Predation-induced morphological and behavioral defenses in a hard coral: implications for foraging behavior of coral-feeding butterflyfishes

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ABSTRACT: In clonal organisms, such as corals, one consequence of partial predation may be an elaboration of defenses in remaining portions of the clone, thereby reducing the probability or severity of future predation events. Inducible defenses have been found in terrestrial and marine plants and in several taxa of marine invertebrates. Predators can detect differences in various aspects of prey quality that translate into preferences for certain prey items. Differences in quantity or types of defenses may determine which species, individuals or parts of a prey item are consumed. Coral-feeding butterflyfishes show distinct preferences for certain coral species, and may prefer particular individuals of a species over others. This study examines the potential for inducible defenses in a hard coral in response to grazing by a natural coral predator, the butterflyfish *Chaetodon multicinctus*. Pairs of genetically identical fragments of the Hawaiian coral *Porites compressa* were exposed to grazed and ungrazed treatments. These colonies were then offered to naïve fish in preference tests at various intervals following the treatment period. Grazing by butterflyfishes induced changes in polyp behavior (prolonged withdrawal of coral polyps) in the short term, and increases in nematocyst density over the longer term, and these changes were associated with reductions in palatability and subsequent predation rates on the damaged corals. These inducible responses may play a role in regulating the intensity of grazing, and ultimately territory size and the density of corallivorous reef fishes.

KEY WORDS: Inducible defenses · Morphological defenses · Behavioral defenses · Foraging behavior · Corallivory · Corals · Chaetodontidae · Clonal organisms

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INTRODUCTION

Many terrestrial plants increase their defenses in response to damage by herbivores (see reviews by Karban & Myers 1989, Tallamy & Raupp 1991, Karban & Baldwin 1997). Such inducible defenses are distinguished from constitutive defenses in that they are produced or enhanced as a direct result of grazing. Inducible defenses are believed to be advantageous to plants under conditions where the probability of grazing is unpredictable or intermittent, the presence of grazers provides some reliable nonfatal cue, and there are costs associated with maintaining defenses in the

absence of grazers (Adler & Harvell 1990, Harvell 1990). Like plants, the architecture of clonal animals is especially conducive for the evolution of inducible defenses in several respects: most are sessile and are subject to partial predation, which provides a reliable, nonfatal cue to the presence of grazers, and allows the remaining parts of the clone to survive and employ inducible defenses (Harvell 1990). In addition, the costs of producing enhanced defenses may be distributed among clone-mates (Harvell & Padilla 1990). Examples of predation-induced defenses have been found in several clonal animals, including a sponge (Hill & Hill 2002), a bryozoan (Harvell 1986, 1992,

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1999), a gorgonian (West 1997), a hydroid (Gaulin et al. 1986) and numerous species of zooplankton (reviewed by Havel 1987, Tollrian & Harvell 1999).

Hard corals are long-lived sessile animals, many of which form colonies of polyps belonging to a clone. Like plants, the capacity for rapid regeneration of damaged tissue enables corals to survive a large degree of partial predation (Hughes & Jackson 1985, Glynn 1988, Meesters et al. 1996, Gochfeld 1997), although intense grazing might preclude regeneration of lost tissue and could ultimately cause colony mortality (Kinzie 1970, Bak & Steward-Van Es 1980, Gochfeld & Aeby 1997). Because clones can both survive and regenerate following grazing, there is the potential for defenses to be induced in either remaining and/or newly produced tissue. Corals are also able to respond behaviorally to grazing by withdrawing their polyps into the corallum. Although predation-induced defenses in hard corals have not been previously reported, many hard corals produce highly modified nematocyst-laden sweeper tentacles in response to competitors (Richardson et al. 1979, Wellington 1980, Chornesky 1983).

Porites compressa is the most abundant coral on shallow reefs in Hawaii (Jokiel 1987), and although this species commonly occurs in territories of coral-feeding butterflyfishes, it is of consistently low preference to these fish in both laboratory and field studies (Reese 1977, Hourigan et al. 1988, Tricas 1989a). Low preference may result from colony morphology, low nutritional content, high handling time, nematocyst size or density, or noxious secondary metabolites (Hourigan 1987, Hourigan et al. 1988, Tricas 1989a).

Many coral-feeding butterflyfishes defend territories in which they perform all of their foraging activities. For some species, the same pair of fish may occupy the same territory for up to at least 8 yr (Reese 1991). Because all of the foraging activities of butterflyfishes are directed at the corals within their territories, the establishment and maintenance of a territory must reflect a balance between feeding intensity and coral growth, reproduction and survival. High levels of predation by butterflyfishes (e.g. 575 to 700 bites h^{-1} fish $^{-1}$ for the endemic Hawaiian species *Chaetodon multicinctus*; Hourigan 1987, Tricas 1989b, author's pers. obs.) are indeed capable of reducing coral growth rates (Cox 1986, Gochfeld 1997), and even causing coral mortality (author's unpubl.). However, under natural conditions this rarely occurs (Harmelin-Vivien & Bouchon-Navaro 1981, 1983, Hourigan 1987), suggesting that both butterflyfishes and corals have evolved mechanisms that prevent excessive predation on individual coral colonies within butterflyfish territories. This might be accomplished by butterflyfishes maintaining territories large enough to sustain this repeated

grazing (Gochfeld 1997). Among the cues that butterflyfishes might use to regulate territory size include those relating to coral condition.

Using natural butterflyfish predators of *Porites compressa* in laboratory experiments, I addressed the following questions: (1) Does predation by butterflyfishes induce responses in the coral? (2) Do the observed responses reduce subsequent predation rates? (3) What is the mechanism for the induced response? (4) Is the induced response localized or systemic? Two potentially inducible characters were examined in this study: polyp withdrawal and nematocyst density. Inducible chemical defenses were also examined and are discussed elsewhere (Gochfeld 1997). These characters were selected because polyp withdrawal in the vicinity of a butterflyfish bite is believed to be the proximate cue responsible for the foraging behavior of these fishes, which take a few bites from a coral colony before moving on to the next colony (Hourigan 1987, Cox 1991), and because nematocysts are known to be both important in cnidarian defense (Mariscal 1974, Bigger 1988, Stachowicz & Lindquist 2000) and inducible (Hidaka et al. 1987, Bigger 1988, Adler & Harvell 1990, Buss 1990). *Porites compressa* possesses both a higher density and larger (Glynn & Krupp 1986, Tricas 1989a) nematocysts than do most other Hawaiian corals, and this may be one reason that *P. compressa* is of low preference to butterflyfishes. Therefore, it was predicted that changes in these characters should affect the rate at which butterflyfish feed on their coral prey and their preferences for these corals, which may have implications for foraging behavior and the size of territories that these fish must defend.

MATERIALS AND METHODS

Animal collection and overview of experimental design. All colonies of *Porites compressa* were collected from shallow (<1.5 m at high tide) reef flats on patch reefs in Kaneohe Bay, Oahu, HI. Coral-feeding fishes and other corallivores are rarely observed on these shallow reef flats, and therefore initial levels of predation on all colonies were assumed to be both similar and negligible. In addition, Kaneohe Bay is a relatively sheltered embayment and reefs are rarely exposed to high wave action that might damage corals. Corals experienced minimal damage to living tissue during removal from the reefs as only colonies that could be removed from the substratum by hand were used. Corals were placed in buckets of seawater and transported to the Hawaii Institute of Marine Biology on Coconut Island in Kaneohe Bay, where they were maintained in outdoor tanks with flow-through seawater, aeration and a 30 % shade cloth cover.

