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The behavioral ecology of three species of butterflyfishes (family Chaetodontidae)

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University of Hawaii, 1987

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THE BEHAVIORAL ECOLOGY OF THREE SPECIES OF BUTTERFLYFISHES
(FAMILY CHAETODONTIDAE)

A DISSERTATION SUBMITTED TO THE GRADUATE DIVISION OF THE
UNIVERSITY OF HAWAII IN PARTIAL FULFILLMENT
OF THE REQUIREMENTS FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY IN ZOOLOGY

DECEMBER 1987

BY

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This work is dedicated to my mother, Hazel, K. Hourigan,

whose love and encouragement have made all the difference.

ACKNOWLEDGMENTS

I would like to thank the following persons and institutions, without whose generous help and support this dissertation would not have been possible:

The field work presented in this dissertation required many long hours of underwater observation and the collection of many samples, and I would like to thank: Bruce Carlson, Therese Hayes, Robin Hori, Stan Jazwinski, Scott Johnson, Chris Kelley, Phil Motta, Ernie Reese, S. Laurie Sanderson, Frank Stanton, Tim Tricas, Bill Tyler, and Dave Walsh. Special thanks to the many Earthwatch Vollunteers, who spent long hours underwater watching butterflyfishes.

My dissertation has benefited discussions with many researchers and fellow gaduate students, and from their critical comments on this manuscript and other papers. In this respect, I would like to thank: Dave Booth, Bruce Carlson, Sybil Carrere, Tom Clarke, Jared Cook, Fenny Cox, Lev Fishelson, Lenny Freed, Gordon Grau, Mike Hadfield, Mark Hixon, Ron Johnson, Sid Kraul, George Losey, Marv Lutnesky, Mike Michael, Phil Motta, Jim Parrish, Steve Ralston, Ernie Reese, Bob Ross, D. Ross Robertson, Peter Sale, Jim Stretch, John Stimson, Teresa Telecky, Tim Tricas, Bill Tyler, and Bill Walsh. Sue Nakamura assisted with the preparation of many of the figures. Ernie Reese provided support, encouragement and inspiration throughout the study.

Financial support was provided by the Center for Field Research, Hawaii Institute of Marine Biology, National Science Foundation, H.H. Kroesen Foundation, and Coral Reef Foundation.

ABSTRACT

This dissertation examines the behavioral ecology of Hawaiian butterflyfishes (family: Chaetodontidae), with particular emphasis on their community ecology, feeding behavior and social systems. Among terrestrial vertebrates, food resources have been shown to be important determinants of the distribution and behavior of individuals, and thereby of their mating systems and community structure. The present research indicates that food resources, especially reliance on coral tissue as a major source of energy has contributed to the unique patterns of distribution and mating systems shown by butterflyfishes.

The distribution and abundance of butterflyfishes was investigated over a four year period on leeward reefs of the Island of Hawaii. The distribution of both planktivorous and corallivorous butterflyfishes is related to the distribution of food resources. Planktivores congregate at the edges of reefs where plankton first reaches the reef. All corallivorous butterflyfishes prefer to feed on the same coral species, but some butterflyfishes specialize on certain corals, while other species are generalist, feeding on nearly all corals. The distribution of coral feeding butterflyfishes is correlated with the distribution of preferred food corals, not total coral cover. Field removal experiments showed that the number of breeding pairs of two abundant species, _C. multicinctus_ and _C. quadrimaculatus_ is limited by intraspecific territoriality, whereas the numbers of less abundant species appear to be limited by low larval recruitment.

Three species, *C. multicinctus*, *C. quadrimaculatus*, and *C. fremblii* were chosen to examine the feeding behavior, energetics and ecology in relation to mating systems. Adults of both *C. multicinctus* and *C. quadrimaculatus* form long lasting monogamous pairs which defend feeding territories from members of their own species. *Chaetodon multicinctus* feeds on corals, with preferences for those species which are most energetically profitable. The second species, *C. quadrimaculatus* feeds only on the most profitable coral, *Pocillopora meandrina* but supplements its diet with algae and non-coralline invertebrates. Both species show differences in feeding behavior and food choice among different sexes and age classes. In addition, food choice by individuals changes at different times of the day. *C. quadrimaculatus* exhibits a unique lunar rhythm to feeding: feeding on the lunar day rather than the solar day. This rhythm can change to nocturnal feeding in areas where diurnal feeding is restricted by the attacks of territorial pomacentrids. Male *C. fremblii* defend harems containing one to four individual female feeding territories. Energy budgets of each species indicate that female reproduction, particularly for the paired, corallivorous species, is limited by feeding time.

Females which form pair-bonds benefit by increased feeding. This occurs by a division of labor whereby males contribute disproportionately to the defense of the feeding territory. When a

male pair-mate is removed, female feeding rates and territory size decrease. In contrast, no such decrease occurs in male feeding rates and territory size when the female pair-mate is removed. Females in the haremic species receive no such advantages. The increased efficiency of energy absorption from the diet of C. fremblii frees males from assisting females, and evidently allows the defense of more than one female leading to harem polygyny.

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CHAPTER I

INTRODUCTION: MATING SYSTEMS OF REEF FISHES

The spatial and temporal association of males and females, and how they mate determine the mating systems of animals. Mating systems result from sum of the interactions of individual male and female behaviors. These behaviors may be considered adaptations to the environment as individuals compete with members of their own sex for genetic representation in the following generations (e.g. Maynard-Smith 1977; Wrangham and Rubenstein 1986). The observed mating system is a compromise of optimal strategies of individuals of each sex, given the constraints of the environment and of the phylogeny of the species.

Coral reef fishes form the most diverse of vertebrate assemblages, and this diversity is reflected in their social and mating systems. These fishes exhibit practically every mating system found in terrestrial vertebrates, as well as several which are unique to fishes (Warner 1978). Thus there are monogamous fishes with parental care (e.g. gobies: Lassig 1976, 1977; damselfishes of the genus Amphiprion: Fricke 1974; Moyer and Bell 1976; Moyer and Nakazono 1978a; and Acanthochromis polyacanthus: Thresher 1984) and without parental care (butterflyfishes: Reese 1975; Hourigan 1984; and angelfishes: Moyer et al. 1983); haremic systems with male parental care (e.g. damselfishes of the genus Dascyllus: Fricke and Holtzberg 1974; Fricke 1977, 1980a; and gobies: Lassig 1976; 1977), with female parental care (sharp nosed puffers: Kobayashi 1986; triggerfishes: Fricke 1980b; Thresher 1984), and without parental care (e.g. wrasses: Robertson 1972; Nakazono and Tsukahara 1974; Warner and Robertson 1978, Nakazono 1979; Tribble 1982; Warner 1984; parrotfishes: Choat and Robertson 1975; Robertson and Warner 1978; boxfishes: Moyer 1979; and angelfishes: Moyer and Nakazono 1978b, Hourigan and Kelley 1985); lek-like mating systems (reviewed by Loiselle and Barlow 1978; Moyer and Yogo 1984); apparently promiscuous mating by one or more fishes (Thresher 1984) and group spawning events (Johannes 1978; Thresher 1984). This diversity is compounded by the occurrence of more than one mating strategy or social organization within the same species (Warner 1984). In addition, fishes show a range of reproductive options unavailable to terrestrial vertebrates, including simultaneous and sequential hermaphroditism, exclusive paternal care and pelagic dispersal of eggs and larvae. The reproduction of haremic and monogamous reef fishes is reviewed Kuwamura (1984) and Barlow (1984, 1986) respectively, while a more general review of reproduction in reef fishes is provided by Thresher (1984).

Life history characteristics of reef fishes.

The mating systems of reef fishes, compared to their terrestrial counterparts, reflect fundamental differences in life history strategies. Coral reef fishes are characterized by moderately sedentary and long-lived adults with young which disperse widely. Tropical marine fishes typically produce hundreds, to hundreds of thousands of externally fertilized zygotes at frequent intervals over an extended breeding season of many months. Most spawn pelagic eggs which are fertilized in the water column and dispersed by currents. With only one exception (Acanthochromis polyacanthus), species with demersal eggs also retain a planktonic larval stage. This planktonic dispersal stage reduces the genetic isolation of populations (Hourigan and Reese 1987), and precludes extended parental care and probably kin selection. These factors should make the environmental constraints on fish social systems clearer (Thresher 1977; Barlow 1984), making reef fishes ideal model systems for tests of sociobiological theory.

The life history strategy of pelagic larvae with high dispersal capabilities has major adaptive consequences. Larval dispersal serves to remove larvae from the predator-rich environment of the reef (Johannes 1978). It may also be adaptive to permit dispersal of the young to find either suitable pelagic environments for larval growth (Doherty et al. 1985) or suitable reef habitats for adult survival (Barlow 1982). Because of the high degree of unpredictable mortality suffered by larvae, there is selection for high fecundity spread over time, to maximize the chance that some larvae will successfully return to the reef (Murphy 1968). Most reef fishes breed repeatedly, and most live at least several years with many living much longer. Thus, adaptations of adults, especially in terms of survival and resource use, which increase the chances of producing additional clutches will be favored. These adaptations may be in the nature of generalist traits rather than specializations to local conditions, since dispersal will disrupt local coadapted gene complexes (Strathmann 1986).

Mating systems will reflect the adaptations of males and females to increase the number of successful larvae which recruit back to reefs. Factors which will affect this success include the sources of mortality acting on adults, juveniles, and larvae; and the density, variability and predictability of resources (such as food, shelter and mates) in time and space. These factors, in turn, will affect intraspecific competition within and between sexes, and interspecific competition for limiting resources. Environmental or social factors which affect males and females differently are of special importance to the understanding of mating systems.

Environmental factors affecting male and female associations.

A. Sources of mortality and their effects.

Predation is probably the major source of mortality for fishes after they recruit to reefs (Hobson 1978; Sale 1980). Other sources of mortality are poorly understood or less general in their action. Coral reefs are less affected by environmental extremes than are temperate marine environments, or freshwater and terrestrial environments. However, fishes living in the intertidal zone, or fishes exposed to occasional strong storms, may experience high or unpredictable levels of mortality from physical forces (Walsh 1983). Other types of mortality, such as starvation, will be mediated through limiting resources, and will be dealt with below. Most fish mortality occurs during the planktonic dispersal stage, but the factors involved are poorly understood.

Mortality may influence mating systems in several ways (Warner 1980):

1. Low or variable juvenile survival and/or high or constant adult survival should select for low reproductive effort and iteroparity (Murphy 1968; Charnov and Schaffer 1973). This will affect the sexes differently if there is differential investment in reproduction, as is the case for most fishes.

2. Predation pressure may limit movement of animals to certain sheltered areas. If shelters are small, this will favor monogamy (e.g. gobies: Lassig 1977) and protandry (e.g. anemonefishes: Moyer and Nakazono 1978a). In contrast, shelters or sheltered areas which are large enough for more than two fish (i.e. spatially aggregated shelters), will increase the environmental potential for polygyny (EPP sensu Emlen and Oring 1977). In some damselfishes of the genus Dascyllus one male is able to defend shelters necessary for more than one female, resulting in haremic polygyny (Fricke 1980a). Low predation pressure will enhance the defendability of a territory (Geist 1974), favoring an even distribution of females and a low EPP.

3. Predation will also affect group size. Fishes which must feed away from cover may form aggregations or schools to reduce the chances of predation on individuals (Hamilton 1971; Pitcher 1986). If groups are small (e.g. Anthias: Shapiro 1979) polygyny may be selected. As group

size increases, individual males will have less control over mating by females, and group spawning may be favored (Ralston 1981).

4. Predation may affect males and females differently if mating strategies require one sex to be more conspicuous than the other. Predation rates may be higher for males courting females or defending demersal eggs. Since most fish predators consume fish whole, larger fishes may be expected to be less subject to predation than smaller fishes (Hobson 1978; Shulman 1985a). This will result in different size classes of individuals within or between sexes having differential mortality, which may act as a constraint on possible mating options. In general, species which reach larger sizes or are less subject to predation due to body shape or antipredator defenses, will experience different constraints on their mating systems than do smaller, unprotected fishes.

5. Predation on eggs may cause the aggregation of fishes around preferred spawning areas, or colonial nesting for demersal spawners. The restriction of males to a nest or spawning territory will reduce the potential for males to defend or sequester mates. If predation on eggs varies predictably over time, spawning synchrony or asynchrony may be favored, to avoid the time when predators are feeding, or to swamp predators, or reduce the chances of predators aggregating. Spawning synchrony will reduce the operational sex ratio and thereby the EPP. Other sources of mortality on eggs or larvae may also favor a degree of spawning synchrony.

6. Finally, high mortality of either adults (Talbot et al. 1978) or juveniles (Doherty 1981, 1983) may reduce population densities below the level where other resources such as food or shelters are limiting.

B. Limiting resources.

The effects of resources on mating systems will vary depending on their density, variability and predictability in space and time (Warner 1980). The distribution of resources necessary for fish will determine the distribution of fish. This may result in the temporary or permanent association of fish, and will affect group size and the defendability of mates. If resources necessary for the limiting sex (usually females) are clumped in space, this may allow males to monopolize more than one female, or resources necessary for more than one female, resulting in polygyny (Emlen and Oring 1977).

Shelters are often considered to be limiting resources for fishes (Lassig 1977; Fricke 1980a; Reviewed by Walsh 1984). These are generally considered to act as refuges from predators. Competition for shelters and consistent use of the same shelters has been shown by several authors (Robertson and Sheldon 1979; Walsh 1984; Shulman 1985a; see also Chapter II), but most experimental manipulations have failed to show that shelters are limiting for adults (Robertson and Sheldon 1979; Sale 1980). Nevertheless, if shelters are unevenly distributed, this may lead to an uneven distribution of females which may allow males to monopolize more than one female (e.g. *Dascyllus*: Fricke 1980a).

Preferred spawning or nesting sites may also be limiting for reef fishes. For broadcast spawning fishes, such sites are are often along the leeward edge of reefs where eggs may be carried away from the reef (Johannes 1978). If preferred spawning areas are limited and defendable, this may favor lek-like mating systems where large males control access to these spawning areas as occurs in many wrasses (Loiselle and Barlow 1978). If preferred nesting sites for demersal spawners are limiting, then some males may mate with more than one female. This may have led to the evolution of male parental care (Baylis 1981). This in turn may allow females a greater latitude of mate choice, and opportunities to deposit eggs in the nests of more than one male.

Finally, food resources may limit the reproductive success of individuals. At one level, food resources are necessary for survival to reproductive age. In addition, increased food ration should result in increased reproductive output (Luquet and Watanabe 1986; other references in Chapter V). This should be especially important for all females, since increased food ration is correlated with increased fecundity (Bagenal 1966; Hirshfield 1980) or increased numbers of clutches within a breeding season (Wootton 1977, 1985) in many species. Food resources may also limit reproduction of males where sperm competition is important, as when males spawn in groups with other males. The effects of food limitation on the reproductive success of males has rarely been investigated (Luquet and Watanabe 1986).

Grouping by females and the extent to which males can defend these groups depend on the variability, density and predictability of food resources in time and space.

1. Food resources are aggregated (i.e. clumped or patchy) in space, their locations are predictable, and their availability is stable in time (i.e. of long duration relative to the life cycle of the fish).

If food patches are small, only one fish is able to defend a single patch of food resource. The mating system will depend the distribution of males and females on patches, the ease of movement between patches, and whether the male, or the female, or neither is restricted to the patch by providing parental care. An example of this type of mating system may be the butterflyfish, _Chaetodon trifascialis_, in which individual fish defend heads of coral of the genus _Acropora_. Another example would be damselfishes of the genus _Stegastes_ in which individuals defend small but highly productive algal mats.

If defendable patches are large enough for two fish, heterosexual pairs may be favored. Although such pairs are associated with intermediate size shelters, I am not aware of any examples of pair defense of patchy food resources. Such defense is known among invertebrates (e.g. the starfish-killing shrimp, _Hymenocera picta_: Wickler and Seibt 1970).

As patches become still larger, groups of females may be associated with them. If groups are small, one male may be able to defend more than one female, resulting in harems. This may occur in the wrasses *Labroides dimidiatus* on the Great Barrier Reef (Robertson 1972) and *Halichoeres maculpinna* in Florida (Thresher 1979), although food limitation has not been demonstrated. Both species show different mating patterns in other areas, or patterns which have been interpreted differently. Kuwamura (1984) found no evidence that distributions of female *Labroides dimidiatus* in Japan depend on clumped food resources, and Warner and Robertson (1978) found that *Halichoeres maculpinna* form leks at many sites in the Caribbean.

If food resources are very abundant, densities of fish may be high, and groups may become larger than can be defended by a single male. This may result in groups with dominance hierarchies and multiple males as occurs in the serranid *Anthias squamipinnus* (Shapiro 1978). At still larger densities, group spawning may result (e.g. *Chaetodon miliaris*, Ralston 1981).

2. Food resources are aggregated (i.e. clumped or patchy) in space, but their occurrence in space and time are unpredictable. This is generally the case for plankton.

Food resources under these conditions are not defendable. If resource densities are low, individual fish may be forced to wander over large areas. This might favor heterosexual pair-bonds or simultaneous hermaphroditism, to insure the availability of a mate for spawning.

With increasing densities of food resources, foraging groups may best exploit the ephemeral occurrence of food patches. Individual males may be able to defend small groups of females, although this defense would likely be less effective than in cases where ther was defense of permanent territories. At still higher densities, heterosexual groups and group spawning are expected. This appears to be the case among most larger planktivores.

3. Food resources are evenly distributed in space (i.e. not aggregated), their locations are predictable, and their availability is stable in time.

At low densities, food resources are not defendable, and fish should inhabit large, undefended home ranges. They should travel either as individuals, pairs or groups depending on which association forages most efficiently, or offers the most benefits in terms of protection from predators or access to mates. Group size may vary over hours, days or seasons.

At higher food densities, it becomes advantageous to defend a territory against conspecifics. Whether this territory is defended by the female alone, or by a heterospecific pair is dealt with in Chapter Eight. Both cases are observed among butterflyfishes. At the highest resource levels, it becomes advantageous to defend smaller, interspecific territories, and the situation approaches that of single fish defending a single patch of high quality food resource (e.g. damselfishes of the genus _Stegastes_: Low 1971; Myrberg and Thresher 1974; and others) or a dominant acanthurid, _Acanthurus lineatus_: Robertson et al. 1979; Robertson and Gaines 1986).

In addition to determining group size, food resources can act to allow or restrict grouping for other reasons. Therefore, grouping may occur for reasons other than clumped food resources, as long as the cost do not outweigh the benefits. Thus many large fishes with feeding territories, leave these to spawn at leks, and are still able to return and reclaim their territories (Robertson et al. 1979). The costs of this behavior may be greater for a small fish which might loose its territory or suffer predation.

In general, although food resources are often invoked as determinants of fish mating systems, there have been few tests of these assumptions.

Social systems of butterflyfishes.

Butterflyfishes of the family Chaetodontidae are conspicuous inhabitants of tropical coral reefs (Burgess 1978; Allen 1979). They show a diversity of food habits (Hobson 1974; Reese 1975; Motta 1985), which are often correlated with their social system (Reese 1975). They are exceptional in that many species exhibit apparently monogamous pair-bonds of long duration (Bascheri-Salvadori 1954; Bardach 1958; Lorenz 1962; Fricke 1973, 1986; Reese 1973, 1975, 1981; Steen 1978; Allen 1979; Neudecker and Lobel 1982; Tricas 1985, 1986; Hourigan et al. 1987). Monogamy among freshwater fishes and terrestrial vertebrates is usually associated with biparental care (Williams 1966; Wilson 1975; Barlow 1984). Butterflyfishes spawn pelagic eggs, precluding all parental care.

In this dissertation I examine the ecological constraints on butterflyfish social systems, with special emphasis on the occurrence of heterosexual (male-female) pair-bonds and monogamy. Two complementary approaches are utilized. First, insights into the ultimate environmental factors which have led to the evolution of specific male and female behaviors may be gained by observing the short-term, proximate responses to different ecological constraints (e.g. resource distributions in time and space, and responses to experimental manipulations of resources). This is a case of reasoning by analogy, and there is no assurance that the proximate responses reflect the ultimate causes. A second method is comparative: closely related species with different social systems are assumed to have diverged in response to different environmental pressures. Comparisons of the social behavior and related ecology of these species should therefore provide information on these pressures. This second method is particularly important when the behaviors in question show a degree of invariance within species.

