Prey selection by coral-feeding butterflyfishes: strategies to maximize the profit

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Synopsis

Factors that structure preferences among food corals were examined for the obligate coral-feeding butterflyfish *Chaetodon multicinctus.* In the field, fish show a simple repetitious pattern of foraging composed of (1) pre-encounter search for coral colonies, and (2) post-encounter inspection/orientation, bite, and consumption of polyps. Rose coral, *Pocillopora meandrina,* and the massive coral, *Porites lobata,* were taken in higher proportions than their percentage substrate cover, while finger coral, *Porites compressa,* was taken in lower proportion. Paired presentations of coral colonies in the lab gave similar results: *Poc. meandrina* was preferred over *Por. lobata* which was preferred over *Por. compressa. Poc. meandrina tissue* had the highest energy content, lowest handling time, and highest profitability. Energy content did not differ among *Porites tissues,* but handling time was greater and more inspective eye movements were made while foraging on the branched finger coral, *Por. compressa.* Experimental manipulation of coral colony morphology indicate preferences among *Porites* are most likely structured by handling costs. Predictions of a simple prey-choice foraging model are supported in the *C. multicinctus* system if abundance of the branched coral *Por. compressa* is estimated as that available to fishes rather than percentage substrate cover. The relative size and abundance of stinging nematocysts are also consistent with observed foraging patterns in the field, but await immunological confirmation. Coral-feeding butterflyfishes offer unique opportunities to test models of foraging ecology in reef fishes, and the direction of future studies is suggested.

Introduction

Foraging behavior is an important aspect of individual fitness because it accrues metabolic substrates for maintenance, growth, and reproduction. When in short supply, food can limit one or more of these physiological processes. Under more favorable conditions, differential selection of items from a potential diet set may be advantageous when quality or accessibility vary among prey types.

While the selection of food items by animals has been extensively modelled and tested (recently reviewed by Krebs & McCleery 1984, Stephens & Krebs 1986), surprisingly little field and experimental work exists on reef fishes. This paucity is due in part to difficulties in prolonged observations of individuals in the marine environment, identifying prey species and unobtrusively quantifying their abundance, and performing experimental manipulations of prey to test specific models. Cor-

al-feeding butterflyfishes of the family Chaetodontidae offer perhaps the best features available among marine teleosts to conduct long-term field studies of foraging. They are abundant on most shallow coral reefs in tropical and subtropical oceans, feed conspicuously on corals, and can be observed at close range for long periods. Individuals are conspicuous and usually identifiable by unique features in their color patterns, and are site attached in territories or stable home ranges (Reese 1975, Sutton 1985, Tricas 1985, 1989). Corals are non-cryptic, relatively easy to identify, and are a stable food resource. The combined features of butterflyfishes and their food corals make it relatively easy to quantify feeding rates on specific prey items as well as associated behaviors such as search and handling time, defense of resources, and foraging paths. In addition, chaetodontids generally adapt well to aquaria for studies where more control over experiments is necessary (e.g. Zumpe 1965, Reese 1977, Gore 1984).

There is good evidence that the fitness of butterflyfishes is enhanced by maximizing food intake. Growth is extremely rapid during the first year of life, and fecundity increases exponentially with body size in mature females (Ralston 1976a, b, 1981, Tricas 1986). For some species, male body length is positively correlated with feeding territory area and the size of his female mate (Tricas 1989). Food supply can control egg production in fishes (Tyler & Dunn 1976, Wooton 1977, Hirschfield 1980) and food shortages may induce oocyte resorption and atresia (Scott 1962, Hunter & Macewicz 1985) which is known to occur in chaetodontids (Tricas & Hiramoto 1989). Thus, it is likely that strong selection exists for foraging on food items that maximize growth and reproductive output.

Although measurable features of food quality such as prey size (Werner & Hall 1974) or protein content (Milton 1979, Owen-Smith & Novellie 1982) can influence fitness, energy content is most conveniently measured and most commonly modelled because it usually covaries with measures of organic content. For animals with energy maximization strategies, the optimal diet set consists of those items that maximize the net rate of energy intake. Less profitable items should be excluded from the diet if their inclusion would decrease the net rate of return (Pyke et al. 1977, Krebs 1978). The selection of profitable prey, however, may be moderated by toxic compounds that affect feeding patterns in fishes (Lobel & Ogden 1981, Targett et al. 1986). For corallivorous fishes, nematocyst defense by food corals must be considered as a potential influence on food selection as suggested for invertebrate corallivores (Barnes et al. 1970, Glynn & Krupp 1986).

Many studies demonstrate that butterflyfishes show distinct preferences for particular coral species (e.g. Reese 1977, Birkeland & Neudecker 1981, Gore 1984, Tricas 1985, Hourigan et al. 1988) but the proximate factors that structure these patterns are not understood. An a priori model can be developed for the Hawaiian obligate corallivore *Chaetodon multicinctus* based on the natural history of this butterflyfish and the biology of its food corals. This species feeds on the polyps of the corals *Pocillopora meandrina, Porites lobata,* and *Porites compressa* that occur naturally within feeding territories (Hobson 1974, Reese 1975, Tricas 1985, Hourigan et al. 1988, Motta 1988). Both males and females spend over 90% of their daily time budget feeding and behave as energy maximizers constrained primarily by the time available for feeding (Tricas 1989). This paper tests the prediction that corals with the highest energetic profit (defined as energy intake per unit foraging time) are taken preferentially over species of lower profit. Feeding patterns of *C. multicinctus* are examined in the field and compared with food preferences observed in the laboratory. The energy content, gross morphology, polyp density, and nematocyst defense are examined for food corals in reference to how each may influence the feeding patterns of *C. multicinctus* in their coral reef environment.

Methods

Study site and corals

Field data on food abundance and fish foraging patterns were collected at Puako reef on the northwest shore of the island of Hawaii. The primary

study area is located at the base of the shallow reef flat and gradually slopes seaward to depths of about 12 m. This reef habitat consists of extensive fields of the unbranched massive coral, *Por. lobata,* and finger coral, *Por. compressa.* Rose coral, *Poc. meandrina,* is a small, robustly branched species widely scattered in low abundance among *Porites.* In addition, some fish were studied that held feeding territories on the shallow reef flat (<4 m deep) where total coral cover is lower but *Poc. meandrina* is more abundant than on the deep reef.