The coral-feeding butterflyfish *Chaetodon multicinctus* does not occur within Kaneohe Bay, but is found on the deeper reef slope offshore of Kaneohe Bay, where it defends territories composed largely of *Porites compressa*. Adult butterflyfishes (8.4 to 8.9 cm SL) were collected from 10 to 20 m depth using monofilament hand nets, and were transported to the laboratory in buckets of seawater. Fish were maintained in large outdoor tanks supplied with flow-through seawater, and were fed live coral colonies collected from the reef flat as needed. Fish were allowed to acclimate to laboratory conditions for a minimum of 3 d before use in any experiments.

All experiments described in this paper utilized a paired design, in which colonies of *Porites compressa* (ca. 25 cm in diameter) were divided in half using a rock saw. Cutting a colony by this method produces equivalent levels of damage to the cut edge on both colony halves. Tissue heals over the cut within 3 to 4 d (pers. obs.), and does not apparently reduce coral growth, as branches exhibit measurable growth in the 24 h following cutting (J. Stimson pers. comm.). Any potential response of the coral tissue to colony division was controlled for by the paired design and by removing branches for analysis after colony division had taken place. Any changes in defense levels detected in these experiments could therefore be attributed to the effect of the experimental treatments. A separate set of corals was used for each experiment.

Following colony division, the 2 genetically identical colony halves were randomly placed on either side of a 500 l test tank, which was divided in half by a 1 cm² mesh Vexar™ screen. Waterborne compounds were not responsible for inducing defenses in this study (i.e. the 'talking trees' hypothesis; Baldwin & Schultz 1983, Rhoades 1983, reviewed by Karban & Baldwin 1997), as both control and grazed colonies were maintained in the same tank at all stages of the experiment, yet defenses were induced in only 1 colony half (see 'Results'). Test tanks were provided with flow-through seawater, aeration and a shade cloth cover. Corals were maintained in the test tanks for 4 d to allow the cut edges to heal, and then an individual *Chaetodon multicinctus* was added to the experimental (grazed) side of each tank. The screen permitted water to flow freely throughout the tank, but prevented the fish from swimming between the grazed and control (ungrazed) sides of the tank. This paired design eliminated any potential confounding effects of genotypic variation in levels of defenses on treatment outcomes as all comparisons were performed on differences between control and grazed clone-mates.

Short-term defense induction. To determine whether predation by coral-feeding butterflyfishes induces defenses rapidly in *Porites compressa*, individual

corals were exposed to predation for 1 d and were then offered to naïve fish in preference tests on the following day (Fig. 1A). Colonies of *Porites compressa* (n = 18) were divided in half and allowed to acclimate to test tanks. Immediately prior to the treatment period, 1 branch was removed from each coral half. Branches were preserved in 10% formalin in seawater for subsequent nematocyst counts (see below). An individual *Chaetodon multicinctus* was then added to the grazed half of each tank. A separate tank and fish was used for each test coral. Because 1 fish was maintained in a tank with 1 coral during the treatment period, feeding intensity on the experimental coral was much greater than natural levels. To estimate feeding intensity and to establish a relative index of feeding treatment level on each colony, three 15 min observations were made of feeding rates on the grazed corals during the 24 h treatment period. Since feeding rates of *C. multicinctus* on the reef are relatively constant throughout the daylight hours (author's pers. obs.), these observations were considered sufficient to obtain relative measures of feeding intensity. Feeding rates ranged from 16 to 365 bites h⁻¹ on the grazed corals.

At the end of the treatment period, the butterflyfish was removed. One branch was then removed from each coral half and preserved in formalin. The corals were then offered to naïve fish in preference tests (see below).

Long-term defense induction. To test whether there was a lag period between initial predation and defense induction, 11 colonies of *Porites compressa* received the same treatment as in the previous experiment, except that following the 24 h treatment period, fish were removed and the corals were allowed to regenerate the tissue that was lost to predation (Fig. 1B). Complete regeneration of small single-polyp wounds in which no skeleton has been removed, such as those produced by *Chaetodon multicinctus*, requires 7 to 10 d in *P. compressa* (Gochfeld 1997). The regeneration period used in this experiment was 11 d. During this period, corals were maintained in the test tanks. At the end of the regeneration period, 1 branch was removed from each coral half and preserved in formalin; corals were then offered to naïve fish in preference tests.

Preference tests. Preference tests were conducted to determine whether naïve fish were able to detect differences in levels of defense among the 18 corals in the short-term induction experiment and the 11 corals in the long-term induction experiment. Individual butterflyfish were placed in 15 gal (56.8 l) glass aquaria with running seawater and several coral colonies, and were allowed to acclimate to the aquaria for a minimum of 48 h. Only fish that were observed feeding during this period were used in preference tests. A different fish was used for each

Fig. 1. Design of inducible defense experiments. (A) Timeline for short-term induction experiment ($n = 18$; CC = collected and cut corals, TP = predation treatment period, PT = preference tests, N = branches removed for nematocyst counts). (B) Timeline for long-term induction experiment ($n = 11$; RP = regeneration period). (C) Design of defense translocation experiment. Colonies ($n = 12$) of *Porites compressa* were cut in half and a cage was placed over one half of each colony half. The grazed colony half was exposed for 24 h to an individual *Chaetodon multicinctus*, which could feed only on the uncaged part of the colony half. The control colony half was placed in the same tank, but was protected from predation by a mesh screen that divided the tank in half. (D) Two types of preference tests were performed in the translocation experiment ($n = 12$). The first tested for defense induction by exposing both previously uncaged parts of the coral halves to a naïve fish. The second tested for defense translocation by exposing the previously caged parts of the coral halves to the fish

preference test, and all fish were returned to their collection sites at the end of the experiments.

One hour prior to each test, all corals were removed from the aquarium of the test fish. The 2 halves of the test coral were arbitrarily placed at either end of the aquarium, and a VexarTM mesh cage was placed over each coral so that the fish was not able to feed on the coral. This period provided the coral polyps sufficient time to reemerge following handling, but did not cause 'excessive hunger' in the fish, as this might have affected their prey selectivity (see Cronin & Hay 1996).

At the end of the hour, the degree of polyp expansion of each coral half was qualitatively scored: expanded

(tentacles of all polyps extended beyond the corallum and easily visible to the human observer), partially withdrawn (either tentacles of all polyps were visible but not fully extended beyond the corallum, or some polyps were fully extended, generally at the bases of branches, while others, generally at the branch tips, were withdrawn) and fully withdrawn (no tentacles visible to the human observer).

The mesh cages were then removed and the identity of the coral receiving the first bite was recorded. The 15 min tests began as soon as the fish had taken a bite ('tasted') from both coral halves. During the test, the following behaviors were recorded: number of bites on

each coral half, number of head shakes following bites on each coral half, and number of inspections on each coral half. Head shakes were rapid and distinct, occurring immediately following a bite. Inspections occurred when the fish swam over to a coral, examined it closely, but then swam away without feeding and returned to the other coral to feed.

