

Response of herbivorous fishes to crown-of-thorns starfish *Acanthaster planci* outbreaks.

I. Substratum analysis and feeding ecology of *Acanthurus nigrofuscus* and *Scarus frenatus*

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ABSTRACT: A large-scale comparative study of 3 crown-of-thorns starfish (COTS) impacted reefs and 3 non-impacted (control) reefs in the central region of the Great Barrier Reef was undertaken. The principal objective was to investigate a long-term functional response of herbivorous fish to a potentially greater food resource in the form of increased abundances of turf algae on COTS affected reefs. Measurement of substratum cover and feeding ecology of *Acanthurus nigrofuscus* and *Scarus frenatus* was made on the windward reef slope of all reefs at a depth of 3 to 7 m. Significantly higher abundances of turf algae in comparison with live coral cover occurred on COTS affected reefs, while the opposite pattern occurred on non-affected reefs. However, no obvious difference was detected in the overall dietary composition of *A. nigrofuscus*, variability being more apparent at a temporal scale. There was no difference in feeding rates of roving herbivores (2 species) between impacted and control reefs. Furthermore, one component of the turf algal assemblage (thick turfs) showed increases in abundance in winter on affected reefs, while on non-affected reefs, thick turfs did not exhibit this seasonal pattern. A similar trend was observed for Cyanophyta (blue-green algae) in the dietary assemblage of *A. nigrofuscus*, although different sampling times and lack of detailed knowledge of epilithic algal community (EAC) composition made direct correlations difficult to infer. Whether this increased turf algal resource is prompting a numerical or growth response from herbivorous fishes is currently being investigated.

KEY WORDS: Herbivorous fish · Crown-of-thorns starfish · Functional response · Feeding ecology · *Acanthurus nigrofuscus*

INTRODUCTION

Patch creation or the release of space by natural disturbance has been identified to be as important as competitive interactions in regulating benthic communities (Connell 1978, White & Pickett 1985, Reichelt 1988). Changes in benthic communities of coral reefs following environmental disturbances have been documented in Japan (Yamaguchi 1986, Sano et al. 1987),

the Caribbean (Lessios et al. 1983, Liddell & Ohlhorst 1986, Hughes et al. 1987, Smith 1988, Carpenter 1990a), Hawaii (Walsh 1983), American Samoa (Wass 1987), Micronesia (Jones et al. 1976, Colgan 1987) and the Great Barrier Reef (GBR) (Done et al. 1988, 1991, Bradbury & Mundy 1989). The most common response to patch creation on coral reefs has been the replacement of areas of live coral cover with epilithic algal communities (EACs), which represent the major food source of herbivorous fish on coral reefs (Hatcher & Larkum 1983, Carpenter 1985, Klumpp et al. 1987, Scott & Russ 1987).

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On the GBR, large-scale examples of patch creation occurred following outbreaks of crown-of-thorns starfish (COTS), which feed on hard live coral. Outbreaks have been documented for over 30 yr (Barnes & Endean 1964, Endean 1973, Potts 1981, Moran 1986, Kenchington 1987, Reichelt et al. 1990), with 70% of the reefs in the central region being affected in recent times (Moran et al. 1990). The net result of these outbreaks has been a large-scale shift in the relative proportions of the benthic biota. Cover of live coral has been substantially reduced, followed by an increase in percentage cover and biomass of algal turfs (Moran et al. 1985, Moran 1986, Bradbury & Mundy 1989). In effect, this represented a large, additional food resource for herbivorous grazers. A similar phenomenon also occurred on a large scale on reefs in the Caribbean (Lessios et al. 1983, Bak 1985, Liddell & Ohlhorst 1986, Hughes et al. 1987, Carpenter 1990a). In this instance, the cause was mass mortalities of the dominant benthic macrograzer *Diadema antillarum*. More importantly, both these natural disturbances have provided an excellent opportunity to test ecological hypotheses at a scale not possible under controlled experimental conditions.

