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CHAPTER 6

Coral Reef Fishes as Indicators of Environmental Stress in Coral Reefs

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Introduction

Butterflyfishes of the family Chaetodontidae are conspicuous inhabitants of coral reefs throughout the world (Figure 6.1). Many species are obligate corallivores, and thus depend on the live tissue of corals for their food. We believe that these species of butterflyfishes are excellent candidates for indicators of changes in conditions on the coral reef.

The conceptual ideas are simple. Corallivorous butterflyfishes have coevolved with, and are intimately related to, the corals on which they feed. The distribution and abundance of these fishes should be directly correlated with the distribution and abundance of the corals. If the corals are adversely affected by stressful environmental conditions, such as chronic low levels of pollution, their health will deteriorate. This deterioration should be detected by the fishes which feed on them. The corals are sessile and cannot avoid the stress, whereas the fishes are motile, and can emigrate to healthier regions of the reef. Chronic low levels of pollutants on the reef and the slowly deteriorating condition of the corals are difficult to detect by conventional methods (Brown and Howard 1985). In contrast, simply counting the abundance of the brightly colored, diurnal butterflyfishes using conventional census techniques is a relatively simple task. A diver can be taught in a few hours to recognize and census key indicator species along a transect. Our hypothesis can be stated as follows: coral-feeding butterflyfishes respond to declines in coral quality or abundance by spatial adjustments that can be easily and rapidly quantified.

Reese (1981) first proposed that obligate corallivores, such as many butterflyfishes, could serve as indicator organisms. Subsequent experimental studies have increased our knowledge of the relationships between butterflyfishes and corals, and support their potential as indicator species. In the following sections we briefly review the need for indicators to monitor changes in conditions of coral reefs, the biology of butterflyfishes and their relationship with corals, the use of visual censuses to monitor butterflyfish

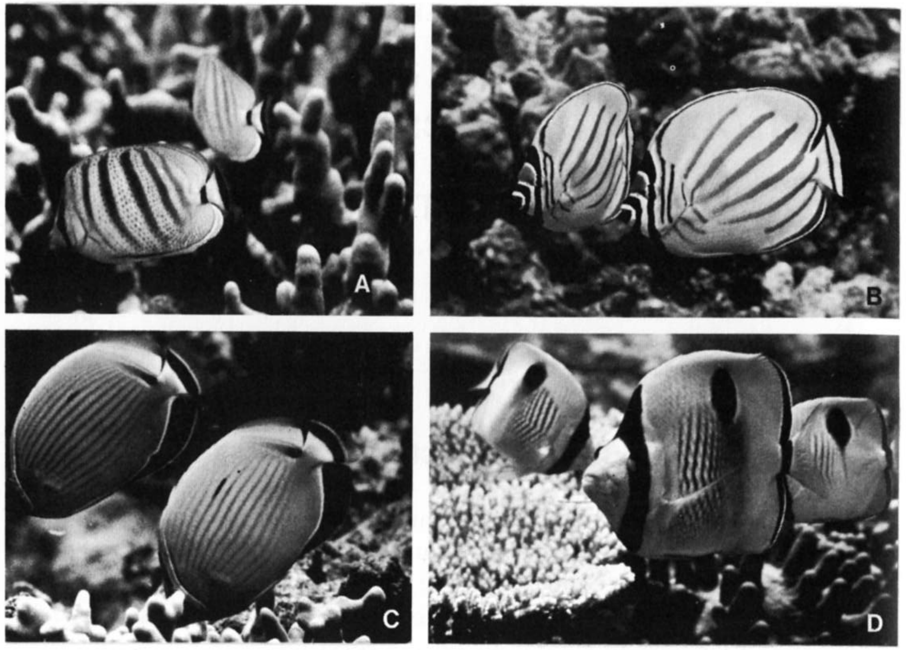


FIGURE 6.1. Four coral-feeding butterflyfishes: (a) *Chaetodon multicinctus*, (b) *Chaetdon ornatissimus*, (c) *Chaetodon trifasciatus*, and (d) *Chaetodon unimaculatus*.

numbers, and evidence of the response of butterflyfishes to natural and artificial perturbations of the corals on which they feed. Furthermore, we describe the studies which must be done to test the predictions which can be generated from this hypothesis.

Environmental Stress and Coral Reefs

Coral reefs are important natural, economic, and recreational resources for many countries throughout the tropics. This is especially true for many of the developing nations in the Indo-Pacific and the Caribbean. Unfortunately, many of these reefs are threatened by activities associated with industrialization and increasing human use. Environmental stresses, such as siltation from construction, logging and agriculture, dredging, sewage, oil spills, and other contaminants, directly affect the scleractinian corals which build the reefs, and indirectly, the rich and diverse biota which inhabit and utilize the reef.

Rosen (1982) defined "stress" on corals as environmental conditions which result in restricted growth and reproduction. Brown and Howard (1985) have recently reviewed the literature on the assessment of stress on coral reefs. Such assessment requires regular monitoring of reefs by repeatable methods. Several common quantitative methods of coral assessment have recently been compared (Dodge et al. 1982, Bouchon 1983). While these methods appear to produce consistent results, problems remain in accurate assessment of coral cover, abundance, and diversity (Kinsie and Snider 1978, Loya 1978, Pichon 1978). In addition, these standard techniques may not detect changes in the complex interactions among corals, or the effects of stress which do not result in immediate coral mortality.

At present, there are insufficient baseline studies of healthy coral reefs to determine the range of natural changes which occur over time. Davis (1982) compared coral reefs in the Caribbean in 1976 to surveys of the same reefs in 1881, and discovered extensive changes in species composition. Other studies of undisturbed reef areas have shown declining coral cover (Dustan 1977; in Florida), increasing coral cover (Done 1981; in Australia), or relatively constant cover with differences in spatial distributions of heads (Bak and Luckhurst 1980; in Curacao). Studies on the effects of natural stress factors on reefs have concentrated on the effects of storms (Goreau 1964, Connell 1973, Stoddart 1974, Shinn 1976, Pearson 1981, Porter et al. 1981, Dollar 1982, Rogers et al. 1983, Laboute 1985), abnormal temperatures (Shinn 1976, Davis 1982), low tides (Loya 1972, 1976), and bacterial infections (Gladfelter 1982). In most cases, stressed coral recovers relatively quickly by regeneration as long as a portion of the colony remains alive. Shallow coral reefs appear to show the least temporal stability (Connell 1973), but corals in these areas may be more resistant to stress (Brown and Howard 1985).

Several authors have suggested that coral reefs may be more susceptible to stress from manmade pollutants than stress from natural occurrences (Johannes 1972, Loya 1976, Rogers et al. 1983). Other studies suggest that reefs may be more resilient to such stresses than previously thought (e.g. Dollar and Grigg 1981). Studies have investigated the effects of human activities such as tourist development (Kelleher and Dutton 1985), dredging (Dahl and Lambert 1978, Dodge and Vaisnys 1977, Bak 1978, Sheppard 1980), oil spills (Hudson et al. 1982, Fischelson 1973, Loya 1976), sewage (Smith 1977, Walker and Ormond 1982), thermal pollution (Jokiel and Coles 1974) and heavy metal pollutants (Brown and Holley 1982). These studies show significant deleterious effects of pollution, and emphasize the importance of early detection and management to preserve the coral reefs.

Many forms of pollution have chronic, long-term effects on corals. Unfortunately, using current survey techniques, many of the critical effects may not be detected until extensive damage has occurred. Interactions may be complex, since different corals respond differently to both natural and manmade stresses (Brown and Howard 1985). Furthermore, because of the diversity of organisms and the number of possible pollutants, conventional methodologies of environmental physiology are difficult to apply to coral communities (Brown and Howard 1985).