The number of bites taken on each coral half, the proportion of bites followed by head shakes on each coral half, and the number of inspections on each coral half were compared using Wilcoxon signed rank tests. The number of times the control versus grazed coral received the first bite was compared using a sign test.

Nematocyst counts. To determine levels of within- and among-colony variation in nematocyst densities, preliminary nematocyst counts were made on 3 branches from each of 5 colonies of *Porites compressa*. As this pilot experiment was not designed to address the question of induction, nor to compare nematocyst density in these corals with those in the induction experiments, branches were removed immediately following collection. These branches were preserved in 10% formalin in seawater and decalcified in 4% nitric acid. The decalcified tissue was cut open and laid flat. Two 4 mm in diameter cores were removed using a cork borer at a distance of 1 cm from the branch tip. Both cores were combined in a tissue grinder with 1 ml seawater and macerated 40 times. One drop of the resulting slurry was pipetted into each chamber of a Hausser Scientific eosinophil counting slide (2.0 mm³ per chamber). Nematocysts were counted using a compound microscope at 100 $\times$. Nematocysts in 12 chambers were counted from each branch. Only the 2 largest types of nematocysts were counted: holotrichous isorhizas (80 $\times$ 15 μ m) and microbasic p-mastigophores (30 $\times$ 10 μ m). These were classified according to Mariscal (1974) and have been described as serving defensive functions (Ewer 1947, Mariscal 1974). Nested random factor ANOVAs compared variability in the densities of both types of nematocysts among colonies and among branches within colonies. To determine the number of chambers to count, cumulative mean nematocyst densities for the 12 replicates from each branch were plotted, and it was determined that 6 replicate chambers represented an adequate sample size.

Densities of nematocysts were determined, as described above, from the preserved branches removed from control and grazed coral halves prior to the treatment period and immediately prior to the preference tests (Fig. 1A,B) in both defense induction experiments. Branches from 6 colonies in the short-term induction experiment and from 11 colonies in the long-term induction experiment were analyzed. Six chambers were counted to produce a grand mean nemato-

cyst density for each branch. Percent change in density of each type of nematocyst in control and grazed corals was compared using Wilcoxon signed rank tests.

Translocation of inducible defenses. To determine whether predation on 1 region of a coral colony could induce defenses in other regions of the colony, 12 colonies of *Porites compressa* were divided in half and allowed to heal. A mesh cage (1 cm² hardware cloth) was constructed to cover one half of each half colony so that the colony was effectively, although not physically, divided into quarters (Fig. 1C). Just prior to the treatment period, 1 branch was removed from each quarter of the colony and preserved in formalin. The colony halves were then randomly assigned to the control or grazed treatment and placed on opposite sides of a divided tank. The cages were placed over each 'caged' quarter and an individual *Chaetodon multicinctus* was added to the grazed side of the tank.

Fish were allowed to feed on the uncaged grazed quarters for 24 h. At the end of the treatment period, the fish and all cages were removed and the corals were allowed to regenerate for 11 d (Fig. 1B). At the end of the regeneration period, 1 branch was removed from each quarter of the colony and preserved in formalin. Both coral halves were transferred to an aquarium containing a naïve fish that had been deprived of food for 1 h. A different fish was used for the preference tests on each of the 12 corals.

Two different preference tests were performed on each colony (Fig. 1D). To test for the presence of inducible defenses, the cages were replaced on the previously caged quarters of each half coral. This enabled the test fish to feed on the previously uncaged portions of the corals, one of which had been directly exposed to predation during the treatment period. To test for translocation effects, cages were placed over the previously uncaged portions of the corals. This exposed the previously caged quarters, neither of which had been directly exposed to predation; however, if translocation of inducible defenses did occur, the caged quarter of the control coral should be preferred over the caged quarter of the grazed coral. The first test lasted 15 min from the time at which the fish 'tasted' both coral halves. At the conclusion of this test, the cages were switched immediately, and the second 15 min test was conducted using the same fish. Data from the preference tests were analyzed as described for the induction experiments, with data from the 2 types of preference tests analyzed separately.

Percent change in nematocyst density in branches from the 4 treatment groups was arcsin transformed and analyzed by a randomized block ANOVA in PROC GLM (SAS Institute 1990), using coral colonies as blocks. Tukey's multiple comparison tests were then used to compare the means of all treatment groups.

RESULTS

Short-term defense induction

Preference tests

In the short-term induction experiment, preference tests were performed immediately following the 1 d predation treatment. Naïve butterflyfishes directed their first bites to the control coral significantly more often than to the grazed coral (sign test, $n = 18$, $p = 0.0075$; Fig. 2A). Polyp expansion was significantly greater on control corals (10 colonies fully expanded, 6 partly expanded, 2 withdrawn) as compared to grazed corals (12 partly expanded, 6 withdrawn; G -test for independence $\chi^2 = 17.996$, $df = 2$, $p < 0.001$; Fig. 3). On only 3 occasions did fish feed on the grazed coral first, and in all 3 cases, the 2 colonies displayed a similar degree of polyp expansion. In addition, grazed colonies were inspected without subsequent feeding significantly more often than were control colonies (6.1 ± 4.8 inspections on grazed corals, 1.6 ± 1.6 on controls; Wilcoxon signed rank test, $n = 18$, $p = 0.001$; Fig. 2B).

Although feeding rates during preference tests varied among fish (range 45 to 328 bites per 15 min), fish

took significantly more bites on control corals ($82.0 \pm 19.0\%$) than on grazed corals ($18.0 \pm 19.0\%$) immediately following the predation treatment (Wilcoxon signed rank test, $n = 18$, $p < 0.001$; Fig. 2C). However, the proportion of bites followed by head shakes did not differ between control and grazed corals ($2.7 \pm 4.6\%$ for controls, $1.6 \pm 3.2\%$ for grazed; Wilcoxon signed rank test, $n = 18$, $p = 0.59$; Fig. 2D).

The preference of fish for control corals was stronger during preference tests in which the grazed coral had been exposed to higher levels of grazing during the treatment period. Percent of bites on grazed corals during preference tests immediately following the treatment period was significantly negatively correlated with the level of grazing on those corals during the treatment period (Fig. 4A; Spearman rank correlation coefficient = -0.71 , $df = 9$, $p < 0.05$; Snedecor & Cochran 1967).

Nematocyst counts

In the preliminary study, a nested random-factors ANOVA on the densities of holotrichous isorhizas indicated significant ($p < 0.001$) variability among colonies,

Fig. 2. *Chaetodon multicinctus*. Preference tests in short-term induction experiment ($n = 18$). (A) Number of first bites by *C. multicinctus* on control and grazed colonies of *Porites compressa*: sign test, $p = 0.0075$. (B) Mean ($\pm$ SE) number of inspections on each coral: Wilcoxon signed rank test, $p = 0.001$. (C) Mean ($\pm$ SE) percent of bites on control and grazed corals: Wilcoxon signed rank test, $p = 0.001$. (D) Mean ($\pm$ SE) proportion of bites followed by head shakes: Wilcoxon signed rank test, $p = 0.59$

Fig. 3. *Porites compressa*. Degrees of polyp withdrawal on *P. compressa*. (A) Polyps fully expanded on control colony. (B) Polyps withdrawn on grazed colony

Fig. 4. Predation response to defense induction. Percent of bites on grazed corals during preference tests as a function of grazing intensity during the initial predation treatment period. (A) Short-term defense induction experiment: Spearman rank correlation coefficient = -0.71 , $df = 9$, $p < 0.05$. (B) Long-term defense induction: Spearman rank correlation coefficient = -0.63 , $df = 9$, $p < 0.05$. In both experiments, $n = 11$ corals

but not among branches within colonies ($p = 0.069$; Table 1A). There was also significant variability in microbasic p-mastigophores among colonies ($p < 0.001$), but not among branches within colonies ($p = 0.223$; Table 1B). These analyses indicate that although nematocyst density shows a high degree of variability among colonies, variability among branches within colonies is low enough that any effects of the treatments on nematocyst densities should be detectable.

