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THE ECONOMICS OF FORAGING IN CORAL-FEEDING BUTTERFLYFISHES OF HAWAII

LES ECONOMIES D'ENERGIE DANS L'ALIMENTATION CHEZ LES POISSONS PAPILLONS CORALLIVORES D'HAWAII

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ABSTRACT

Coral-feeding butterflyfishes (family Chaetodontidae) in Hawaii show a wide variety of social behaviors. Most obligate coral feeders, however, occur in pairs that defend feeding areas against intrusions by other corallivores, especially conspecifics. In these cases fish form stable multi-purpose territories that function to insure food, mates, and shelter resources.

Maximizing food intake is of particular importance among fishes, as it can increase both present and future reproductive success. Food territories of corallivorous butterflyfishes are examined in reference to a simple energetic model where the net benefits of being territorial are expressed as total food (or energy) intake less the costs of territorial defense. Relative to other prey types, corals represent an evenly dispersed, predictable, and long-term renewable food resource that when defended can yield high net energetic benefits. Calorimetric analyses indicate that coral tissues of the Porites spp. complex in Hawaii are of a relatively low energy content. To compensate, fishes engage in activites that increase time spent feeding or maximize net energy consumption. For example, some species exhibit distinct choice preferences for corals with the highest energy density. Studies on Chaetodon multicinctus show that there are fewer aggressive interactions among territorial neighbors in stable undisturbed communities than those subject to recent environmental perturbation. Thus territorial behavior can function to increase access to food resources in a relatively cost-efficient way.

RESUME

Les poissons papillons (famille des Chaeotodontidae) hawaiiens qui se nourrissent sur les coraux montrent une grande gamme de comportements sociaux. La plupart des espèces qui doivent se nourrir sur les coraux, vivent en paires et défendent les zones dans lesquelles elles se nourrissent, contre les intrusions d'autres corallivores, en particulier si ceux-ci sont de la même espèce. Dans ce cas, les poissons forment des territoires stables à usages multiples qui leur fournissent leur nourriture, leurs partenaires, et leurs abris.

Augmenter au maximum la ration alimentaire est d'une importance capitale chez les poissons puisque cela peut augmenter le succès de leur reproduction, présente et à venir. Les territoires trophiques des poissons papillons qui se nourrissent sur les coraux sont examinés en référence à un modèle énergétique simple où le bénéfice net, retiré du fait de l'existence du territoire, s'exprime en ration (ou en énergie) totale, moins le coût de la défense du territoire trophique. Relativement à d'autres types de proies, les coraux représentent une source d'énergie à long terme, à la fois prédictible et régulièrement répartie dans l'espace et, lorsqu'elle est protégée, peut fournir d'importants bénéfices énergétiques. Les analyses calorimétriques indiquent que les tissus des complexes de coraux du genre Porites d'Hawaii contiennent une énergie relativement basse. Afin de compenser cela, les poissons s'engagent dans des activités qui augmentent le temps passé à se nourrir ou qui portent à un maximum la consommation nette d'énergie. Par exemple, certaines espèces manifestent des préférences évidentes pour les coraux ayant la plus forte énergie. Des études sur les Chaetodon multicinctus montrent qu'il y a moins d'interventions agressives avec les voisins territoriaux dans les communautés stables et tranquilles que dans celles qui sont sujettes à une perturbation environnementale récente. Donc, le comportement territorial peut servir à augmenter l'accès aux ressources d'une façon à augmenter le rapport énergétique du comportement alimentaire.

INTRODUCTION

Fish communities on coral reefs exhibit a remarkably diverse species composition in habitats often limited in area. In spite of the obvious importance of living space to members of coral reef communities, relatively little is known about the ecological factors that influence the spacing patterns of individuals. Early workers in terrestrial systems recognized that the dispersion of resources could influence the social structure and dispersion of animal populations. For example, Orians (1961) and Horn (1968) demonstrated that a clumped ephemeral food supply could be most efficiently harvested by blackbirds residing at a central colony. In constrast, a stable evenly distributed food supply was better harvested if nest sites were evenly spaced. In reef fishes, social groupings may also be influenced by the abundance and distribution of resources or competitors (e.g. Barlow, 1974; Sale, 1978; Robertson et al., 1979; Robertson, 1984) but further study is needed to clarify whether the concepts developed for terrestrial systems also apply to reef fishes.