A primary requisite for an organism as a biological indicator is a close functional relationship to the resource being monitored. Many species of butterflyfishes feed almost exclusively on corals (Hobson 1974, Reese 1977, Motta 1980, Harmelin-Vivien and Bouchon-Navaro 1981, 1983, Hourigan 1987). Corals and butterflyfishes have coexisted since the late Eocene, and there is evidence of coevolution in the broad sense between the corals and the fishes that feed on them (Reese 1977). Most species efficiently remove the coral tissue without harming the underlying corallite. The functional morphology of the feeding apparatus and the feeding behavior of many butterflyfishes are adapted to the species of corals on which they most often feed (Motta 1980, 1985). Reese (1981) suggested that this close relationship would mean that factors which affected one organism, the corals, would probably have measurable effects on the coevolved fishes feeding on these corals as well. Our understanding of the relationships of butterflyfishes to their food resources comes from laboratory feeding experiments and field observations on numerous species.

Laboratory feeding experiments on several coral-feeding butterflyfishes show that most species have distinct feeding preferences. Reese (1977) presented *Chaetodon trifasciatus* and *C. ornatissimus* with three different species of common corals, *Pocillopora damicornis, Montipora verrucosa*, and *Porites compressa*. Both butterflyfishes consistently preferred *P. damicornis* over the other two corals, and *M. verrucosa* over *P. compressa*. Cox (1983) found that *Chaetodon unimaculatus* strongly preferred *M. verrucosa* to *P. compressa*, often feeding little or not at all on the latter species.

More extensive tests on *Chaetodon multicinctus* and *C. quadrimaculatus* showed distinct and consistent preferences among five common Hawaiian coral species (Hourigan 1987). *Chaetodon quadrimaculatus* preferred *Pocillopora meandrina*, and fed very little on other corals, even when only one species was offered (Figure 6.2a). In contrast, *C. multicinctus* fed on almost all of the corals when species were offered singly (Figure 6.2b). However, in paired presentations with different coral species, it showed significant preferences for certain corals over others. Coral preferences of

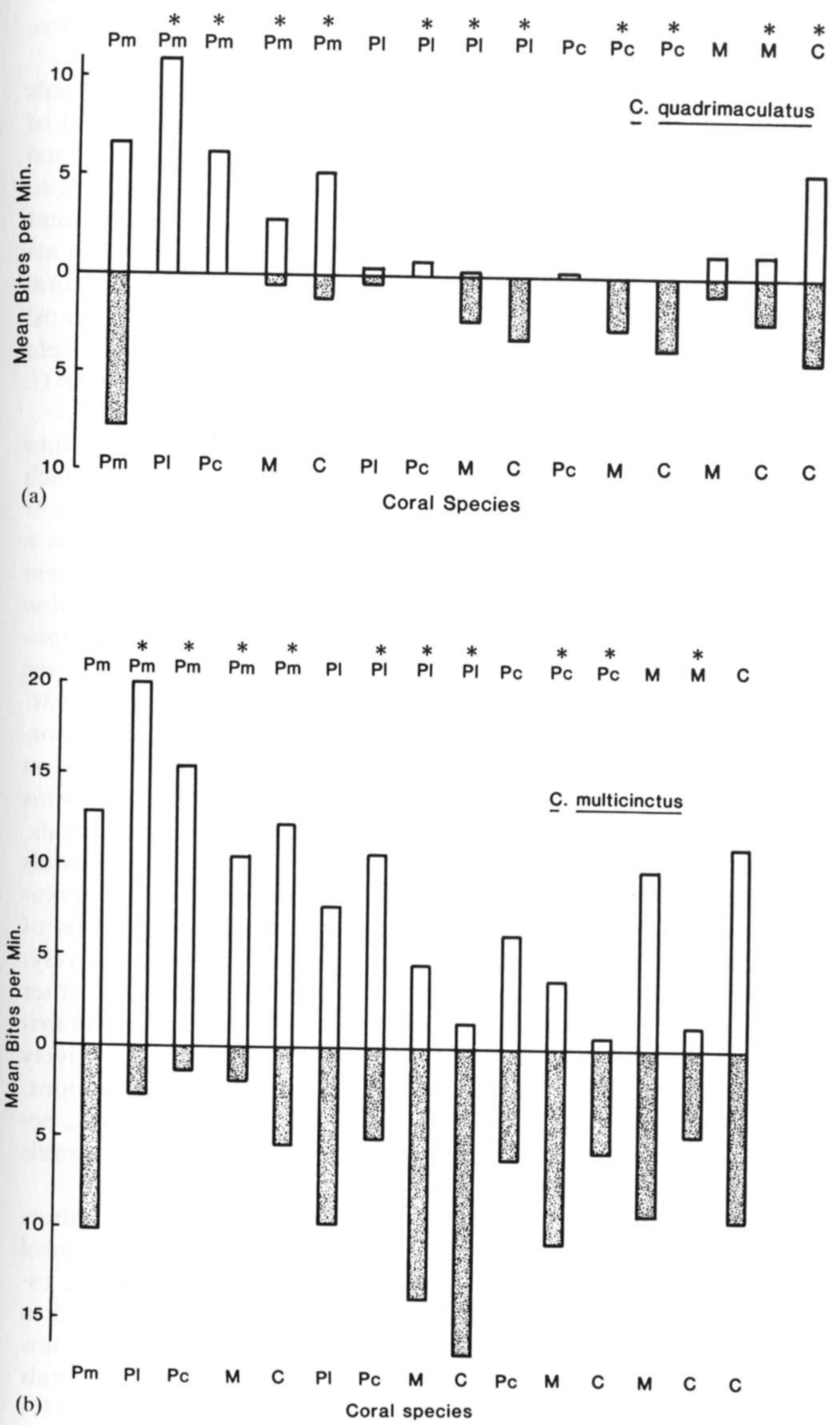


FIGURE 6.2. Laboratory experiments on feeding preferences of (a) *C. quadrimaculatus* and (b) *C. multicinctus* for different species of corals. Each bar represents the mean feeding rate for paired coral presentations to 10 different individuals. Coral species are: Pm = *Pocillopora meandrina*; Pl = *Porites lobata*; Pc = *Porites compressa*; M = *Montipora verrucosa*; C = *Cyphastrea ocellina*. * = $p < 0.05$; Wilcoxon's signed-ranks test.

five species of butterflyfishes in the lab are compared in Table 6.1. All five species showed generally the same ranking of coral preferences.

Coral preferences observed in the lab were also found among individuals in natural populations on reefs along the leeward coast of the Island of Hawaii (Hourigan 1987). Feeding preferences in the field were determined by comparing the occurrence of corals in the diet of five chaetodontids to the occurrence of each species of coral within each of four different habitats. Feeding bites on each species of coral were counted. The habitats differed in the occurrence and abundance of different corals. Distinct coral preferences were shown by all butterflyfishes (Figures 6.3a–e). In almost all cases, the same coral species were preferred in both the lab and the field (Table 6.1). Tricas (1985) found the same patterns of preferences for *C. multicinctus* in the field.