Nematocyst counts were performed on both initial and final branches from control and grazed corals for 6 colonies in the short-term induction experiment. The percent change in nematocyst density between initial branches and branches removed immediately following the treatment period was compared for both holotri-

Table 1. Nested random factors analysis of variance on the density of nematocysts in *Porites compressa*

Source	df	SS	MS	F	p
(A) Holotrichous isorhizas					
Colony	4	1130.48	282.62	47.72	<0.001
Branch (Colony)	10	59.22	5.92	1.78	0.069
Error	165	550.29	3.34		
Total	179	1739.99			
(B) Microbasic p-mastigophores					
Colony	4	31769.3	7942.3	609.91	<0.001
Branch (Colony)	10	130.2	13.0	1.32	0.223
Error	165	1626.3	9.9		
Total	179	33525.8			

chous isorhizas and microbasic p-mastigophores. There was no significant difference in the percent change in density of holotrichous isorhizas between the control ($+6.3 \pm 15.4\%$) and grazed ($-7.5 \pm 18.7\%$) corals (Wilcoxon signed rank test, $n = 6$, $p = 0.30$). Percent change in density of microbasic p-mastigophores was also not significantly different between control ($+3.0 \pm 9.2\%$) and grazed ($+0.94 \pm 12.5\%$) corals (Wilcoxon signed rank test, $n = 6$, $p = 0.30$).

Long-term defense induction

Preference tests

In preference tests conducted 11 d following the predation treatment, there was no difference between which colony received the first bite (sign test, $n = 11$, $p = 0.55$; Fig. 5A), and this corresponded to similarities in degree of polyp expansion between the control (6 fully expanded, 5 partly expanded) and grazed corals (4 fully expanded, 7 partly expanded; G-test for independence $\chi^2 = 0.738$, $df = 2$, $p > 0.5$). There was also no difference in the number of inspections without subsequent feeding on the 2 corals (5.2 ± 3.9 for controls, 4.6 ± 2.4 for grazed; Wilcoxon signed rank test, $n = 11$, $p = 0.66$; Fig. 5B). Fish still took significantly more bites on the control ($65.1 \pm 19.2\%$) than on the grazed corals ($34.9 \pm 19.2\%$) after the regeneration period (Wilcoxon signed rank test, $n = 11$, $p = 0.021$; Fig. 5C). The proportion of bites followed by head shakes was significantly greater for the grazed corals ($8.2 \pm 12.2\%$) than for the control corals ($2.6 \pm 2.1\%$; Wilcoxon signed rank test, $n = 11$, $p = 0.045$; Fig. 5D). Percent of bites on the grazed corals during preference tests following the regeneration period was significantly negatively correlated with the level of grazing on those corals during the treatment period (Spearman rank correlation coefficient = -0.63 , $df = 9$, $p < 0.05$; Fig. 4B).

Fig. 5. *Chaetodon multicinctus*. Preference tests in long-term defense induction experiment ($n = 11$). (A) Number of first bites by *C. multicinctus* on control and grazed colonies of *Porites compressa*: sign test, $p = 0.55$. (B) Mean ($\pm$ SE) number of inspections on each coral: Wilcoxon signed rank test, $p = 0.66$. (C) Mean ($\pm$ SE) percent of bites on control and grazed corals: Wilcoxon signed rank test, $p = 0.021$. (D) Mean ($\pm$ SE) proportion of bites followed by head shakes: Wilcoxon signed rank test, $p = 0.045$

Nematocyst counts

Nematocyst densities were determined from all 11 colonies from the long-term induction experiment. Percent change in density of holotrichous isorhizas over the course of this experiment did not differ between the control ($-5.8 \pm 25.6\%$) and grazed corals ($-1.7 \pm 32.2\%$; Wilcoxon signed rank test, $n = 11$, $p = 0.82$; Fig. 6A). Densities of microbasic p-mastigophores increased significantly following the treatment period in the grazed corals ($+22.3 \pm 20.3\%$; Wilcoxon signed rank test, $n = 11$, $p = 0.037$), and this increase was significantly different from the percent change in density of this nematocyst type in the control corals ($-0.34 \pm 14.3\%$; Wilcoxon signed rank test, $n = 11$, $p = 0.009$; Fig. 6B).

The percent increase in density of microbasic p-mastigophores in the grazed corals following the regeneration period was significantly positively correlated with the intensity of grazing on those corals during the treatment period (Spearman rank correlation coefficient = 0.773, $df = 9$, $p < 0.01$; Fig. 7).

Translocation of inducible defenses

Preference tests

Two sets of preference tests were conducted on corals in the translocation experiment. To test for defense induction, the previously uncaged control and grazed coral halves were offered to naïve fish. A preference for one colony over the other in this test indicates that predation during the treatment period caused changes in the coral that affected feeding preferences by the fish 11 d later. In this test, there was no difference in which colony received the first bite (sign test, $n = 12$, $p = 0.39$; Fig. 8A). Grazed corals also did not receive significantly more inspections than control corals (3.5 ± 3.6 for controls, 2.0 ± 1.6 for grazed corals; Wilcoxon signed rank test, $n = 6$, $p = 0.14$; Fig. 8B). For all treatment groups, polyps were expanded to similar

Fig. 6. Change in nematocyst density. Percent change in nematocyst density from initial branches to branches removed following 11 d of regeneration. (A) Holotrichous isorhizas: Wilcoxon signed rank test on the differences between control and grazed corals, $p = 0.82$. (B) Microbasic p-mastigophores: Wilcoxon signed rank test on the difference between control and grazed corals, $p = 0.009$. Lines connect clone-mates for $n = 11$ corals

Fig. 7. Change in nematocyst density as function of grazing intensity. Percent change in density of microbasic p-mastigophores in grazed corals (solid circles, $n = 11$) as a function of grazing intensity during the predation treatment period for corals after 1 d of treatment and 11 d of regeneration. Control corals (mean $\pm$ SE) shown by open circle, $n = 11$ were not exposed to grazing during the treatment period. Spearman rank correlation coefficient for grazed corals only = 0.773, $df = 9$, $p < 0.01$

degrees from Day 5 through the end of the regeneration period. However, fish did feed more heavily on control ($69.2 \pm 20.0\%$) than on grazed corals ($30.8 \pm 20.0\%$; Wilcoxon signed rank test, $n = 12$, $p = 0.013$; Fig. 8C), and a greater proportion of bites were followed by head shakes on the grazed corals ($13.5 \pm 12.5\%$ vs $3.1 \pm 4.2\%$ on controls; Wilcoxon signed rank test, $n = 12$, $p = 0.021$; Fig. 8D).