Arising from these impacts was the question: Do roving herbivorous fish communities respond in any manner to the increased turf algal resource? Previous studies have observed a tight coupling between roving grazers and their algal food resource (Carpenter 1986, Lewis 1986, Scott & Russ 1987, Polunin & Klumpp 1992). For example, Scott & Russ (1987) demonstrated that short-term exclusion of large herbivorous grazers significantly altered the abundance of individual species and, consequently, the composition of the EAC. In all instances, herbivory by roving grazers was regarded as being fundamentally important in determining EAC composition. Thus, the immediate hypothesised response of roving herbivorous fish to the starfish outbreaks is a functional response. Has there been an increase in grazing intensity and/or a shift in diets? Carpenter (1990b) detected an immediate increase in grazing intensity of parrotfishes and surgeonfishes following *Diadema antillarum* mortalities in the Caribbean. This increased grazing pressure, however, fell back to pre-mortality levels within a few months. Following this, Carpenter (1990b) also observed an increase in numbers of parrotfish and surgeonfish, thus supporting the hypothesis that exploitative competition for the algal food resource had occurred prior to the mass mortalities of *D. antillarum*.

In this study, we compare substrate cover and feeding ecology of roving herbivores from 3 COTS affected and 3 control reefs within the central GBR to establish if there has been a functional response to a new food resource. Grazing rates were estimated for 2 representative species, a surgeonfish *Acanthurus nigrofuscus* and a parrotfish *Scarus frenatus*. In addition, dietary choice of *A. nigrofuscus* was examined in detail.

MATERIALS AND METHODS

Study sites. The study was conducted on 3 adjacent pairs of 'impacted/control' reefs in the central region of the GBR, Queensland, Australia (Fig. 1). These reefs were 'Grub/Centipede', 2 mid-shelf reefs, and 'Yankee/Bowl' and 'Dip/Coil', 4 outer-shelf reefs. All COTS affected reefs had experienced outbreaks in the last 5 to 7 yr (Moran et al. 1990). Sampling was carried out in a single topographic zone, the windward reef slope (3 to 7 m depth). This was the reef area most consistently experiencing starfish outbreaks (Moran 1986).

Substratum analysis. Data for substratum cover was collected along the same 45 × 6 m transect utilised for the surveys of density and biomass of herbivorous fish (Hart et al. 1996—this issue). Following completion of the fish counts, the recorder (A.M.H.) swam back along the transect and recorded substrate cover at a point at each 1 m interval. This resulted in 46 'point intercepts' (0 to 45 m). To distinguish between intensively grazed surfaces and damselfish territories, turf algal cover was split into 2 arbitrary categories: <1 and

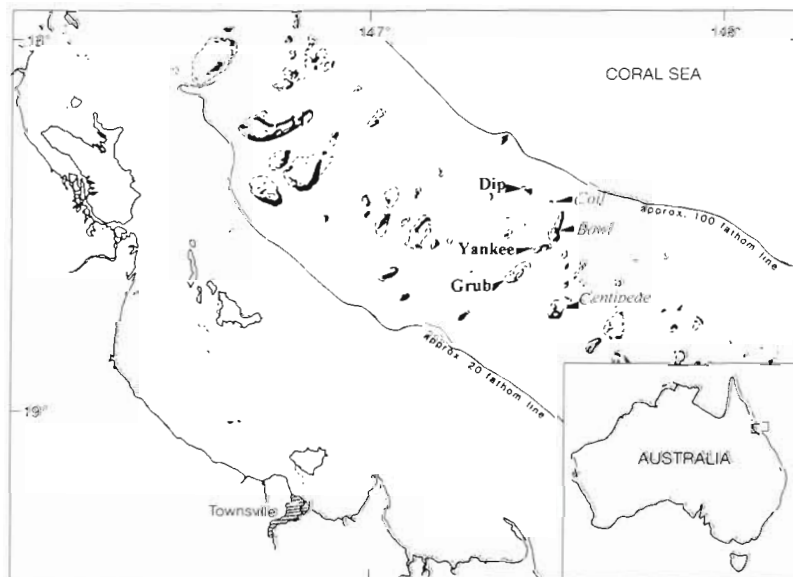


Fig. 1. Location of study reefs in the central region of the Great Barrier Reef. Crown-of-thorns starfish (COTS) impacted reefs in bold, non-impacted reefs in italics