Based on preliminary observations on one species which forms heterosexual pair-bonds: the fourspot butterflyfish, _Chaetodon quadrimaculatus_, an _a priori_ hypothesis on the adaptive significance of pair bonding and monogamy in butterflyfishes was proposed:

> Pair-bonding and monogamy are of selective advantage to both sexes, because fecundity is food limited, and pairing increases the fecundity of females, and enables the male pair-mate to share in the benefits of this increased fecundity.

Tests of predictions from the hypothesis were conducted on: 1) C. quadrimaculatus, 2) a second pair-bonded species, the banded butterflyfish, Chaetodon multicinctus and 3) the closely related bluestripe butterflyfish, Chaetodon fremblii, which did not appear to form pairs (Reese 1975). I have chosen to present the material as a series of chapters which comprise the observational and experimental background for the species in question, with the hypothesis and its tests presented in the final chapter.

Chapter Two presents a survey of the butterflyfish assemblage on coral reefs at Puako, on the Island of Hawaii. The purpose is to investigate major trends in the distribution of butterflyfishes with respect to food and shelter resources, predation, and intra- and interspecific competition. The results allowed comparisons of the patterns in distribution and abundance of butterflyfishes to the predictions of three major hypotheses concerning the structuring of reef fish assemblages.

Results from the surveys of butterflyfishes indicated that food resources were likely limiting the numbers of breeding adults of at least two species, C. multicinctus and C. quadrimaculatus. Chapter Three presents a detailed analysis of the feeding behavior and use of space by these two species. Special emphasis is placed upon different feeding strategies of males and females, since these differences relate directly to hypotheses concerning the relationship between feeding behavior and social strategies. Chapter Four investigates the feeding and space related behavior of Chaetodon fremblii a haremic butterflyfish. A series of food reduction and mate removal experiments reveal the fine structure of a haremic social system unlike that of most terrestrial vertebrates or other fishes.

Many sociobiological models are implicitly energetic models, but the actual energy budgets of the animals in question are seldom if ever measured. As a result of anisogamy (unequal investment in gametes between the sexes), reproductive success of females is generally assumed to be resource (often energy) limited. Male reproduction is assumed to be limited primarily by the number of females with which he can mate. Chapter Five reports the results of a series of eight experiments conducted to determine the sexual differences in energy intake and assimilation efficiencies, and the partitioning of this energy among somatic, storage and reproductive tissues in the three species of butterflyfishes during different seasons of the year. The results of these experiments are compared to field observations of feeding and activity presented in the previous chapters.

Chapter Six presents a series of field experiments designed to investigate how pair bonds are formed in C. multicinctus and C. quadrimaculatus. Differences in the population structure of the two species affect the pairing process, and thereby, the entrance of new fishes into the breeding population. These experiments are primarily intended to test predictions of the hypothesis concerning pair-bonding in these fishes, and are similar to experiments conducted on the third species C. fremblii and reported in Chapter Four. Food reduction tests the effects of changes in food resources on male and female behavior, while mate removals test the contribution of each mate to the social unit (pair-bond).

In the final chapter my hypothesis on the adaptive significance of monogamy to butterflyfishes and other fishes without parental care is presented. It serves as a summary of the results of the previous chapters, and places them in the larger theoretical framework of the evolution of mating systems. Evidence from previous chapters is marshalled to support the assumptions and test the predictions of the hypothesis.

CHAPTER II

THE STRUCTURE OF THE CHAETODONTID ASSEMBLAGE AT PUAKO, HAWAII, WITH SPECIAL REFERENCE TO CORALLIVORES

INTRODUCTION

The pattern of distribution and abundance of species of fishes defines the structure of a fish assemblage. The great diversity of fishes on coral reefs provides a source of lively controversy concerning the mechanisms which underlie the observed structure of their assemblages. Three major theories have been proposed to explain the factors which structure reef fish assemblages. These are the Resource Limitation Hypothesis, the Lottery Hypothesis and the Non-Equilibrium Hypothesis.

The Resource Limitation Hypothesis is based on theory developed from terrestrial communities. It assumes that the number of individuals (i.e. population density) of each species in an assemblage is at or near the carrying capacity of the habitat, and is limited by the availability of resources (Mac Arthur 1972; Cody 1974). For reef fishes, the limiting resources are usually considered to be food or space (Sale 1980). If resources are stable over time, population densities of each species will also be stable. Species which exploit the same class of resources in a similar way can be classed as members of a guild (Root 1967). The resource limitation hypothesis assumes that coexisting species in the same guild are not equal competitors for the same limiting resources, and either specialize on different resources (resource partitioning), or the inferior competitor is excluded (habitat partitioning). Guilds of fishes are predicted to have stable and predictable compositions given resource stability, summing to a predictable assemblage. This view of reef fish assemblages has been proposed by several authors (Smith and Tyler 1972, 1973; Smith 1978; Gladfelter and Gladfelter 1978; Molles 1978; Brock et al. 1979; Anderson et al. 1981; Ogden and Ebersole 1981). Ross (1986) reviewed the literature on resource partitioning in fish assemblages. He found evidence for substantial differences in habitat and microhabitat use (54% of all species studied) and size and kind of food (64% of all species) among fishes in 20 studies of fish assemblages. Few of these studies included field experiments to determine if the observed differences in resource use were a response to competition.

In a series of papers, Sale (1974, 1977, 1978) and Sale and Dybdahl (1975, 1978) argued that there was little evidence for stable compositions of reef fish assemblages, and proposed the "Lottery Hypothesis" as an alternative. This hypothesis also assumes that space is limiting. Guild members however have similar spatial requirements and are assumed to be equal competitors for space. When an individual dies, the open space is filled by the first individual of any species in the guild to recruit to this space. Once an individual has settled in a space, it can defend this area against other fishes. Thus, the assemblage of fishes is a function of the composition of the larval pool, and the rate at which new spaces became available, rather than being internally regulated.

Doherty (1981, 1982, 1983) proposed a non-equilibrium hypothesis in which the population densities of species on a reef remain well below the levels where resources would be limiting. This may occur when larval recruitment is inadequate for populations to reach the carrying capacity of the habitat. This type of recruitment limitation is shown by some temperate fishes (Stephens and Zerba 1981). A similar non-equilibrium model was proposed by Sale and Douglas (1984) and Sale and Steel (1986), in which the observed structure of an assemblage is determined solely by the chance of an individual recruiting and surviving on a reef, uninfluenced by the fishes already present in the assemblage. Alternately, population densities below the carrying capacity of the habitat may result from high levels of post-recruitment mortality due to predation (Talbot et al. 1978) or to other disturbances. Doherty (1981, 1983) presented convincing experimental evidence that populations of two damselfishes on lagoonal patch reefs were indeed recruitment limited, and mortality was independent of resource limitation or intra- and inter-specific competition. Neither space nor food appeared to be limiting. Sale (1980) reviewed the literature, and found few convincing cases in which either food or space appeared to limit population densities of coral reef fishes.

The mechanisms underlying the structure of an assemblage may be most clearly seen in the analysis of individual populations which compose the assemblage. This "mechanistic" approach to community ecology has been adopted by a growing number of researchers (reviewed by Schoener 1986). The manner in which individuals of different species are recruited to reefs and respond to competitors, predators and resources may differ. The sum of these processes will determine the observed assemblage structure. Phylogenetically related species may show the most similarities in these processes (Ross 1986). Related species in the same guild are also most likely to be in competition for resources (Root 1967; Mac Arthur 1972). The most extensive studies of reef fish guilds have been conducted on damselfishes of the family pomacentridae (Emery 1973; Itzkowitz 1977; Sale 1976, 1977, 1978; Robertson & Lassig 1980; Williams 1980; Waldner and Robertson 1980; Robertson et al. 1981; Robertson 1984; Ebersole 1985). Damselfishes are usually small, site attached, demersal spawning fishes, and may not provide a representative model for most reef fishes (Hourigan 1986a). These studies did not directly measure food availability, feeding preferences and use of space for these fishes. Such measurements are a necessary first step in a mechanistic approach to the study of an assemblage in order to identify possible limiting resources and competitive interactions. These observations can then serve as the basis of the controlled field experiments which are necessary to falsify one or more of the hypotheses (Schoener 1983).

Butterflyfishes (family Chaetodontidae) are conspicuous inhabitants of coral reefs throughout the world. They include the largest number of corallivores, and may thereby have an important impact on the corals themselves (Neudecker 1977, 1979; Reese 1977; Cox 1986). They are easily observed, and their patterns of distribution have been documented in Hawaii (Hobson 1974), the Caribbean (Clarke 1977), Australia's Great Barrier Reef (Anderson et al. 1981; Williams 1983, 1986), the Red Sea (Bouchon-Navaro 1979, 1986) and French Polynesia (Bouchon-Navaro 1981; Harmelin-Vivien and Bouchon-Navaro 1983; Bell and Galzin 1984; Bell et al. 1985; Bouchon-Navaro et al. 1985; Findley and Findley 1985). Their diets and feeding behavior have also been investigated (Hiatt and Strasburg 1960; Talbot 1965; Hobson 1974; Reese 1975, 1977; Ralston 1981; Motta 1980, 1985; Harmelin-Vivien and Bouchon-Navaro 1981, 1983; Birkeland and Neudecker 1981; Cox 1983, 1986; Gore 1984; Neudecker 1985; Tricas 1985, 1986; Bouchon-Navaro 1986; Hourigan et al. 1987; Hourigan Chapter III, IV).

The present study describes the structure of the chaetodontid assemblage in six contiguous habitats on Hawaiian reefs. The similarity of the same assemblages over time and the similarity of geographically separated assemblages in similar habitats are analyzed to determine the degree of temporal and spatial predictability of assemblage structure. The Resource Limitation Hypothesis, Lottery Hypothesis and Non-Equilibrium Hypothesis differ in the relative importance of larval recruitment, inter- and intraspecific interactions, and limited resources to the assemblage structure. To investigate the mechanisms underlying the observed structure, five factors were investigated: 1) The distribution and abundance of successful larval recruits; 2) The use of nocturnal shelters by butterflyfishes and their response to experimental removal of nocturnal shelters. 3) The abundance and behavior of potential competitors and predators; 4) The distribution of food resources, with special reference to corals, and the feeding behavior and food preferences of the coral-feeding chaetodontids; 5) The use and defense of space by butterflyfishes. These factors are compared to the observed patterns of distribution and abundance of chaetodontids and to the predictions of the three major hypotheses concerning the assemblage structure of reef fishes.

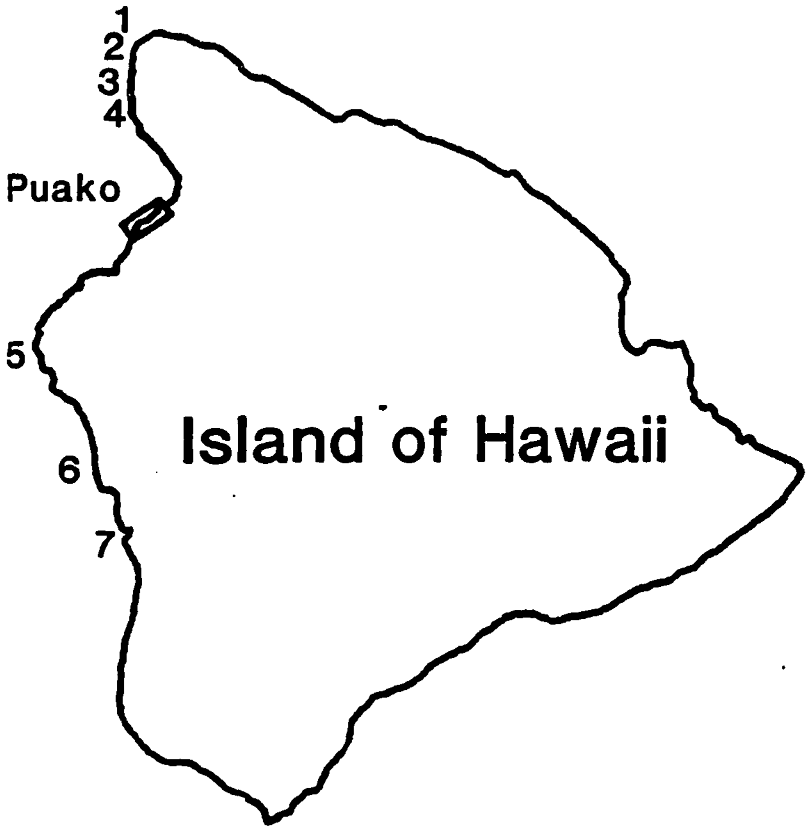
METHODS

Study sites:

The study was conducted by scuba divers on coral reefs along the leeward coast of the island of Hawaii (Fig. 2.1). Most fish censuses, observations and experiments were conducted at two sites (Sites A and B) on extensive fringing reefs at Puako, Hawaii. Sites A and B were separated by 6 km and large areas of sand, so that reef habitats were not continuous between the two areas. Within each site, six distinct but contiguous habitat zones were distinguished (Fig. 2.2): 1) a shallow surge zone; a shallow reef platform with both 2) shallow coral-rich and 3) shallow coral-poor areas; 4) a zone at the base of a cliff separating the shallow and deeper areas; 5) a deep coral-rich zone; and 6) a zone of interface between the reef and deeper sand areas. These habitat zones are described in Table 2.1 and in Hayes et al. (1982).

The structural characteristics of each habitat were measured as possible correlates to the structure of the chaetodontid assemblage. These characteristics were: 1) Depth at high and low tide; 2) Surge, classified qualitatively as low (little perceptible water motion), medium (diver is swept back and forth) and high (diver is unable to retain position, often accompanied by breaking surf); 3) Rugosity, a measure of topographic relief measured as the mean of the ratios of contour distance to linear distance (Luckhurst and Luckhurst 1978). Contour distance was measured by positioning a 5m chain to follow the contours of the reef as closely as possible. Within each habitat, 22

Figure 2.1. Locations of the study sites on the Island of Hawaii. Primary study sites (Sites A and B) were located at Puako. Other study sites are 1) Upolu Point; 2) Kapaa; 3) Mahukona; 4) Lapakahi; 5) Old Kona Airport; 6) South Kona; 7) Honaunau.


1
2
3
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Puako
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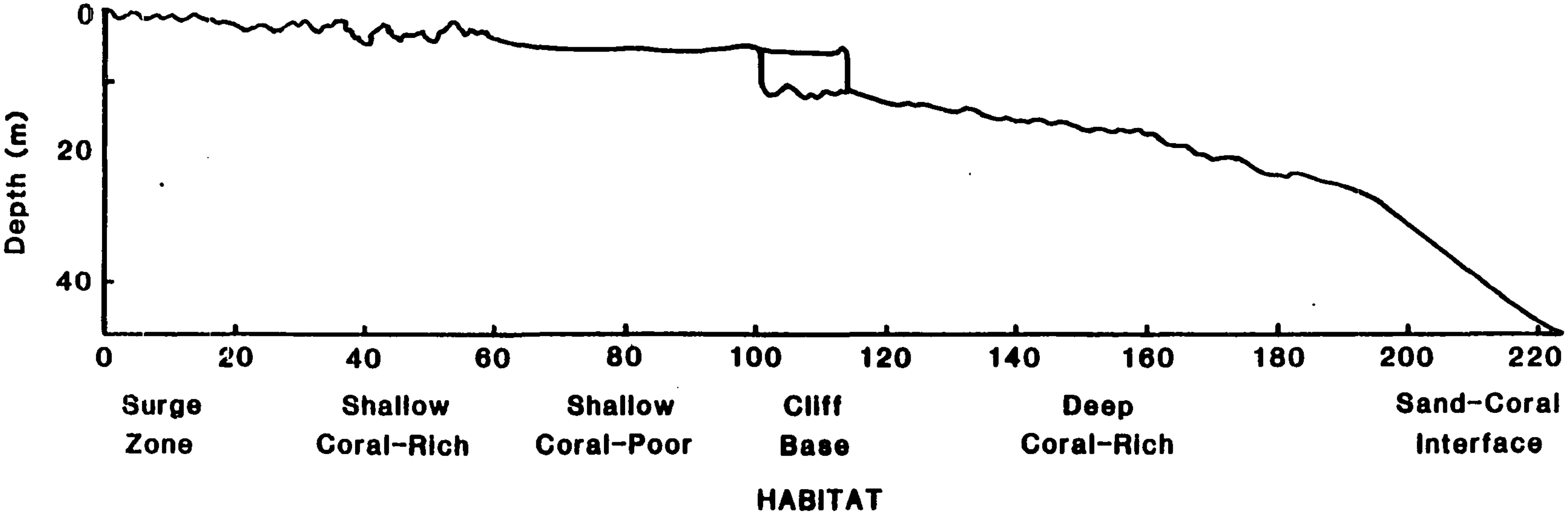
Island of Hawaii

Figure 2.2. Underwater topography of study sites at Puako, showing the major habitat zones.



0
20
40
Depth (m)
0
20
40
60
80
100
120
140
160
180
200
220
Surge Zone
Shallow Coral-Rich
Shallow Coral-Poor
Cliff Base
Deep Coral-Rich
Sand-Coral Interface
HABITAT

Table 2.1 Habitat zones of the fringing reefs of Puako, Hawaii.

HABITAT ZONE	DEPTH m	SURGE	RUGOSITY	BOTTOM COVER Type	%	DESCRIPTION
Surge Zone (SZ)	0-1	mod.-high	1.09 SD=0.04	Sand	0	Shallow, wave washed area where the lava rocks meet the water. Characterized by heavy surge, low relief and little live coral cover.
				Hard substrata	70.8	
				Coralline Algae	15.9	
				Coral	13.2	
				Other	0.1	
Reef top shallow coral-rich zone (SCR)	1-3	low - high	1.15 SD=0.1	Sand	2.3	Shallow zone characterized by large mounds of the coral _Porites_ _lobata_, separated by rubble filled gullies. High structural complexity and moderate vertical relief (1-2 m). Major coral species are _P._ _lobata_ and _P._ _meandrina_. This is the major habitat of the territorial damselfish _S._ _fasciolatus_. This habitat grades into the shallow coral-poor habitat.
				Hard substrata	47.5	
				Coralline algae	18.3	
				Coral	31.9	
				Other	0	
Reef Top - shallow coral-poor zone (SCP)	1-4	mod.-high	1.10 SD=0.05	Sand	0	Shallow basalt reef platform exposed to greater surge than the SCR zone. There are large flat expanses of hard substratum with occasional cracks and furrows < 0.5 m deep. Coral cover consists of small patches of _P._ _lobata_ and _P._ _meandrina_.
				Hard substrata	73.0	
				Coralline algae	10.4	
				Coral	16.0	
				Other	0.6	

Table 2.1 (cont.) Habitat zones of the fringing reefs of Puako, Hawaii.

HABITAT ZONE	DEPTH m	SURGE	RUGOSITY	BOTTOM COVER Type	%	DESCRIPTION
Cliff base zone (CB)	5-15	low	1.27 SD=0.14	Sand Hard substrata Coralline algae Coral Other	0 29.4 4.8 65.2 0.8	The shallow reef-top ends about 150m from shore in a 4-7m cliff with numerous overhangs, caves and ledges. The bottom of this cliff consists of boulders, rubble and large heads of <u>P. lobata</u> as well as some <u>Porites compressa</u>. It is an area of high structural complexity and relief. This zone grades into the deep coral-rich habitat.
Deep Coral-rich Zone (DCR)	15-25	low	1.30 SD=0.16	Sand Hard substrata Coralline algae Coral Other	0 30.7 6.2 63.1 0	This is a gently sloping area of low surge and high coral cover. <u>P. lobata</u> and dense beds of <u>P. compressa</u> are the dominant corals, in an area of high complexity and vertical relief.
Sand-coral interface zone (SCI)	20-30	low	1.15 SD=0.11	Sand Hard substrata Coralline algae Coral Other	25.2 41.7 10.3 22.8 0	At depths of 18 to 25m the bottom slopes more steeply forming a deeper drop off zone. At depths of 20 to 30m the coral reef ends and the sand begins. This interface may be sharp, or it may include an area of coral rubble and sand. Major coral species are the same as in the DCR zone.

separate measurements were made at randomly selected intervals perpendicular to a 50 m transect line bisecting the survey area. 4) Bottom cover, estimated by quadrat sub-sampling. A 0.5 m^2 quadrat (0.05 m grid) was placed at 5 m intervals along the transect line. The coral species or other substratum underlying each grid intersection point was recorded.