Translocation across the colony of defenses, or of the stimuli to induce defenses, was tested by offering the previously caged control and grazed coral halves to fish in preference tests. Neither caged half was directly exposed to predation during the treatment period; however, if translocation did occur, fish would be

expected to show a preference for the control coral over the grazed coral. No such preference was observed. First bites were distributed equally over both corals (sign test, $n = 12$, $p = 1.0$; Fig. 9A), and there was no difference in the number of inspections on either colony (1.8 ± 1.2 for controls, 2.3 ± 1.2 for grazed corals; Wilcoxon signed rank test, $n = 6$, $p = 0.40$; Fig. 9B). Fish also did not feed more heavily on control corals ($47.0 \pm 14.7\%$) than on grazed corals ($53.0 \pm 14.7\%$; Wilcoxon signed rank test, $n = 12$, $p = 0.72$; Fig. 9C), and there was no difference in proportion of bites followed by head shakes on either colony ($3.4 \pm 6.1\%$ for controls, $2.9 \pm 2.0\%$ for grazed corals; Wilcoxon signed rank test, $n = 12$, $p = 0.22$; Fig. 9D).

Nematocyst counts

Nematocyst densities were determined for 6 colonies in the translocation experiment. Table 2A shows the percent change in density of holotrichous isorhizas and microbasic p-mastigophores in all treatment groups. There was a significant effect of treatment group on percent change in density of both holotrichous isorhizas (Table 2B) and microbasic p-mastigophores (Table 2C). In both cases, the uncaged grazed group showed a significantly greater increase in nematocyst density than did the other 3 treatment groups, which did not differ significantly from each other (Tukey's test with $\alpha = 0.05$; Table 2A).

DISCUSSION

This study demonstrated that *Porites compressa* responds to intense grazing by *Chaetodon multicinctus* by withdrawal of polyps into the corallum in the short term, and by increasing nematocyst density in grazed parts of colonies in the longer term. Both of these induced coral responses have impacts on butterflyfish feeding behavior and prey preferences. In preference

Fig. 8. *Chaetodon multicinctus*. Preference tests for defense induction during translocation experiment ($n = 12$). During preference tests, cages were placed over the previously caged halves. (A) Number of first bites by *C. multicinctus* on control and grazed colonies of *Porites compressa*: sign test, $p = 0.39$. (B) Mean ($\pm$ SE) number of inspections on each coral: Wilcoxon signed rank test, $p = 0.14$. (C) Mean ($\pm$ SE) percent of bites on control and grazed corals: Wilcoxon signed rank test, $p = 0.013$. (D) Mean ($\pm$ SE) proportion of bites followed by head shakes: Wilcoxon signed rank test, $p = 0.021$

Fig. 9. *Chaetodon multicinctus*. Preference tests for translocation during translocation experiment ($n = 12$). During preference tests, cages were placed over the previously uncaged coral halves. (A) Number of first bites by *C. multicinctus* on control and grazed colonies of *Porites compressa*: sign test, $p = 1.0$. (B) Mean ($\pm$ SE) number of inspections on each coral: Wilcoxon signed rank test, $p = 0.40$. (C) Mean ($\pm$ SE) percent of bites on control and grazed corals: Wilcoxon signed rank test, $p = 0.72$. (D) Mean ($\pm$ SE) proportion of bites followed by head shakes: Wilcoxon signed rank test, $p = 0.22$

tests performed immediately following the predation treatment period, naïve fish were able to detect differences between corals that had been previously exposed to grazing and ungrazed controls. First bites were directed toward control corals more often than toward grazed corals, and grazed corals were inspected without subsequent feeding more often than were controls (Fig. 2A,B). Both of these behaviors indicate that fish could distinguish the quality of the coral by

visual means. Butterflyfishes are known to rely on visual cues for locating prey, although chemical or other cues may then determine prey preferences (Alino et al. 1988, 1992). In the short-term, therefore, it appears that the external appearance of the colony contributes to prey selection. Two aspects of colony appearance may play a role here: polyp number and degree of polyp expansion. Although the predation treatment reduced the available number of polyps, most polyps remained on the grazed corals (Fig. 3B), they were just fully withdrawn into the corallum. The fact that fish still found those corals desirable enough to inspect even when an alternative prey source was readily available, suggests that the reduction in polyps itself was an insufficient deterrent. Indeed, the overall greater degree of polyp withdrawal on the grazed corals reduced the ease with which fish could consume the remaining polyps and forced them to feed on the control corals.

When butterflyfishes forage, they take only a few bites from a colony and then move on to feed on another colony (Gochfeld 1997). This brevity of feeding bouts may increase foraging efficiency as the polyps in the area surrounding a bite withdraw, resulting in an increase in handling time for subsequent bites. This behavior may also distribute feeding across colonies within the territory so that individual coral colonies are not subjected to high levels of predation that might reduce coral productivity. This distribution of feeding activity may maintain feeding at an intensity that is not sufficient to induce increased levels of defenses in a coral colony. Withdrawal of polyps in the vicinity of a bite is believed to serve as the proximate cue for a coral-feeding fish to move on to the next colony (Motta 1980, Hourigan 1987, Cox 1991, Gochfeld 1991). Polyps need not remain withdrawn for longer than a few seconds before the fish has moved on, and therefore, a brief period of withdrawal following a feeding bout may increase colony fitness, even if polyp withdrawal were to temporarily incur some cost to the colony. Hourigan (1987) found that polyps within a

Table 2. Comparison of percent change in density of nematocysts in *Porites compressa* ($n = 6$) from 4 treatment groups in the translocation experiment. (A) Mean ($\pm$ SD) percent change in density of holotrichous isorhiza and microbasic p-mastigophore nematocysts. Superscripts of the same letter indicate that group means are not significantly different from each other at $p = 0.05$ (Tukey's test). (B) Randomized block ANOVA on percent change in density of holotrichous isorhizas (arcsin-transformed data). (C) Randomized block ANOVA on percent change in density of microbasic p-mastigophores (arcsin-transformed data)

(A)					
Treatment group	Percent change in density of holotrichous isorhizas		Percent change in density of microbasic p-mastigophores		
Uncaged control	0.82 ± 15.7 ^b		0.35 ± 0.73 ^b		
Caged control	2.5 ± 11.5 ^b		2.5 ± 5.8 ^b		
Uncaged grazed	25.2 ± 13.2 ^a		21.0 ± 7.6 ^a		
Caged grazed	9.4 ± 7.4 ^b		6.3 ± 6.2 ^b		
(B)					
Source	df	SS	MS	F	p
Treatment	3	0.19	0.074	9.45	0.0009
Coral	5	0.53	0.037		
Error	15	0.12	0.0079		
Total	23	0.53			
(C)					
Source	df	SS	MS	F	p
Treatment	3	0.16	0.052	26.09	0.0001
Coral	5	0.061	0.012		
Error	15	0.030	0.0020		
Total	23	0.25			

10 to 15 mm radius of a bite on *Porites* spp. remain withdrawn for 3 to 6 min following a feeding bout, whereas polyps on *P. compressa* remained withdrawn for approximately 5 d following intense predation in the present study. The results of this experiment support the contention that polyp withdrawal is the proximate cause of feeding bout brevity on individual colonies. In addition, fish also fed more heavily on the control corals in these preference tests (Fig. 2C), which may reflect a distastefulness of the coral tissue from the grazed colony or greater efficiency of feeding on the control corals. Since *Chaetodon multicinctus* feeds on coral polyps without removing any of the coral's skeleton, these fish are presumably able to feed with greater efficiency on corals with expanded tentacles, as they could potentially ingest more energy per bite on fully expanded polyps.