Field measurements and observations

Coral abundance was estimated within 30 fish territories in the deep coral-rich habitat and five on the shallow reef flat. A 1 m² quadrat (0.1 m grid) was placed at 20 randomly determined locations within each territory and the coral species under each grid intersection tallied. Percentage coral cover for each species was calculated from its proportion of the total counts for all substrates.

Feeding data for resident pairs in each of the 35 territories were recorded between 1000 and 1400 h. Divers followed at distances (1–2 m) that did not disturb the foraging paths of focal fish, and scored on underwater paper the coral species taken in each bite. Each member of a pair was observed during alternate 5 min observation periods for a total of at least 50 min per fish. Qualitative descriptions of foraging behaviors during travel between feeding sites, encounters with coral heads, and handling of corals during feeding bouts were recorded. In addition to direct observations of feeding, gut contents of six fish collected in the afternoon were examined and their volumetric proportions estimated to verify food items in the diet.

Encounter rates of food corals were estimated three times from movements made by fish within territories on the deep reef. Fifty small consecutively-numbered plastic tags were placed along the foraging paths of focal fish at 1 min time intervals. Tag locations were carefully recorded on a 1 m² grid map of the territory, handling and chase times subtracted from total foraging time, and average distance traveled per unit search time determined. It was assumed that the average horizontal visual field of a foraging fish was a frontal semi-circular field of 25 cm radius. Thus for every 1.0 cm of linear movement a rectangular area of substrate 50 cm² was encountered. Encounter rate (λ) for each coral was calculated as the product of the average area surveyed in the visual field per unit time and the proportion of coral polyp cover in the territory. This can be expressed as,

$$\lambda = 50 \text{ v pd},$$

where v = the average rate of movement during searching, p = proportion of bottom cover for that coral, d = polyp density, and the constant, 50, a conversion factor for substrate area encountered during linear movement.

Energy and water content of coral tissues

The caloric content of the three food corals was determined by microbomb calorimetry (Phillipson 1964). Surface tissue was removed from fresh collected corals with a stream of distilled water shot from a dental water jet (Johannes & Wiebe 1970). Samples were then frozen, lyophylized, pelletized, and bombed. The calorimeter was calibrated using benzoic acid standards. When appropriate, endothermic processes due to combustion of carbonate were adjusted (Paine 1966). Inorganic ash content was determined by ashing pellets for 3 h at 500° C in a muffle furnace. The water content of *Porites* corals was determined by dry weight analysis. Individual coral colonies were drip-dried, placed inside a large dry plastic bag, and surface tissue removed with a high-pressure stream of air. The resultant viscous blastate was transferred from the plastic bag into pre-weighed pans, weighed wet, oven-dried at 40° C, and then reweighed.

Polyp density

The density of coral polyps per unit surface area was estimated for the corals. A circular template (2 cm diameter) was placed haphazardly at 10 locations accessible to fish on the surface of a coral

colony and the number of polyps enumerated. Ten colonies were sampled for each species of *Porites* and five for *Poc. meandrina*.

Nematocyst density and size

The relative density and size of stinging nematocysts in polyp tentacles were determined for each coral. Fresh collected colonies were fixed in 10% formalin for two days, rinsed, and whole polyps removed (from colony tips in branching corals) with small needles and forceps. The distal 1 mm of the polyp was then removed, opened by a incision along the oral-aboral axis, and placed flat on a glass slide. The polyp was squashed under a glass cover slip and examined at 400× under a compound microscope. Nematocysts were classified according to Mariscal (1971, 1974). The number of nematocysts in five ocular fields (1 ocular field = approximately 4.2 mm^2) was counted for ten polyps of each coral species. The length (l) and diameter (d) of ten undischarged nematocysts of each species was measured with an ocular micrometer. From these data nematocyst size was estimated by the formula for volume of an ellipse,

$$4/3 \, \pi \, d^2 \, l \, .$$

Laboratory experiments

Fish used in laboratory tests were obtained from shallow coral reefs on the leeward coast of Oahu by divers using handnets and acclimatized for 3 days in aquaria supplied with fresh sea water at Hawaii Institute of Marine Biology. Fish were maintained with fresh colonies of the finely branched coral *Pocillopora damicornis* which occurs on shallow reefs of Kaneohe Bay and is not a normal food for *C. multicinctus*.

Handling time. – Total foraging time is normally defined as that time spent in search and handling of prey. For laboratory study, I defined handling time as that required to locate and ingest polyps after enountering a coral head. This is synonymous with the post-encounter handling component of natural foraging behavior (described in Results) but differs from the more traditional definition of handling time which begins after a prey is captured (e.g. Werner & Hall 1974). Butterflyfish encounter coral colonies sequentially and then must invest additional time to locate polyps on the colony and position their head for a bite. As shown below, this post-encounter inspection/orientation time differs for each coral species and therefore is considered analogous to handling time costs of manipulating prey after capture (e.g. Kislalioglu & Gibson 1976). The beginning of a foraging bout in the tank was defined by the approach to and orientation within one head-length of a coral colony and terminated when the fish departed. Handling time was calculated as the average time interval between bites during foraging bouts.

Relative inspection costs during handling were determined for *Porites* corals. Movement of the black vertical band which passes through the center of the eye made it easy to tally eye movements while fish foraged on colonies. Each of five fish was presented a single coral colony for 10 min and observed from behind a black plastic blind placed against the aquarium glass. For each colony presentation the following were recorded: (1) total foraging bout time, (2) total number of bites, and (3) number of eye movements during foraging bouts. Each test fish was presented each species of *Porites* three times in a randomized sequence.

Coral morphology. – The effect of colony morphology on handling time was tested experimentally. If food preferences were due to handling constraints, the prediction can be made that no preference should exist if handling times are equalized by masking gross coral colony morphology.