Territoriality is a common behavioral adaptation for the defense of resources. Among fishes, defended areas are usually multi-purpose territories that contain some combination of food, mates, spawning, and shelter sites. The aggressive behavior involved in territorial defense is a means of interference competition for these resources and can be directed at either conspecific or heterospecific individuals (Low, 1971; Myrberg and Thresher, 1974).

Brown's (1964) theory of economic defendability provides a useful framework for tests of the adaptiveness of territorial behavior. Simply stated, in order for territoriality to evolve, any benefits that can ultimately contribute to increased fitness must exceed additional costs incurred by territory defense. This concept is especially relevant to studies of reef fishes with planktonic larvae because it allows for costs and benefits to be defined in units that contribute to, but are not necessarily a direct measure of, fitness.

Butterflyfishes of the family Chaetodontidae are abundant members of most tropical reef communities. *Chaetodon multicinctus* Garrett is endemic to the shallow coral reefs of the Hawaiian Islands and Johnston Atoll (Burgess 1978). It has a small, highly compressed body with a series of five or six conspicuous brown vertical bands on a white background. Adults are monogamous, obligate coral feeders (Reese, 1975) that vigorously defend a feeding area against intrusion by other coral-feeding fishes (Tricas, ms). Studies of corallivorous butterflyfishes provide strong evidence for behavioral (Reese, 1977; 1981) and morphological (Motta, 1980) coevolution with their food corals thus emphasizing the importance of assuring access to these resources.

This paper examines the use of space by *C. multicinctus* and other coral-feeding chaetodontids within the theoretical framework outlined above to explain the evolution of territoriality. Herein, I compare the ecology, distribution, and energetics of food corals with adaptations of butterflyfishes to the defense of these resources within a coral reef community.

METHODS

Field data were collected at Puako reef located on the west coast of the island of Hawaii. The study area begins in 7 m of water near the base of a shallow reef flat and extends seaward along a gently sloping shelf to depths of about 12 m. This region is characterized by expansive fields of *Porites lobata* and *Porites compressa* corals. A third species, *Pocillopora meandrina* is interspersed within the *Porites* stands but is much less common. Characteristics of the various habitats at Puako have been reported in detail elsewhere (Hayes et al., 1982).

Coral abundance was estimated by quadrat subsampling. A 1-m^2 quadrat with a .1-m grid was placed at randomly determined locations across the study habitat and the coral species underlying each grid intersection tallied. Percent cover was calculated from the proportion of total counts for each species. Coral abundance within 14 fish territories (see below) was estimated by random sampling of 20 quadrats per territory.

The caloric content of three species of corals was determined using a Phillipson microbomb calorimeter (Phillipson, 1964). Corals were collected from reef habitats on the island of Oahu and transported to the lab. Surface tissue was removed with a stream of recirculating distilled water shot from a dental water jet. Samples were then frozen, lyophylized, pelletized, and bombed. The calorimeter was calibrated using a benzoic acid standard. Endothermic processes due to combustion of carbonate were adjusted for according to Paine (1966). Non-organic content was determined by ashing pellets for 3 hours at 500 °C in a muffle furnace.

Divers using scuba watched pairs of *Chaetodon multicinctus* forage and defend areas of the reef. Boundaries of feeding territories were marked with strips of plastic surveyor's tape weighted with galvanized nails. Territory sizes were estimated as total surface area by placing a line along the major territory axis and then measuring the rugose (relief) distance with a chain to territory borders at 1-m intervals.

Feeding data for *C. multicinctus* were also recorded by scoring the coral species taken in each bite by each pair member during alternate 5-minute observation periods. Agonistic interactions of territorial residents were also recorded as the number of chases directed at and received from other fishes. To estimate costs of territorial defense, an index of aggression was calculated for each fish species as the product of the proportion of total agonistic acts in which *C. multicintus* was the aggressor and the proportion of total *C. multicinctus* that showed agonistic interactions with that particular species. For five fish pairs, agonistic interactions were further categorized as ritualized feeding bouts (primarily accelerated feeding), lateral displays, fin flicks and flaring, or face-offs at territory borders. These displays were distinguished from other aggressive behaviors by a lack of overt chasing.

RESULTS

Corals formed 37% of bottom cover in the study area with *Porites lobata* the most abundant

Table 1. Coral abundance (means and standard deviations) across the study habitat and within 14 territories of *Chaetodon multicinctus* at Puako, Hawaii. Ratios of variance to mean for proportion of coral cover given in parentheses.