≥ 1 mm (sensu Klumpp & McKinnon 1989). This resulted in 7 physiognomic categories of substrate cover: (1) fine turf algae (< 1 mm), (2) thick turf algae (≥ 1 mm), (3) total turf algae (fine + thick), (4) coralline algae, (5) macro algae (mainly *Halimeda* sp.), (6) live hard coral cover, and (7) other, including biotic and abiotic substrata not falling into the former categories.

Sampling design and data analysis. Data for substrate cover and density and biomass of fish were collected simultaneously, allowing direct correlations between habitat type and fish abundance. Results from fish-habitat studies are reported in the companion paper (Hart et al. 1996). There were 3 sampling occasions (June 1991, January 1992, March 1993), 2 COTS status treatments (+ impacted, - non-impacted), and 3 reefs within COTS status. At each reef, on each occasion, 6 sites were selected and 3 replicate transects examined within each site. Data were analysed with a 4-factor mixed model ANOVA. Sampling occasions and COTS status were treated as fixed and orthogonal, while reefs were orthogonal with occasions, but nested within COTS status. Cochran's test was carried out to test for heterogeneous variances. Tukey's pairwise comparison of means test was applied where the ANOVA detected a significant effect (Day & Quinn 1989). Data for percentage substrate cover were transformed ($\arcsin \sqrt{p}$) to normalise distributions (Zar 1984).

Feeding rates of herbivorous fish. The sample unit was a 5 min observation period for each individual (Montgomery et al. 1989), with the observers recording total number of bites taken during this time interval. Fork length of *Acanthurus nigrofuscus* was estimated visually, with each individual being assigned into 1 cm size classes. For *Scarus frenatus*, observations were made on initial phase females, as males are usually engaged in complex mating behaviour (D. R. Bellwood pers. comm.). All counts were taken between 10:00 and 16:00 h, when the fish were feeding actively (Bellwood & Choat 1990).

Sampling design and data analysis. Seven replicate observations were taken at each of 8 sites within each reef. The data were analysed with a 3-factor mixed-model ANOVA, with the factors being COTS status (fixed), Reef (nested within COTS status), and Sites (nested within reef and COTS status).

Dietary analysis. Ninety-four stomach samples of *Acanthurus nigrofuscus* were analysed for composition of diets, 53 from impacted reefs and 41 from non-impacted reefs. Specimens were collected with spear-guns and monofilament nets (15 mm mesh size) at all reefs on 2 separate occasions, April and October 1992. The stomach was dissected out and preserved in 70% seawater formalin. An adaptation of the method of Jones (1968) was utilised to quantify the diets (see

laboratory procedure). Identifications follow those of Price & Scott (1992) and Cribb (1983), with algal taxon being identified to the level of genus.

Laboratory procedure. The excised portion of the gut was split open and the contents washed into a petri dish. This material was mixed with tap water and broken up with a dissecting needle. Using fine grade forceps (INOX 5), a 'clump' of this material was placed on a microscope slide, and further teased apart with the forceps and dissecting needle under low power. At a magnification of $\times 100$, 4 areas of each slide were examined using an ocular micrometer with 25 intersection points. Any alga falling across one or more of these points of intersection was identified and counted. This procedure was repeated 3 times for each stomach sample. Thus, for each gut sample there was a total of 300 points of intersection (i.e. 3 slides \times 4 observations \times 25 points).

Data analysis. Multidimensional scaling (MDS) was utilised to delineate the dietary assemblage. The analysis was performed on the 15 most common algal taxa which comprised approximately 92% of the total diet composition. Normal or q-type analysis procedure (Field et al. 1982) was followed.