Head shakes in cnidarian-feeding fishes are distinctive movements that occasionally occur immediately following a bite, presumably as a response to the mouth being stung by nematocysts (Stachowicz & Lindquist 2000). The proportion of *Chaetodon multicinctus* bites followed by head shakes on grazed corals was not greater than on control corals immediately following the predation treatment period (Fig. 2D), suggesting that nematocyst densities were not higher in the grazed corals than in the controls. Indeed, there was no change in density of either type of nematocyst immediately following the predation treatment period. In addition to the observed differences in polyp behavior, unpalatability of the experimental coral tissue at this time could be the result of elevated levels of chemical defenses (Gochfeld 1997), which can be induced rapidly (within minutes or hours) in some plants (Edwards et al. 1991, Karban & Baldwin 1997, Hammerstrom et al. 1998). Inducible morphological defenses, on the other hand, generally require at least a few days to develop (Adler & Harvell 1990, Harvell & Padilla 1990), although there are exceptions (Kuhlmann & Heckmann 1994).

After full regeneration of the coral tissue, fish still preferred to feed on the control corals (Fig. 5C). This preference is apparently not based on visual cues as neither first bites nor number of inspections differed between corals (Fig. 5A,B), and both polyp presence and the degree of polyp expansion in the 2 corals were similar. The decision to feed more heavily on the control coral occurred only after the fish 'tasted' both colonies. Evidence that the grazed colony was less palatable than the control after the regeneration period comes from the greater proportion of grazed bites followed by head shakes (Fig. 5D) and the concomitant increase in density of microbasic p-mastigophores in grazed colonies (Fig. 6B). These nematocysts are localized in the mesenterial filaments (T. Work

pers. comm.), and are therefore consumed with the polyp. The induced responses of corals in these experiments support Rhoades' (1979) hypothesis that rapidly induced defenses should be 'qualitative' in nature, since they incur relatively little cost and are effective against a variety of grazers. Delayed inducible responses should involve more 'quantitative' types of defenses. The evolution of a combination of both rapid and delayed inducible defenses may result if a predation threat is continually present (Tollrian & Harvell 1999). In *Porites compressa*, the rapid behavioral responses and delayed induction of nematocysts meet these predictions, and presumably act in concert to reduce overall grazing intensity to sustainable levels.

The increase in nematocyst densities in the grazed colony following regeneration of the coral tissue, but not immediately following the predation treatment, probably reflects the time required for the coral to produce new nematocysts or for nematocysts to migrate within the colony. Few studies have addressed the mechanisms of nematocyst production in anthozoans, although migration of nematocysts has been demonstrated in octocorals (Schmidt & Moraw 1982) and hydroids (Campbell 1988, Robson 1988), and is presumed to occur in other cnidarians (Buss 1990). Since this subject has not been examined in scleractinian corals, it is premature to speculate whether the elevated nematocyst densities observed in this experiment result from increased densities in regenerating polyps or in remaining polyps as a result of new cell production or migration of cells from other regions of the polyp or colony.

In response to grazing, defenses may be induced locally in the region of damage or systemically throughout the prey organism (Karbon & Baldwin 1997). This 'translocation' of inducible defenses, or of the cue to induce these defenses, could act to disperse grazing (Agrawal & Karban 1999, Jaremo et al. 1999), which may reduce the overall cost of grazing (Edwards et al. 1991, Karban & Baldwin 1997, Wold & Marquis 1997). Corals possess a primitive nervous system and translocation of energy occurs at various scales within a coral colony. Therefore, there exists the potential for translocation of defense induction within coral colonies. Indeed, Hidaka & Yamazato (1984) found that the coral *Galaxea fascicularis* developed sweeper tentacles not only on the side of the colony facing a competitor, but also on the opposite side of the colony. If translocation of defenses occurred in *Porites compressa*, butterflyfish would be expected to prefer the caged half of the control coral over the caged half of the grazed coral in the translocation experiment. However, fish did not show a preference, nor did they exhibit a difference in head shake frequency (Fig. 9C,D), for either caged control or caged grazed

corals. Nematocyst density also did not differ significantly between the 2 caged treatment groups (Table 2A). Horridge (1957) used electrical stimuli to study polyp retraction behavior in several species of corals and found that *Porites* spp. respond to a single stimulus by withdrawal of polyps within a 4 cm² area around the stimulus, and after only a few stimuli, an asymptote was reached at approximately 16 cm². This suggests that translocation, at least by any mechanism requiring the nerve net, is limited to a very localized area in *Porites* spp. This may explain the absence of translocation of inducible defenses in *P. compressa*, although it is not impossible to rule out alternative mechanisms of translocation following more sustained stresses. However, Jaremo et al. (1999) suggested that localized defenses are less costly and more beneficial when defenses are effective in small doses or when the expected degree of damage is low, as is most often the case with butterflyfishes that only remove individual polyps.

Physical damage to the coral tissue appears to be a necessary cue for increased nematocyst density, as disturbance of the coral without associated tissue damage did not induce changes similar to those observed in response to grazing. Other types of physical damage to *Porites* spp. tissue also appear sufficient to cause increases in nematocyst densities. Aeby (1998) found elevated densities of microbasic p-mastigophores in *Porites compressa* polyps infected by cysts of a digenetic trematode, as compared to uninfected polyps, and *Porites lobata* accumulated a high density of holotrichous isorhizas on the oral surface where algal filaments had become 'rooted' in the coral epidermis (C. Hunter pers. comm.). Thus, increased densities of nematocysts may serve as a generalized defense against or response to tissue damage, rather than a specific defense against grazers.

Inducible defenses are generally predicted to occur in organisms that are exposed to unpredictable or intermittent periods of predation (Harvell 1990, Haukioja 1990), although temporal variability in grazing pressure is not always considered necessary for the evolution of inducible defenses (Jaremo et al. 1999). Clearly, corals living within territories of long-lived butterflyfishes would ordinarily experience relatively constant levels of predation pressure. However, under certain circumstances, individual coral colonies could be exposed to elevated feeding intensities. This might occur under conditions of reduced food supply, reduced territory size, or increased rates of territory intrusion by other coral-feeding fishes, any of which might be due to overall deterioration in the condition of the coral community (Hourigan 1987, Tricas 1989b, Gochfeld 1997). In general, the intensities of predation to which individual coral colonies were exposed in

these experiments were significantly greater than levels of predation by *Chaetodon multicinctus* on individual coral colonies on the reef. On Hawaiian reefs, individual colonies of *Porites compressa* within *C. multicinctus* territories are revisited a maximum of once or twice per hour, with only a few bites taken at a time (pers. obs.). Therefore, the lowest intensity of feeding during the treatment period in the defense induction experiments most closely resembles the natural situation. These lower treatment levels did not result in as strong a preference for control corals as did colonies exposed to higher treatment levels (Fig. 4), suggesting that corals are able to tolerate such levels of grazing with minimal fitness costs. These correlations, when considered with the positive correlation between grazing treatment level and percent increase in nematocyst density (Fig. 7), suggest that a coral colony exposed to predation above some threshold intensity is likely to produce increased densities of nematocysts. Coral-feeding butterflyfishes are able to detect such changes in behavior and palatability of their food resource and these reduce the quality of that colony as food.