Species	Percent Cover Study Area	 Fish Territories
P. lobata	29.2 ± 18.3 (.12)	29.9 ± 7.4
P. compressa	7.9 ± 6.8 (.06)	7.4 ± 4.0
P. meandrina	<1.0 ± .1 (.01)	< 1.0 ± .1
Total Coral	37.2 ± 3.2 (<.01)	37.3 ± 7.3

species (Table 1). Other corals were much less common. Non-coral substrata included small patches of exposed basalt, dead coral, rubble, and sand.

The morphologies of *Porites* colonies make it difficult to quantify their dispersion patterns because of problems associated with identifying discrete individuals. A simple estimate of dispersion was made, however, by comparing the sample distributions of percent coral cover in quadrats. Variance to mean ratios (Table 1) show that variation was low in relation to the average coral cover among sample quadrats, and indicate a dispersed distribution of coral cover within the study area.

Caloric densities of coral tissues are shown in Table 2. Mean values for *P. lobata* and *P. compressa* did not differ (Wilcoxon 2-sample test). In contrast, *P. meandrina* had a higher mean caloric density than the pooled *Porites* data ($p < .002$, Wilcoxon 2-sample test).

Fish territories shared contiguous borders that changed only slightly over a one-year period. Mean area of territories was 57.2 m^2 (SD = 18.7; n = 34). Although mate fidelity appeared to be strong on a short term basis, in only two of eight territories could both original residents be identified after one year. It was not possible to determine whether mate separation was due to natural mortality, eviction by another conspecific, or voluntary abandonment. One territory monitored near the study area, however, contained the same two paired individuals for over 3 years, indicating a potential for long-term site attachment by this species.

P. lobata was the most frequent food item and comprised 69% of the total number of bites (Table 3). In addition to coral tissues, fish consumed small quantities of benthic filamentous algae that grew on the surface of dead corals. This food item, however, comprised less than 1% of the total stomach content volume.

High indices of aggression were recorded for a variety of coral feeding species (Fig. 1, Table 4). The most intense and lengthy agonistic bouts occurred when neighboring conspecifics intruded within a territory. Juvenile corallivores also received high levels of aggression from territory residents but all non-corallivorous fishes did not. Although conspecific agonistic encounters were frequent, 36% involved behaviors that involved displays rather than the more energy costly and potentially damaging chases and fights (Table 4).

Table 2. Caloric values (mean and standard deviation) for soft tissues of three species of Hawaiian corals. AFDW = Ash Free Dry Weight.

Species	(n)	Calories / mg AFDW
Pocillopora meandrina	(7)	5.29 ± .08
Porites lobata	(8)	4.65 ± .32
Porites compressa	(3)	4.53 ± .10

Table 3. Feeding activities on various substrates in the field for 8 pairs of *C. multicinctus*. Total observation time = 1795 min. Total number of bites = 17,097. Feeding rates calculated as average mean rates (and standard deviation) for each pair.

Food Item	Percent of Total Bites	Feeding Rate bites/min.)
Porites lobata	69	6.69 ± 1.91
Porites compressa	6	.52 ± .59
P. meandrina	<1	.02 ± .04
Hard Substrate	25	2.38 ± 1.20
Other items	<1	.05 ± .15

DISCUSSION

Corals: Predictable, dispersed, and stable resources

Although there are over 40 species of hermatypic corals in Hawaii, only a few are common on shallow reefs. In the study area at Puako, three species in two genera comprised over 99% of the living coral cover. In spite of this low species diversity, corals form a major portion of the bottom substrate and are widely distributed across the reef. This is evident for both species of *Porites* and collectively for total coral cover. Although considerable variability existed in percent species cover between quadrats, both *Porites* spp. were present in over 95% of the samples. This even pattern of distribution was also found within fish territories.

Physical forces in the environment are the most important influence on the diversity and temporal stability of Hawaiian coral communities. On the island of Hawaii, Dollar (1982) found that four distinct coral habitats were structured by normal patterns of low-level wave actions but were also subject to massive destruction by severe storms approximately every 40 years. Disturbances from biological sources appear to have relatively mild effects on Hawaiian coral

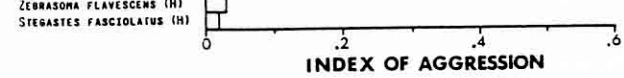

Figure 1. Aggressive interactions between *C. multicinctus* and other fishes. C. = *Chaetodon*, P. = *Plectroglyphidodon*. (H) = herbivore, (I) = invertebrate picker, (P) = planktivore.