Two identical feeders were constructed for paired presentation of live coral fragments (Fig. 1). Sides were made from opaque 6 mm plexiglass and the surface from 2 mm white vinyl. Overall dimensions were 20 × 20 × 5 cm. A square matrix of sixteen 2 cm^2 holes was drilled on the surface, and rows of elastic bands strung so that they crossed under each hole. Small pieces of fresh coral were positioned on the underside of the feeder and held flush with the surface by the bands.
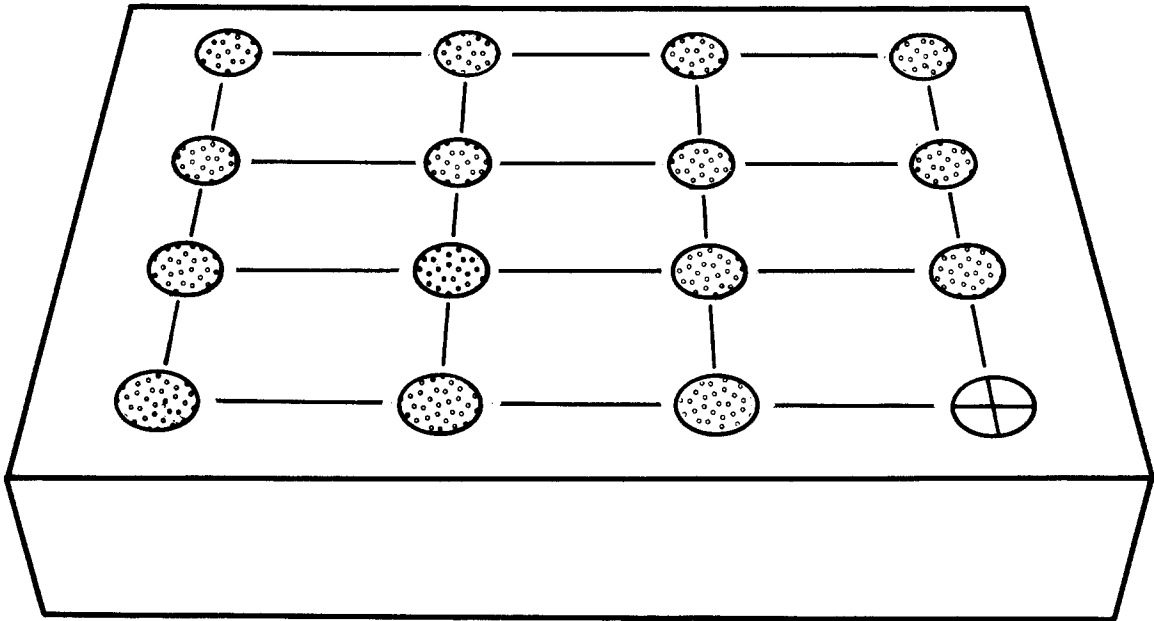
Fig. 1. Feeder used to mask gross morphology of the food corals of *C. multicinctus*. Sixteen fragments from a single coral colony were presented to fish through sixteen 2 cm² holes on the surface and held in place by elastic bands that crossed under each hole. A hole without a coral fragment that shows crossed bands is illustrated in right front corner of feeder. Dimensions of feeder are 20 × 20 × 5 cm.

Food preference experiments were performed in a 140 l aquarium. Individuals were presented corals under treatment classes (1) two separate coral colonies, and (2) two corals in separate feeders. In one set of experiments, *Poc. meandrina* was tested with *Por. lobata*. In the second set, all three possible permutations of the two *Porites* species were used in paired treatments: paired conspecific (*Por. lobata* + *Por. lobata* and *Por. compressa* + *Por. compressa*) and heterospecific (*Por. lobata* + *Por. compressa*) combinations. Considerable effort was made to minimize cues that could produce visual or gustatory biases. Coral heads of approximately 20 cm diameter were used in whole colony presentations. Color differences and polyp condition between species were controlled by matching species for color and polyp length, respectively. Coral pieces placed in feeders were taken from the same mother colony as those used in whole colony presentations. The location of paired colonies or feeders in the aquarium (left or right side) was randomized to eliminate position effects. Prior to each test subjects were given a minimum of 5 min to sample each paired colony or feeder for at least 5

feeding bouts. The first presentation treatment (colonies or feeders) was followed immediately by the other. The order of presentation for whole colonies and feeders was randomized for each test sequence and run in triplicate. Experiment durations were 15 min for whole colony and 30 min for feeder presentations. Data were compared between colony and feeder presentations by analysing pooled means of each fish. A paired-comparisons test was used to detect directional changes common to all fish.

Results

Foraging behavior

The foraging of *C. multicinctus* in the field involves a repetitious sequence of search, encounters with colonies, and handling of coral prey (Fig. 2). Search involves travel between individual coral heads or small areas on large *Porites* colonies. As corals are encountered, they are either approached for inspection (the first stage of handling) or passed
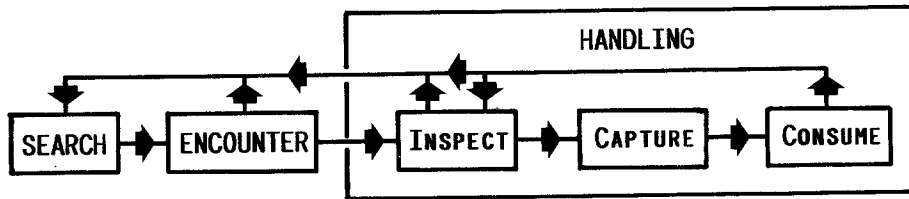
Fig. 2. Flow diagram of foraging patterns among food corals in the field for *C. multicinctus* showing pre-encounter search and post-encounter handling of prey. Handling time includes post-encounter inspection of polyps and orientation of the body for a bite.

for further search behavior. Inspection involves the examination of colonies for polyps and orientation of the body for feeding. When no bites are taken (polyps captured), the fish abandons the colony and returns to search. Captured polyps are consumed (masticated and swallowed) followed by either further inspection of the same colony or departure to search for another colony. This pattern of feeding is only occasionally interrupted by agonistic defense of the feeding territory, brief periods of sheltering, or cleaning by symbiotic cleaner wrasses. In this analysis handling is considered to include time spent during pre-capture inspection and orientation for a bite since it is a function of prey morphology rather than encounter rates with coral colonies.