Many herbivores have evolved foraging behaviors that allow them to circumvent plant defenses (reviewed by Futuyma & Keese 1992, Karban & Baldwin 1997). Whitham (1987) proposed that territoriality among herbivores may have evolved as a counter-adaptation against plant defenses, and this seems likely among butterflyfishes as well. If corals increase their defenses in response to high levels of grazing, the evolutionary response of corallivores could well be the development of a mechanism that limits their density and distributes individuals more uniformly over the reef. Indeed, butterflyfish territories may need to be larger than would be required simply to include sufficient food to meet the metabolic needs of the resident fishes, but maintenance of large territories also incurs costs in terms of defense from intruders. The sizes of butterflyfish territories often vary inversely with coral abundance (Reese 1981, Sutton 1985, Hourigan 1987, Hourigan et al. 1988, Tricas 1989b, Wrathall et al. 1992), and butterflyfishes may respond to changes in coral abundance by concomitant adjustments in the size of their territories (Hourigan 1987, Tricas 1989b, Gochfeld 1997). This variation in territory size may be the mechanism by which fish can control the amount of food to which they have access, and information from the corals themselves may provide essential cues for determining territory size. Indeed, polyp withdrawal and induced defenses could provide rapid and reliable feedback relating to coral condition. Territoriality could thus maintain grazing levels on individual coral colonies below an intensity that would both prevent corals from regenerating and induce defenses in those corals. Since territorial butterflyfishes rely on the same

corals for food for many years, maintaining a sustainable quantity of high quality food is crucial to their survival.

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LITERATURE CITED

- Adler FR, Harvell CD (1990) Inducible defenses, phenotypic variability and biotic environments. *Trends Ecol Evol* 5: 407–410
- Aeby GS (1998) Interactions of the digenetic trematode, *Podocotyloides stenometra*, with its coral intermediate host and butterflyfish definitive host: ecology and evolutionary implications. PhD thesis, University of Hawaii, Manoa, HI
- Agrawal AA, Karban R (1999) Why induced defenses may be favored over constitutive strategies in plants. In: Tollrian R, Harvell CD (eds) *The ecology and evolution of inducible defenses*. Princeton University Press, Princeton, NJ, p 45–61
- Alino PM, Sammarco PW, Coll JC (1988) Studies of the feeding preferences of *Chaetodon melannotus* (Pisces) for soft corals (Coelenterata: Octocorallia). *Proc 6th Int Coral Reef Symp, Townsville* 3:31–36
- Alino PM, Coll JC, Sammarco PW (1992) Toxic prey discrimination in a highly specialized predator *Chaetodon melannotus* (Block et Schneider): visual vs. chemical cues. *J Exp Mar Biol Ecol* 164:209–220
- Bak RPM, Steward-Van Es Y (1980) Regeneration of superficial damage in the scleractinian corals *Agaricia agaricites* F. *purpurea* and *Porites astreoides*. *Bull Mar Sci* 30: 883–887
- Baldwin IT, Schultz JC (1983) Rapid changes in tree leaf chemistry induced by damage: evidence for communication between plants. *Science* 221:277–279
- Bigger CH (1988) The role of nematocysts in anthozoan aggression. In: Hessinger DA, Lenhoff HM (eds) *The biology of nematocysts*. Academic Press, New York, p 295–308
- Buss LW (1990) Competition within and between encrusting clonal invertebrates. *Trends Ecol Evol* 5:352–356
- Campbell RD (1988) Migration of nematocytes in hydrozoans. In: Hessinger DA, Lenhoff HM (eds) *The biology of nematocysts*. Academic Press, New York, p 123–142
- Chornesky EA (1983) Induced development of sweeper tentacles on the reef coral *Agaricia agaricites*: a response to direct competition. *Biol Bull (Woods Hole)* 165:569–581
- Cox EF (1986) The effects of a selective corallivore on growth rates and competition for space between two species of Hawaiian corals. *J Exp Mar Biol Ecol* 101:161–174
- Cox EF (1991) Interactions between trophic levels on coral reefs: scleractinian corals and corallivorous butterflyfishes in Hawaii. PhD thesis, University of New Mexico, Albuquerque
- Cronin G, Hay ME (1996) Susceptibility to herbivores depends on recent history of both plant and animal. *Ecology* 77:1531–1543
- Edwards PJ, Wratten SD, Gibberd RM (1991) The impact of inducible phytochemicals on food selection by insect herbivores and its consequences for the distribution of grazing damage. In: Tallamy DW, Raupp MJ (eds) *Phytochemical induction by herbivores*. Wiley-Liss, New York, p 205–221
- Ewer RF (1947) On the functions and mode of action of the nematocysts of hydra. *Proc Zool Soc Lond* 117:365–376
- Futuyma DJ, Keese MC (1992) Evolution and coevolution of plants and phytophagous arthropods. In: Rosenthal GA, Berenbaum MR (eds) *Herbivores: their interactions with secondary plant metabolites*. Ecological and evolutionary processes, Vol 2. Academic Press, San Diego, CA, p 440–475
- Gaulin G, Dill L, Beaulieu J, Harris LG (1986) Predation-induced changes in growth form in a nudibranch-hydroid association. *Veliger* 28:389–393
- Glynn PW (1988) Predation on coral reefs: some key processes, concepts and research directions. *Proc 6th Int Coral Reef Symp, Townsville* 1:51–62
- Glynn PW, Krupp DA (1986) Feeding biology of a Hawaiian sea star corallivore *Culcita novaeguineae* Muller & Trotschel. *J Exp Mar Biol Ecol* 96:75–96
- Gochfeld DJ (1991) Energetics of a predator-prey interaction: corals and coral-feeding fishes. *Pac Sci* 45:246–256
- Gochfeld DJ (1997) Mechanisms of coexistence between corals and coral-feeding butterflyfishes: territoriality, foraging behavior, and prey defense. PhD thesis, University of Hawaii, Manoa, HI
- Gochfeld DJ, Aeby GS (1997) Control of populations of the coral-feeding nudibranch, *Phestilla sibogae*, by fish and crustacean predators. *Mar Biol* 130:63–39
- Hammerstrom K, Dethier MD, Duggins DO (1998) Rapid phlorotannin induction and relaxation in five Washington kelps. *Mar Ecol Prog Ser* 165:293–305
- Harmelin-Vivien ML, Bouchon-Navaro Y (1981) Trophic relationships among chaetodontid fishes in the Gulf of Aqaba (Red Sea). *Proc 4th Int Coral Reef Symp, Manila* 2: 537–544
- Harmelin-Vivien ML, Bouchon-Navaro Y (1983) Feeding diets and significance of coral feeding among chaetodontid fishes in Moorea (French Polynesia). *Coral Reefs* 2: 119–127
- Harvell CD (1986) The ecology and evolution of inducible defenses in a marine bryozoan: cues, costs, and consequences. *Am Nat* 128:810–823
- Harvell CD (1990) The ecology and evolution of inducible defenses. *Q Rev Biol* 65:323–340
- Harvell CD (1992) Inducible defenses and allocation shifts in a marine bryozoan. *Ecology* 73:1567–1576
- Harvell CD (1999) Complex biotic environments, coloniality, and heritable variation for inducible defenses. In: Tollrian R, Harvell CD (eds) *The ecology and evolution of inducible defenses*. Princeton University Press, Princeton, NJ, p 231–244
- Harvell CD, Padilla DK (1990) Inducible morphology, heterochrony, and size hierarchies in a colonial invertebrate monoculture. *Proc Natl Acad Sci* 87:508–512