Point intercept data were converted into proportions to obtain relative abundance estimates. Next, a dissimilarity matrix was constructed between samples using the standard Euclidean distance measure (Faith et al. 1990). MDS essentially seeks to scale (minimise) the dissimilarity matrix down to physical distances on a 2- or 3-dimensional map, so that the between point distances have the same rank order as the higher dimensional dissimilarity matrix. Importantly, the final map is determined only within an arbitrary orientation, location and scale and hence axis scales are omitted (Field et al. 1982).

Number of genera, divisions of turf algae, and the 9 most common taxa were subjected to a 2-fixed-factor ANOVA (Reefs, Time). All data were $\arcsin \sqrt{p}$ transformed and a *a posteriori* testing procedures were as for substratum analysis.

RESULTS

Analysis of substratum cover

Fine and thick turf algae were much higher in abundance on impacted reefs (Table 1; Fig. 2) and this pattern was maintained over time. Cover of fine turf increased consistently across occasions on affected reefs, however on control reefs there was an initial increase in fine turf from June 1991 to January 1992, then no change up to March 1993 (Fig. 2). This is evidenced by a significant interaction between Occasions and COTS status (Table 1). Cover of thick turf on impacted reefs was highest in June 1991, and similar

Table 1. ANOVA results from the analysis of percentage cover of the 5 major physiognomic categories of substrate

Source of variability	df	MS	F	p	MS	F	p	MS	F	p
		Fine turf (<1 mm)			Thick turf (≥1 mm)			Total turf algae		
Occasions	2,90	0.125	45.1	***	0.021	2.01	ns	0.372	28.8	***
COTS status	1,90	0.549	197	***	1.684	164.1	***	6.823	529	***
Reefs	4,90	0.021	7.66	***	0.118	11.5	***	0.249	19.3	***
Occasions × COTS	2,90	0.059	21.2	***	0.01	9.79	***	0.131	10.14	***
Occasions × Reefs	8,90	0.011	4.04	***	0.014	1.34	ns	0.044	3.38	**
Sites	90,216	0.0028	1.48	*	0.010	1.75	***	0.013	1.56	**
Residual	216	0.0019			0.0019			0.0083		
		Live coral			Coralline algae					
Occasions	2,90	0.047	4.08	*	0.568	43.9	***			
COTS status	1,90	4.55	399	***	0.003	1.87	ns			
Reefs	4,90	0.047	4.08	*	0.568	43.4	***			
Occasions × COTS	2,90	0.014	1.26	ns	0.003	1.90	ns			
Occasions × Reefs	8,90	0.008	0.68	ns	0.004	2.25	*			
Sites	90,216	0.011	2.07	***	0.001	1.72	***			
Residual	216	0.0055			0.0008					