On the basis of these observations, the butterflyfishes can be divided into coral-feeding specialists and generalists. Specialists are those species which consistently favor certain prey items whether these items are common or rare (Birkeland and Neudecker 1981). In contrast, generalists feed on a wider variety of prey items, and the amount of each type of prey item ingested will depend on the relative abundances available. *Chaetodon quadrimaculatus* is a specialist on *Pocillopora meandrina*, and *C. unimaculatus* is a specialist on *P. meandrina* and *Montipora* spp. (Figures 6.3a, b). Cox (1983) found that *C. unimaculatus* specialized on the coral *M. verrucosa* in Kaneohe Bay, Hawaii, and Motta (1985) described morphological and behavioral adaptations which enable it to feed efficiently on *Montipora*. In contrast, *C. multicinctus*, *C. ornatissimus*, and *C. trifasciatus* are coral-feeding generalists (Figures 6.3c,d,e), feeding on many corals, but still showing preferences for certain species by feeding on these corals in greater proportion than they occur in the environment. Field observations elsewhere in Hawaii (Motta 1980) support these observations of feeding preferences, although coral cover was not measured quantitatively.

Reese (1975, 1981) and Motta (1980, 1985) have studied another specialized corallivore, *Chaetodon trifascialis* (formerly *Megaprotodon strigangulus*), the chevron butterflyfish. This species feeds almost exclusively on *Acropora* corals, and shows a strong preference for table *Acropora*. *Chaetodon trifascialis* is of particular interest as an indicator species, because it is widely distributed throughout the Pacific, wherever these corals occur (Reese 1981).

Similar patterns of feeding preferences are shown in studies of butterflyfishes in other areas. In Guam, Neudecker (1979) showed that the coral *Pocillopora damicornis* was a preferred food for several corallivores, especially butterflyfishes, and was quickly overgrazed when transplanted to deeper habitats where these fishes were common. Randall's (1974) review of coral-feeding fishes found that in most reports, corallivores fed on corals of the genera *Acropora* and *Pocillopora*. Birkeland and Neudecker (1981)

TABLE 6.1. Comparison of ranked coral-feeding preferences by five chaetodontids in the laboratory and in the field.

	Butterflyfish (*Chaetodon*) Species									
	C. quadrimaculatus		*C. unimaculatus*		*C. multicinctus*		*C. ornatissimus*		*C. trifasciatus*	
Coral	Lab	Field	Lab	Field	Lab	Field	Lab	Field	Lab	Field
P. meandrina	1	1	2	1	1	1	1	1	1	1
P. damicornis	2	—	3	—	2	—	2**	—	2**	—
Cyphastrea sp.	3	2	4	2	3	2	—	1	—	2
Montipora sp.	4	3	1*	1	4	3	3**	2	3**	3
P. lobata	5	4	5	3	5	4	—	3	4	4
P. compressa	6	5	6*	4	6	5	4**	3	5**	5

Laboratory ranks are based on Wilcoxon's signed-ranks test ($N = 10$, $p < 0.05$; * data supplemented from Cox 1983, ** data supplemented from Reese 1977). Field ranks are based on the Waller-Duncan K ratio t-test of mean electivity indices for 20 individuals of each fish species. Tied ranks signify no significant differences.

found that the diet of the Caribbean butterflyfish, *Chaetodon capistratus*, included many species of scleractinian corals, and concluded that it was a generalist. Gore (1984) found that *C. capistratus* fed on 16 different species of corals as well as zoanthids, gorgonids, and other prey items. When the number of bites taken was compared to the abundance of each prey species in the environment, *C. capistratus* showed preferences for specific coral species. Lasker (1985) also found preferential feeding by *C. capistratus* on certain gorgonian species.

While many butterflyfishes exhibit distinct food preferences among their coral food resources, the causal factors that structure these preference patterns are poorly understood. Tricas (1985) studied feeding preferences in a natural population of *Chaetodon multicinctus* in relation to the coral abundance and energy content of food coral tissues. The tissues of the highly preferred but relatively rare coral, *Pocillopara meandrina*, contained 14% more calories (on an ash-free dry weight basis) than *Porites lobata*, the most abundant coral in the habitat. The abundant but least preferred species, *Porites compressa,* however, had an energy content similar to *P. lobata*. Thus energetic quality could not explain the intrageneric food preference. Similar results were found when the energy ingested per bite by *C. multicinctus* on different corals was measured (Table 6.2; Hourigan 1987). In addition, the branching shape of *P. compressa* colonies increased the time required by fish to locate and feed on polyps, compared to fish feeding on the rounded colonies of *P. lobata*. In more recent comparative studies, it was found that *P. compressa* has larger and more numerous tentacular nematocysts than *P. lobata* (Tricas 1986). This inverse relationship between nematocysts and feeding preference also includes the highly preferred *P. meandrina*. Thus, feeding patterns observed in the field may represent foraging strategies to enhance energy intake per unit time that are balanced by the defensive biology of the coral prey.

These observations provide important information pertaining to the use of butterflyfishes as indicator organisms. Since butterflyfishes show preferences for some corals, they may respond most strongly only when preferred corals are affected. This is of special importance, since different corals respond differently to stress (Brown and Howard 1985).

Coral-feeding specialists may respond differently to changes in corals than do species with more generalized diets. Specialists would be expected to emigrate rather than change their diets if environmental stress caused a deterioration in their preferred corals. Under this scenario, specialists may be the best indicator species. Specialists, however, should respond only to changes in preferred corals, and therefore may not indicate stress on other corals. In contrast, generalists may show different feeding responses. Their broader diets may allow them to switch feeding from one coral species to a less preferred one as the habitat deteriorates. This response might be expected to occur before any movement of individuals out of the area. Emigration of generalist species from a reef might therefore indicate stress factors affecting most or all corals.