- Haukioja E (1990) Induction of defenses in trees. *Annu Rev Entomol* 36:25–42
- Havel JE (1987) Predation-induced defenses: a review. In: Kerfoot WC, Sih A (eds) *Predation: direct and indirect impacts on aquatic communities*. University Press of New England, Hanover, NH, p 263–278
- Hidaka M, Yamazato K (1984) Intraspecific interactions in a scleractinian coral, *Galaxea fascicularis*: induced formation of sweeper tentacles. *Coral Reefs* 3:77–85
- Hidaka M, Miyazaki I, Yamazato K (1987) Nematocysts characteristic of the sweeper tentacle of the coral *Galaxea fascicularis* (Linnaeus). *Galaxea* 6:195–207
- Hill MS, Hill AL (2002) Morphological plasticity in the tropical sponge *Anthiosigmella varians*: responses to predators and wave energy. *Biol Bull (Woods Hole)* 202:86–95
- Horridge GA (1957) The co-ordination of the protective retraction of coral polyps. *Phil Trans R Soc Lond B Biol Sci* 240:495–529
- Hourigan T (1987) The behavioral ecology of three species of butterflyfishes (family Chaetodontidae). PhD thesis, University of Hawaii, Manoa, HI
- Hourigan TF, Tricas TC, Reese ES (1988) Coral reef fishes as indicators of environmental stress in coral reefs. In: Soule DF, Kleppel GS (eds) *Marine organisms as indicators*. Springer-Verlag, New York, p 107–135
- Hughes TP, Jackson JBC (1985) Population dynamics and life histories of foliaceous corals. *Ecol Monogr* 55:141–166
- Jaremo J, Tuomi J, Nilsson P (1999) Adaptive status of localized and systemic defense responses in plants. In: Tollrian R, Harvell CD (eds) *The ecology and evolution of inducible defenses*. Princeton University Press, Princeton, NJ, p 33–44
- Jokiel PL (1987) Ecology, biogeography and evolution of corals in Hawaii. *Trends Ecol Evol* 2:179–182
- Karban R, Baldwin IT (1997) Induced responses to herbivory. University of Chicago Press, Chicago
- Karban R, Myers JH (1989) Induced plant responses to herbivory. *Annu Rev Ecol Syst* 20:331–348
- Kinzie RA III (1970) The ecology of the gorgonians (Cnidaria, Octocorallia) of Discovery Bay, Jamaica. PhD thesis, Yale University, New Haven
- Kuhlmann HW, Heckmann K (1994) Predation risk of typical ovoid and 'winged' morphs of *Euplotes* (Protozoa, Ciliophora). *Hydrobiology* 284:219–227
- Mariscal RN (1974) Nematocysts. In: Muscatine L, Lenhoff HM (eds) *Coelenterate biology: reviews and new perspectives*. Academic Press, New York, p 129–178
- Meesters EH, Wesseling I, Bak RPM (1996) Partial mortality in 3 species of reef-building corals and the relation with colony morphology. *Bull Mar Sci* 58:838–852
- Motta PJ (1980) Functional anatomy of the jaw apparatus and related feeding behavior of butterflyfishes (Chaetodontidae) including a review of jaw protrusion in fishes. PhD thesis, University of Hawaii, Manoa, HI
- Reese ES (1977) Coevolution of corals and coral feeding fishes of the family Chaetodontidae. *Proc 3rd Int Coral Reef Symp, Miami* 1:267–274
- Reese ES (1981) Predation on corals by fishes of the family Chaetodontidae: implications for conservation and management of coral reef ecosystems. *Bull Mar Sci* 31:594–604
- Reese ES (1991) How behavior influences community structure of butterflyfishes (family Chaetodontidae) on Pacific coral reefs. *Ecol Int Bull* 19:29–41
- Rhoades DF (1979) Evolution of plant chemical defense against herbivores. In: Rosenthal GA, Janzen DH (eds) *Herbivores: their interaction with secondary plant metabolites*. Academic Press, New York, p 3–54
- Rhoades DF (1983) Herbivore population dynamics and plant chemistry. In: Denno RF, McClure MS (eds) *Variable plants and herbivores in natural and managed systems*. Academic Press, New York, p 155–220
- Richardson CA, Dustan P, Lang JC (1979) Maintenance of living space by sweeper tentacles of *Montastrea cavernosa*, a Caribbean reef coral. *Mar Biol* 55:181–186
- Robson EA (1988) Problems of supply and demand for cnidae in Anthozoa. In: Hessinger DA, Lenhoff HM (eds) *The biology of nematocysts*. Academic Press, San Diego, CA, p 179–207
- SAS Institute (1990) SAS/STAT user's guide. Version 6, Vol 2, 4th edn. SAS Institute, Cary, NC
- Schmidt J, Moraw B (1982) Die Cnidogenese der Octocorallia (Anthozoa, Cnidaria): II. Reifung, Wanderung und Zerfall von Cnidoblast und Nesselkapsel. *Helgol Meeresunters* 35:97–118
- Snedecor GW, Cochran WG (1967) *Statistical methods*, 6th edn. Iowa State University Press, Ames, IA
- Stachowicz JJ, Lindquist N (2000) Hydroid defenses against predators: the importance of secondary metabolites versus nematocysts. *Oecology* 124:280–288
- Sutton M (1985) Patterns of spacing in a coral reef fish in two habitats on the Great Barrier Reef. *Anim Behav* 33:1332–1337
- Tallamy DW, Raupp MJ (1991) *Phytochemical induction by herbivores*. Wiley-Liss, New York
- Tollrian R, Harvell DC (1999) *The ecology and evolution of inducible defenses*. Princeton University Press, Princeton, NJ
- Tricas TC (1989a) Prey selection by coral-feeding butterflyfishes: strategies to maximize the profit. *Environ Biol Fishes* 25:171–185
- Tricas TC (1989b) Determinants of feeding territory size in the corallivorous butterflyfish, *Chaetodon multicinctus*. *Anim Behav* 37:830–841
- Wellington GM (1980) Reversal of digestive interactions between Pacific reef corals: mediation by sweeper tentacles. *Oecology* 47:340–343
- West JM (1997) Plasticity in the sclerites of a gorgonian coral: tests of water motion, light level, and damage cues. *Biol Bull (Woods Hole)* 192:279–289
- Whitham TG (1987) Evolution of territoriality by herbivores in response to host plant defense. *Am Zool* 27:359–369
- Wold EN, Marquis RJ (1997) Induced defense in white oak: effect on herbivores and consequences for the plant. *Ecology* 78:1356–1369
- Wrathall TJ, Roberts CM, Ormond RFG (1992) Territoriality in the butterflyfish *Chaetodon austriacus*. *Environ Biol Fishes* 34:305–308