*p < 0.05. **p < 0.01. ***p < 0.001, ns = not significant

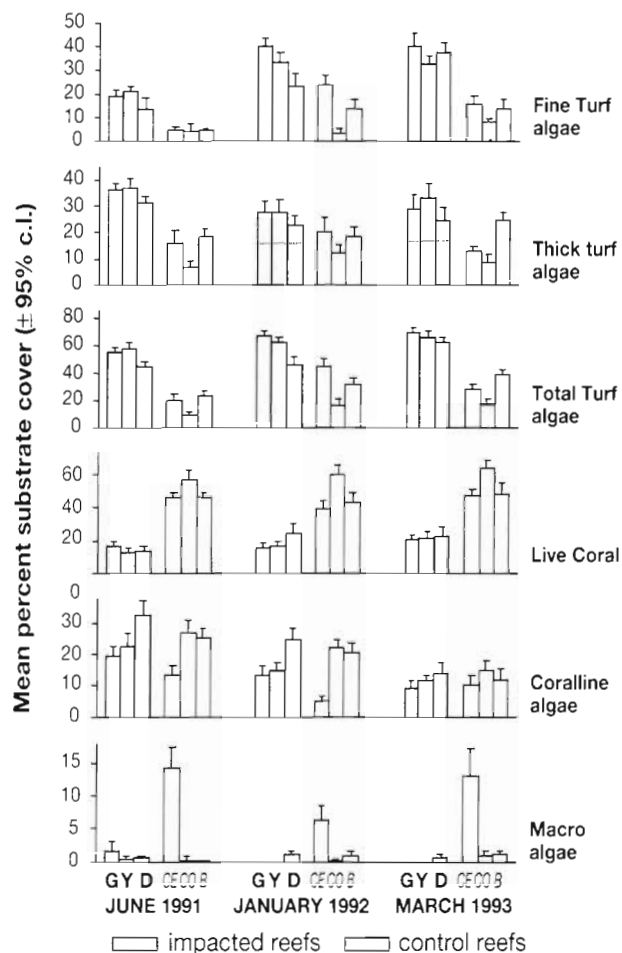


Fig. 2. Mean % cover of all physiognomic categories of substrate at impacted (□) and non-impacted reefs (■) during each sampling occasion. G: Grub, Y: Yankee, D: Dip, CE: Centipede, CO: Coil, B: Bowl

in January 1992 and March 1993. On the other hand, thick turf remained relatively consistent across all occasions on control reefs (Fig. 2). The pattern for total turf algae was similar to that of fine turf. Tukey's test distinguished Grub as having the highest cover of fine turf, Yankee and Dip showing the next highest, and Centipede, Coil, and Bowl having a similarly lower cover of fine turf (Fig. 2). In general, the pattern of live coral cover was opposite to that of turf algae, being highest on control reefs Centipede and Bowl and lowest on COTS impacted reefs (Fig. 2).

Feeding rates of *Acanthurus nigrofuscus* and *Scarus frenatus*

No significant differences in bite rates of *Acanthurus nigrofuscus* or *Scarus frenatus* were detected between affected and non-affected reefs (Table 2). However, bite rate of *A. nigrofuscus* was significantly higher on Coil than all other reefs, except Dip (Table 2). This was directly related to size of *A. nigrofuscus* (Pearson, $r = -0.278$, $n = 314$, $p < 0.001$), with smaller individuals exhibiting faster bite rates. Furthermore, a 1-way ANOVA detected significantly lower sizes of *A. nigrofuscus* at Coil Reef ($F = 85.17$, $p < 0.001$).

Turf algal assemblage in the diet of *Acanthurus nigrofuscus*

MDS ordinations showed no obvious separation of samples due to COTS status (Fig. 3a). Diets of *Acanthurus nigrofuscus* from non-impacted reefs tended to

Table 2. ANOVA results and Tukey's test for analysis of feeding rates of *Acanthurus nigrofuscus* and *Scarus frenatus* (impacted reefs in bold; non-impacted reefs in italics). Underlines indicate Tukey's groups

Source of variability	df	<i>Acanthurus nigrofuscus</i>			<i>Scarus frenatus</i>		
		MS	F	p	MS	F	p
COTS status	1,4	95675	1.32	ns	12186	2.08	ns
Reef	4,42	72462	6.17	***	5851	1.34	ns
Sites	42,288	11745	2.63	***	4360	4.18	***
Residual	288	4457			1043		

Tukey's test for effect of reef on mean bite rates (bites/5 min) of <i>A. nigrofuscus</i>						
<i>Coil</i>	Dip	<i>Bowl</i>	<i>Centipede</i>	Grub	Yankee	
195	<u>142</u>	129	120	119	82	

***p < 0.001, ns = not significant

be more tightly clustered than those from impacted reefs, indicating a more uniform composition. In contrast, there was a clear temporal difference between the April and October samples (Fig. 3b). Hence, the variability in the dietary assemblage of *A. nigrofuscus* was most likely related to the time of year, and was least likely to result from the COTS status of the reef.