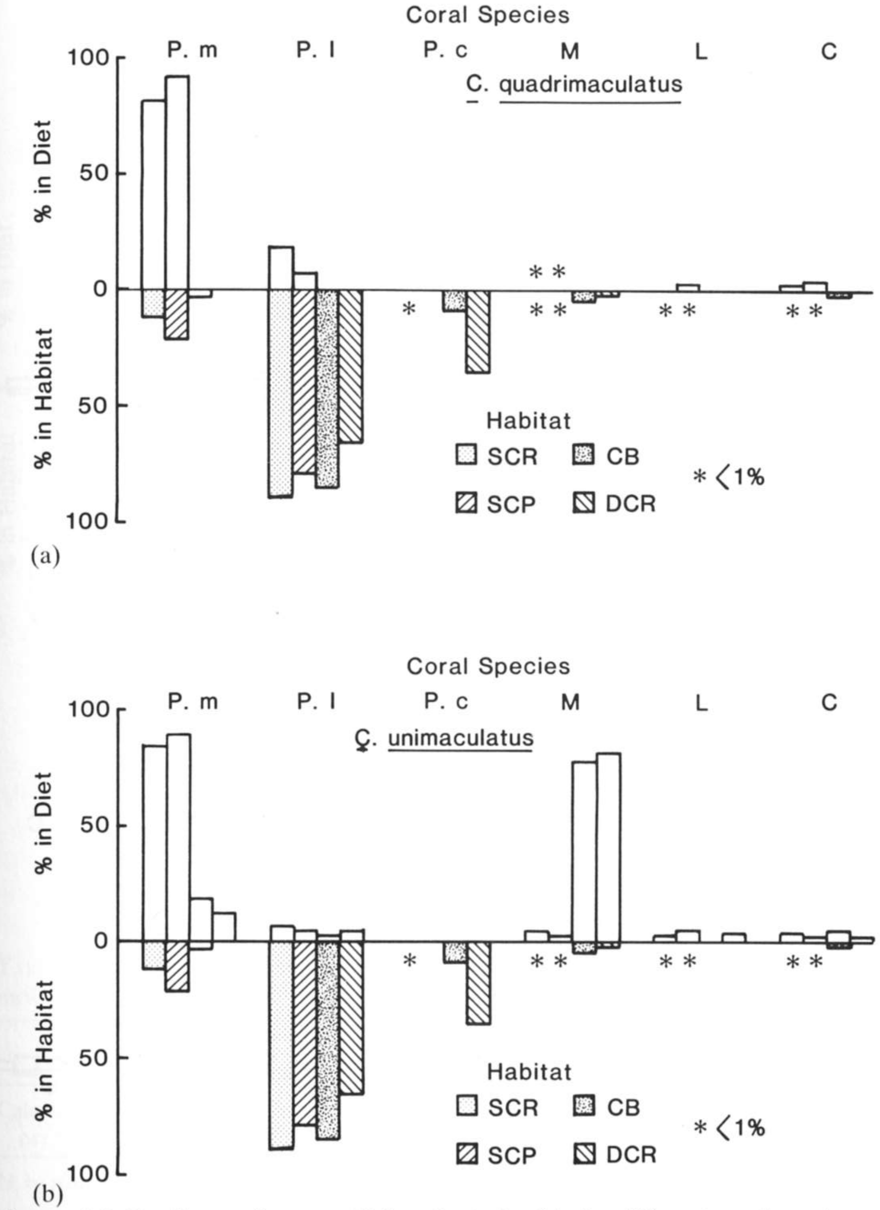
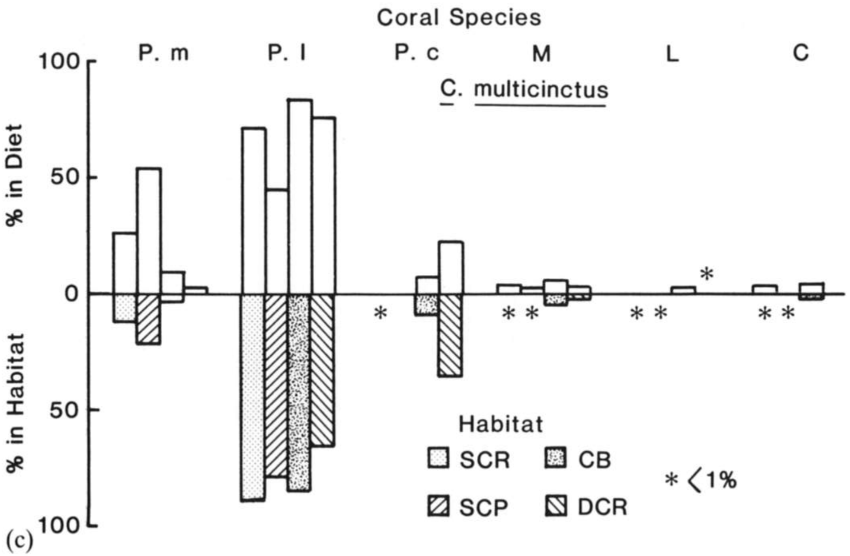


FIGURE 6.3. Feeding preferences of five chaetodontids for different coral species. Feeding on each coral species is shown in relation to the abundance of that coral within each of four habitats at Puako, Hawaii. Percent occurrence of corals in the diet was determined from 25 min feeding observations of at least five individuals of each species in each habitat. Percent occurrence of corals in the habitat was determined by quadrat methods. Habitats are: SCR = shallow coral rich; SCP = shallow coral poor; CB = cliff base; DCR = deep coral rich. Coral species are: Pm = *Pocillopora meandrina*; Pl = *Porites lobata*; Pc = *Porites compressa*; M = *Montipora* spp.; L = *Leptastrea* spp.; C = *Cyphastrea ocellina*. c,d,e: Generalists.



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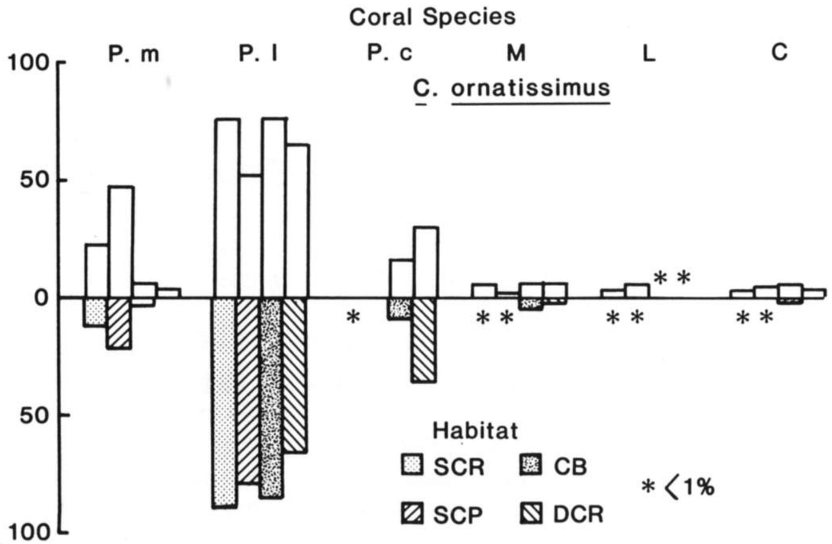

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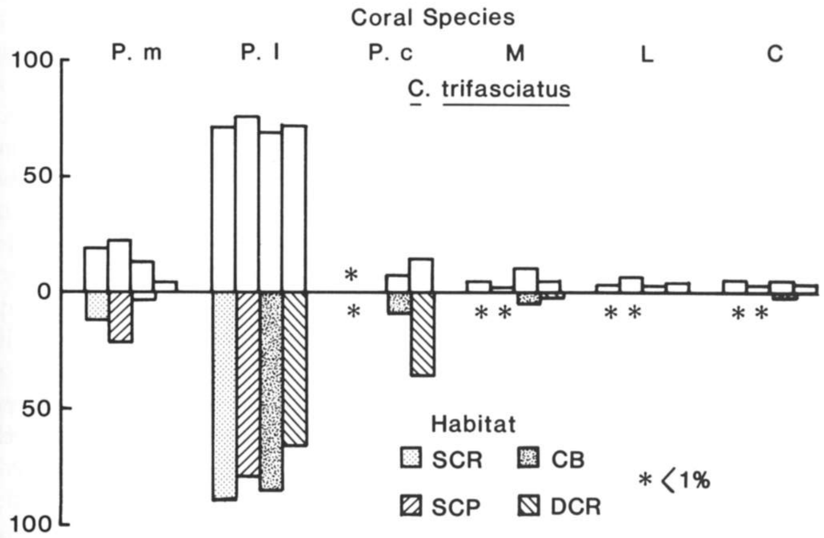


(e)

TABLE 6.2. Mean caloric intake per bite by *Chaetodon multicinctus* on the three most common coral species in Hawaii

	P. meandrina $N = 8$	*P. lobata* $N = 8$	*P. compressa* $N = 8$
Calories per bite	0.25*	0.19	0.13

N = 10 trials for each coral species; Waller-Duncan K ratio t-test: * = $p < 0.05$.