Table 4. Relative frequency of display and chase events between adjacent territorial pairs of Chaetodon multicinctus and other corallivorous chaetodontids. 10 fish (5 pairs), 1270 min. observation time.

Species	Total Agonistic Acts	Chase/Display Ratio
C. multicinctus	58	1.8
C. ornatissimus	4	.3
C. trifasciatus	2	1.0
C. unimaculatus	1	0.0

community structure. Predation by Acanthaster starfish is apparently not as severe in Hawaii as in other tropical areas (Branham et al., 1971). Fishes can limit coral distributions through predation (Neudecker, 1977, 1979; Cox, 1983), and algal mat grooming (Kaufman, 1977; Potts, 1977; Wellington, 1982). In Hawaii, the yellow-eye damselfish, Stegastes fasciolatus, defends large algal mats that can overgrow and kill adjacent P. lobata corals (Tricas, unpublished), but its overall impact remains to be determined.

In summary, coral communities in Hawaii typically show a relatively low species diversity but a high total cover. To coral feeding fishes that forage over these reefs, this presents food resources dispersed evenly over a wide area. The long average intervals between major disturbances of inshore reefs make coral food resources spatially and temporally stable in relation to the duration of residence (and probably life span) of the fishes.

Corals as food resources

Coral resources present unique opportunities for foraging reef fishes. Unlike other invertebrate prey that must be located by searching the interstices of the reef, corals are non-cryptic and form the substrate over which fish forage. This results in small search and travel times between feeding sites. In addition, changes in food abundance or quality should be relatively easy to assess. Tricas (ms) experimentally demonstrated that C. multicinctus could detect decreased coral abundance within feeding territories and respond by territorial expansion.

Basic metabolic processes impose minimal food requirements for maintenance of normal body functions. For a species that must forage within a limited area, the supply of food must be replaced at a rate equal to that at which it is removed, or the resource will eventually be depleted. The assurance of a constant and predictable food supply is important in view of the low energy content of coral tissues. Corals of the genus Porites showed a caloric density only slightly above that of carbohydrates (4.10 cal/mg AFDW), and well below that of either pure protein or lipid (5.65 and 9.45 cal/mg AFDW, respectively). The higher energy content of P. meandrina is probably due to lipids as this species often has small fat bodies within the soft tissue and mucus (J. Stimson, pers. comm.). The congener, Pocillopora damicornis, shows about the same caloric content of adult tissue (Richmond, 1982). As a consequence of the relatively low caloric density of coral tissue, fishes using this food resource should invest large amounts of time feeding to harvest sufficient energy. This is the case for C. multicinctus as individuals spend greater than 90% of their time budget in feeding-related activies (Tricas, ms).

Most butterflyfishes feed selectively on corals with high energy contents. Reese (1977) and Cox (1983) found P. damicornis was preferred over Montipora verrucosa and P. compressa by C. ornatissimus and C. trifasciatus. In the present study, P. meandrina was rare in the field, hence it represented only a small portion of the total diet. This coral, however, was highly preferred by C. multicinctus when transplanted into experimental territories (Tricas, ms). In contrast, the preference for P. lobata over P. compressa is not adequately explained by differences in energy content. It may instead reflect relative abundances in relation to energy or nutrient-based foraging strategies (Birkeland and Neudecker, 1981), differential perforation of the corallite, nematocyst size and densities, or toxins like those common to octocorals (e.g. Coll et al., 1982).

Food requirements are not a simple function of metabolic needs. Egg production in some fishes is directly related to food supply (Tyler and Dunn, 1976; Hirschfield, 1980). Female fecundity is limited by body cavity size (Bagenal, 1966; Williams, 1966), therefore in species with few opportunities to reproduce, selection may favor rapid growth. Furthermore, large size may be advantageous in contexts of intraspecific social dominance (Jenkins, 1969; Constantz, 1975), reproductive success (Kodric-Brown, 1977), and interspecific competitive dominance (Robertson, 1984). The low levels of predation on adult chaetodontids may be related to their highly compressed body form and spinous dorsal fins (Gosline, 1965), and may reflect a size refuge from predation. Thus, even though metabolic requirements are met within a foraging area, exclusive access to additional food may be an important aspect of fitness for coral-feeding fishes. Defensive behaviors like territoriality, should be selectively advantageous if food resources can be defended so that food requirements can be met and production levels maintained.