Feeding patterns in the field

Total coral cover within fish territories in the coral rich habitat ranged from 30 to 91%, and averaged 51%. *Por. lobata* was the most abundant species followed by *Por. compressa* (Table 1). *Poc. meandrina* comprised less that 1% of total bottom cover. Other encrusting corals such as *Montipora verruco-*

sa, Leptastrea purpurea, and *Leptastrea bottae* occurred in patches less than a few centimeters in diameter and were very rare in quadrat samples.

Eighty-two percent of all feeding bites were taken from live corals (Table 1). Fish also consumed small quantities of benthic filamentous algae on dead coral and basalt substrates, and occasionally invertebrates such as amphipod crustaceans and fragments of polychaete worms. Although 18% of the total bites were taken on non-coral substrates, non-coral invertebrate food items comprised less than 5% of the total stomach content volume and algae less than 1% which confirms that the diet of *C. multicinctus* consists largely of scleractinian coral polyps. Undigested filamentous algae and symbiotic coral zooxanthellae were often recognized in the hind gut and indicates that assimilation of all plant material is incomplete.

No individual fish foraged on food items in equal ratios to the proportion of substrate cover (independent G-test: n = 60: df = 3, all test $P<0.001$). Fish fed upon *Por. lobata* in excess of its abundance (Table 1). Although relatively rare in the study area, *Poc. meandrina* was also taken in higher proportion than its abundance. In contrast *Por. compressa* and non-coral substrates (which contained

Table 1. Substrate composition in *C. multicinctus* feeding territories (n = 30) and feeding patterns of resident pairs (n = 60) in the coral rich habitat at Puako. Total observation time = 9025 min. Total number of bites = 93638. B/C = ratio of proportion of bites to proportion of bottom cover. Data expressed as means and standard deviations. *P* determined by Wilcoxon's two-sample test for equal proportions of cover and bites.

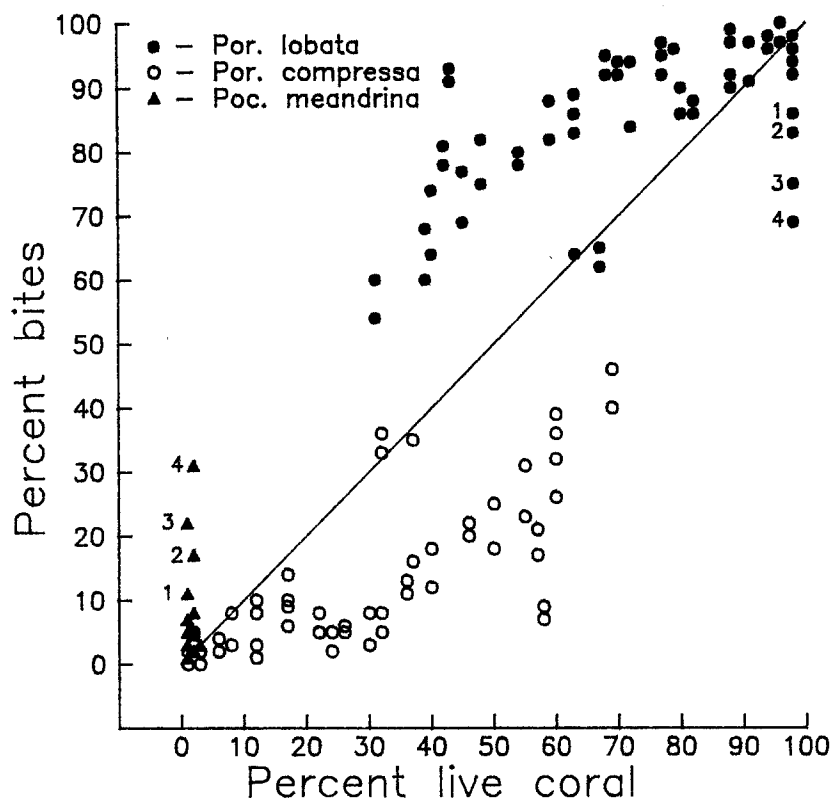| Food item	% Total cover	% Total bites	B/C	P
Porites lobata	34.8 ± 12.4	71.9 ± 12.6	2.1	<0.0001
Porites compressa	15.9 ± 14.6	10.1 ± 9.0	0.6	<0.0001
Pocillopora meandrina	0.1 ± 0.1	0.3 ± 0.8	3.0	<0.0001
Hard substrate (non-coral)	49.2 ± 13.5	17.7 ± 10.6	0.4	<0.0001

Fig. 3. Relationship between proportion of live coral cover and proportion of feeding bites for individual *C. multicinctus* at Puako. Solid line indicates equal proportions. Examples of the strong preference for *Poc. meandrina* that reduced feeding on *Por. lobata* are shown by numbered points that indicate feeding by 4 fish in territories that contained *Poc. meandrina*.

filamentous algae and invertebrates in much lower densities) were grazed less frequently than expected by their proportion of cover.

Feeding patterns among living corals (exclusive of bites on non-coral substrates) in relation to their relative abundance from the primary study area and the coral-poor reef flat are shown in Figure 3. The relatively uncommon *Poc. meandrina* was taken in greater proportion than expected by its abundance (Wilcoxon's two-sample test: n = 18, $P<0.05$). *Por. lobata* was also taken in a higher proportion than its abundance (Wilcoxon's two-sample test: n = 57, $P<0.05$) except when it cooccurred with the highly preferred *Poc. meandrina*. Finger coral, *Por. compressa*, was taken less than expected (Wilcoxon's two-sample test: n = 53, $P<0.05$). Thus, the feeding relationships observed among live food corals by *C. multicinctus* are consistent with those observed for all food types combined.