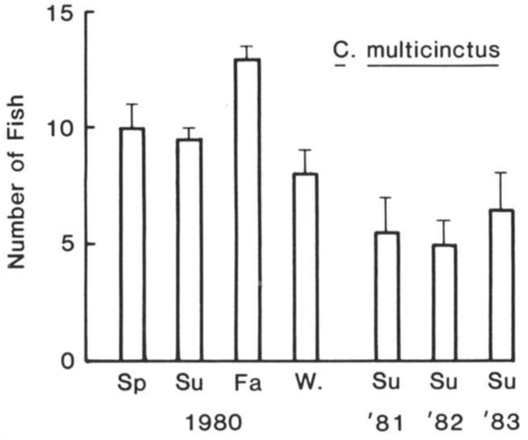


FIGURE 6.4. Mean abundance of the coral-feeding butterflyfish *C. multicinctus* per 500 m^2 in two replicate censuses per season for four seasons in 1980 and Summer 1981, 1982, and 1983 in the shallow coral-rich habitat at Puako, Hawaii Sp = Spring; Su = Summer; Fa = Fall; Wi = winter.

Censusing of Butterflyfish Numbers

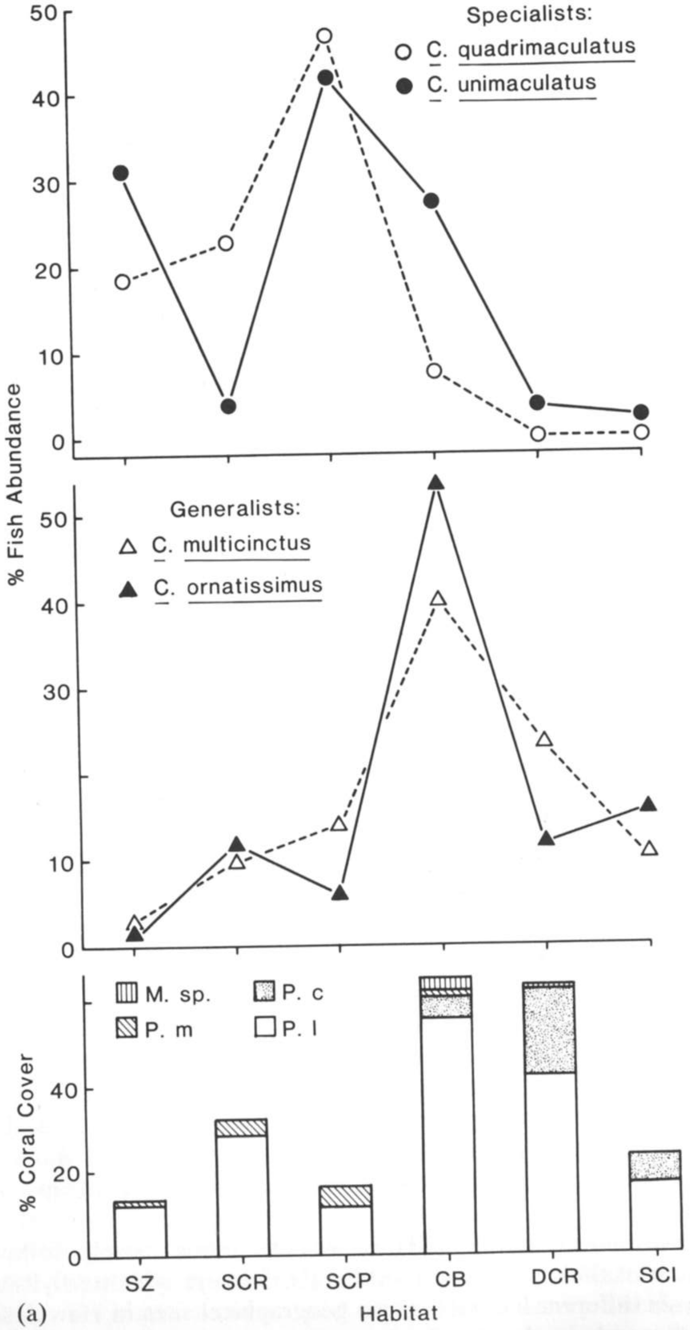
Most butterflyfishes are relatively large, diurnally active, and conspicuous, characteristics which facilitate census counts. Visual censuses are the most common, nondestructive methods to quantify fish abundances (Sale 1980). Most censuses are based on modifications of the methods of Brock (1954), where fishes are counted along strip transects, or on the rapid visual technique of Jones and Thompson (1978), which ranks abundances of fishes according to the frequency of encounter. These census methods are fairly accurate for conspicuous, site attached species such as butterflyfishes (Brock 1982), require little special training, and provide replicable results (Sanderson and Solonsky 1986). Each method however, has advantages and unavoidable biases. Transect methods underestimate cryptic fishes, and their accuracy depends on strip width (Keast and Harker 1977, Sale and Douglas 1981, Sale and Sharp 1983). Since butterflyfishes are conspicuous, and planned comparisons would use standardized strip lengths and widths, these biases can be minimized. Harmelin-Vivien et al. (1985) reviewed the use of visual surveys, especially strip transects in estimating fish abundances. The rapid visual technique overemphasizes the relative abundance of widely dispersed, rare species, while underestimating the abundance of patchily distributed, common species (DeMartini and Roberts 1982). To insure accuracy and replicability, survey areas must be large enough to provide representative samples of areas, and must include sufficient replicates to determine between-sample variability (Pielou 1969). Choice of an appropriate indicator species will depend on factors affecting its ease of censusing. The species chosen for survey must be relatively common, with small home ranges relative to the size of the census area. Populations must be monitored regularly, and care must be taken that single census areas do not include habitats which differ greatly in coral cover and species composition.

Several studies of butterflyfish populations have used visual censuses along strip transects (Clarke 1977, Bouchon-Navaro 1979, 1981; Harmelin-Vivien and Bouchon-Navaro 1981, 1983; Bouchan-Navaro et al. 1985, Bell and Galzin 1984, Bell et al. 1985, Hourigan 1987). Modifications of the rapid visual technique were used by Williams (1982) and Hourigan (1987). Most of these studies have not looked at temporal stability of butterflyfish populations over time. If corallivorous butterflyfishes are to be used as indicators of change on coral reefs, it must first be demonstrated that populations are stable (within the limits of the census techniques) when coral reefs are not disturbed.