The defendability of corals

The ability of coral feeding fishes to defend their food resources is promoted largely by the even distribution of corals across the reef. Species like C. multicinctus that hold small territories can efficiently monitor most of the territory for intruders from almost any point within. Similarly, residents can advertise their presence to potential intruders from the same distance. Other species like C. ornatissimus or C. trifasciatus that range over much larger areas, however, are unable to survey the entire foraging area from one place. Thus, agonistic activities among these later species become a function of encounter rates during foraging movements and are infrequent (Reese, 1975; Tricas, unpublished data).

There is reasonable evidence to predict the existence of defensive behaviors among coral feeding butterflyfishes. Reese (1975) noted that agonistic interactions were more frequent among ecologically similar species and suggested the possiblility of competition for food or space.

Studies on the distributions of coral feeding butterflyfishes fit predicted patterns of reduced spatial overlap between potentially competing species. For example, Bouchon-Navaro (1981) found that each of three reef zones was dominated by only one or two coral feeding species. Broader geographical replacement was also reported for coral feeding buterflyfishes on the Great Barrier Reef (Anderson et al., 1981). Although the association of species with particular habitats may indicate competitive processes, further experiments are required to validate the role of extant interspecific competition in structuring butterflyfish distributions such as those done for other fishes (Hixon, 1980; Larson, 1980; Williams, 1980).

At present, territoriality among chaetodontids is generally considered to be uncommon (Ehrlich et al., 1977). Reese (1975) reported very low levels of intraspecific aggression among Pacific chaetodontids in the field and classified only two species, *C. trifascialis* (=*Megaprotodon strigangulus*) and *C. baronessa* (=*C. triangulum*), of approximately 20 as territorial. Both of these fishes were obligate coral feeders and defended their food resources. The majority of the remaining species were classified as "home ranging" based primarily on the lack of overt defensive behaviors used to defend territory boundaries. Among these "home ranging" species in Hawaii are the territorial coral feeders *C. quadrimaculatus* (T. Hourigan, pers. comm.) and *C. multicinctus*. In stable communities, these two species show low levels of overt aggression but maintain well-defined territory borders against conspecifics. *C. multicinctus* spends less than 5% of its time budget in territorial defense (Tricas, ms). Furthermore, the data in Table 4 indicate that one agonistic interaction occurred approximately every 20 minutes, and the more easily detected overt chases occurred on average only once every 34 minutes. Thus, it would be very easy to conclude that species with such low levels of aggression are not defending a territory. Future studies must provide detailed analyses of the patterns of spatial use, activity budgets, and estimate the temporal stability of home ranges.

The high number of attacks on *C. multicinctus* by other species that reside within the territory have a negligible influence on the maintenance of its own territorial boundaries. Therefore, the costs associated with territorial defense are not a direct function of the total number of agonistic interactions with other species, but are considerably less. For example, most agonistic interactions with the corallivorous damselfish, *Plectroglyphidodon johnstonianus*, involved chases directed against *C. multicinctus* in the defense of only a small portion of coral heads within the butterflyfish's territory (< 1% total area). Similarly, of 130 agonistic interactions with the herbivorous damselfish, *Stegastes fasciolatus*, only 10 involved chases initiated by *C. multicinctus*. These high levels of aggression probably function to protect nest sites (in addition to food resources) since *C. multicinctus* is an opportunistic egg predator on nests of the damselfish, *Abudefduf abdominalis*.

Adult *C. multicinctus* spend considerable time chasing coral-feeding juvenile chaetodontids that have recently settled within their territories. Attempts to evict small juveniles are usually unsuccessful, however, because of the inability of adults to pursue them into the reef interstices. As juveniles grow their ability to refuge within the territory abates, and they are eventually driven out. As a result, subadult pairs will often establish territories in suboptimal areas or between existing territories. The selective advantage of driving off coral-feeding juveniles may be to protect food resources and insure future territorial sovereignty. Similar accounts of spatial refuging within the territories of adults were observed among *C. trifascialis* and *C. ornatissimus* (Reese, pers. comm.) and damselfishes (Doherty, 1983).