Energy and water content of food corals

Caloric densities of coral tissues are shown in Table 2. Mean values for *Por. lobata* and *Por. compressa* were very low on an ash-free dry weight basis and did not differ (t-test: $P<0.3$). The tissues of both species have a water content of about 95%. Thus, energy content on a wet weight basis is also approximately equivalent between the two species of *Porites*. In contrast, *Poc. meandrina* had a mean caloric density approximately 16% higher than the pooled *Porites* data (t-test: $P<0.05$).

Table 2. Caloric densities and water content ($\bar{x} \pm$ SD) of coral tissues. n = number colonies assayed.

Species	Calories mg^{-1} AFDW (n)	% water (n)
Pocillopora meandrina	5.29 ± 0.08 (7)	– –
Porites lobata	4.63 ± 0.31 (9)	96.1 ± 0.4 (4)
Porites compressa	4.50 ± 0.24 (7)	94.4 ± 0.3 (3)

Nematocyst size, distribution, and abundance

Nematocysts differed qualitatively between the two genera of corals examined. Two types of small nematocysts were observed in *Poc. meandrina* (Table 3). The largest (type 1) and most common had a translucent capsule with the undischarged shaft prominently visible in the interior and was classified as a microbasic mastigophore by Mariscal (1971). The second smaller and less abundant type was not classified although similar in size to cnidocysts described for *Poc. damicornis* by Glynn & Krupp (1986).

Nematocysts were qualitatively similar for both species of *Porites* but much larger than those found in *Poc. meandrina*. Nematocysts of *Por. compressa* have been classified as holotrichous isorhiza (Glynn & Krupp 1986). Threads of some discharged nematocysts were almost 50× their capsule length. A between-species comparison of estimated cell volume shows that nematocysts of *Por. compressa* are larger than those of the preferred *Por. lobata* (t-test: $P<0.001$) although of much lower magnitude than the inter-generic size differences. Nematocyst density in polyp squashes was higher in *Por. compressa* than in *Por. lobata* (t-test of square-root transformed data: $t = 3.14$, $df = 18$, $P<0.01$). The distribution of nematocysts in *Por. compressa* was also more clumped than in *Por. lobata*. This is reflected by a higher coefficient of dispersion (ratio of variance to mean, Sokal & Rohlf 1981) of 1.60 for *Por. compressa* than 1.03 *Por. lobata*.

Polyp densities

Corals of the genus *Porites* have similar calyx morphologies but some minor differences exist. Calyxes were on average smaller in *Por. lobata* than *Por. compressa* and their overall density was higher in the former species (Table 4, t-test: $P<0.005$). In addition, calyxes (and presumably polyps) were more variable in size for *Por. compressa* due to the coral's more complex surface relief. Unlike *Porites*, the surface of *Poc. meandrina* is covered with small verrucae that underlie polyp clusters. The variable size of the verrucae and numbers of associated polyps produce considerable variability in local polyp density although it did not differ from either species of *Porites* (Tukey's multipe comparisons test: $P>0.05$).

Handling costs

In laboratory feeding experiments, fish took 71% more bites per unit foraging time on *Poc. meandrina* than on *Por. lobata* (paired t-test: $P<0.05$), and 47% more bites per unit foraging time on *Por. lobata* than on *Por. compressa* (Table 5, paired t-test: $P<0.05$). The high feeding rate on *Poc. meandrina* was influenced by intense feeding bouts by fish on polyp clusters located on colony verrucae. Assuming a linear inverse relationship between handling time and feeding rate, handling time was 83% greater for *Por. lobata* and 151% greater for *Por. compressa* compared to *Poc. meandrina*. The high handling time for *Por. compressa* is reflected in the greater number of eye

Table 3. Nematocyst dimensions, volume, and density ($\bar{x} \pm$ SD) for three food corals measured in a compound microscope ocular field (4.2 mm²). Ten polyps were sampled for each species.

Species	Length (mm)	Diameter (mm)	Volume ($\times 10^{-5}$ mm³)	Density (no. per ocular field)
Porites lobata	0.063 ± 0.003	0.017 ± 0.001	7.36 ± 0.92	4.30 ± 2.1
Porites compressa	0.076 ± 0.001	0.018 ± 0.0	10.21 ± 0.20	6.40 ± 3.2
Pocillopora meandrina				
Type 1	0.040 ± 0.003	0.005 ± 0.0	0.39 ± 0.04	>40
Type 2	0.022 ± 0.003	0.003 ± 0.0	0.06 ± 0.01	$-$

movements made to inspect polyps while feeding compared to *Por. lobata* (paired t-test: $P<0.01$), and over twice as many eye movements per bite (paired t-test: $P<0.05$). Eye movement data support the hypothesis that foraging on *Por. compressa* has a higher handling cost related to coral inspection that results in fewer bites per unit time compared to *Por. lobata*.

Food preference and the constraint of coral morphology

C. multicinctus shows the same preference for corals in the laboratory as observed in the field. Whole colonies of *Poc. meandrina* were highly preferred over those of *Por. lobata* (Fig. 4) which were preferred over *Por. compressa* (Fig. 5). No preference was found in any conspecific colony or feeder presentation.