In addition to these main study sites, censuses of butterflyfishes were conducted at seven other geographically separated sites on the leeward coast of Hawaii (Fig. 2.1).

Species of butterflyfishes studied:

Seventeen species of butterflyfishes occurred in the study sites. A summary of the literature on the distribution, diet, feeding behavior and social system of each species is presented in Table 2.2.

Distribution and abundance of chaetodontids: Survey methods:

Two types of surveys were used to determine the abundances of fishes in different habitats. The first method was a standard census of fishes along a strip transect. All quantitative data were collected using a modified version of the visual survey method of Brock (1954). This method has been found relatively accurate for large, non-cryptic, diurnal species such as butterflyfishes (Brock 1982, in Hawaii). Permanent 50m transect lines were placed parallel to shore well within each habitat zone. Markers were placed 5m from

Table 2.2 Summary of the distribution, diet, feeding behavior and social systems of chaetodontids observed at Puako, Hawaii.

Species	Distribution(1,2)	Diet	Feeding Behavior(10)	Social System
Chaetodon auriga	Indo-Pacific Hawaii to Red Sea	Pieces of larger sessile inverts. & algae (3,5,6,10)	Tears with front or side of mouth	Paired or Single (6)
C. citrinellus	Indo-Pacific Hawaii to Indian Ocean	Benthic inverts. & coral? (6)	?	Paired or Single (2)
C. fremblii	Hawaii Endemic	Benthic inverts. & algae (5)	?	Haremic (13)
C. kleinii	Indo-Pacific Hawaii to Red Sea	Plankton (5,12)	?	?
C. lineolatus	Indo-Pacific Hawaii to Red Sea	Benthic inverts. (3,6)	?	Paired (2,6)
C. lunula	Indo-Pacific Hawaii to Red Sea	Benthic inverts. (3,5)	?	Paired or Groups?
C. miliaris	Hawaii Endemic	Plankton & some benthic inverts. (5,7,10)	Small mouth & teeth. Feeds by suction.	Schooling (6,7)
C. multicinctus	Hawaii Endemic	Coral (5,6,13,14)	Nips coral polyps and tissue	Paired (2,6,13,14,17)
C. ornatissimus	Central & West Pacific; Hawaii to Philippines	Coral (3,5,6,9,10)	Scrapes corals with lower jaw	Paired (2,6,17)
C. quadrimaculatus	Oceanea Hawaii to Micronesia	Coral, algae & benthic inverts. (5,6,13)	Nips or scrapes corals, tears inverts. & algae	Paired (6,13,17)

Table 2.2 (cont.) Summary of the distribution, diet, feeding behavior and social systems of chaetodontids observed at Puako, Hawaii.

Species	Distribution(1,2)	Diet	Feeding Behavior(10)	Social System
C. reticulatus	Central & West Pacific; Hawaii to Philippines	Coral (Algae?) (3)	Scrapes corals?	Paired? (2)
C. trifasciatus	Indo-Pacific Hawaii to Red Sea	Coral (3,4,5,6,8,9,10)	Bites corals or scrapes with lower jaw.	Paired (6,15)
C. unimaculatus	Indo-Pacific Hawaii to Indian Ocean	Coral & some benthic inverts. (3,5,6,8,9,10,11)	Lunges at corals, biting corallium Very strong teeth	Single, Paired or small groups (2,6)
Forcipiger flavissimus	Indo-Pacific Mexico to Red Sea	Pieces of larger benthic inverts. (5,8,9,16)	Tears benthic prey	Single, Paired or small groups (16)
F. longirostris	Central & West Pacific Hawaii to Philippines	Shrimp, other small inverts. & small fishes (5,8,9,16)	Feeds by suction	Paired? (16)
Hemitaurichthys polylepis	Central & West Pacific; Hawaii to Philippines	Plankton (5,6)	?	Schooling (2,6)
H. thompsoni	Hawaii Endemic	Plankton (5,6)	?	Schooling (2,6)

Data are summarized from: 1. Burgess (1978); 2. Allen (1979); 3. Hiatt and Strasburg (1960); 4. Talbot (1965); 5. Hobson (1974); 6. Reese (1975, 1977, 1978, 1981); 7. Ralston (1976, 1981); 8. Anderson et al. (1981); 9. Harmelin-Vivien & Bouchon-Navaro (1981, 1983); 10. Motta (1980,1983,1985); 11. Cox 1983; 12. Sano et al. (1984); 13. Hourigan (1986a, 1986b); 14. Tricas (1985); 15. Sutton (1985); 16. Ludwig (1984); 17. Driscoll and Driscoll (in prep).

this line. Each survey area was separated from other survey areas by at least 200 m. Two divers swam in parallel, one on either side of the transect line, each counting all butterflyfishes occurring within five meters of the line, for a total area censused of $500m^2$. Divers swam at a constant pace, slow enough to assure that almost all fishes were counted, but not so slow as to allow fishes to swim ahead and cross the transect area and be counted repeatedly. Each sample consisted of two replicates for each habitat zone. Replicates were conducted at the same time on consecutive days.

Annual censuses of fishes were conducted during the summers of 1980, 1981, 1982, and 1983. Seasonal censuses were conducted during the spring, summer, fall and winter 1980, in five of the six habitats at sites A and B at Puako. Censuses of the surge zone were not possible during periods of high surf during the winter and spring.

A more extensive survey of fishes in habitats in different areas at Puako (21 unreplicated censuses, each covering $500m^2$) was conducted during the summer of 1980. This survey was used for comparison to a similar survey in the same area (42 censuses, each covering $500m^2$) conducted in 1974 by Kimmerer and Durbin (1975).

Sale and Sharp (1983) reviewed sources of bias for strip transects. They found that the estimated densities of eight chaetodontids were only weakly affected by differing transect widths. All transects in the present study were of the same width (5 m per diver), and all divers followed the same procedures. Nevertheless, such transects suffer other unavoidable biases (Keast and Harker 1977, Sale and Sharp 1983). Since most data were used for comparisons among transects rather than as estimates of actual densities, these biases should be minimal. Harmelin-Vivien et al. (1985) reviewed the use of visual censuses in the estimation of reef fish populations.

The second survey method was a modification of the Jones and Thompson (1978) rapid visual survey method, and was used to quantify relative abundances of butterflyfishes at other sites along the leeward coast of Hawaii. A single diver swam steadily through a habitat and noted the occurrence of each species of butterflyfish in each 5 min interval, for a total of 25 min. Those species which were noted in all 5 min intervals were given a rank of five, those which occurred in four intervals a rank of four and so on. This method gives relative rather than absolute measures of abundance, and also suffers from distinct biases (De Martini and Roberts 1982; for a comparison of the Jones and Thompson and Brock survey methods for use with Hawaiian fishes see Sanderson and Solonsky 1986). Surveys were conducted at the following sites: (from North to South) Upolu Point, Kapaa, Mahukona, Lapakahi, Puako, Old Kona Airport, South of Kona, and Honaunau (Fig. 2.1). The purpose of these surveys was to document broad geographical patterns and to determine to what extent relative abundances of chaetodontids at Puako were representative of this coastline.

Biases in visual censuses due to different observers have been reported for both census methods (Sale and Douglas 1981; Kaufman and Ebersole 1984). Sanderson and Solonsky (1986) surveyed fish faunas in Hawaii similar to those in the present study, and found no observer bias for strip transects, but significant observer bias for the rapid visual technique. All rapid visual censuses in the present study were conducted by the author. Most censuses along the strip transects had at least one of the observers in common. Censuses from 1974, at Puako, were conducted by other observers with some variations in census techniques (Kimmerer and Durbin 1975).

Patterns of butterflyfish recruitment:

Larval recruitment of most Hawaiian chaetodontids occurs in the late spring and summer (Walsh 1984, 1987). Juveniles which recruited in the same year were less than 50mm in total length and easily distinguishable from larger fish of previous year classes.

Surveys of recently recruited juveniles were conducted in August of each year. A single diver swam over an area of approximately 2000 m^2 within each habitat, looking carefully for juvenile butterflyfishes. Juveniles counted were considered successful recruits, defined as the fish which both settled in the habitat, and subsequently survived until the time of the census (Sale and Steel 1986).

Nocturnal activity and use of shelters:

Surveys of butterflyfishes were conducted at night on two occasions in each of four habitats to determine sheltering behavior and use of shelter resources. Numbers of butterflyfishes in shelters were counted, and the type of shelter noted. The areas censused at night were the same as the diurnal census areas. Because of logistical problems associated with night diving, no observations were made in the shallow surge zone, or in the deep, sand-coral interface zone.

The importance of specific nocturnal shelters was investigated by experimentally covering shelters. Three replicate experiments were conducted in 1980 with _C. multicinctus_ and _C. quadrimaculatus_. For each species, the nocturnal shelter of one member of each of three pairs was completely covered with cloth material. The shelters of pair mates were unmanipulated and served as controls.

Distribution of predators and potential competitors:

The numbers of piscivores, corallivorous fishes other than butterflyfishes, and territorial damselfishes (identified according to Hobson 1974; Hayes et al. 1982) were also counted during all censuses in 1980. Piscivores were considered to be potential predators on butterflyfish adults or juveniles. Corallivores are potential competitors of coral-feeding butterflyfishes, and territorial damselfishes are known to chase some butterflyfishes (Hourigan 1986a). The effects of predation and competition are often difficult to measure without controlled field experiments. At their simplest level however, they may manifest themselves in habitat exclusion, producing negative correlations between numbers of fishes.

The gut contents of common piscivorous fishes at Puako were examined for the occurrence of butterflyfishes in the diets. In addition, interactions of eight species of butterflyfishes with piscivores, other corallivores, and territorial damselfishes were recorded during more than 700 hours of underwater field observations.

Feeding observations in the field:

Feeding observations were conducted on the five most abundant corallivorous butterflyfishes at Puako. The number of bites on corals and other substrata was counted during four 5 min intervals for at least five fish of each species in each of four habitats. To determine coral feeding preferences, an electivity index E, (Gore 1984, modified from Ivlev 1961) was used to compare the number of bites with the coral cover for each species of coral within each habitat:

$$E = (b_i - c_i)/(b_i + c_i)$$

where b_i is the proportion of bites on all corals which were directed toward the ith coral species, and c_i is the proportion of the total coral cover made up by that one species. Positive values show a preference for that particular species, while negative values show that it is fed upon less than would be expected by chance. To verify feeding observations, a cursory analysis of stomach contents of common butterflyfishes was conducted, and contents were sorted into major taxonomic categories.

Feeding preferences in the laboratory:

Feeding preferences of five species of corallivorous butterflyfishes were tested in the laboratory by offering individual fish a choice of coral species. Butterflyfishes were collected using hand nets and transported to the laboratory where they were placed singly in 40 l aquaria. After a minimum of 24hrs acclimation in the presence of several species of corals, the fish were subsequently kept without food for 18 to 24 hrs. Following this period, two similar size coral colonies of the same or different species were presented simultaneously to individual fish. Bites on each colony were recorded in 5 min intervals for 30 min, after which the corals were removed. The order of presentation of coral species was randomized for different fish, with ten replicates of each presentation of two coral species. Fresh coral colonies were used for each presentation. Due to the limited availability of fishes and some corals, the same individuals were used for different choices, and not all choices were offered to all species. Species of corals tested included Porites lobata, P. compressa, Pocillopora meandrina, Cyphastrea ocellina and Montipora verrucosa.

Use of space and interactions with other fishes:

Home ranges of individuals of abundant species were measured. Individuals were identified using natural markings, and followed over a period of at least five hours, during which colored markers were dropped at the outer perimeter of the foraging areas. The locations of these markers were then mapped on underwater paper. The occurrence of agonistic encounters or other interactions with conspecifics and other species was recorded for each minute interval during feeding observations, and the locations of territorial displays and chases were recorded on the home range maps.

Statistical Analyses:

All distributions of data were tested for normality using the Kolmogorov-Smirnov D test with a rejection level of 5% (i.e. at least a 5% probability that the sample came from a population with a normal distribution). Most data were counts (e.g. numbers of fishes or numbers of bites on corals) and were distributed in a Poisson fashion. Data from common species or behaviors could be normalized using a square root transformation. Data presented as a proportion or percentage were normalized using an arcsine transformation. Simultaneous comparisons of multiple means were conducted using the Waller-Duncan K-Ratio t-test. In some cases, multiple comparisons of means were conducted on samples with heterogeneous variances and non-normal distributions (Tables 2.3, 2.4, 2.12, 2.13). In these cases, these results are presented for descriptive purposes only. Data from rare species and infrequent behavior could not be normalized, and other analyses used standard, non-parametric tests.

The total chaetodontid assemblage at Site A was compared to the assemblage at Site B based on all censuses conducted in 1980. Each species in a census was ranked according to its abundance. Each pair of censuses taken at the same time of year in similar habitats at sites A and B were then matched, and a single Spearman rank correlation coefficient (r_s) was calculated from the ranks of all censuses conducted at each of the two geographic sites.

Dendrograms were constructed to show the similarity of the chaetodontid assemblages among individual censuses conducted at different times and in different habitats and sites. The numbers of individual fish recorded for each species during the two replicate censuses were averaged, and pairwise similarity coefficients (Bray and Curtis 1957) were calculated between each pair of averages. Dendrograms were constructed from an unweighted pair-group clustering of these coefficients (McCammon and Wenninger 1970).

The similarity in diets of corallivorous butterflyfishes was calculated using two separate methods. First, Schoener's (1968) Index of dietary similarity was calculated as:

$$T = 1 - 0.5 \sum_{i=1}^{n} |p_{xi} - p_{yi}|$$

where p_{xi} and p_{yi} are the proportions of total bites on the i^{th} resource (prey category) for all fish species pairs x and y. This index ranges from 0 for species with no dietary overlap, to 1 for species with all food items eaten in the same proportions. This index has been used for reef fishes by Gladfelter and Johnson (1983) and Hourigan et al. (in press). A second measure of dietary similarity employed discriminant function analysis. Bites on each food resource category were transformed using a square-root transformation and analyzed by habitat. Each five minute feeding observation was then independently assigned a posteriori to a species using the discriminant function. The proportion of assignments to the correct species is a measure of the uniqueness of that species' diet in that habitat. All of these measures of similarity are primarily descriptive, since confidence limits for these analyses are not generally available.

RESULTS

Distribution and abundance of chaetodontids:

Thirteen species of butterflyfishes were observed during visual surveys along transects in the six habitats at Puako, Hawaii (Fig. 2.3a,b,c). An additional four species, Chaetodon citrinellus, C. lineolatus, C. reticulatus and Hemitaurichthys thompsoni, were observed in the area, but were rare, and were not recorded during the quantitative surveys.

Population densities of most species differed among the contiguous habitats within each geographic site (Table 2.3; Kruskal-Wallis test, $p<0.05$). The distribution of each species among the six habitats was similar at both geographic sites and the large scale censuses conducted in 1980 and 1974 (Table 2.3; Fig. 2.3a,b,c), indicating that the distribution was not random. For example, for each site, C. multicinctus was consistently most abundant in the cliff base habitat and least common in the surge zone. Within any one site, adult individuals were capable of moving between habitats.

Comparisons between the the two sites showed that the composition of the chaetodontid assemblage was similar in habitats which resembled each other in terms of depth, coral cover and physical structure. In most cases there was good agreement in the absolute abundances of different species in similar habitats compared among the two sites and the large scale censuses (Fig. 2.3a,b,c). The relative rankings of the different species within each habitat, also were comparable among

Figure 2.3a Mean abundance of corallivorous butterflyfishes observed in visual censuses of fishes in different habitats at sites A and B at Puako during 1980 (N=8 censuses at the same locations in each habitat). These abundances are compared to censuses conducted during the summer of 1980 (single censuses at two to five different locations in each habitat) and censuses conducted six years earlier by Kimmerer and Durbin (1975) during the summer of 1974 (single censuses at 5 to 21 different locations in each habitat). Thin and thick error bars show the standard error of the mean and the range respectively. NC = Habitat Not Censused. Habitat zones are: SZ = Surge Zone, SCR = Shallow Coral-Rich, SCP = Shallow Coral-Poor, CB = Cliff Base, DCR = Deep Coral-Rich, and SCI = Sand-Coral Interface.

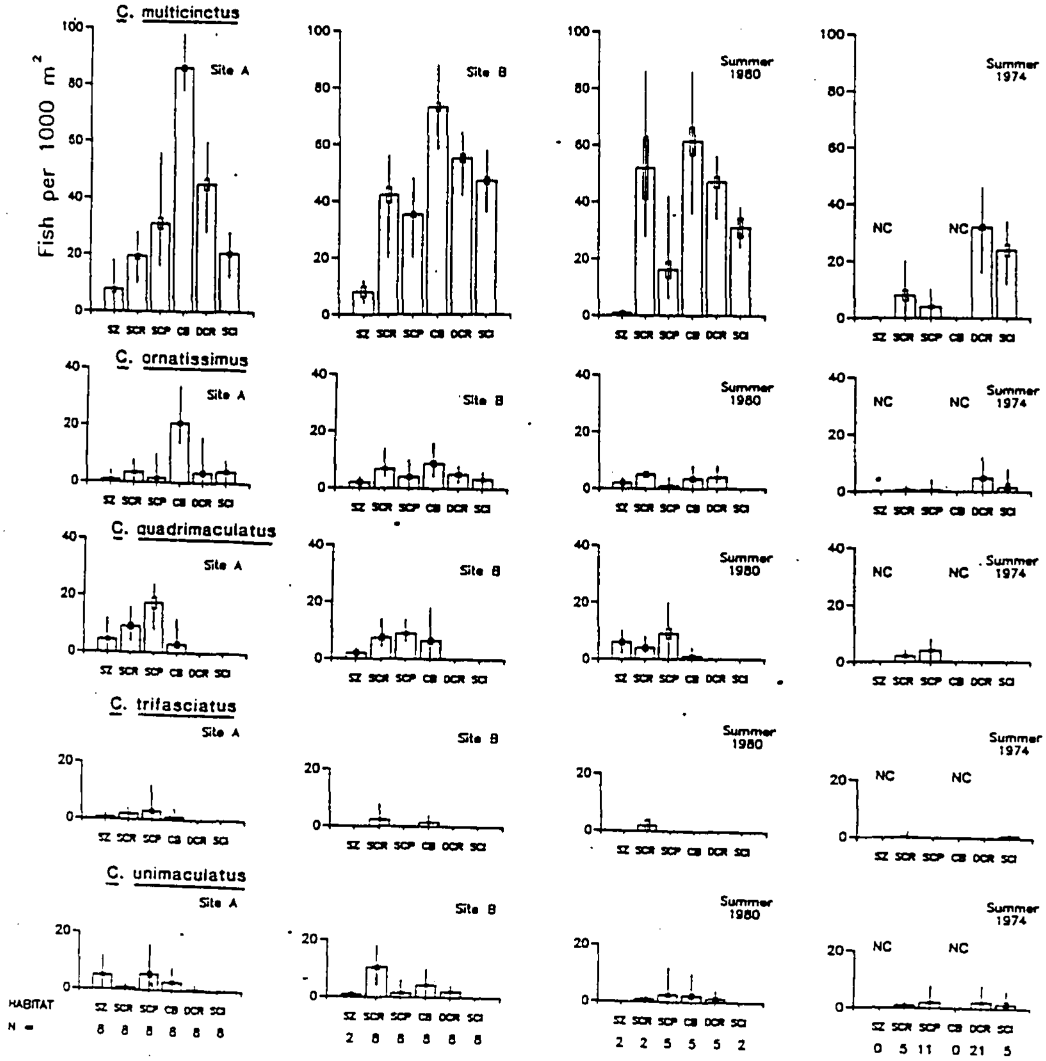

C. multicinctus
C. ornatissimus
C. quadrimaculatus
C. trifasciatus
C. unimaculatus
Site A
Site B
Summer 1980
Summer 1974
NC
Fish per 1000 m^2
0
20
40
60
80
100
SZ SCR SCP CB DCR SCI
HABITAT
N =
8 8 8 8 8 8
2 8 8 8 8 8
2 2 5 5 5 2
0 5 11 0 21 5

Figure 2.3b Mean abundance of omnivorous butterflyfishes observed in visual censuses of fishes in different habitats at sites A and B at Puako during 1980 (N=8 censuses at the same locations in each habitat). These abundances are compared to censuses conducted during the summer of 1980 (single censuses at two to five different locations in each habitat) and censuses conducted six years earlier by Kimmerer and Durbin (1975) during the summer of 1974 (single censuses at 5 to 21 different locations in each habitat). Thin and thick error bars show the standard error of the mean and the range respectively. NC = Habitat Not Censused. Habitat zones are: SZ = Surge Zone, SCR = Shallow Coral-Rich, SCP = Shallow Coral-Poor, CB = Cliff Base, DCR = Deep Coral-Rich, and SCI = Sand-Coral Interface.