Analysis of diets by divisions and generic richness

A significantly higher number of genera (11.9 ± 0.7) occurred in the diets from April 1992, as opposed to October 1992 (10.4 ± 0.7 ; Table 3). On impacted reefs (Grub, Yankee, Dip), Cyanophyta comprised a significantly greater percentage of diets in April, as opposed to October 1992 (Fig. 4). On control reefs (Centipede, Coil, Bowl), there was no difference in percentage composition of Cyanophyta between April and October 1992. Diet samples from Dip had a significantly higher percentage composition of Rhodo-

phyta than those from Yankee (Table 3; Fig. 4). Conversely, diets from Yankee contained a significantly higher percentage composition of Chlorophyta than Grub, Dip or Centipede, and this was consistent over both sampling times (Fig. 4).

Analysis of diet by genera

There was no significant difference in percentage diet composition between affected and control reefs for any genera. However, *Enteromorpha* sp. was more prevalent in diets from impacted reefs (6.3 ± 3.1) than non-impacted reefs (2.8 ± 1.1). *Ceramium* sp. and *Enteromorpha* sp. were more common in April 1992 than October 1992, while *Laurencia* sp. exhibited the opposite pattern. Differences in percentage diet composition of genera between reef are summarised in Table 4.

DISCUSSION

In studies of localised regions of coral reefs, it is important to recognize that processes no longer evident may have been critical to the current distribution patterns (Reichelt 1988). This was well documented by Hughes (1989), who demonstrated the synergistic effects of 2 separate environmental disturbances on the benthic composition of a coral reef. The patchy nature of outbreaking COTS populations (Moran 1986) makes it difficult to establish whether a particular area of reef actually has a history of COTS disturbance. Since this posed potential problems in interpretation of within reef patterns, it was desirable to keep all analyses at the level of reefs to circumvent this.

The distinction between fine turf and thick turf was an important one, as differences in algal community structure have been shown to correspond with the frequency and intensity of herbivore-induced disturbance (Steneck 1988). Firstly, a decrease in cover of thick turfs occurred on impacted reefs from winter (June 1991) to summer (January 1992); however, this phenomenon did not occur on control reefs. In addition, there was some evidence of roving herbivores targeting this 'winter food' arising from dietary analysis of *Acanthurus nigrofuscus*. On affected reefs, Cyanophyta was in much higher

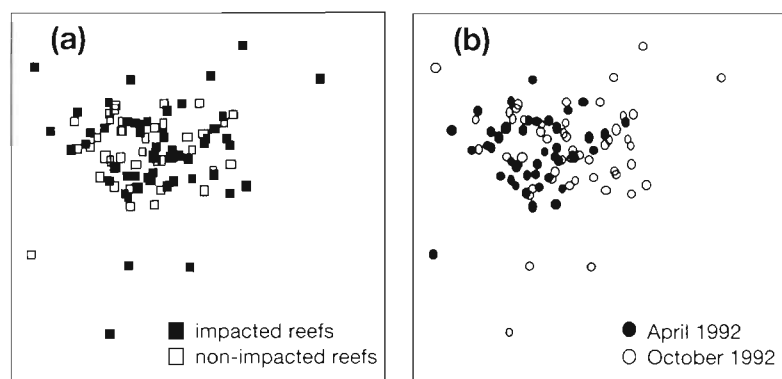


Fig. 3. *Acanthurus nigrofuscus*. MDS ordination plots of dietary assemblage. Results are grouped by (a) COTS status, and (b) time

Table 3 *Acanthurus nigrofuscus*. ANOVA results for generic richness and the 4 principal divisions present in the diet

Source of variability	df	MS	F	p	MS	F	p
				Cyanophyta		Rhodophyta	
Time	1,82	0.513	16.5	***	212.0	1.46	ns
Reef	5,82	0.058	1.86	ns	398.4	2.74	*
Time × Reef	5,82	0.210	6.75	***	159.5	1.90	ns
Residual	82				145.3		
				Chlorophyta		Phaeophyta	
Time	1,82	1.52	0.013	ns	268.1	2.16	ns
Reef	5,82	612.8	5.39	***	74.6	0.60	ns
Time × Reef	5,82	79.8	0.69	ns	70.6	0.57	ns
Residual	82	115.5			124.1		
Number of genera							
Time	1,82	55.8	10.23	**			
Reef	5,82	7.23	1.33	ns			
Time × Reef	5,82	8.44	1.55	ns			
Residual	82	5.45					