Fish discriminated between *Poc. meandrina* and *Por. lobata* when gross coral morphology was masked by the feeders (Fig. 4). The proportion of bites on *Pocillopora* in whole colony presentations (98%) remained very high when the two corals were presented in the feeders (88%). The preference for whole colonies of *Por. lobata* over *Por. compressa*, however, was not replicated when coral fragments were presented in feeders (Fig. 5). For pooled feeding data, fish did not show a preference for either coral when morphology was masked (Wilcoxon signed-ranks test: $P<0.05$) and a decreased proportion of bites on *Por. lobata* in feeder experiments compared with associated presentations of whole colonies (Wilcoxon's two-sample test: $P<0.05$, one-tailed test). Fish did not show selective feeding among *Porites* when the variable of gross morphology was controlled.
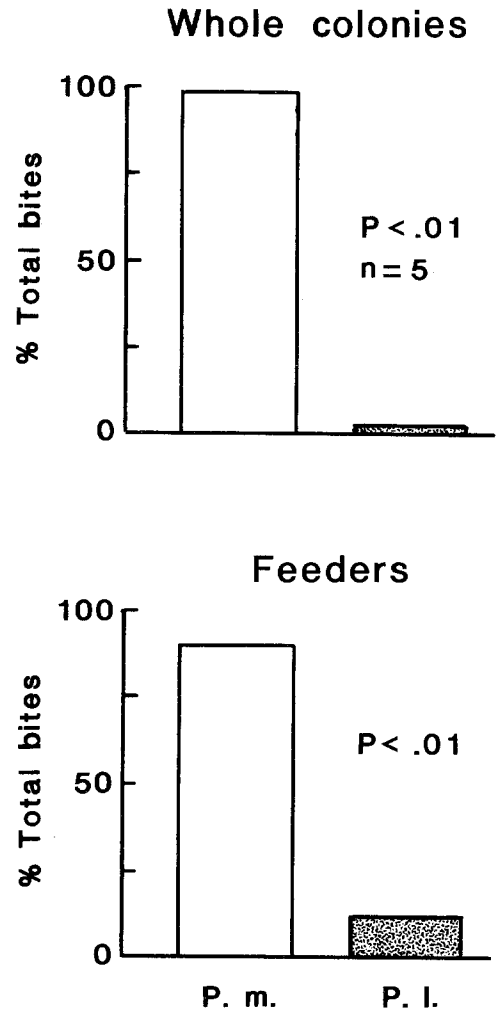

Fig. 4. Feeding preferences of five *C. multicinctus* on the corals *Pocillopora meandrina* (P. m.) and *Porites lobata* (P. l.) in paired presentations of whole coral colonies and paired presentations of coral fragments in experimental feeders that masked coral gross morphology. *P* determined by Wilcoxon's two-sample test of proportions of bites within each treatment.

Table 4. Polyp densities (number per cm^2) of three food corals. Coefficient of dispersion (CD) = variance/mean, n = number of colonies examined.

Species	n	$\bar{x} \pm SD$	CD
Pocillopora meandrina	5	66.4 ± 15.3	3.5
Porites lobata	10	76.7 ± 5.7	0.4
Porites compressa	10	61.0 ± 10.5	1.8

Table 5. Feeding rates and frequency of eye movements ($\bar{x} \pm SD$) of *C. multicinctus* during foraging on coral colonies.

Species	Bites	Eye movements	
	minute^{-1}	minute^{-1}	bite^{-1}
Porites lobata	19.3 ± 7.8	33.3 ± 8.0	2.1 ± 0.9
Porites compressa	13.1 ± 8.1	42.1 ± 11.4	4.6 ± 2.4
Pocillopora meandrina	33.0 ± 8.6	–	–

Whole colonies
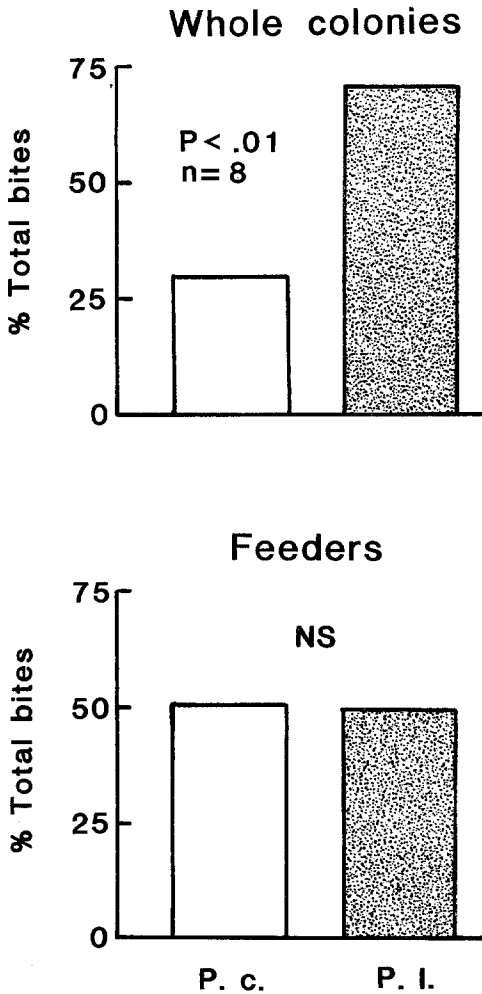

P < .01
n = 8

Feeders

NS

P. c.   P. l.

Fig. 5. Feeding preferences of eight *C. multicinctus* on the corals *Porities compressa* (P. c.) and *Porites lobata* (P. l.) in paired presentations of whole coral colonies and paired presentations of coral fragments in experimental feeders that masked coral gross morphology. *P* determined by Wilcoxon's two-sample test of proportions of bites within each treatment.

Discussion

Field studies on corallivorous chaetodontids indicate corals of the genus *Pocillopora* to be a preferred food (Randall 1974, Neudecker 1979, Tricas 1985, Hourigan et al. 1988). Although relatively uncommon on the Puako reef, *Poc. meandrina* was grazed by *C. multicinctus* more frequently than expected both in its proportion of total live coral and total bottom cover. The preference for *Poc. meandrina* by *C. multicinctus* was reported in four

different reef habitats by Hourigan et al. (1988) where this coral species comprised as high as 55% of the coral diet but only 25% of live coral cover.

For many fish, feeding on *Por. lobata* was reduced when *Poc. meandrina* was present in feeding territories. Similarly, the focus on these two corals reduced feeding upon finger coral, *Por. compressa*, which often was the most common coral within feeding territories but rarely taken in proportion to its percentage of bottom cover. Thus the low occurrence of *Por. compressa* in the diet may be due to concentrated feeding on other species rather than active avoidance. In laboratory feeding experiments with corallivorous chaetodontids, corals of the genus *Pocillopora* have been shown to be the preferred food in paired presentations while *Por. compressa* was often the least preferred although the latter species is readily fed upon when presented alone (Reese 1977, Cox 1983, Hourigan et al. 1988).