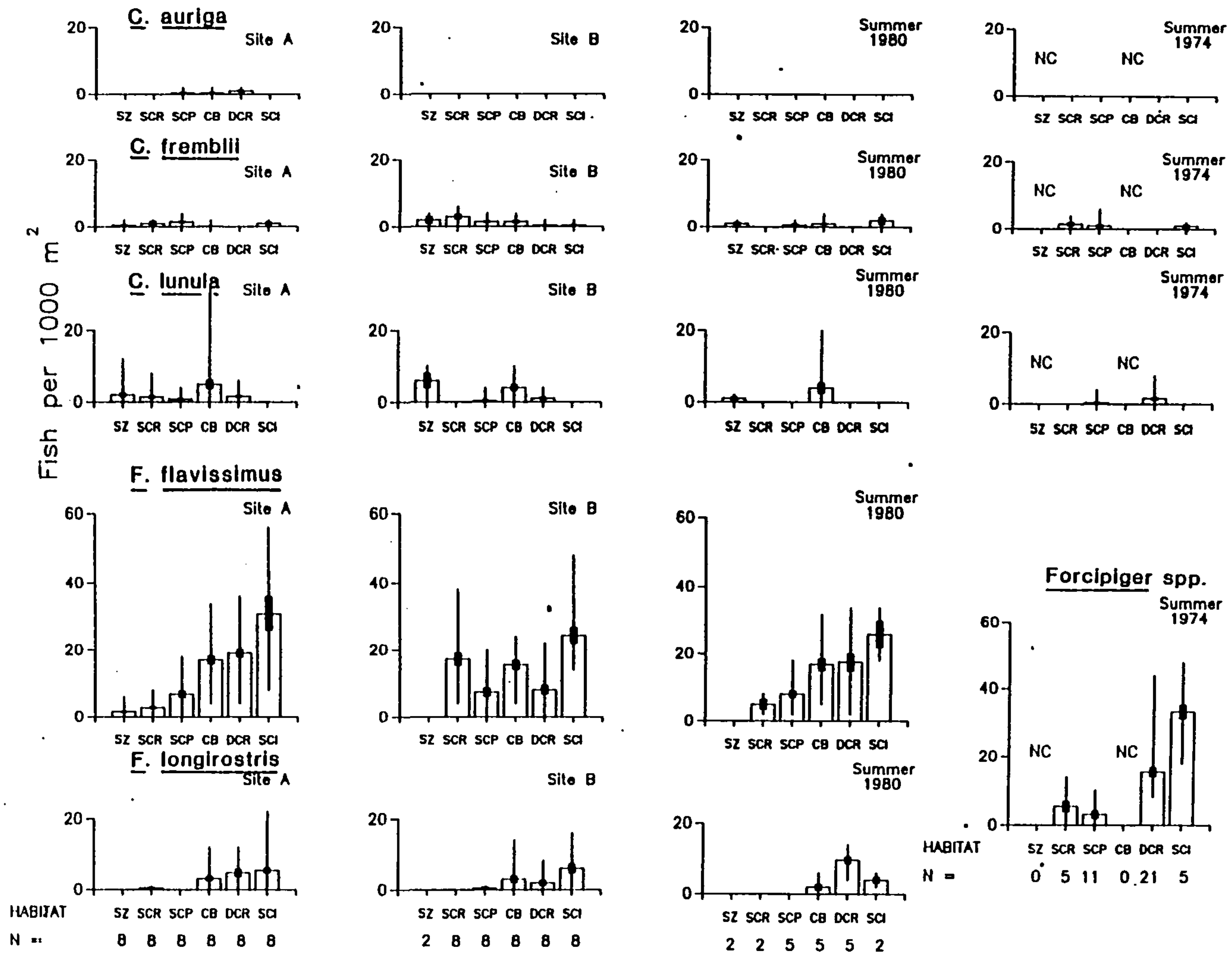

Fish per 1000 m2
C. auriga
Site A
Site B
Summer 1980
Summer 1974
C. fremblii
C. lunula
F. flavissimus
F. longirostris
Forcipiger spp.
NC
20
0
40
60
SZ SCR SCP CB DCR SCI
HABITAT
N =
8 8 8 8 8 8
2 8 8 8 8 8
2 2 5 5 5 2
0 5 11 0 21 5

Figure 2.3c Mean abundance of planktivorous butterflyfishes observed in visual censuses of fishes in different habitats at sites A and B at Puako during 1980 (N=8 censuses at the same locations in each habitat). These abundances are compared to censuses conducted during the summer of 1980 (single censuses at two to five different locations in each habitat) and censuses conducted six years earlier by Kimmerer and Durbin (1975) during the summer of 1974 (single censuses at 5 to 21 different locations in each habitat). Thin and thick error bars show the standard error of the mean and the range respectively. NC = Habitat Not Censused. Habitat zones are: SZ = Surge Zone, SCR = Shallow Coral-Rich, SCP = Shallow Coral-Poor, CB = Cliff Base, DCR = Deep Coral-Rich, and SCI = Sand-Coral Interface.

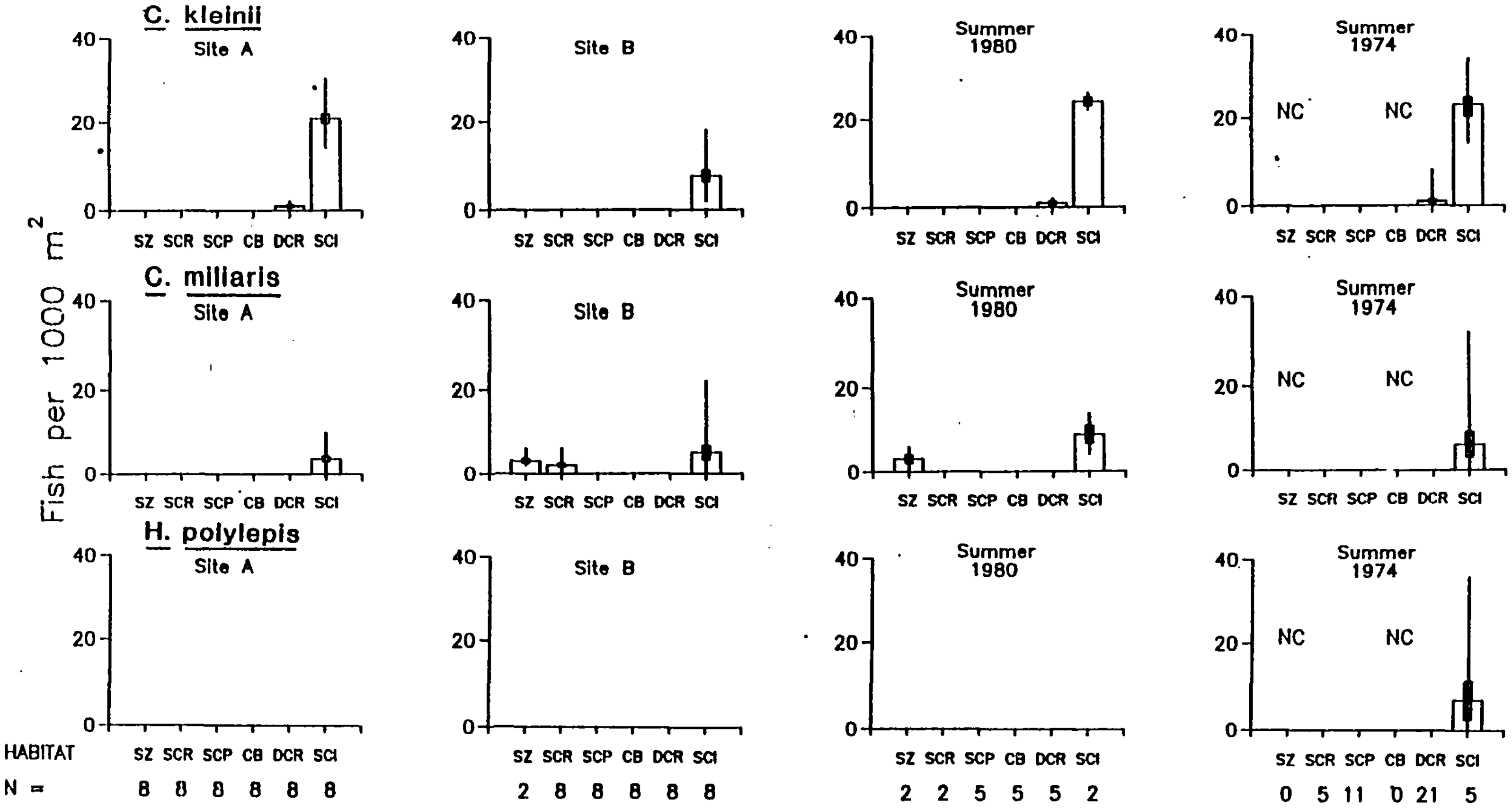

Fish per 1000 m^2
C. kleinii
Site A
Site B
Summer 1980
Summer 1974
C. miliaris
Site A
Site B
Summer 1980
Summer 1974
H. polylepis
Site A
Site B
Summer 1980
Summer 1974
NC
NC
0
20
40
SZ SCR SCP CB DCR SCI
HABITAT
N =
8 8 8 8 8 8
2 8 8 8 8 8
2 2 5 5 5 2
0 5 11 0 21 5

Table 2.3 Comparisons of population density of each species of butterflyfish in different habitats. Habitats are ranked from left to right, from highest to lowest mean number of fish of that species seen in censuses at the two different sites at Puako (Site A, N=16 censuses in each habitat; and Site B, N= 10 censuses), and the large scale transects at Puako (Summer 1980, N= 2 to 5 censuses in each habitat, and Summer 1974, N = 5 to 21 censuses, conducted by Kimmerer and Durbin, 1976). Kruskal-Wallis non-parametric test for differences in rank of population densities among habitats (* = $p<0.05$). Differences in mean ranks were compared using the parametric Waller-Duncan K-ratio test for multiple comparisons: Underlines connect those habitats whose means were not significantly different for that species ($p>0.05$).

SPECIES:	SITE A	SITE B	SUMMER 1980	SUMMER 1974
C. auriga	DCR CB - - - -	- - - - - -	- - - - - -	- - - -
C. fremblii	SCP SCR SCI SZ CB - *	SCR SZ SCP CB DCR SCI*	SCI CB SZ SCP - -	SCR SCI SCP - *
C. kleinii	SCI DCR - - - - *	SCI - - - - - *	SCI DCR - - - - *	SCI DCR - - *
C. lunula	CB SZ DCR SCP SCR - *	SZ CB DCR SCP - - *	SZ CB - - - -	DCR SCP - -
C. miliaris	SCI SZ - - - - *	SCI SZ SCR - - - *	SCI SCP - - - - *	SCI SCR SCP DCR*
C. multicinctus	CB DCR SCP SCR SCI SZ *	CB DCR SCI SCR SCP SZ *	CB SCR DCR SCI SCP SZ *	DCR SCI SCR SC *
C. ornatissimus	CB SCI DCR SCR SCP SZ *	CB SCR DCR SCP SCI SZ *	SCR DCR CB SZ SCP SCI*	DCR SCI SCP SCR*
C. quadrimaculatus	SCP SCR SZ CB - - *	SCP SCR CB SZ - - *	SCP SCR SZ CB - - *	SCP SCR - - *
C. trifasciatus	SCP SCR CB SZ - - *	SCR CB SCP - - - *	SCR - - - - - *	SCI SCR - - *
C. unimaculatus	SCP SZ CB SCR DCR SCI*	SCR CB DCR SCP SZ - *	CB DCR SCP SCR - -	DCR SCP SCI SCR
F. flavissimus	SCI DCR CB SCP SCR SZ *	SCI SCR CB DCR SCP - *	SCI CB DCR SCP SCR - *	SCI DCR SCR - *1
F. longirostris	SCI DCR CB SCR - - *	SCI CB DCR SCP - - *	DCR SCI CB - - - *	
	Highest -------- Lowest	Highest -------- Lowest	Highest -------- Lowest	Highest - Lowest

---

1. *Forcipiger* species were not differentiated in data from 1974.
Abbreviations for habitats are the same as in Table 1.

the sites and the large scale censuses (Table 2.4). The total assemblages at site A and B were highly correlated (Spearman Rank coefficient $r_s = 0.84$; $p<0.01$) when censuses were matched for similar habitats censused at the same time of year. General patterns of distribution of fishes were similar at both sites and for other areas along the leeward coast (Table 2.5).

Population densities of the most abundant species, such as C. multicinctus, were similar in the same habitats over different seasons and years at each site (Fig. 2.4). Only five species, C. kleinii, C. multicinctus, C. ornatissimus, C. quadrimaculatus and F. flavissimus, could be compared using parametric tests (Table 2.6; Kolmogorov-Smirnov D test for normality after square root transformation $p<0.95$). These five species were analyzed using a nested ANOVA (Model II). The component of the total variance attributable to differences among sites, habitats and seasons was calculated (Table 2.7). The major component of the variance was due to differences among habitats within sites. Very little was due solely to difference between similar habitats at different geographic sites.

Analysis of the similarity of habitats as a function of butterflyfish abundances showed greatest similarities between seasons and years at the same habitat and site, and also great similarities between the same habitats at different sites (Fig. 2.5). This indicated a degree of both spatial and temporal stability in the chaetodontid assemblage. The deep and shallow habitats were the most distinct in terms of their butterflyfish assemblages.

Table 2.4 Comparisons of population densities of different species of butterflyfishes in each habitat. Species are ranked from left to right, from highest to lowest mean number of fish seen in censuses at the two different sites at Puako (Site A, N=16 censuses in each habitat; and Site B, N= 10 censuses), and the large scale transects at Puako (Summer 1980, N= 2 to 5 censuses in each habitat). Kruskal-Wallis non-parametric test for differences in rank of population densities among species (* = p<0.05). Differences in mean ranks were compared using the parametric Waller-Duncan K-ratio test for multiple comparisons: Underlines connect those species whose means were not significantly different in that habitat (p>0.05).

HABITAT	SITE A	SITE B	SUMMER 1980
SZ	CMU CUN CQU CLU FFL COR CFR CTR*	CMU CLU COR CMI CFR CQU CUN	CQU COR CFR CMU CLU*
SCR	CMU CQU COR FFL CTR CLU CFR CUN FLO*	CMU FFL CUN CQU COR CFR CTR CMI*	CMU COR FFL CQU CTR CUN*
SCP	CMU CQU FFL CUN CTR CFR COR CLU*	CMU CQU FFL COR CFR CUN CLU FLO*	CMU CQU FFL CMI CUN COR CFR*
CB	CMU COR FFL CLU FLO CQU CUN CTR CFR*	CMU FFL COR CQU FLO CUN CLU CFR CTR*	CMU FFL COR CUN FLO CFR CQU CLU*
DCR	CMU FFL FLO COR CLU CKL CAU CUN*	CMU FFL CUN FLO COR CLU CFR*	CMU FFL FLO COR CUN CKL*
SCI	FFL CKL CMU COR CMI FLO CFR CUN*	CMU FFL CKL FLO CMI COR CFR*	CMU FFL CKL CMI CFR FLO*
	Highest ---------------- Lowest	Highest ---------------- Lowest	Highest ---------------- Lowest

Species abbreviations are: CAU = *C. auriga*, CFR = *C. fremblii*, CKL = *C. kleinii*, CLU = *C. lunula*, CMI = *C. miliaris*, CMU = *C. multicinctus*, COR = *C. ornatissimus*, CQU = *C. quadrimaculatus*, CTR = *C. trifasciatus*, CUN = *C. unimaculatus*, FFL = *F. flavissimus*, FLO = *F. longirostris*.
Abbreviations for habitats are the same as in Table 1.

Table 2.5 Abundance of butterflyfishes in shallow (SH< 5m) and deep (D> 5m) habitats along the leeward coast of the Island of Hawaii. Numbers refer to the number of five minute (out of 25 min observation) intervals in which fish of a particular species were noted within that habitat.

	Upolu		Kapaa		Mahukona		Lapakahi		Puako		Kona		South Kona		Honaunau	
	SH	D	SH	D	SH	D	SH	D	SH	D	SH	D	SH	D	SH	D
# of Censuses =	1	1	1	1	1	1	2	2	5	7	1	1	1	1	2	2
Species:																
C. auriga	0	0	0	1	0	0	0.5	0	0.4	0.1	0	0	0	0	0	1
C. citrinellus	0	0	0	0	0	0	0	0	P	0	0	0	0	0	0	0
C. fremblii	1	3	1	0	3	1	2	2	0.4	0.4	0	0	0	0	0	0
C. kleinii	0	2	0	2	0	2	0	1	0	1.4	0	5	0	2	0	1
C. lineolatus	0	0	0	0	1	0	0.5	0	0	P	1	0	1	0	1	0
C. lunula	0	2	0	3	1	2	2.5	0	1.6	1.7	1	3	3	1	1	2
C. miliaris	0	0	0	0	0	0	0	1	0.2	0.4	0	5	0	0	0	0
C. multicinctus	3	5	3	5	3	5	3	4	3.4	4.3	3	5	4	5	4	5
C. ornatissimus	4	5	1	3	1	3	2.5	3	2.4	2.6	2	4	3	3	2	3
C. quadrimaculatus	3	0	3	0	3	0	3	0	3.4	0.3	2	0	4	0	3	0
C. trifasciatus	0	0	0	0	0	1	0.5	0	0.4	0.1	0	0	1	0	0	0
C. reticulatus	0	0	0	0	0	0	0.5	0	P	0	0	0	1	0	1	0
C. tinkeri	0	0	0	0	0	0	0	0	0	P	0	0	0	0	0	0
C. unimaculatus	0	1	0	0	0	0	1	0	1.8	0.7	0	0	1	0	2	0
F. flavissimus	2	4	3	4	2	3	2.5	3	2.4	3.9	1	3	2	3	3	4
F. longirostris	0	1	0	3	0	2	0	1	0	1.7	0	1	0	1	0	0
H. polylepis	0	0	0	0	0	2	0	0	0	P	0	1	0	1	0	0
H. thompsoni	0	0	0	0	0	0	0	0	0	P	0	1	0	0	0	0

P = Present in habitat but not observed during census.

Figure 2.4. Numbers of the most abundant butterflyfish, *C. multicinctus*, at sites A and B at Puako. Two replicate censuses were conducted in most habitats during four seasons in 1980 and during the summer of 1981 at both sites. Additional censuses were conducted at site A during the fall of 1979 and the summers of 1982 and 1983.