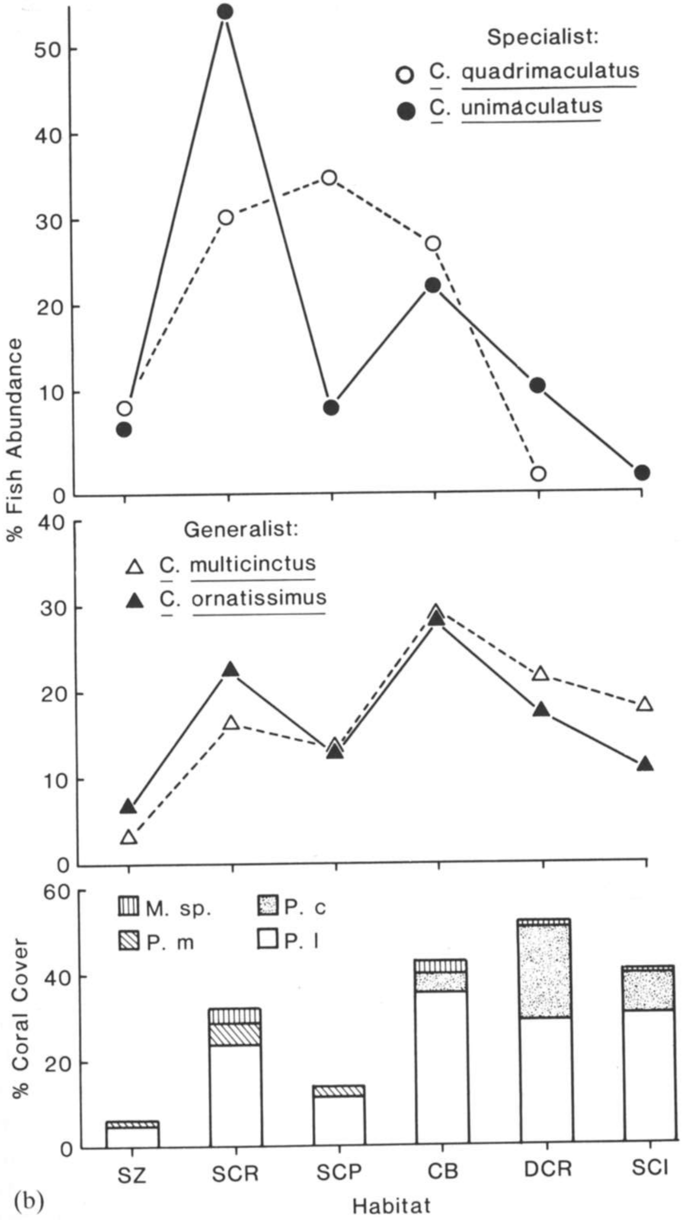
Butterflyfishes are long-lived animals, and on undisturbed reefs, individuals of most species remain in the same home range throughout their adult life. Reese (1981) observed adult individuals of two species (*Chaetodon trifascialis* and *C. trifasciatus*) in the same home ranges at Enewetak Atoll for 7 years. We have observed individuals of two additional species (*C. multicinctus* and *C. quadrimaculatus*) in the same home ranges year-round up to 4 years. This stability of the adult population is probably due to low adult mortality, and perhaps low recruitment to limited spaces on the reef. Most coral-feeding species are territorial, with pairs defending areas where all feeding and sheltering takes place (Hourigan 1987). The stability of populations is observed in the Hawaiian butterflyfish, *C. multicinctus*. Numbers of this fish over 4 seasons and 4 years were relatively stable (Figure 6.4), compared to carnivorous and herbivorous fishes censused concurrently in the same habitat (Hourigan 1987).

Obligate coral-feeding butterflyfishes are exclusively associated with living coral, a necessary requirement for their use as indicator species. Positive correlation between coral cover and butterflyfish numbers is common (Clarke 1977, Anderson et al. 1981, Harmelin-Vivien and Bouchon-Navaro 1981, 1983, Bouchon-Navaro et al. 1985, Bell and Galzin 1984, Bell et al. 1985, Findley and Findley 1985). Sano et al. (1984) compared patch reefs composed of living and dead coral. None of the coral polyp feeders, including many butterflyfishes which were found as residents or visitors to the live coral patches, were observed on the dead patches.

The distribution and abundance of the fishes closely follows the distribution of their preferred food corals. Surveys of butterflyfishes and corals in six different habitats at two geographical sites in Hawaii showed consistent trends in the distributions of specialist and generalist corallivores (Figures 6.5a, b). *Chaetodon quadrimaculatus* fed almost exclusively



(a)



(b)

FIGURE 6.5. Percent occurrence of two coral-feeding specialists and two coral-feeding generalists in six different habitats compared with the abundance of the four most common species of corals. Patterns are similar at the two geographically separated sites: (a) Puako and (b) Mauna Lani Bay, Hawaii. Habitats in order of increasing depth are: SZ = surge zone; SCR = shallow coral rich; SCP = shallow coral poor; CB = cliff base; DCR = deep coral rich; SCI = sand coral interface. Coral species are: Pm = *Pocillopora meandrina*; Pl = *Porites lobata*; Pc = *Porites compressa*; M. sp = *Montipora* sp.

on the coral *Pocillopora meandrina*, although it supplemented its diet with algae and polychaetes. The distribution of this species closely followed the distribution of the coral *P. meandrina*, which occurred primarily in shallow waters. Total coral cover was much greater in deeper waters, but *P. meandrina* was nearly absent there. In Tahiti, *C. quadrimaculatus* is found in very similar habitats, and also feeds on *Pocillopora* spp. (Bouchon-Navaro 1981). The distribution of the second specialist, *C. unimaculatus*, also followed more closely the distribution of preferred corals, *P. meandrina* and *Montipora* spp., rather than total coral cover. The distribution of *C. unimaculatus* among patch reefs in Kaneohe Bay, Hawaii, closely follows the distribution of *Montipora* spp. (Cox 1983).

Reese (1981) has compiled extensive evidence on the distribution of another coral specialist, *C. trifascialis*. This species feeds almost exclusively on table *Acropora*. It is found in areas where these corals occur. Recently, *C. trifascialis* was observed to feed occasionally on *Montipora* spp. in habitats where *Acropora* spp. are rare (Irons in press).

The distribution and abundance of coral-feeding generalists in relation to food-coral distributions differs from that of specialists. *Chaetodon multicinctus* is the most common coral-feeding butterflyfish in Hawaii (Hobson 1974, Hourigan 1987). It has a much broader distribution across different habitats than the coral specialists, *C. quadrimaculatus* and *C. unimaculatus* (Figures 6.5a, b), and more closely follows the distribution of total coral cover. Nevertheless, numbers appear to be influenced little by the presence of *Porites compressa*, the abundant, but least preferred, coral. A second coral generalist, *C. ornatissimus*, has similar coral preferences and a similar distribution to *C. multicinctus*.

Other studies compared the distributions of butterflyfishes and total coral cover (Bell and Galzin 1984, Bell et al. 1985, Findley and Findley 1985). Although they found a positive correlation between coral cover and numbers of coral-feeding butterflyfishes, different types of corals and feeding preferences were not distinguished. Bouchon-Navaro et al. (1985) censused butterflyfishes in Moorea, and found strong correlations between the species richness, density of corallivores, and the distribution of long-branched coral colonies of the genera *Acropora* and *Pocillopora*. Future studies of the distribution and abundance of corallivorous fishes and their food must include analyses of food preferences to adequately model the relationship.

The size of foraging areas varies as a function of coral cover, especially preferred coral cover. This is evidently the basis for differences in fish abundance in different areas. There is a general negative correlation between preferred coral cover and feeding-territory size in *C. multicinctus* (Tricas 1985, 1986; Hourigan 1987) and *C. quadrimaculatus* (Hourigan 1987). Sutton (1985) found a similar relationship between territory size and coral cover in *C. trifasciatus* on the Great Barrier Reef, Australia. This supports the contention that individual fish adjust their use of space in response to coral cover.

The data presented thus far are correlative. They indicate that populations of butterflyfishes on healthy reefs are relatively stable, and vary directly with changes in preferred coral resource abundance. Bell et al. (1985) censused butterflyfish assemblages at widely separated sites in French Polynesia. Although they found a rough correlation of coral feeders to coral cover, numbers of different species differed between sites with similar coral cover. These differences may be due to the presence of different species of corals, or as they suggest, to different rates of fish recruitment to different sites. This emphasizes the point that a single estimation of the butterflyfish assemblage should not be used to determine relative coral abundance and quality. Rather, the usefulness of these fishes as indicators is in monitoring changes in the assemblage relative to baseline data prior to environmental stress. It remains to be shown how these fishes respond to changes in coral abundance or quality, and whether these changes are detectable by conventional census methods.

Changes in Numbers of Coral-Feeding Butterflyfishes in Response to Disturbances on Coral Reefs

The effects of severe storms and other natural disturbances on coral communities and associated reef fishes may parallel changes caused by pollution. Studies of the colonization of damaged reefs and artificial reefs, suggest that obligate coral-feeding butterflyfishes are prime candidates for indicator species.