*p < 0.05, **p < 0.01, ***p < 0.001, ns = not significant

abundance in diets from autumn as opposed to spring, while no temporal difference occurred on non-affected reefs. Certainly, there is evidence of *A. nigrofuscus* switching diets to make use of winter blooms of Chlorophyta in the Red Sea (Fishelson et al. 1987). This

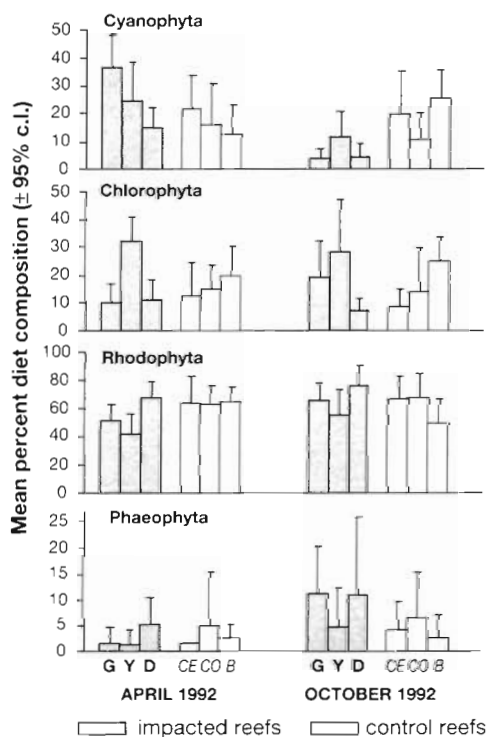


Fig. 4. *Acanthurus nigrofuscus*. Mean % dietary composition (by division) at all impacted (□) and non-impacted (■) reefs during April and October 1992. Reefs as defined in Fig. 2

hypothesis could be tested by specifically identifying EAC composition on impacted and non-impacted reefs, and analysing the diets of grazers (specifically *A. nigrofuscus*) observed feeding on the substrate.

Impacted reefs increased in percentage cover of live coral from June 1991 to March 1993. This is possible evidence of a recovery; however, there was a concomitant increase in live coral on control reefs from January 1992 to March 1993. Certainly, the rate and direction of coral recovery is highly species- and disturbance-specific, depending more on local rather than on regional processes (Done et al. 1991). At the extreme scale, Done et al. (1988) predicted a recovery time in excess of 50 yr for massive corals *Porites* spp. damaged by starfish outbreaks. In Thailand, sedimentation caused a 30% reduction

in live coral cover, yet percentage cover was back to pre-disturbance levels within 2 yr of the cessation of dredging (Brown et al. 1990). With respect to COTS outbreaks, a major factor influencing rates of recovery is the extent to which the spatial heterogeneity in reef structure has been damaged. Total collapse of the structural heterogeneity of a reef flat in Japan has resulted in very slow recovery rates (Sano et al. 1987). In contrast, reefs from Guam (Colgan 1987) had achieved pre-impact coverage of live coral within 12 yr of COTS outbreaks, despite coral cover being reduced to <1% on most reefs. This was attributed to the persistence of the structural integrity of the reef matrix (Colgan 1987).

Two criteria were chosen as providing evidence of an additional algal food resource. Firstly, cover of algal turfs on COTS impacted reefs must be greater than on non-impacted reefs. Secondly, this pattern must be maintained over the 2 yr sampling period. Results of this study show this to be clearly the case, and subsequent investigations were devoted to answering the question: Have *Acanthurus nigrofuscus* and *Scarus frenatus* exhibited a functional response to this available food resource?