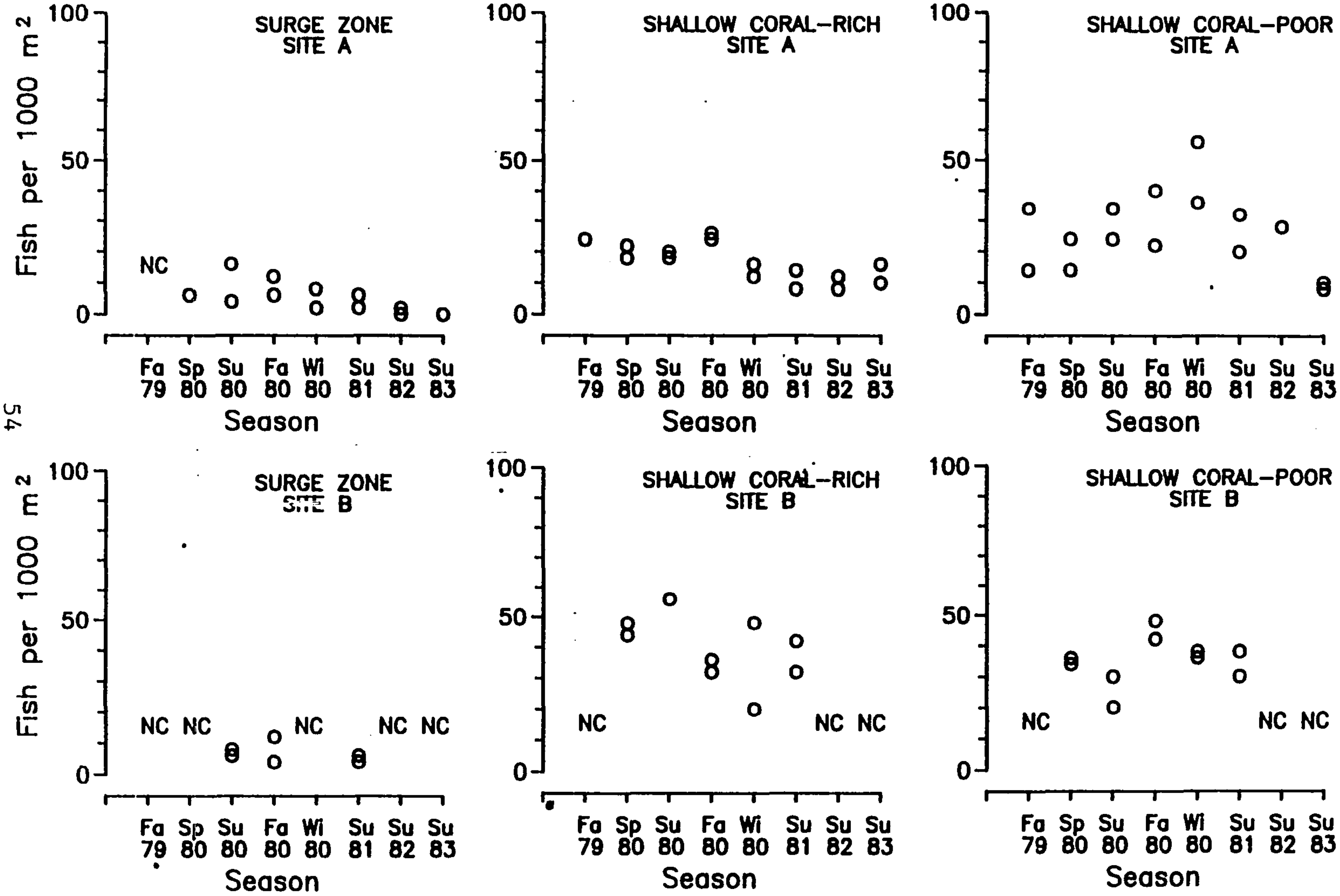

SURGE ZONE SITE A
SHALLOW CORAL-RICH SITE A
SHALLOW CORAL-POOR SITE A
SURGE ZONE SITE B
SHALLOW CORAL-RICH SITE B
SHALLOW CORAL-POOR SITE B
Fish per 1000 m 2
100
50
0
Fa 79
Sp 80
Su 80
Fa 80
Wi 80
Su 81
Su 82
Su 83
Season
NC

Figure 2.4 (cont.). Numbers of the most abundant butterflyfish, _C. multicinctus_, at sites A and B at Puako. Two replicate censuses were conducted in most habitats during four seasons in 1980 and during the summer of 1981 at both sites. Additional censuses were conducted at site A during the fall of 1979 and the summers of 1982 and 1983.

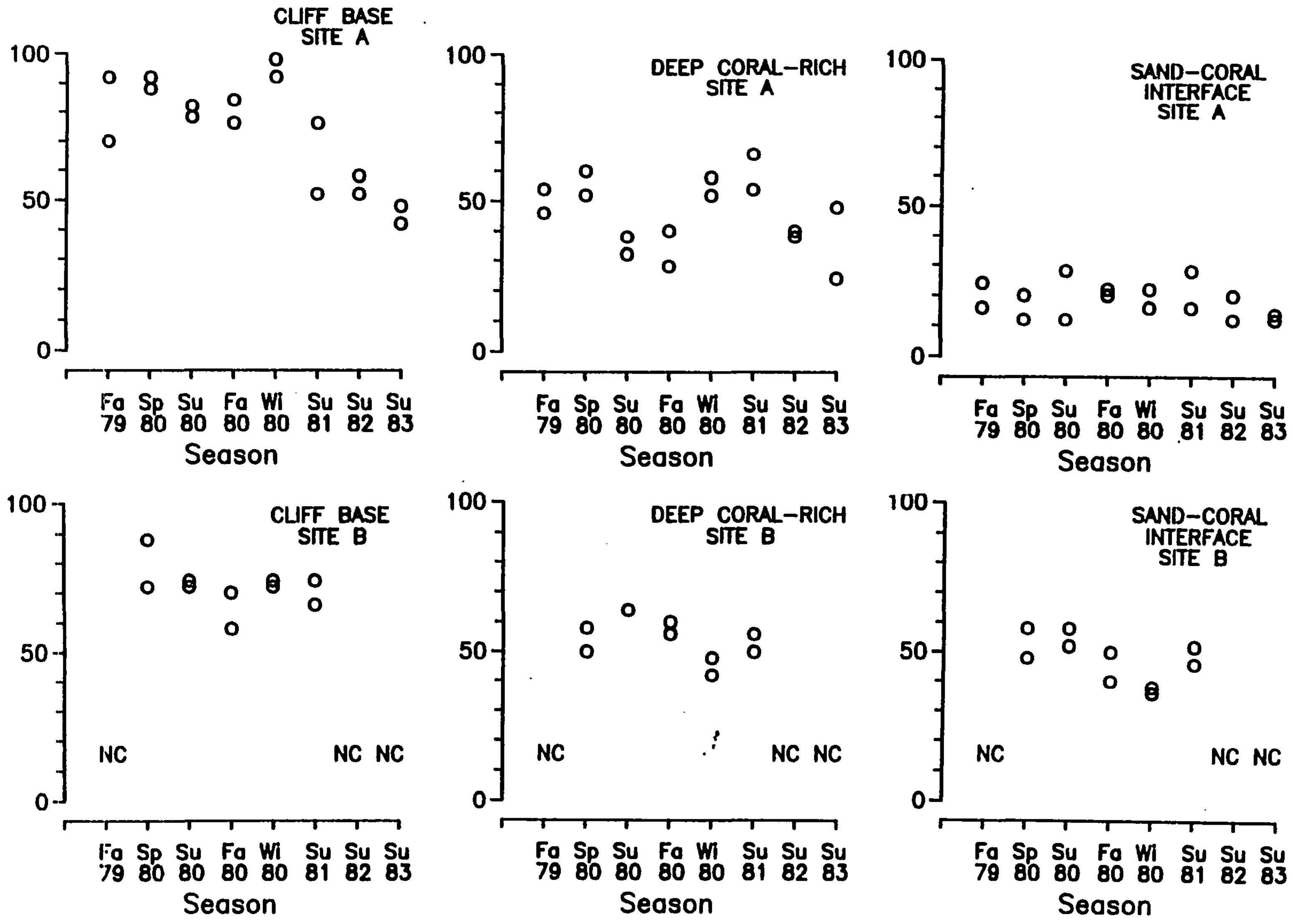

CLIFF BASE
SITE A
DEEP CORAL-RICH
SITE A
SAND-CORAL
INTERFACE
SITE A
CLIFF BASE
SITE B
DEEP CORAL-RICH
SITE B
SAND-CORAL
INTERFACE
SITE B
100
50
0
Fa 79
Sp 80
Su 80
Fa 80
Wi 80
Su 81
Su 82
Su 83
Season
NC
NC NC

Table 2.6 Test of goodness of fit to a normal distribution of census data for each species of butterflyfish by site and habitat. Kolmogorov-Smirnov D-test: Values represent the probability that sample came from a population with a normal distribution. < = p less than 0.05, i.e. sample does not meet normality criteria. Numbers of butterflyfishes have been transformed using a square root transformation.

	SITE A						SITE B					
HABITAT:	SZ	SCR	SCP	CB	DCR	SCI	SZ	SCR	SCP	CB	DCR	SCI
Species:												
C. auriga	-	-	<	<	<	<	-	-	-	-	-	-
C. fremblii	<	<	<	<	<	<	<	0.4	0.05	<	<	<
C. kleinii	-	-	-	-	-	0.4	-	-	-	-	-	0.7
C. lunula	<	<	<	<	<	-	-	<	<	<	<	-
C. miliaris	<	-	-	-	-	<	<	<	-	-	-	0.1
C. multicinctus	0.4	0.6	0.9	0.5	0.2	0.3	<	0.4	0.1	0.5	0.3	0.4
C. ornatissimus	<	0.1	<	0.2	0.05	0.05	<	0.6	0.5	0.2	<	<
C. quadrimaculatus	0.05	0.1	0.4	<	-	-	<	0.5	0.4	<	-	-
C. trifasciatus	<	<	<	<	<	-	<	<	<	<	<	-
C. unimaculatus	0.09	<	<	<	<	-	<	0.3	<	<	0.9	-
F. flavissimus	<	<	<	0.1	0.4	0.95	<	0.9	0.5	0.3	0.6	0.3
F. longirostris	-	-	-	<	<	<	-	-	-	0.1	<	0.6

	SUMMER 1980						SUMMER 1974			
HABITAT:	SCR	SCP	CB	DCR	SCI		SCR	SCP	DCR	SCI
Species:										
C. auriga	-	-	-	-	-		-	-	-	-
C. fremblii	-	<	0.6	<	0.9		0.4	<	<	<
C. kleinii	-	-	-	-	0.9		-	-	-	0.7
C. lunula	-	-	<	-	-		-	<	<	-
C. miliaris	-	-	-	-	<		-	-	-	<
C. multicinctus	0.2	0.1	0.3	0.2	0.5		0.6	<	0.3	0.2
C. ornatissimus	0.4	0.06	0.3	0.2	-		<	<	<	<
C. quadrimaculatus	0.3	0.7	<	-	-		0.06	<	-	-
C. trifasciatus	<	-	-	-	-		<	-	-	<
C. unimaculatus	<	<	<	0.3	-		<	<	<	<
F. flavissimus	<	0.6	0.9	0.4	0.7	F. spp.[1]	0.2	0.05	0.99	0.9
F. longirostris	-	-	<	<	<					

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[1] Forcipiger species were not differentiated in data from 1974.
Abbreviations for habitats are the same as in Table 1.

Table 2.7 Percent of the variance component of butterflyfish numbers among censuses attributable to different sites (or years), habitats, and seasons. Error term is the amount of variance between replicates in the same season, habitat and site. Analysis is by nested ANOVA of square root transformed numbers of the five most abundant species of butterflyfishes at Puako.

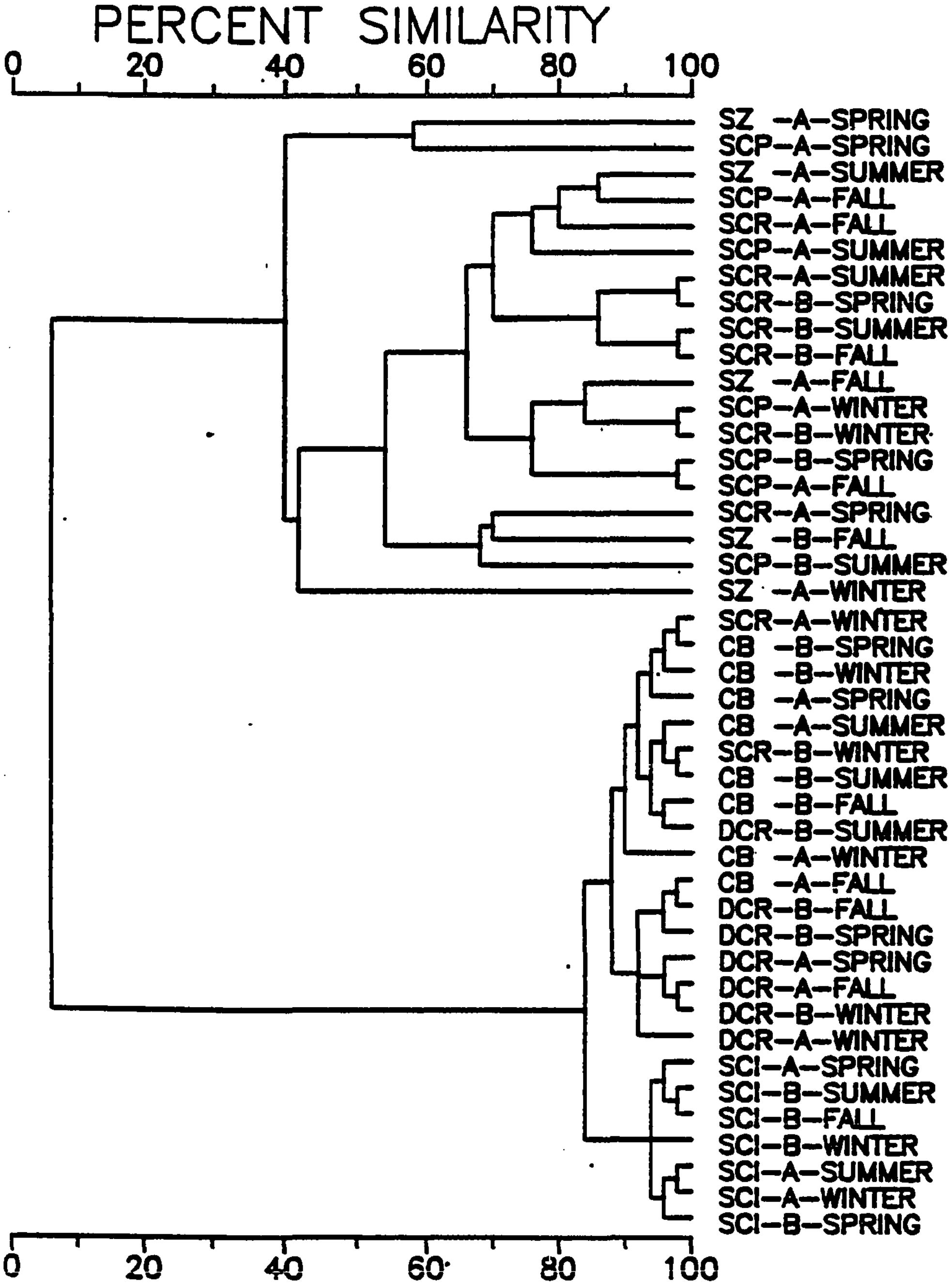
1980
SITE A vs. SITE B

SPECIES:	Site	Habitat	Season	Error	Total
C. kleinii	0	92.6	0	7.4	100
C. multicinctus	0	83.1	9.7	7.2	100
C. ornatissimus	0	61.7	3.1	35.2	100
C. quadrimaculatus	0	47.4	27.6	25.0	100
F. flavissimus	0	60.1	6.3	33.6	100

Summer 1980 vs. Summer 1974

	Year	Habitat	Error	Total
C. kleinii	0	91.1	8.9	100
C. multicinctus	0	77.6	22.4	100
C. ornatissimus	0	26.4	73.6	100
C. quadrimaculatus	10.5	49.8	39.7	100
Forcipiger spp.	0	48.9	51.1	100

Figure 2.5. Dendrogram showing the similarity of butterflyfish assemblages analyzed from visual censuses conducted during different seasons during 1980, in different habitats at sites A and B at Puako. Similarities were analyzed using the Bray-Curtis index of similarity. Assemblage labels give the habitat (SZ - Surge Zone, SCR - Shallow Coral-Rich, SCP - Shallow Coral-Poor, CB - Cliff Base, DCR - Deep Coral-Rich, and SCI - Sand-Coral Interface), the site (A or B), the season. N - 2 censuses at each time, for each habitat.


PERCENT SIMILARITY
0
20
40
60
80
100
SZ -A-SPRING
SCP-A-SPRING
SZ -A-SUMMER
SCP-A-FALL
SCR-A-FALL
SCP-A-SUMMER
SCR-A-SUMMER
SCR-B-SPRING
SCR-B-SUMMER
SCR-B-FALL
SZ -A-FALL
SCP-A-WINTER
SCR-B-WINTER
SCP-B-SPRING
SCP-A-FALL
SCR-A-SPRING
SZ -B-FALL
SCP-B-SUMMER
SZ -A-WINTER
SCR-A-WINTER
CB -B-SPRING
CB -B-WINTER
CB -A-SPRING
CB -A-SUMMER
SCR-B-WINTER
CB -B-SUMMER
CB -B-FALL
DCR-B-SUMMER
CB -A-WINTER
CB -A-FALL
DCR-B-FALL
DCR-B-SPRING
DCR-A-SPRING
DCR-A-FALL
DCR-B-WINTER
DCR-A-WINTER
SCI-A-SPRING
SCI-B-SUMMER
SCI-B-FALL
SCI-B-WINTER
SCI-A-SUMMER
SCI-A-WINTER
SCI-B-SPRING
0
20
40
60
80
100

Comparisons of data from large scale surveys in 1980 and 1974 showed similar trends among habitats for most species. The two species in the genus *Forcipiger* were not differentiated in 1974, so comparisons were conducted with numbers of both species pooled. Censuses in the same habitat, regardless of year, were most similar (Fig. 2.6).

Patterns of butterflyfish recruitment.

Recently settled butterflyfishes (<50mm in total length) of eight species were observed. For most species, settlement occurred between March and July. Generally, juvenile corallivores were found in the same habitats as the adults. *Chaetodon multicinctus* juveniles were the most abundant juveniles observed (Table 2.8). Juvenile *C. ornatissimus* and *C. quadrimaculatus* were observed each year but in low numbers. In each of these species, juveniles were generally sheltered, and were chased whenever they were encountered by conspecific adults.

Juveniles of two non-corallivore species, *C. lunula* and *C. miliaris*, showed highly disjunct adult-juvenile distributions, with juveniles only occurring in the shallow surge zone or in tide pools (Table 2.8).

Juveniles of less abundant species showed distinct annual fluctuations. For example, *C. miliaris* juveniles were very common in 1982, and three *C. reticulatus* juveniles were observed in 1983, the

Figure 2.6. Dendrogram showing the similarity of the butterflyfish assemblage analyzed from visual censuses conducted during the summers of 1974 (Data from Kimmerer and Durbin 1975) and 1980 in different habitats at Puako. Similarities were analyzed using the Bray-Curtis index of similarity. Assemblage labels give the habitat and the year of the census. The habitats are: SZ - Surge Zone (1980: N - 3; 1974: not censused), SCR - Shallow Coral-Rich (1980: N - 3 censuses; 1974: N - 5 censuses), SCP - Shallow Coral-Poor (1980: N - 6 censuses; 1974: N - 11 censuses), CB - Cliff Base (1980: N - 6 censuses; 1974: not censused), DCR - Deep Coral-Rich (1980: N - 6 censuses; 1974: N - 21 censuses), and SCI - Sand-Coral Interface (1980: N - 3 censuses; 1974: N - 5 censuses).