The preference for Pocillopora over Porites

The observed preferences for *Poc. meandrina* by *C. multicinctus* is consistent with its relatively high energy content. Surface tissues of *Poc. meandrina* had a mean caloric density 16% higher than *Porites*. This difference is probably due to fat bodies that comprise approximately 32% of the dry tissue weight of *Poc. meandrina* (Stimson 1987) and the occurrence of all tissue on the surface of the imperforate corallite skeleton. In contrast, *Porites* corals have a perforate skeleton where much of the living tissue and most fat bodies are located beneath the corallite surface (Stimson 1987) and are inaccessible to polyp pickers like *C. multicinctus*. Thus, more tissue (and its energy-rich components) may be available on a per bite basis to foragers on the imperforate *Poc. meandrina*. Hourigan et al. (1988) estimated that 32% more calories per bite are taken by *C. multicinctus* on *Poc. meandrina* than on *Por. lobata*, and found no difference in calories per bite among the two species of *Porites*. The congener, *Poc. damicornis*, which is a highly preferred species by corallivorous chaetodontids (Randall 1974, Reese 1977, Neudecker 1979), also

shows a high caloric (Richmond 1982, Glynn & Krupp 1986) and lipid content (Stimson 1987). The acquisition of lipid is important for *C. multicinctus* as seen in pronounced seasonal deposition of body fat (Tricas 1986) and high lipid fraction in reproductively active ovaries (21%) and testes (33%) (Tricas, unpublished data).

Although polyps did not differ in average density among genera, their clustered distribution on *Poc. meandrina* verrucae is probably the primary factor responsible for the low handling time of this coral relative to *Porites*. Fish continued to discriminate *Poc. meandrina* when gross morphology was masked indicating possible cues from surface microstructure. The extreme differences in nematocyst size, however, is also consistent with the preference for species of *Pocillopora* and may also influence feeding patterns and choices among these corals.

The preference for Porites lobata *over* Porites compressa

The preference for *Por. lobata* over *Por. compressa* in the field and in whole colony presentations is probably not a function of energy content of tissues since their caloric densities and water contents are similar. In this case differences in the rate at which fish can harvest polyps also may structure feeding patterns. The branched morphology of *Por. compressa* colonies greatly reduces the number of polyps available to fish compared to *Por. lobata*. More time is required to locate suitable polyps, more inspective eye movements per unit handling time are made, and fewer bites per unit handling time are taken. The indiscriminate feeding among the two species of *Porites* when their gross morphologies were masked supports the existence of a handling time constraint. The differences in gross morphology apparently outweigh microstructural differences between the species such as larger average polyp size for *Por. compressa*. The larger size, higher abundance, and clustered distribution of nematocysts among *Porites* corals are also consistent with observed foraging preferences. Since fish did not show preferences among *Porites* over the

30 min duration of the coral feeder experiments, however, any nematocyst-mediated feeding probably operates over a longer time period. Clearly, more research is needed to determine the role of nematocyst defense in food corals.

The prey choice model

The basic assumptions of the classic prey choice model for energy maximizers (reviewed by Stephens & Krebs 1986) are met by the *C. multicinctus* system, and allow a simple predictive model. Foraging consists of a repetitious pattern of searching among coral heads that are encountered sequentially and in approximate proportion to their abundance. Because fish must forage over wide areas to feed on benthic non-mobile prey, handling and search time are discrete events. Coral tissues contain no large undigestible components (although some portion of the symbiotic zooxanthellae may pass undigested through the gut), thus the assimilable fraction of energy is probably similar among coral species. Each coral has a predictable average energy content and handling time is determined largely by morphological constraints of each prey coral. Energetic cost per unit time of searching and handling are approximately equivalent for different prey. Since handling primarily involves inspection, energetic costs are probably only slightly higher than standard metabolic rates and can be ignored as a differential cost to be subtracted directly from energy intake.

The diet set that will maximize rate of energy intake can be predicted by applying the empirically derived parameters for each coral species (n = 3), in order of ranked profitability until the following equality is maximized,

$$\frac{E_n}{T} = \frac{\sum_{i=1}^{n} \lambda_i E_i}{1 + \sum_{i=1}^{n} \lambda_i h_i},$$

where E = energy gain, h = handling time, T = time foraging, and λ = encounter rate of each coral type during search.

The energy return per bite is highest and handling time lowest for *Poc. meandrina* (Pm) which combine to give this coral the highest profitability (Table 6). *Por. compressa* (Pc) has the highest handling time but approximately equivalent profitability as *Por. lobata* (Pl) because of its higher estimated energy content per bite. By this model only *Poc. meandrina* should be taken,

$$\frac{\lambda_{Pm} \, E_{Pm}}{1 + \lambda_{Pm} \, h_{Pm}} = 0.05 < \frac{E_{Pl}}{h_{Pl}} = \frac{E_{Pc}}{h_{Pc}} = 0.01.$$

However, fish can not sustain themselves on the rare *Poc. meandrina* alone and therefore should take both species of *Porites* when encountered. The predicted preference for *Poc. meandrina* by *C. multicinctus* is supported in habitats where the coral occurs in higher abundance (Hourigan et al. 1988) and also when it is supplemented in feeding territories (Tricas 1989) where it is then taken almost exclusively.

The inconsistency between the predicted diet set and the apparent partial preference for *Por. compressa* observed in the field can be explained at least partially by the expression of abundance of *Por. compressa* as percentage total substrate cover. At Puako, beds of *Por. compressa* are a thick matrix of highly twisted, 1–2 cm diameter branches that are broadly spaced. As a result, much of the area covered by this coral does not contain polyps due to large inter-branch gaps and inaccessible covered branches. The 'available abundance' of *Por. compressa* was estimated for some colonies to be less than half that of the total surface area (Tricas, unpublished data) and therefore this coral may actually be taken in equal or greater proportion than its availability to fish. While this consideration is less critical for massive and encrusting corals like *Por. lobata* where virtually all polyps are exposed, coral abundance would be better estimated for food preference studies in terms of that available to the fish rather than simple measures of total substrate cover. This is especially crucial for tests of the prey choice model if branched corals are of the highest profitability ranks because encounter rates (a function of abundance) are used to determine the predicted diet set.