Feeding rates of *Acanthurus nigrofuscus* and *Scarus frenatus*

No differences in bite rates of either species was detected between COTS affected and control reefs. Carpenter (1990b) did detect a short-term feeding response from roving herbivores to increases in biomass of turf algae. This, however, lasted only a few

Table 4. Tukey's test for the effect of reefs (reefs as defined in Fig. 2) on percentage diet composition of 5 common genera of algal turfs (R: Rhodophyta; CH: Chlorophyta). Means (% composition) are shown and underlines indicate Tukey's groups

<i>Polysiphonia</i> (R)						<i>Cladophora</i> (CH)						<i>Enteromorpha</i> (CH)					
CO	Y	D	CE	B	G	Y	CO	B	D	CE	G	Y	G	CE	CO	B	D
18.0	17.2	16.3	8.7	7.2	6.6	16.3	10.4	8.9	4.9	3.3	2.1	12.6	5.9	3.4	2.7	2.4	1.6
<hr/>						<hr/>						<hr/>					
<i>Herposiphonia</i> (R)						<i>Caulerpa</i> (CH)											
CO	D	B	Y	CE	G	B	G	CE	D	CO	Y						
10	5.2	3.8	2.4	2.4	1.6	8.8	7.3	3.5	2.1	1.6	0.9						

months before feeding rates returned to prior-impact levels (Carpenter 1990b). Furthermore, in the present study the opposite trend to the predicted response occurred, with both *Acanthurus nigrofuscus* and *Scarus frenatus* exhibiting highest mean feeding rates on non-impacted reefs.

Coil Reef experienced the highest mean bite rates of *Acanthurus nigrofuscus* and *Scarus frenatus*. This was a function of size of fish as small fish bite faster and Coil had a significantly lower mean size of *A. nigrofuscus* than all other reefs. Furthermore, Coil exhibited the lowest mean percentage cover of both fine and thick turfs on all occasions (Fig. 2). Thus, in addition to being smaller, the fish simply may have had to feed more rapidly on Coil to obtain their nutritional requirements.

Diets of *Acanthurus nigrofuscus*

This is the first instance of quantification of diets of *Acanthurus nigrofuscus* on the GBR. Utilising substrate analysis and availability of algal taxa, Scott & Russ (1987) identified the dominant turf algal taxa which would be expected to be major components of the diets of roving herbivores (e.g. *Enteromorpha*, *Polysiphonia*, *Cladophora* sp.). Indeed, all of these algae were common in the diets of *A. nigrofuscus*.

Little difference in composition of diets existed between impacted and non-impacted reefs, variability being more apparent on a temporal scale. This concurred with results from the analysis of feeding rates. Diets of *Acanthurus nigrofuscus* from control reefs did, however, show evidence of a more uniform composition. The present study also found some evidence of high abundance of Chlorophyta in the diet in autumn, with *Enteromorpha* sp. being more abundant in diets from April.

Although the trend of winter high abundances and summer low abundances of Cyanophyta (from diets) and thick turfs (from substrate) on impacted reefs appear related, it is difficult to infer direct correlations due to different sampling times (June and January thick turfs; April and October diets). Moreover, in a companion paper, Hart et al. (1996) showed that on

impacted reefs, roving herbivores may be avoiding areas of thick algal turfs. The proportion of thick turfs represented by Cyanophyta is unknown, although it is probably substantial. Wilkinson et al. (1984, 1985) reported that blue-green algae (Cyanophyta) were more abundant on grazed than on ungrazed substrata, while Scott & Russ (1987) demonstrated the opposite pattern.

In conclusion, there was primary evidence of an additional food resource on affected reefs, expressed as significantly higher percentage cover of algal turfs compared to control reefs. However, no evidence of a functional response in terms of differences in grazing intensity by an acanthurid and scarid was detected. Limited evidence of a functional response in terms of composition of diets of *Acanthurus nigrofuscus* was observed. Both the thick turf algal assemblage and Cyanophyta in the diets of *A. nigrofuscus* showed a temporal change on impacted reefs, but did not exhibit this trend on non-impacted reefs. However, Hart et al. (1995) demonstrated negative correlations between roving herbivores and thick turf algae on impacted reefs. Implications of this are discussed in related studies on grazing fish population densities and correlations between fish and habitat structure (Hart et al. 1996).

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