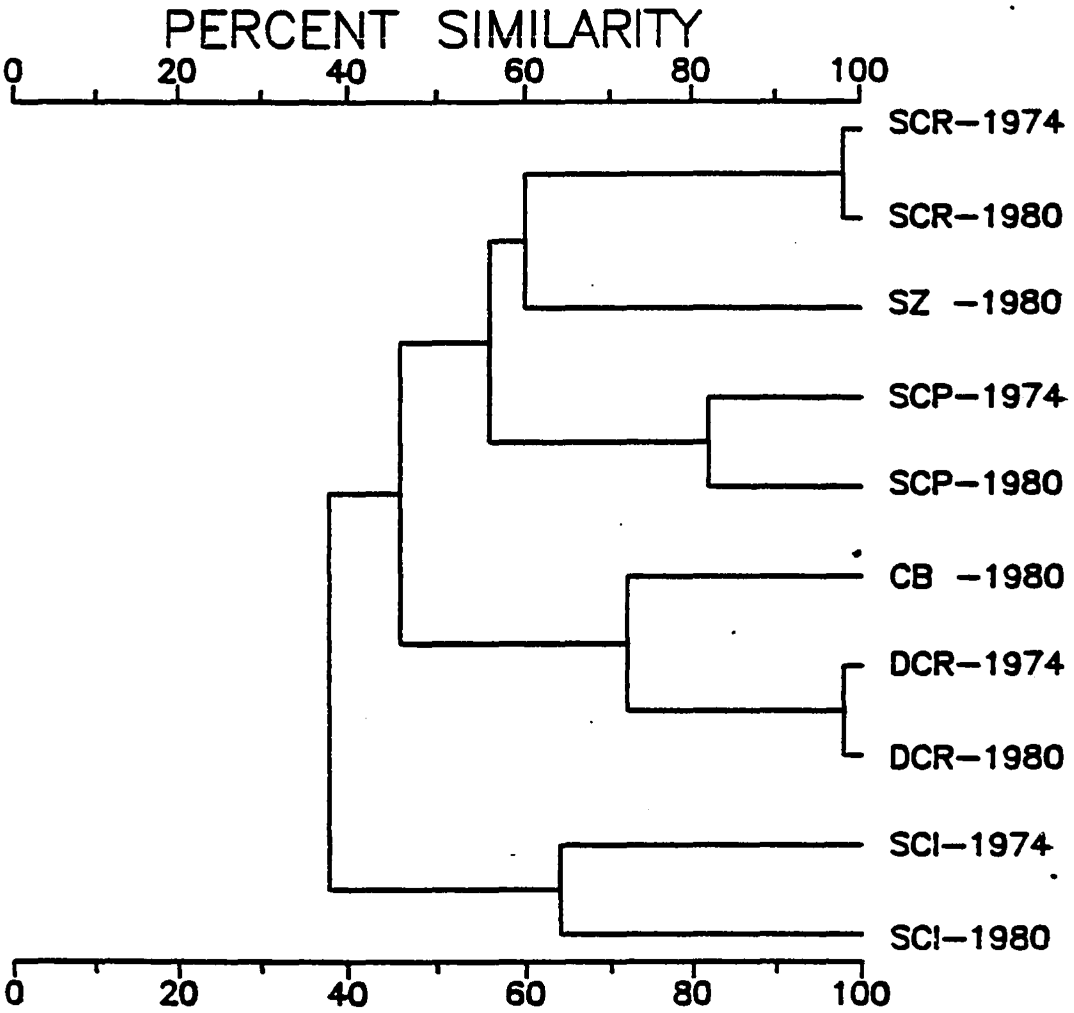

PERCENT SIMILARITY
0
20
40
60
80
100
SCR–1974
SCR–1980
SZ –1980
SCP–1974
SCP–1980
CB –1980
DCR–1974
DCR–1980
SCI–1974
SCI–1980
0
20
40
60
80
100

Table 2.8 Abundance of juvenile butterflyfishes observed in different habitats at Puako, Hawaii, during 2 hr surveys (approximately 2000m^2) in each habitat during August 1979, 1980, 1981, 1982 and 1983.

	HABITAT																						
	Surge Zone			Shallow Coral-Rich					Shallow Coral-Poor					Cliff Base					Deep Coral-Rich				
Year:	81	82	83	79	80	81	82	83	79	80	81	82	83	79	80	81	82	83	79	80	81	82	83
Species:																							
C. fremblii	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
C. lunula	1	3	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C. miliaris	1	13	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C. multicinctus	0	0	0	0	2	1	1	4	1	0	2	1	2	6	3	4	5	9	4	2	3	4	5
C. ornatissimus	0	0	0	0	1	0	0	1	0	0	0	0	0	2	1	1	1	7	1	0	2	1	3
C. quadrimaculatus	0	0	1	2	3	0	0	1	1	5	1	1	0	0	2	1	0	0	0	0	0	0	0
C. reticulatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	2
C. unimaculatus	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0

only year this species was found. Unfortunately, I was not able to follow these year classes.

Butterflyfishes often did not mature to adulthood in the same location that they settled. No adult _C. miliaris_ or _C. lunula_ were observed in the shallow surge zone where the juveniles occurred. Juveniles of the two abundant corallivores, _C. multicinctus_ and _C. quadrimaculatus_ left the territories of adults where they had settled. This appeared to occur when they became too large to shelter in the coral from attacks by the territorial adults. Sub-adult _C. multicinctus_ ranged as singles, pairs or trios over large areas, skirting the territory boundaries of adults. Sub-adult _C. quadrimaculatus_ gathered in small groups of varying composition, which ranged widely along the cliff base at the edge of the shallower adult territories.

Nocturnal activity and use of shelters:

Surveys of fishes at night showed qualitatively similar distributions to those seen during the day (Table 2.9). Butterflyfishes were usually found sheltered beneath overhanging ledges, in large crevices or at the bases of coral heads. Although the fish were quiescent, they appeared aware of their surroundings and moved off when approached. Pair-mates always sheltered within their diurnal territories (N=30 pairs of _C. multicinctus_, 24 pairs of _C. quadrimaculatus_, 3 pairs of _C. ornatissimus_ and 2 pairs of _C. trifasciatus_), and in all but two cases, pair-mates had separate

Table 2.9 Presence of butterflyfishes in different habitats at night, and occurrence of sheltered fish as single individuals (S), pairs (P) or groups (G; number in group in parentheses). No observations were made at night in the surge zone or sand coral interface habitats.

SPECIES	HABITAT											
	Shallow Coral-Rich			Shallow Coral-Poor			Cliff Base			Deep Coral-Rich		
	S	P	G	S	P	G	S	P	G	S	P	G
<u>C. fremblii</u>	1	0	0	0	0	0	1	0	0	0	0	0
<u>C. lunula</u>	0	0	0	0	0	0	1	0	0	0	0	0
<u>C. multicinctus</u>	4	0	0	7	0	0	16	1	0	9	0	0
<u>C. ornatissimus</u>	0	0	0	2	0	0	6	0	0	2	0	0
<u>C. quadrimaculatus</u>	4	0	0	6	0	0	2	0	0	0	0	0
<u>C. trifasciatus</u>	0	0	0	0	0	0	0	0	0	0	0	0
<u>C. unimaculatus</u>	0	0	0	1	0	0	2	0	0	0	0	0
<u>F. flavissimus</u>	0	0	0	0	0	0	5	2	6(3-9)	4	1	0
<u>F. longirostris</u>	0	0	0	0	0	0	2	0	0	1	0	0

shelters. Individual C. multicinctus and C. quadrimaculatus were observed to use the same shelters over a period of three years. Shelters of most species appeared unspecialized. Forcipiger flavissimus was observed to shelter upside-down in caves, often in groups of two or more (Table 2.9). The only other example of group sheltering was one group of seven C. unimaculatus sheltered near each other in a $2m^2$ area.

Most butterflyfishes foraged continuously during the day and used shelters exclusively at night. A notable exception was C. quadrimaculatus which fed on a lunar day (i.e. between moonrise and moonset) regardless of whether it was dark or light (see Hourigan 1986a, Chapter III). Chaetodon lunula was often observed in shelters or in non-feeding groups during the day, and may also feed at night.

When shelters were experimentally blocked, fishes quickly found new shelters within their territories. The nocturnal shelters of three C. multicinctus and three C. quadrimaculatus were covered. On the first night, all but one fish had switched to a new shelter within its territory. One C. quadrimaculatus sheltered in front of its old shelter on the first night, but subsequently switched shelters. There was no mortality among these fish during the subsequent year, nor were there any changes in the shelters of the six concurrent controls.

Distribution of predators and potential competitors:

Twenty-two species of piscivorous fishes were observed in the visual surveys at Puako. These species included muraenids

(*Enchelynassa canina*, *Gymnothorax (Lycodontis) eurostus*, *G. flavimarginatus*, *G. petelli*, *G. meleagris*, *G. undulatus*, *G. steindachneri*), one cirrhitid (*Paracirrhites forsteri*), one mullid (*Parupeneus cyclostomus*), holocentrids (*Sargocentron spiniferum* and *Holotrachys lima*), one carangid (*Caranx melampygus*), two lutjanids (*Aphareus furcatus*, *Lutjanus kasmira*), one grouper (*Cephalopholis argus*), two scorpaenids (*Scorpaenopsis cacopsis* and *S. diabolus*), one cornetfish (*Fistularia commersonii*), one trumpetfish (*Aulostomus chinensis*), two lizardfishes (*Synodus* sp. and *Saurida flamma*) and one wrasse (*Cheilinus unifasciatus*). The wrasse was especially abundant. All predators observed were large enough to feed on newly settled juvenile chaetodontids. Most adult muraenids and scorpaenids as well as the carangid, grouper and wrasse fed on fishes of the same size as the small and medium sized adult chaetodontids, as determined from gut content analyses.

Piscivores were most abundant in the deeper habitats (Fig. 2.7). The shallow surge zone contained the fewest predators. With the exception of one chaetodontid, *C. quadrimaculatus*, the occurrence of butterflyfishes was not negatively correlated with the occurrence of piscivores, as would be expected if butterflyfishes avoided habitats with predators (Table 2.10).

Butterflyfishes did not avoid predators when they were encountered during the day. On the contrary, when a predator, especially a moray eel, was discovered within the territory, individuals displayed in front of it, either laterally or facing the predator head down, with extended dorsal and anal spines. *Chaetodon*

Figure 2.7. Mean numbers of planktivorous, omnivorous and corallivorous butterflyfishes in six habitats at Site A at Puako during 1980 (N = 8 censuses in each habitat). Narrow bars represent 95% confidence limits around the mean. The mean numbers of non-chaetodontid corallivores (including P. johnstonianus), territorial pomacentrids and potential predators are also shown for each habitat.

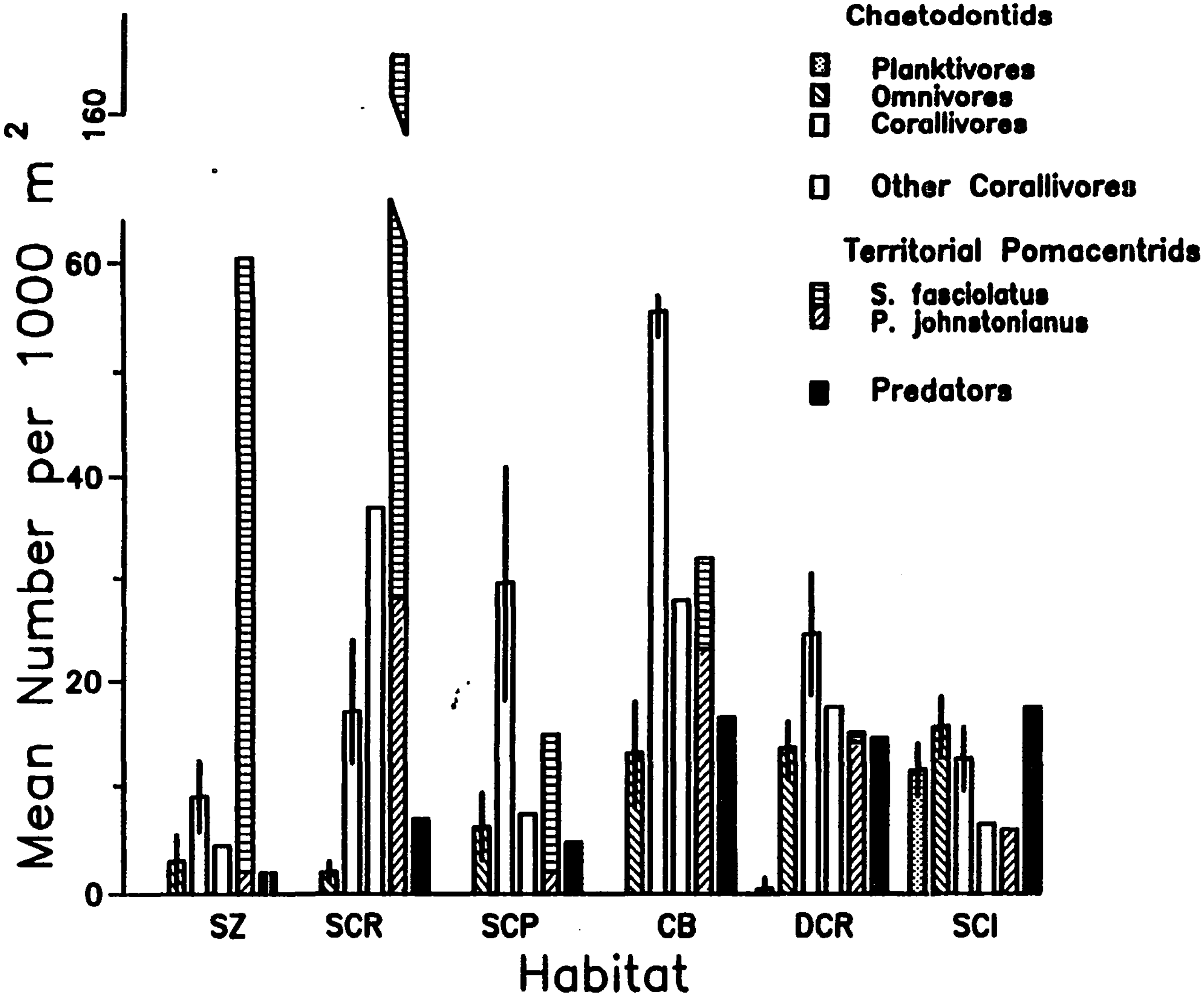

Chaetodontids
Planktivores
Omnivores
Corallivores
Other Corallivores
Territorial Pomacentrids
S. fasciolatus
P. johnstonianus
Predators
Mean Number per 1000 m²
0
20
40
60
160
SZ
SCR
SCP
CB
DCR
SCI
Habitat

Table 2.10 Correlation of the abundance of butterflyfishes seen during censuses with the abundance of piscivores, non-chaetodontid corallivores, and the territorial damselfishes *S. fasciolatus* and *P. johnstonianus*. r_s = Spearman rank correlation coefficient; p = probability of no correlation.

		Piscivores	Non-Chaetodontid Corallivores	*Stegastes fasciolatus*	*Plectroglyphidodon johnstonianus*
All Chaetodontids	r_s	0.602	0.421	- 0.290	0.433
	$p <$	0.001	0.001	0.001	0.001
Corallivorous Chaetodontids	r_s	0.415	0.509	- 0.013	0.493
	$p <$	0.01	0.001	NS	0.001
C. multicinctus	r_s	0.525	0.506	- 0.192	0.520
	$p <$	0.001	0.001	0.01	0.001
C. ornatissimus	r_s	0.316	0.415	- 0.004	0.462
	$p <$	0.001	0.001	NS	0.001
C. quadrimaculatus	r_s	- 0.250	0.002	0.590	- 0.098
	$p <$	0.01	NS	0.001	NS

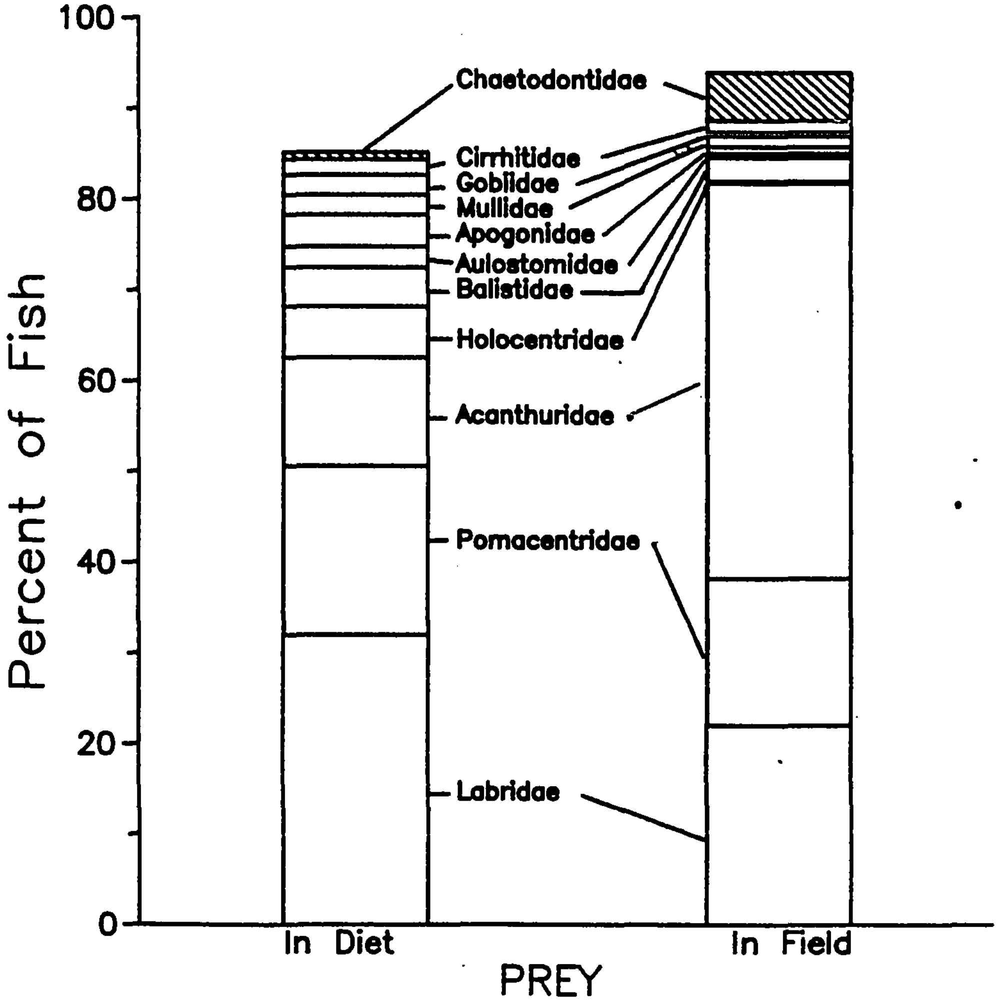
Data from all censuses at Site A and Site B, as well as data from large scale censuses in the summer of 1980 have been consolidated (N= 199 censuses).

multicinctus chased the large grouper, *Cephalopholis argus* on several occasions when it ventured into the butterflyfish's territory. The only exception observed was one occasion when a large jack, *Caranx melampygus*, swam over several *C. multicinctus* territories, and the territory holders dashed for cover. Most butterflyfishes remained within one meter of the substratum during normal activities. In contrast, the planktivores, *C. kleinii*, *C. miliaris*, *H. polylepis* and *H. thompsoni* swam well up into the water column when feeding, and ventured out over sand areas away from the coral reef. Juveniles of all species stayed very close to the bottom and were often sheltered.

During more than 700 hrs of daytime observations of fishes, numerous observations of piscivory were made, but none of these were directed toward butterflyfishes. Gut contents of 120 piscivores from Puako contained fish parts identifiable to family. One moray eel, *Gymnothorax meleagris* had eaten an adult *C. multicinctus* (SL = 78mm). The gut of one lizardfish, *Synodus* sp. contained a single scale tentatively identified as belonging to a chaetodontid. When the number of fish eaten per family was compared to the abundance of each family in the environment, it was found that chaetodontids were less common in the guts of piscivores than expected by chance (Fig. 2.8).