Nutrient constraints and toxic properties of food items may also alter predictions of the simple prey choice model in reef fishes (Lobel & Ogden 1981). The need for rare but essential amino acids or inorganic nutrients unavailable in preferred corals may require searching for less abundant species, or energetically unprofitable and time costly filamentous algae or invertebrates among non-coral substrates. Although untested, foraging on coral tissues may also be limited by the need to add roughage to the diet to facilitate movement of gelatinous coral tissue through their gut. Hobson (1974) reported a similar complement of filamentous algae in the gut of *C. multicinctus* and *Chaetodon ornatissimus* as did Harmelin-Vivien & Bouchon-Navaro (1983) for numerous corallivorous chaetodontids. Nematocyst toxins or metabolic compounds present in live corals may set an upper limit to the number of bites taken per unit time from otherwise energetically profitable corals. In this regard, Glynn & Krupp (1986) reported no adverse affects of crude coral extracts of *Por. compressa* on a freshwater fish. While the differences found for nematocysts among prey corals are consistent with observed foraging patterns, more work is necessary

Table 6. Estimates for parameters that characterize foraging returns for *Chaetodon multicinctus* on food corals. See Appendix for estimate of E.

	Energy gain (E) (cal bite^{-1})	Handling time (h) (sec bite^{-1})	Profitability (E h^{-1})	Encounter rate (λ) (polyps sec^{-1})
Pocillopora	0.10	1.82	0.06	21
Porites lobata	0.04	3.11	0.01	8407
Porites compressa	0.06	4.58	0.01	3055

to establish whether any toxic compounds in corals function as aversive stimuli to coral-feeding butterflyfishes.

Future direction

Coral-feeding butterflyfishes offer many advantages to field studies of foraging ecology, energy allocation, and feeding behavior of fishes. While there currently exists considerable data on the food habits of many species, much work remains to develop and test models of their foraging patterns. Below are suggested topics to address the decision, currency, and constraint assumptions of butterflyfish foraging systems:

(1) *Does maximization of some component of food best characterize the foraging strategies of coral-feeding butterflyfishes?* This important question must be addressed before any rate-maximization model can be tested. Life history data for individual species are needed to establish how reproductive success varies with food intake. If the relationship exists, preferred food items that maximize the rate of intake can be predicted by estimating their relative profitability. In addition to energy content, analyses are needed to assess the relative protein, lipid, and carbohydrate content of coral tissues and how they are allocated in physiological pathways of butterflyfishes. Food choice experiments where energy or component content of food corals are manipulated and compared to controls (for example, by spiking the autotrophic symbiotic zooxanthellae with inorganic nutrients) could provide a direct test of a maximization strategy.

(2) *What features of coral tissues other than energy content influence selection (or avoidance) of food types?* In addition to component and energy content, critical inorganic or rare organic nutrients may govern the selection of relatively non-profitable coral prey. These questions require knowledge of the physiology of growth and assimilation in the fishes and the relative abundance of nutrients in prey corals. In addition, aversion to coral species can be addressed through immunological assays of

antibodies to nematocyst toxins and surveys for metabolic compounds such as those known to occur in marine macroalgae (e.g. Targett et al. 1986), soft corals, and gorgonians (Fenical 1982, Gerhart 1984).

(3) *Patch vs. prey models.* In the present study foraging preferences were compared to a classical 'prey choice model' that addressed 'what corals should be included in the diet?'. Alternatively, individual colonies can be regarded as discrete patches of prey and derivatives of the classical 'prey-patch model' used to ask 'how long should a fish feed before moving to another coral head' (sensu Charnov 1976). This question also deals with maximization strategies and would include analyses of polyp depletion, withdrawal, and regeneration rates. Butterflyfish systems offer exciting field and laboratory opportunities to vary the number of polyps per patch, travel time between patches, and patch encounter rates by manipulation of individual coral colonies.

(4) *Feeding ontogeny and periodicity.* Ontogenetic studies of age-specific food preference patterns could be used to address trade-offs between the acquisition of protein for growth in juveniles and lipids for reproduction in adults. Also, unlike adults that are often site attached for long periods (Reese 1973, 1975, Sutton 1985), new recruits to the reef often experience intense predation (Tricas, unpublished data), and may exhibit habitat and food preferences mediated by predation risk (e.g. Mittlebach 1984). Finally, diel, lunar, or seasonal shifts in feeding patterns may follow changes in profitability of food corals such as shown for chaetodontids feeding on gorgonians (Lasker 1985). Closely monitoring changes in foraging behaviors in relation to coral spawning activity would provide valuable insight into the relationships of butterflyfishes and their coral prey.

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Appendix

Energy gain per bite (E) was estimated for each coral by the combined product of (1) the estimated volume (mm^3) of coral tissue per bite (see below), (2) the density of coral tissue (assumed to be equivalent for all three corals and that of water, 1.0 mg mm^{-3}), (3) the proportion of dry tissue in a bite (a dimensionless constant estimated as 1 − proportion of water from Table 2, assumed to be 0.05 for *Poc. meandrina,* and tissue ash content assumed to be equivalent for all species), and (4) calories mg AFDW^{-1} from Table 2.

Bites upon *Porites* corals usually remove only polyp tentacles while bites upon *Poc. meandrina* usually take tentacles, the oral disk, and a distal portion of the polyp column (Hourigan 1987, Tricas unpublished data). Mean tentacle length (1) and radius (r) were estimated from photographs of live polyps, and volume for 12 tentacles calculated from the formula for the volume of a cylinder, 12 (π r^{2}l). The volume of an additional 0.5 mm length of polyp column taken in the imperforate *Poc. meandrina* was calculated by the same method and summed with the tentacle volume estimate. Mean tentacle radii (0.1 mm) and lengths (0.6 mm) were equivalent for both *Porites* corals providing an estimate of 0.23 mm^3 tissue per bite. Mean *Poc. meandrina* tentacle radius (0.1 mm) and length (0.5 mm) gave a tentacle volume estimate of 0.19 mm^3; oral disk/polyp column volume was 0.19 mm^3 for a 0.38 mm^3 total bite volume estimate. These estimates do not include other coral tissues which may also be ingested (e.g. inter-polyp coenosarc), thus they may underestimate actual energy content.