An important function of the conspicuous color pattern of *Chaetodon multicinctus* is to advertise their presence to neighbors and inhibit territory intrusions. Residents vigorously attack both living and dead bottled conspecifics placed within their territories (Tricas, ms) which emphasizes the importance of color patterns to intra-specific recognition. The maintenance of well-defined territory borders in conjunction with low levels of intraspecific aggression supports the postulate that an advertisement strategy with occasional aggressive reinforcement can greatly reduce the cost of territorial defense. When intraspecific confrontations do occur, the response of *C. multicinctus* territory holders to intruders is well described by Lorenz's (1966) original observation as, "...furious reactions of territorial defence in every fish of the same species". While the proximate function of intraspecific aggression among territorial butterflyfishes like *C. multicinctus* is best explained in terms of resource defense, a clear result is the even patterns of distribution of the species as originally conjectured by Lorenz. Hence, the apparent paradox of territoriality in the absence of high levels of overt defense is resolved for *C. multicinctus*, but remains to be tested among the variety of other coral feeding butterflyfishes.

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REFERENCES

Anderson G.V.R., A.H. Erhlich, P.R. Erhlich, B.C. Russell, and F.H. Talbot, 1981. The community structure of coral reef fishes. *Am. Nat.* 117:476-495.

Bagenal T.B., 1966. The relationship between food supply and fecundity in brown trout *Salmo trutta* L. *J. Fish Biol.* 1:167-182.

Barlow G.W., 1974. Contrasts in social behavior between Central American cichlid fishes and coral-reef surgeon fishes. *Amer. Zool.* 14:9-

34.

Birkeland, C. and S. Neudecker, 1981. Foraging behavior of two Caribbean chaetodontids: *Chaetodon capistratus* and *Chaetodon aculeatus.* Copeia 1981 (1):169-178.

Bouchon-Navaro Y., 1981. Quantitative distribution of the Chaetodontidae on a reef of Moorea Island (French Polynesia). *J. exp. mar. biol. ecol.* 55:145-157.

Branham J.M., S.A. Reed, J.H. Bailey, and J. Caperon, 1971. Coral-eating sea stars *Acanthaster* in Hawaii. *Science* 172:1155-1157.

Brown J.L., 1964. The evolution of diversity in avian territorial systems. *Wilson Bull.* 76:160-169.

Burgess W.E., 1978. Butterflyfishes of the world. T.F.H. Publ., Neptune City, New Jersey. 832 pp.

Coll J.C., S. LaBarre, P.W. Sammarco, W.T. Williams and G.J. Bakus, 1982. Chemical defences in soft corals (Coelenterata: Octocorallia) of the Great Barrier Reef: A Study of comparative toxicities. *Mar. Ecol. Prog. Ser.* 8:271-278.

Constantz G.D., 1975. Behavioral ecology of mating in the male gila topminnow, *Poeciliopsis occidentalis* (Cyprinodontiformes: *Poeciliidae*). *Ecology* 56:966-973.

Cox E.F., 1983. Aspects of corallivory by *Chaetodon unimaculatus* in Kaneohe Bay, Oahu. M.S. Thesis, University of Hawaii.

Doherty P.J., 1983. Tropical territorial damselfishes: is density limited by aggression or recruitment? *Ecology.* 64(1):176-190.

Dollar S.J., 1982. Wave stress in coral community structure in Hawaii. *Coral Reefs* 1:71-81.

Ehrlich P.R., F.H. Talbot, B.C. Russell and G.R.V. Anderson, 1977. The behaviour of chaetodontid fishes with special reference to Lorenz's "poster colouration" hypothesis. *J. Zool., Lond.* 183:213-228.

Gosline, W. A., 1965. Thoughts on systematic work in outlying areas. *Syst. Zool.* 14:59-61.

Hayes T.A., T.F. Hourigan, S.C. Jazwinski, Jr., S.R. Johnson, J.D. Parrish, and D.J. Walsh, 1982. The coastal resources, fisheries and fishery ecology of Puako, West Hawaii. Haw. Coop. Fish. Unit Tech. Rept. 82-1. 159 pp. + appendix.

Hixon M.A., 1980. Competitive interactions between California reef fishes of the genus *Embiotoca. Ecology* 61:918-931.

Hirschfield M.F., 1980. An experimental analysis of reproductive effort and cost in the Japanese medaka *Oryzias latipes. Ecology* 61:282-292.

Horn H.S., 1968. The adaptive significance of colonial nesting in the brewer's blackbird, (*Euphagus cyanocephalus*). *Ecology* 49:682-694.