Several species of corallivores other than butterflyfishes also occurred on the reef. These included a blenny (*Exallias brevis*), three monocanthids (*Cantherhines dumerili*, *C. sandwichiensis*, *Pervagor melanocephalus*), two puffers (*Arothron hispidus*, *A. meleagris*), and the most abundant corallivore, the pomacentrid, *Plectroglyphidodon*

Figure 2.8. The occurrence of fishes by family in the diets of piscivores collected at Puako, compared to the relative abundance of those families on the reef. Chaetodontids were eaten less than would be expected by chance.


100
80
60
40
20
0
Percent of Fish
Chaetodontidae
Cirrhitidae
Gobiidae
Mullidae
Apogonidae
Aulostomidae
Balistidae
Holocentridae
Acanthuridae
Pomacentridae
Labridae
In Diet
In Field
PREY

johnstonianus (Fig. 2.7). The latter often chased butterflyfishes which attempted to feed in its territory (Fig. 2.9a). The butterflyfishes usually moved off, or less often, extended their dorsal spines toward the damselfish, preventing successful attacks. No other chases of chaetodontids by other species of corallivores were observed. Although C. multicinctus chased other species of corallivorous butterflyfishes, it was not observed to chase corallivores of other families (Fig. 2.9b). The distribution of non-chaetodontid corallivores was positively correlated with the distribution of corallivorous butterflyfishes (Table 2.10; Fig. 2.7).

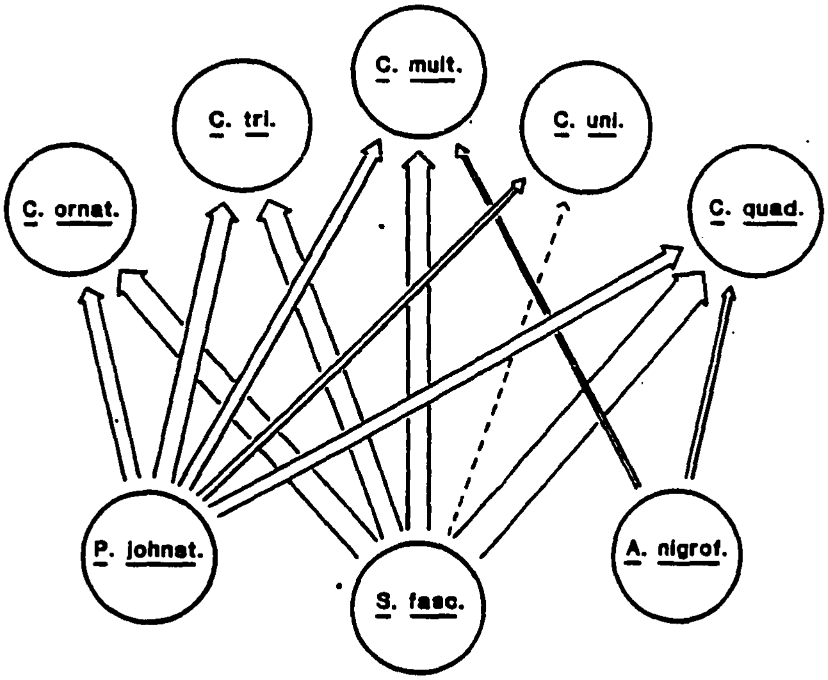
In addition to P. johnstonianus, a second species of damselfish, Stegastes fasciolatus, was observed to chase most butterflyfishes (Fig. 2.9). Stegastes fasciolatus, a territorial herbivore, was especially abundant in the shallow coral-rich zone (Fig. 2.7). Attacks on butterflyfishes by this species were more vigorous than attacks by P. johnstonianus, and feeding, especially by C. multicinctus and C. quadrimaculatus was often interrupted by such attacks. The distribution of butterflyfishes was negatively correlated with the distribution of this damselfish (Table 2.10). Chases of butterflyfishes by the herbivorous surgeonfish, Acanthurus nigrofuscus were also observed (Fig. 2.9a).

Field observations of corallivore feeding:

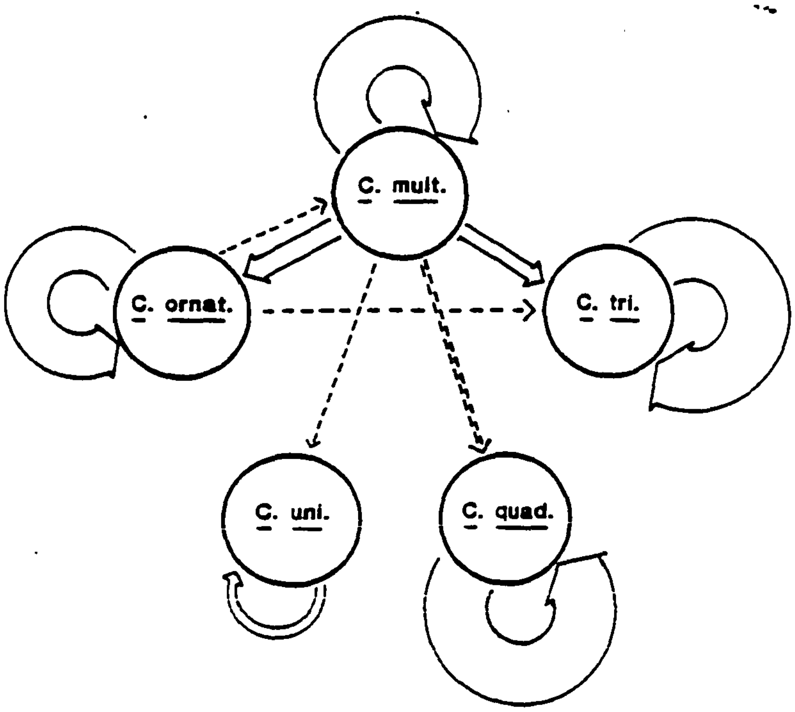
The feeding behavior of five species of corallivores (C. multicinctus, C. ornatissimus, C. quadrimaculatus, C. trifasciatus and

Figure 2.9. Chases of butterflyfishes by a) fishes other than butterflyfishes, and by b) other butterflyfishes. The width of the arrows is proportional to the number of chases observed per hour divided by the abundance of the chasing fish in the habitat (a measure of the opportunity for the chase to occur). Species are: *C. ornat.* - *Chaetodon ornatissimus*, *C. tri.* - *C. trifasciatus*, *C. mult.* - *C. multicinctus*, *C. uni.* - *C. unimaculatus*, *C. quad.* - *C. quadrimaculatus*, *P. johnst.* - *Plectroglyphididon johnstonianus*, *S. fasc.* - *Stegastes fasciolatus*, *A. nigrof.* - *Acanthurus nigrofuscus*.

a


C. mult.
C. tri.
C. uni.
C. ornat.
C. quad.
P. johnst.
S. fasc.
A. nigrof.

b


C. mult.
C. ornat.
C. tri.
C. uni.
C. quad.

C. unimaculatus) was observed. Brief observations were made of one other species of corallivore (*C. reticulatus*), three species of omnivores (*C. auriga*, *C. fremblii* and *C. citrinellus*) and one planktivore (*C. kleinii*). The results are shown in Table 2.11.

Within each habitat, butterflyfishes of different species differed in the number of feeding bites taken on each coral species (Kruskal-Wallis test, $p<0.05$; Table 2.12), indicating that they were not using food resources in the same manner. Within each species, the number of feeding bites on the three most abundant species of corals varied among habitats (Kruskal-Wallis test; $p<0.05$; Table 2.13). The percent of all bites on coral comprised by bites on each species of coral was compared to the percent of total coral cover in each habitat which was comprised of that coral species (Fig. 2.10). This allowed a determination of electivities and preferences for different coral species in the field (Table 2.14). A test of independence between percent coral abundance and percent of each coral in the diet showed that no species foraged on coral species in proportion to their abundance (Independent G-tests for five species of corallivores: $df = 3$, $p< 0.01$).

Each of the five species of butterflyfishes had similar coral preferences in the field, indicated by similar ranks of electivity indices (Table 2.14). All corallivorous butterflyfishes fed on *P. meandrina* more than expected from its relative abundance in the habitats. The less abundant corals of the genera, *Montipora*, *Cyphastrea* and *Leptastrea* were also fed on by all species somewhat more than expected by chance (i.e. positive electivity indices). The

Table 2.11 Feeding behavior of nine Hawaiian butterflyfishes. Feeding behavior is reported in bites per min, averaged over all habitats at Puako, Hawaii[1].

BITES PER MINUTE

	Minutes					Coral^2				Hard	Crevi-	Plank-	Sand	Other	Total
Species	observed	PM	PL	PC	MV	Msp.	L	CO	OC	Subtr.	ces	ton			
C. auriga	50	0	0	0	0	0	0	0	0.12	1.93	3.29	0	0.02	0.01	5.35
C. citrinellus	50	0.15	0	0	0	0	0	0	0	6	1.6	0	0.2	0.19	8.14
C. fremblii	1335	0	0	0	0	0	0	0	0	9.08	0.18	0.01	0.82	0.12	10.21
C. kleinii	125	0	0	0	0	0	0	0	0	0.36	0	9.2	0	0	9.56
C. multicinctus	2530	0.96	7.8	1.93	0.04	<.01	<.01	<.01	<.01	1.27	<.01	<.01	<.01	<.01	12.03
C. ornatissimus	400	3.29	7.88	1.56	0.2	0.19	0.19	0.04	0.20	0.01	0	0	0	<.01	13.57
C. quadrimaculatus	1765	2.09	0.39	0	<.01	<.01	0.01	<.01	<.01	2.9	3.74	0	0.01	0.01	9.17
C. reticulatus	20	1.15	4.6	0.25	0.9	0.25	0.7	0.8	2.3	0.45	0	0	0	0	9.17
C. trifasciatus	400	1.29	6.62	0.58	0.14	0.14	0.21	0.17	0.18	0.25	0	0	0	<.01	9.58
C. unimaculatus	400	7.14	0.46	0	1.18	1.84	0.26	0.04	0.05	0.03	0	0	0	0	11.00

---

1. Data for *C. fremblii* were gathered at Kahe Pt. Oahu, not Puako.

2. Corals are: PM = *Pocillopora meandrina*; PL = *Porites lobata*; PC = *Porites compressa*; MV = *Montipora verrucosa*; Msp. = *Montipora petelli* and *M. verrilli*; L = *Leptastrea purpureum*; CO = *Cyphastrea ocellina*; OC = Other Corals.

Table 2.12 Comparisons of feeding rates of butterflyfishes on different species of corals in each of four habitats at Puako. Species are ranked from left to right, from highest to lowest mean feeding rate for each species of coral. Kruskal-Wallis non-parametric test for differences in rank of population densities among species (* = $p<0.05$). Differences in mean ranks were compared using the parametric Waller-Duncan K-ratio test for multiple comparisons: Underlines connect those species whose mean feeding rates were not significantly different in that habitat ($p>0.05$).

	HABITAT			
Coral:	SHALLOW CORAL-RICH	SHALLOW CORAL-POOR	CLIFF BASE	DEEP CORAL-RICH
Porites lobata	CMU COR CTR CQU CUN*	CTR COR CMU CUN CQU*	COR CTR CMU CQU CUN*	COR CMU CTR CUN*
P. compressa[1]			COR CTR CMU CQU CUN*	COR CMU CTR CUN*
Poc. meandrina	CUN CMU COR CTR CQU*	CUN COR CMU CQU CTR*	CUN CQU CTR COR CMU*	CUN CTR COR CMU*
Other Corals	CTR CUN COR CQU CMU*	COR CTR CUN CMU CQU*	CUN CQU CTR COR CMU*	CUN COR CTR CMU*
All Coral	CMU CUN COR CTR CQU*	COR CUN CMU CTR CQU*	COR CMU CTR CUN CQU*	COR CMU CTR CUN*
Total Bites	CMU CUN COR CTR CQU*	COR CUN CMU CQU CTR*	COR CMU CTR CUN CQU*	COR CMU CTR CUN*

---

1. *P. compressa* did not occur in the shallow reef areas.

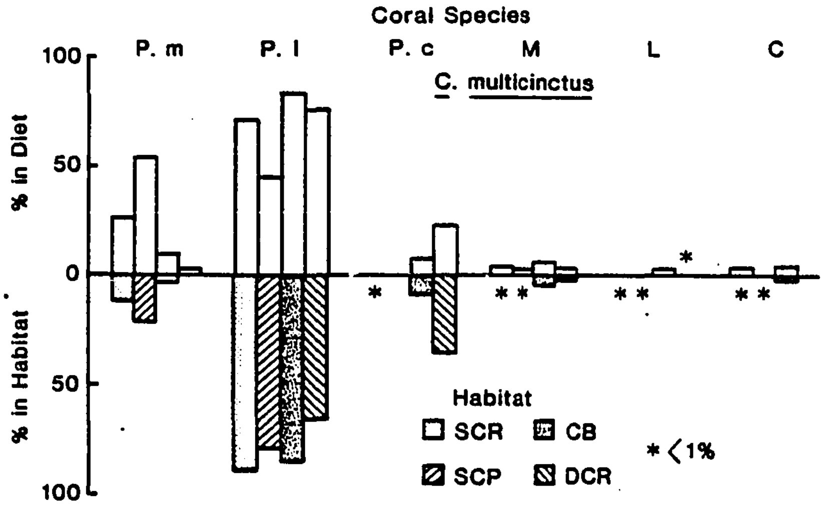
Butterflyfish species abbreviations are: CMU = *C. multicinctus*, COR = *C. ornatissimus*, CQU = *C. quadrimaculatus*, CTR = *C. trifasciatus*, CUN = *C. unimaculatus*.

Table 2.13 Comparisons of feeding rates of butterflyfishes in different habitats at Puako, Hawaii, on each coral species. Habitats are ranked from left to right, from highest to lowest mean feeding rate for each habitat. Kruskal-Wallis non-parametric test for differences in rank of population densities among species (* = $p<0.05$). Differences in mean ranks were compared using the parametric Waller-Duncan K-ratio test for multiple comparisons: Underlines connect those species whose mean feeding rates were not significantly different in that habitat ($p>0.05$).

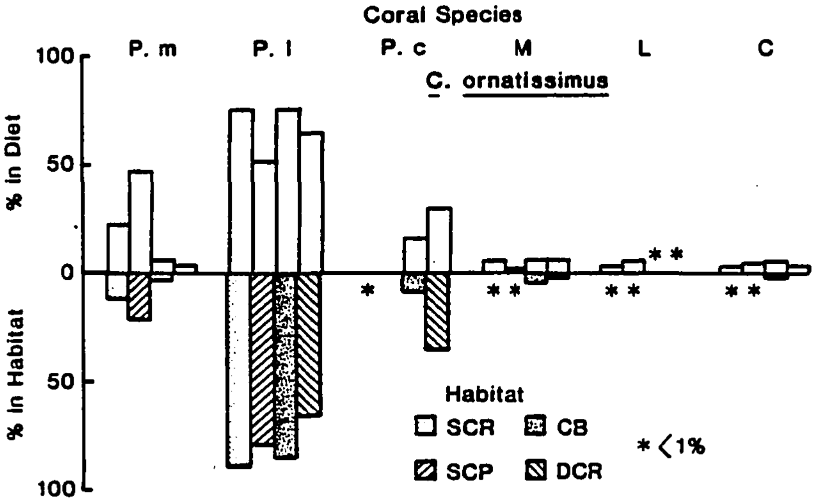
	BUTTERFLYFISH SPECIES				
Coral:	*C. ornatissimus*	*C. trifasciatus*	*C. unimaculatus*	*C. multicinctus*	*C. quadrimaculatus*
Porites lobata	CB DCR SCR SCP*	CB DCR SCP SCR*	SCP SCR CB DCR*	DCR SCR CB SCP*	CB SCP SCR*
P. compressa	DCR CB SCR SCP*	DCR CB SCR SCP*	- - - -	DCR CB SCR SCP*	- - -
Poc. meandrina	SCP SCR CB DCR*	SCR SCP CB DCR*	SCP SCR CB DCR*	SCP SCR CB DCR*	SCP SCR CB *
Other Corals	CB DCR SCR SCP	SCR CB SCP DCR	DCR CB SCP SCR*	SCP DCR CB SCR	SCP SCR CB
All Coral	SCP DCR CB SCR	DCR CB SCR SCP*	SCP SCR CB DCR*	DCR SCR SCP CB	SCP CB SCR*
Total Bites	SCP CB DCR SCR	DCR CB SCR SCP*	SCP SCR CB DCR*	DCR SCP CB SCR*	SCP CB SCR*

Abbreviations for habitats are the same as in Table 1.

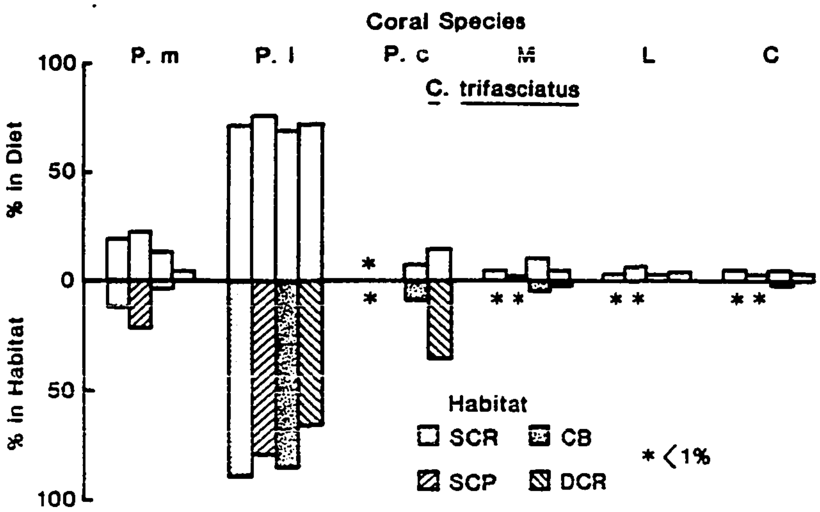
Figure 2.10. Feeding preferences of five chaetodontids on coral species in relation to coral abundance within each of four habitats at Puako, HI. Habitats are: SCR - shallow coral rich; SCP - shallow coral poor; CB - cliff base; DCR - deep coral rich. Percent occurrence of corals in the diet was determined 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. Coral species are: Pm - *Pocillopora meandrina*; Pl - *Porites lobata*; Pc - *Porites compressa*; M - *Montipora* spp. L - *Leptastrea* spp.; C - *Cyphastrea ocellina*. * indicates a percent occurrence of less than 1% for that coral in the habitat or in the diet.