Many common herbivores such as damselfishes, surgeonfishes, and parrotfishes move to deeper waters during severe storms. Within a few days or weeks after the storm, these fishes return to the devastated reefs, sometimes in increased numbers despite extensive coral damage (Kaufmann 1983, Walsh 1983). In contrast, coral-feeding butterflyfishes usually do not return to reefs until the corals on which they feed are reestablished. Reefs at Yanuka Island off the south coast of Fiji were damaged in a series of severe hurricanes in 1985 (Reese unpubl. data). Large overturned heads of table *Acropora* were scattered over the reef and in sand channels between reef structures. *Chaetodon trifascialis*, which is common in Fiji and normally associated with these corals, was completely absent. A few newly settled *C. baronessa* were in close association with the scattered, small heads of *Acropora* which remained intact. These were the only corallivores present on the reefs.

Periodic infestations of coral reefs by the crown of thorns starfish *Acanthaster planci* cause extensive damage to corals. Endean and Stablum (1973) studied Australian reefs on which living corals had been killed by the starfish. They found that butterflyfishes and other coral-feeders initially remained in the vicinity of the dying corals, but disappeared when the coral skeletons were overgrown with algae.

The best evidence in support of the association between coral health and butterflyfish abundance comes from quantitative observations of butterflyfishes and coral abundances before and after a crown of thorns starfish infestation at Moorea (Bouchon-Navaro et al. 1985). The starfish caused as much as 50% mortality in corals, especially of the genera *Acropora* and *Pocillopora*. Concomitant with the coral mortality, the density of coral-feeding chaetodontids decreased by 47%. *Chaetodon trifascialis*, a specialist on *Acropora*, disappeared completely from the barrier reef flat. A second common corallivore, *C. trifasciatus*, was replaced at many sites by the omnivore, *C. citrinellus*. The interdependence of corallivores and living coral is clear from species lists of the recolonization of reefs following coral damage, as well as colonization of artificial reefs lacking corals (Nolan 1975, Talbot et al. 1978, Sale 1980). Corallivores are notably absent on these reefs. Four years of observations on coral reefs in Hawaii showed that recruitment of juvenile coral-feeding butterflyfishes occurred only in areas where corals were present (Hourigan 1987). In contrast, recruitment of other species of chaetodontids was not so restricted.

Coral destruction by *Acanthaster planci* on the Great Barrier Reef in Australia was also followed by measurable changes in the numbers of coral-feeding butterflyfishes (Williams 1986). The numbers of the two most abundant species of corallivorous butterflyfishes, *Chaetodon aureofasciatus* and *C. rainfordi*, were significantly reduced on three reefs following coral destruction by *A. planci*. Two other coral-feeding chaetodontids also decreased in abundance on the most extensively damaged reef. There were no significant changes in abundance for these species on undisturbed reefs during the same 4 year period. Changes in the abundances of fishes of the four other families surveyed (Acanthuridae, Labridae, Pomacanthidae and Scaridae) did not appear to be directly related to the effects of *A. planci*.

Sano et al. (1984) experimented with small patch reefs in Okinawa. Small colonies of living *Acropora* sp. were placed in the sandy bottom 3 to 4 m from the coral reef, and fishes were censused daily. After 20 days, the fishes from some colonies were removed, and the colonies replaced. On other colonies, the living coral tissue was allowed to die before the colonies were replaced. Resident coral-feeders, including butterflyfishes, returned to the live colonies, but not to the dead colonies. Other butterflyfishes which were not residents regularly visited the live colonies, but avoided the dead colonies.

There are fewer studies which have observed the effects of pollutants on butterflyfish populations. Neudecker (1977) censused butterflyfish populations in areas affected by thermal effluent from a power plant in Guam, compared to two control areas. Coral abundance, survival, and recruitment was reduced near the area of thermal outfall. Three species of coral-feeding butterflyfishes, *Chaetodon ornatissimus, C. quadrimaculatus,* and *C. trifascialis* occurred at both control sites, but not near the thermal effluent. The latter two species were observed in surveys of the same area before the plant became operational.

The only other study of which we are aware was conducted before and after a large scale dredging operation to improve the airport at Johnston Island in the Central Pacific (Brock, Jones, and Helfrich 1965; Brock, Van Heukelem, and Helfrich 1966). In the course of the 2 year study, from 1963 to 1965, reef fishes were censused in nine habitats. These habitats ranged from pristine areas with no visible impact of the dredging, to areas in the lagoon where the effects were apparent. Besides the physical destruction of the reef by dredging, the pollution included increased turbidity and siltation. Both were measured quantitatively. The areas of greatest siltation showed the greatest coral morality.

Twelve species of butterflyfishes were reported, eight of which were obligate or facultative corallivores (Reese 1975). These fishes showed decreased abundances in the areas of greatest siltation and coral mortality. The most striking effect was on *Chaetodon trifascialis*, the most abundant and most specialized of the obligate corallivores. In 1964, it was common in the shallow lagoon habitat characterized by winding coral ridges with small heads of table *Acropora*. In 1965 the area was resurveyed. The dredging operation covered the area with a layer of silt and murky water. Almost all the corals were dead and no *C. trifascialis* were observed. *Chaetodon trifascialis* also disappeared from two other areas which suffered siltation damage.

Response to Experimental Perturbation of Coral Food Resources

The prediction that the abundance of coral-feeding butterflyfishes should decrease as food quality declines is strongly supported by survey data obtained from many coral reefs. However, while such "natural experiments" may point to associations between these factors, they do not provide verification of the proximate causal relationships. To demonstrate that changes in fish abundance are a direct result of altered food supplies, experimental manipulations of food resources are necessary, in conjunction with the use of proper experimental controls. There is experimental evidence that decreased coral abundance can directly affect the spatial requirements of corallivorous butterflyfishes.

Experimental maniplations of food supply have been performed on the obligate corallivore, *Chaetodon multicinctus,* at Puako, Hawaii (Tricas 1986, Hourigan 1987). This species forms monogamous pairs that defend contiguous feeding territories from intrusions by conspecific neighbors and other coral-feeding fishes (Tricas 1985). Coral abundance was decreased by covering portions of the substratum with 1 m^2 covers within fish territories. The amount of coral reduced in six experimental territories ranged from 19 to 57%. In all cases, territories increased in size by expansion of foraging areas into territories of neighboring pairs (Table 6.3) and stabilized approximately 2 to 4 weeks after coral reductions. At high levels of food reduction, territorial expansion was vigorously resisted by neighboring pairs, while at lower levels fish slowly encroached into territories of smaller

TABLE 6.3. Summary of spatial responses to experimentally decreased corals in feeding territories of *Chaetodon multicinctus*.

Experimental Territory	Premanipulation Territory Area (m^2)	Percent Coral Reduction	Percent Area Change
1	82	19	+40
2	83	25	+11
3	66	38	+29
4	61	37	+ 7
5	81	46	+12
6	74	57	+14

neighbors. In contrast, no changes in territory size were observed at seven control territories where corals were left undisturbed.

The defense of space by coral-feeding butterflyfishes is emerging as a more common phenomenon than previously believed. This oversight is due largely to the low natural levels of aggression observed between individuals in undisturbed communities (e.g., Reese 1975, Ehrlich et al. 1977). Many species, however, show strong site fidelity for long periods of time (Reese 1973, 1975, 1981; Sutton 1985; Tricas 1985; Hourigan 1987). Scleractinian corals are extremely long-lived (Connell 1973), making them spatially and temporally predictable resources, and thus economically defendable (sensu J.L. Brown, 1964). As a result of intraspecific territoriality, expansion of feeding ranges in response to decreased food availability may be opposed by interaction with other individuals, as was demonstrated for *C. multicinctus* (Tricas 1986).