Jenkins T.M., 1969. Social structure, position choice and microdistribution of two trout species (*Salmo trutta* and *Salmo gairdneri*) resident in mountain streams. *Anim. Beh. Monogr.* 2:57-123.

Kaufman L.S., 1977. The three-spot damselfish: effects on benthic biota of Caribbean coral reefs. Proc. 3rd Int. Coral Reef Symp. 1:559-564.

Kodric-Brown A., 1977. Reproductive success and the evolution of breeding territories in pupfish (*Cyprinodon*). *Evolution* 31:750-766.

Larson R.J., 1980. Influence of territoriality on adult density in two rockfishes of the genus *Sebastes. Mar. Biol.* 58:123-132.

Lorenz K., 1966. On aggression. Harcourt, Brace, and World Inc. 306 pp.

Low R.M., 1971. Interspecific territoriality in a pomacentrid reef fish *Pomacentrus flavicauda* Whitley. *Ecology* 52:648-654.

Motta P., 1980. Functional anatomy of the jaw apparatus and the related feeding behavior of the butterflyfishes (Chaetodontidae) including a review of jaw protrusion in fishes. Ph.D. Thesis, University of Hawaii. 435 pp.

Myrberg A.A. Jr. and R.E. Thresher, 1974. Interspecific aggression and its relevance to the concept of territoriality in reef fishes. *Amer. Zool.* 14:81-96.

Neudecker S., 1977. Transplant experiments to test the effect of fish grazing on coral distribution. Proc. 3rd Int. Coral Reef Symp. 1:317-323.

Neudecker S., 1979. Effects of grazing and browsing fishes on the zonation of corals in Guam. *Ecology* 60:666-672.

Orians G.H., 1961. Social stimulation within blackbird colonies. *Condor* 63:330-337.

Paine R.T., 1966. Endothermy in bomb calorimetry. *Limnol. Oceanogr.* 11:126-129.

Phillipson J., 1964. A miniature bomb calorimeter for small biological samples. *Oikos* 15:130-139.

Potts D.C., 1977. Supression of coral populations by filamentous algae within damselfish territories. *J. Exp. Mar. Biol. Ecol.* 28:207-216.

Reese E.S., 1975. A comparative field study of the social behavior and related ecology of reef fishes of the family Chaetodontidae. *Z. Tierpsychol.* 37:37-61.

Reese E.S., 1977. Coevolution of corals and coral feeding fishes of the family Chaetodontidae. 3rd Int. Coral Reef Symp. 1:267-274.

Reese E.S., 1981. Predation on corals by fishes of the family Chaetodontidae: implications for conservation and management of coral reef systems. *Bull. Mar. Sci.* 31:594-604.

Richmond R.A., 1982. Energetic considerations in the dispersal of *Pocillopora damicornis* (Linnaeus) planulae. Proc. 4th Int. Coral Reef Symp. 2:153-156.

Robertson D.R., 1984. Cohabitation of competing territorial damselfishes on a Caribbean coral reef. *Ecology* 65:1121-1135.

Roberston D.R., N.V.C. Polunin, and K. Leighton., 1979. The behavioral ecology of three Indian Ocean surgeonfishes (*Acanthurus lineatus*, *A. leucosternon*, and *Zebrasoma scopas*): their feeding strategies, and social and mating systems. *Env. Biol. Fish.* 4:125-170.

Sale P.F., 1978. Reef fishes and other vertebrates: a comparison of social structures. *In*: E. S. Reese and F. J. Lighter (eds.). Contrasts in behavior. John Wiley, New York.

Tyler A.V. and R.S. Dunn, 1976. Ration, growth, and measures of somatic and organ condition in relation to meal frequency in winter flounder, *Pseudopleuronectes americanus*, with hypotheses regarding population homeostasis. *J. Fish. Res. Bd. Can.* 33:63-75.

Wellington G.M., 1982. Depth zonation of corals in the Gulf of Panama: control and facilitation by resident reef fishes. *Ecol. Monogr.* 52:223-241.

Williams G.C., 1966. Adaptation and natural selection. Princeton Univ. Press, Princeton, New Jersey. 307 pp.

Williams D.McB., 1980. Dynamics of the pomacentrid community on small patch reefs in One Tree Lagoon (Great Barrier Reef). *Bull. Mar. Sci.* 30:159-170.