Environmental stress on coral reefs may result in a decrease in food availability to all resident coral-feeding fishes. To compensate for this decrease, adjustments in foraging ranges by fishes should be one of the first responses. On rich coral reefs, where corallivorous butterflyfish populations are often at very high densities, these spatial adjustments will be mediated by high levels of agonistic behavior, and may be important in the early detection of environmental disturbance. In populations where territories or foraging ranges are contiguous, this could lead to severe conflicts that eventually force less competitively dominant individuals out of the preferred habitat, resulting in an overall decrease in population density. As food resources deteriorate still further, emigration to other areas should occur.

The spatial responses of nonterritorial corallivores to decreased food abundance may involve more rapid and direct reactions than those of territorial species. While nonterritorial fishes may have fixed home ranges, they may not experience the energetic constraints and degree of spatial fidelity imposed by defense of a feeding area. Thus, emigration from a food-stressed habitat by nonterritorial species might occur earlier than by territorial species. This proposition remains to be tested. Among Hawaiian corallivores, only *Chaetodon unimaculatus* is nonterritorial (Hourigan 1987).

Other Indications of Changes in Coral Food Resources

Other aspects of the biology of butterflyfishes may be important in their use as indicator organisms. Besides simply leaving an area, butterflyfishes may respond more subtly to poor quality and death of the corals. Fishes may respond with quantifiable changes in feeding behavior. They may change their feeding rate, switch from feeding on one species of coral to another, or even switch to noncoralline prey items. Such switches are more likely in species with more generalized diets, and were observed in food reduction experiments with *Chaetodon multicinctus* (Hourigan 1987). We believe these changes in feeding behavior provide a means of assessing the decline in the physiological condition of corals, which would be difficult to do with other techniques in situ.

Reese (1981) proposed a second possible indication of deteriorating environmental quality. Most species of coral-feeding butterflyfishes occur in heterosexual, monogamous pairs (Reese 1975, Allen 1979, Barlow 1984). In undisturbed, healthy coral reef environments, these pairs are usually very similar in size, indicative of assortative mating by size. Sexually mature individuals form heterosexual pairs with only slight differences in size in the coral-feeding butterflyfishes *Chaetodon trifasciatus* ($N = 15$ pairs, 100% heterosexual; Reese 1981), *C. multicinctus* ($N = 239$ pairs, 97% heterosexual; Tricas 1986; $N = 40$ pairs, 100% heterosexual; Hourigan 1987) and *C. quadrimaculatus* ($N = 30$, 100% heterosexual; Hourigan 1987). In situations of stress there should be fewer pairs, and those that do occur might be homosexual, transitory, or composed of individuals of very different sizes (Reese 1981). This has yet to be demonstrated. Gore (1983) has found transitory, and often homosexual pairs in the butterflyfish *C. capistratus* in Jamaica. It is not known whether the reef or the fish population she studied was stressed.

The judicious selection of key species of butterflyfishes taken as a group in the reef community may provide another sensitive monitoring technique. A method has been developed for benthic communities (Grey 1985, Pearson et al. 1983) which is rapid, easy, and robust. It allows a comparative assessment of changes in the pattern of abundance of species in a stressed community with greater sensitivity than diversity indicies, and permits an objective selection of species as indicators of pollutant effects over time.

The method is based on the log-normal distributions of individuals of species belonging to three groups: (1) rare species comprising 60 to 70% of the total number of species; (2) moderately common species comprising 15 to 20% of the total number of species; and (3) a small number of common species. The numbers of species are plotted on the ordinate against the number of individuals per species in each group along the abscissa. Although there exists some controversy regarding interpretation, there is agreement that the log-normal patterns change under conditions of stress in benthic communities. This method was developed for soft-bottom communities of small, numerous species. We hope to determine if the method can be used with the fewer numbers of species and individuals of butterflyfish assemblages on coral reefs. The advantage is that censuses of the butterflyfish assemblage are much faster and easier than the tedious collecting and identification of small invertebrates. It is generally agreed (Grey 1985) that pollution research must be based on a better understanding of the basic biology of the species which show changes in response to pollution. In this regard, butterflyfishes show great promise, as there exists considerable information on the natural history of at least 10 species.

Other Reef Fishes as Indicator Species

Butterflyfishes are the most common coral-feeding fishes on most reefs, and undoubtedly the most conspicuous and easily censused. Other corallivores are found among the damselfishes (Pomacentridae), gobies (Gobiidae), blennies (Blenniidae), filefishes (Monacanthidae), puffers (Tetraodontidae), and others (Randall 1974). Under specific situations, these fishes may also be suited as indicator species, although many are more difficult to census and their biology is for the most part poorly understood.

Corals, while the most important, are not the only major constituents of coral reefs. Researchers have recently emphasized the importance of monitoring the effects of stress on noncoralline resources as well as corals (e.g., Benayahu and Loya 1977, Bak et al. 1981, Tursch and Tursch 1982, Brown and Howard 1985). Algae and sponges are both important constituents of reef ecosystems and provide food for many organisms. Herbivorous fishes often compose the major portion of the fish biomass on coral reefs, and studies have investigated the relationship between herbivorous fishes and their food (Ogden and Lobel 1978). Angelfishes (Pomacanthidae) of the genera *Holacanthus* and *Pomacanthus* feed extensively on sponges (Randall and Hartman 1968, Feddern 1968). They are conspicuous and site attached fishes, and relationships between feeding and spacing behavior are beginning to be elucidated (Hourigan et al. in prep). Further studies on these species are required before their suitability as indicator organisms can be gauged.

Concluding Remarks

We have presented data on the potential usefulness of corallivorous butterflyfishes as indicators of the health of coral reefs. In a practical situation, such as in an area near a proposed sewage outfall, common coral-feeding butterflyfishes would be identified, and their numbers regularly assessed by standard census techniques before, during, and after environmental disturbance. Death or deterioration of preferred corals should be accompanied by reduced abundances of these fishes in censuses as they leave the area, and as territories of remaining fishes expand. A more sensitive measure of the effects of environmental stress would be obtained by monitoring changes in proportions of bites on different coral species by individual fish. This technique may provide an early warning to deteriorating conditions on the reef, allowing time for remedial action and management.

Further study is clearly needed to confirm the practicality of our proposed method. To date, there have been no comprehensive studies that document the decline of corals in response to environmental pollutants, concomitant with measures of the responses of coral-feeding butterflyfish populations.

We have reviewed the responses of coral-feeding butterflyfishes to changes in their food resources, the living corals. These relationships may not be as straightforward as had earlier been thought. Strong site attachment by butterflyfishes assures stability on healthy reefs; however, it may also mean that the fishes will remain in their territories, making only minor adjustments even as their environment deteriorates significantly. Specialist feeders on certain coral species may be sensitive indicators for changes in those corals. The ability of other species to shift their diets, however, may allow them to remain in an area despite the death of some of their coral food. In addition, little is known about the direct effects of most pollutants on coral reef fishes, independent of the effects on corals. These problems should not detract from the promise of butterflyfishes as indicator organisms, but show that further research is needed on particular species along with their food resources, and the responses of both to particular types of environmental stress.

Coral-feeding butterflyfishes show predictable and quantifiable changes in behavior with changes in their food resources. Further research should concentrate on quantifying the responses of particular species to changes in their food corals before, during, and after pollution or environmental deterioration. Studies such as these are essential if we are to preserve the rich and delicate ecosystems of the coral reefs.

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