Coral Species
P. m
P. l
P. c
M
L
C
C. multicinctus
100
50
0
50
100
% in Diet
% in Habitat
Habitat
SCR
CB
SCP
DCR
* < 1%

a

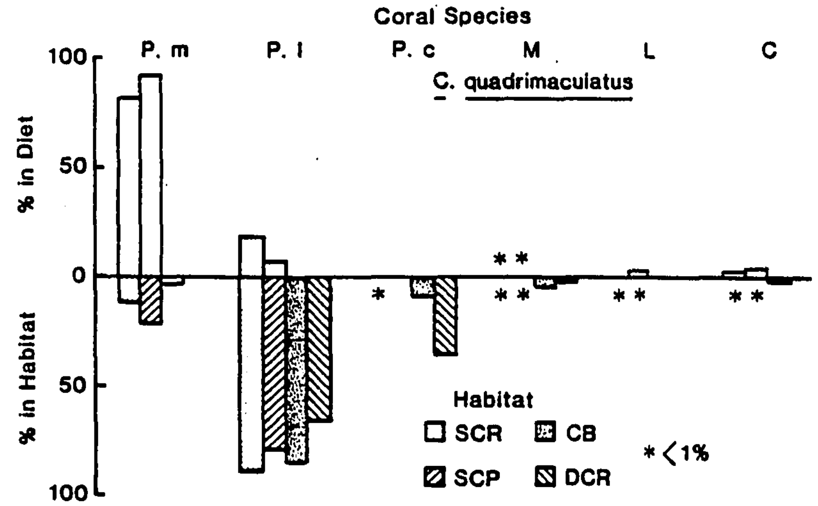

Coral Species
P. m
P. l
P. c
M
L
C
C. ornatissimus
100
50
0
50
100
% in Diet
% in Habitat
Habitat
SCR
CB
SCP
DCR
* < 1%

b

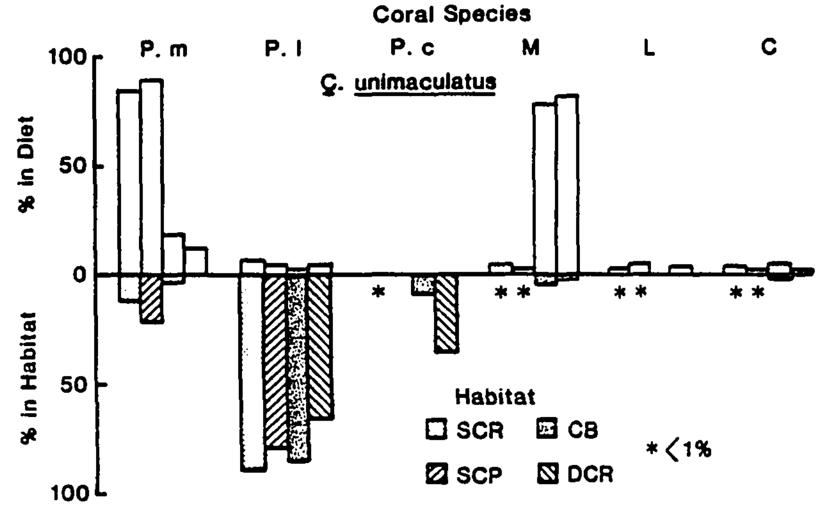

Coral Species
P. m
P. l
P. c
M
L
C
C. trifasciatus
100
50
0
50
100
% in Diet
% in Habitat
Habitat
SCR
CB
SCP
DCR
* < 1%

c

Figure 2.10 (cont.). Feeding preferences of five chaetodontids on coral species in relation to coral abundance within each of four habitats at Puako, HI. Habitats are: SCR - shallow coral rich; SCP - shallow coral poor; CB - cliff base; DCR - deep coral rich. 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. Coral species are: Pm - *Pocillopora meandrina*; Pl - *Porites lobata*; Pc - *Porites compressa*; M - *Montipora* spp. L - *Leptastrea* spp.; C - *Cyphastrea ocellina*. * indicates a percent occurrence of less than 1% for that coral in the habitat or in the diet.


Coral Species
P. m
P. l
P. c
M
L
C
C. quadrimaculatus
% in Diet
% in Habitat
100
50
0
50
100
Habitat
SCR
CB
SCP
DCR
* <1%

d


Coral Species
P. m
P. l
P. c
M
L
C
C. unimaculatus
% in Diet
% in Habitat
100
50
0
50
100
Habitat
SCR
CB
SCP
DCR
* <1%

e

Table 2.14 Comparison of electivity indices and field and laboratory coral-feeding preferences of five chaetodontids. Electivities are based on field observations of 20 individuals of each fish species. Probability (p) of accepting the null hypothesis: that mean electivity = 0, was determined by paired t-tests between the mean proportion of coral in each habitat and the mean proportion of bites on each coral species. Field ranks signify differences in mean electivity indices based on the Waller-Duncan K ratio t-test for multiple comparisons. Laboratory ranks are based on Wilcoxon's signed-ranks test (N=10, p<0.05).

BUTTERFLYFISH SPECIES		CORAL SPECIES[1]					
		PM	C	L	M	PL	PC
C. multicinctus	Electivity	0.504	.0169	0.028	0.099	−0.082	−0.466
	p <	0.05	0.2	0.4	0.5	0.4	0.05
	Field Rank	1	2	2	3	4	5
	Lab Rank	1	2	3	4	5	6
C. ornatissimus	Electivity	0.319	0.313	0.175	0.28	−0.106	−0.238
	p <	0.1	0.1	0.4	0.2	0.05	0.9
	Field Rank	1	1	3	2	4	4
	Lab Rank	1	-	-	2**	3	4**
C. trifasciatus	Electivity	0.447	0.39	0.416	0.264	−0.052	−0.214
	p <	0.05	0.05	0.1	0.1	0.2	0.1
	Field Rank	1	3	2	4	5	6
	Lab Rank	1	-	-	2**	3	4**
C. quadrimaculatus	Electivity	0.684	0.27	0.056	0.005	−0.768	−1
	p <	0.01	0.1	0.2	0.9	0.01	0.05
	Field Rank	1	2	3	4	5	6
	Lab Rank	1	2	3	4	5	6
C. unimaculatus	Electivity	0.75	0.448	0.479	0.789	−0.918	−1
	p <	0.05	0.05	0.1	0.1	0.001	0.02
	Field Rank	1	2	2	1	3	4
	Lab Rank	2	3	-	1*	4	5*

* data supplemented from Cox (1983).

** data supplemented from Reese (1977).

1. Corals are: PM = *Pocillopora meandrina*; M = *Montipora*; L = *Leptastrea purpureum*; C = *Cyphastrea ocellina*; PL = *Porites lobata*; PC = *Porites compressa*.

abundant corals, Porites lobata and Porites compressa, were fed on relatively less than expected by chance.

Although all species were generally similar in their order of coral preferences, two different feeding types - coral-feeding generalists and coral-feeding specialists - could be established. Generalists feed on a wide variety of prey items, and the amount of each type of prey item ingested will depend on the relative abundance available (Birkeland and Neudecker 1980). In contrast, specialists consistently favor certain prey items whether these items are abundant or rare. Chaetodon multicinctus, C. ornatissimus and C. trifasciatus were coral-feeding generalists, feeding on almost all species of corals (Fig. 2.10a,b,c). In contrast, C. quadrimaculatus and C. unimaculatus appeared to specialize on one or two species of coral (Fig. 2.10e,f). These coral species were also preferred by the generalist species. Chaetodon quadrimaculatus supplemented its diet with food other than coral (Table 2.11).

The similarity of the diets of the five corallivores was compared using Schoener's (1968a) similarity index, and by discriminant function analysis in which each food category was a variable (Table 2.15). Both measures of similarity showed that dietary overlap was greatest among the coral-feeding generalists, C. multicinctus, C. ornatissimus and C. trifasciatus. The coral-feeding specialists, C. quadrimaculatus and C. unimaculatus, had the most distinct diets.

Results of gut content analyses agreed with feeding observations. Chaetodon multicinctus, C. ornatissimus, and C. trifasciatus stomachs

Table 2.15 Dietary overlap among corallivorous butterflyfishes at Puako, Hawaii. D = Schoener's Index of Dietary Overlap. P = a posteriori probability of classifying each 5 min feeding observation of an individual as belonging to a particular species. P was determined from discriminant function analysis and expressed as the proportion of all observations classified into each species. The two indices are not numerically comparable, but the trends are similar for both.

		Proportion of Observations Classified into Species:				
From Species:		<u>C. multicinctus</u>	<u>C. ornatissimus</u>	<u>C. trifasciatus</u>	<u>C. quadrimaculatus</u>	<u>C. unimaculatus</u>
<u>C. multicinctus</u>	D =	1	0.779	0.821	0.230	0.129
	P =	0.881	0.049	0.070	0	0
<u>C. ornatissimus</u>	D =	–	1	0.839	0.273	0.335
	P =	0.132	0.553	0.276	0	0.039
<u>C. trifasciatus</u>	D =	–	–	1	0.205	0.239
	P =	0.200	0.267	0.500	0	0.033
<u>C. quadrimaculatus</u>	D =	–	–	–	1	0.274
	P =	0.039	0	0	0.953	0.009
<u>C. unimaculatus</u>	D =	–	–	–	–	1
	P =	0.026	0	0	0	0.973

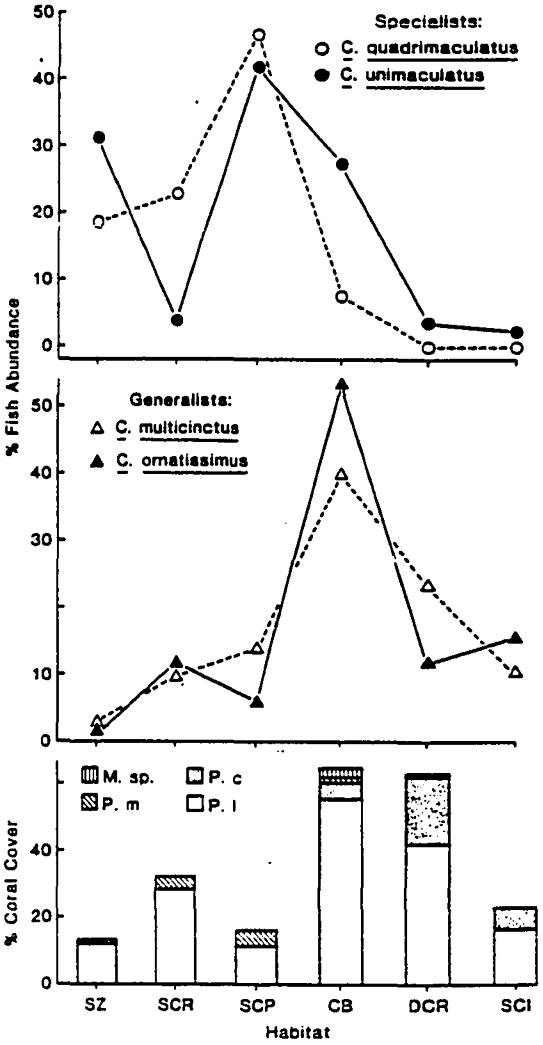
contained predominantly coral tissue, while *C. unimaculatus* stomachs contained coral tissue and calcium carbonate from corals. *Chaetodon quadrimaculatus* ingested coral tissue, polychaetes, small crustaceans and algae.

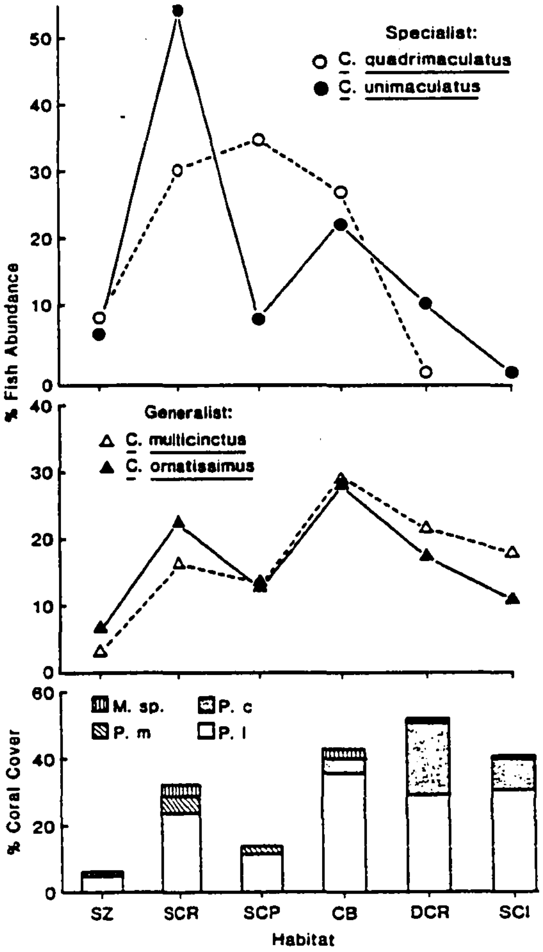
The abundance of corallivorous butterflyfishes in each habitat was related to the abundance of preferred corals in that habitat rather than to total coral cover. The distribution of specialists at both geographic sites most closely followed the distribution of preferred corals (*P. meandrina* for *C. quadrimaculatus*; *P. meandrina* and *Montipora* spp. for *C. unimaculatus*; Fig. 2.11). The generalists were more broadly distributed among habitats (Fig. 2.11), but their numbers appeared to be little influenced by the abundant but least preferred coral, *P. compressa*. The abundances of the coral-feeding generalists, *C. multicinctus* and *C. ornatissimus* observed on each census were positively correlated (Spearman Rank; $N=199$, $r_s = 0.468$, $p<0.0001$). The abundance of the specialist, *C. quadrimaculatus* was not positively correlated to either species (Spearman Rank correlation with *C. multicinctus*: $r_s = -0.166$, $p<0.05$; with *C. ornatissimus* $r_s = -0.015$, $p>0.8$). The remaining two species, *C. trifasciatus* and *C. unimaculatus*, were not abundant enough for statistical comparisons.

Feeding preferences in the laboratory:

The feeding preferences of butterflyfishes which were offered choices of corals in the laboratory matched the feeding preferences of

Figure 2.11. Percent occurrence of two coral-feeding specialists and two coral-feeding generalists in six different habitats compared to the abundance of the four most abundant species of corals. Patterns are similar at the two geographically separated sites at Puako: a) Site A and b) Site B. Habitats listed 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.


Specialists:
○ C. quadrimaculatus
● C. unimaculatus
Generalists:
△ C. multicinctus
▲ C. ornatissimus
% Fish Abundance
% Coral Cover
M. sp.
P. c
P. m
P. l
SZ
SCR
SCP
CB
DCR
SCI
Habitat
0
10
20
30
40
50


Specialist:
○ C. quadrimaculatus
● C. unimaculatus
Generalist:
△ C. multicinctus
▲ C. ornatissimus
% Fish Abundance
% Coral Cover
M. sp.
P. c
P. m
P. l
SZ
SCR
SCP
CB
DCR
SCI
Habitat
0
10
20
30
40
50
60

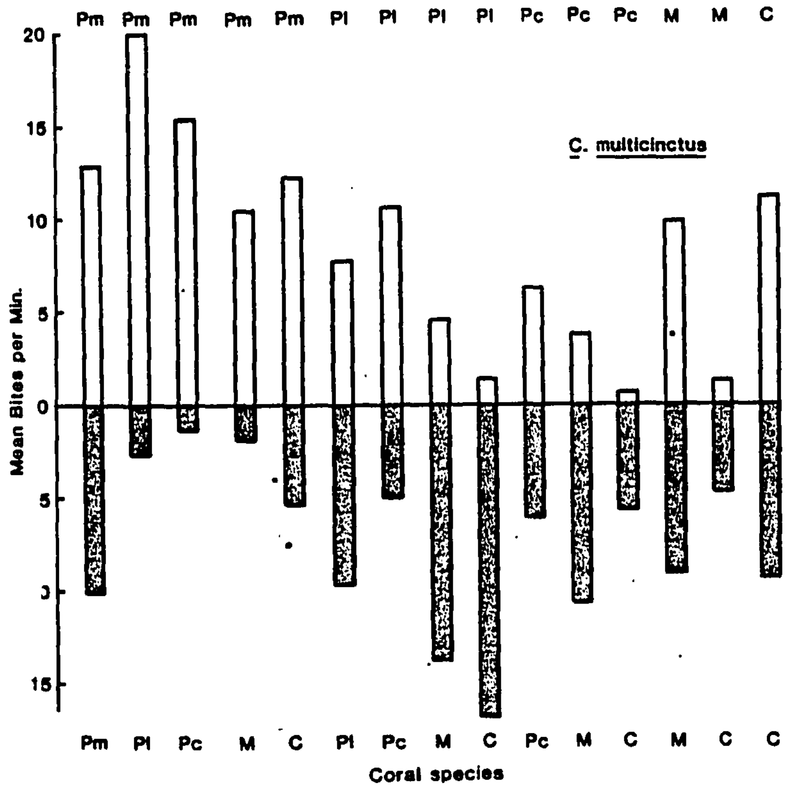
those fishes when observed in the field. Complete determinations of coral preferences in the laboratory were made for two abundant corallivores, C. quadrimaculatus and C. multicinctus (Fig. 2.12). Both species showed consistent preferences for certain corals (Wilcoxon's signed rank test $p < 0.05$) which allowed an independent ranking of coral preferences. Incomplete data on the remaining three species were supplemented with data from Reese (1977) and Cox (1983) and are shown in Table 2.14. All five species showed consistent preferences in the laboratory and in the field. As in the field, C. unimaculatus and C. quadrimaculatus appeared to be specialists on certain species of coral, often refusing to feed on other species even in a no-choice situation (Fig. 2.12b). The remaining three species fed on almost all corals offered, but preferred the same corals as the specialists. Only the mushroom coral, Fungia scuteria was not fed on by C. multicinctus when offered alone.

Use of space and interactions with other fishes:

Home ranges were measured for individuals of five species of corallivores, as well as the omnivore, C. auriga and the planktivore, C. kleinii (Table 2.16). Conspecific individuals of C. multicinctus, C. ornatissimus, C. trifasciatus, C. quadrimaculatus and C. auriga formed male-female pairs which defended territories against conspecifics. Home range boundaries and foraging boundaries of a pair coincided with the area defended and therefore these areas were considered feeding territories. Most aggressive encounters occurred

Figure 2.12. Laboratory feeding experiments on a) C. multicinctus, and b) C. quadrimaculatus. Each bar represents the mean feeding rate for paired coral presentations to ten different individuals. Coral species are: Pm - Pocillopora meandrina; Pl - Porites lobata; Pc - Porites compressa; M - Montipora verrucosa; C - Cyphastrea ocellina. Preferences for one coral species in a paired presentation were determined using Wilcoxon's signed-ranks test: * - $p < 0.05$.

a


Pm Pm Pm Pm Pm Pl Pl Pl Pl Pc Pc Pc M M C
20
15
10
5
0
5
10
15
Mean Bites per Min.
C. multicinctus
Pm Pl Pc M C Pl Pc M C Pc M C M C C
Coral species

b

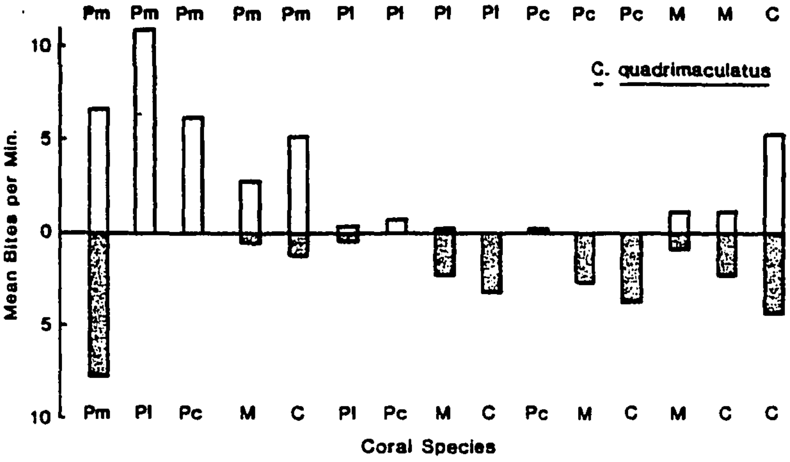

Pm Pm Pm Pm Pm Pl Pl Pl Pl Pc Pc Pc M M C
10
5
0
5
10
Mean Bites per Min.
C. quadrimaculatus
Pm Pl Pc M C Pl Pc M C Pc M C M C C
Coral Species

Table 2.16 Size of home ranges of individuals of seven butterflyfish species at Puako, Hawaii.

	HABITAT					
	Shallow Coral-Poor			Deep Coral-Rich		
	N	Mean m^2	Range m^2	N	Mean m^2	Range m^2
C. auriga	2	11,360	10490-12230	-	-	
C. kleinii	-	-		3	301	231-459
C. multicinctus	15	107	71-171	29	73	44-97
C. ornatissimus	1	1081		3	795	590-848
C. quadrimaculatus	24	276	105-558	-	-	
C. trifasciatus	2	1110	995-1207	1	884	
C. unimaculatus	4	1393	981-1653	-	-	

among conspecifics (Fig. 2.9b). Adults of all corallivores except *C. unimaculatus* chased conspecific juveniles.

Adult *C. multicinctus* defended the smallest territories (Table 2.16). Species with larger body sizes had larger territories. The same pairs defended the same territories throughout the year. Pairs of *C. multicinctus* and *C. quadrimaculatus* were observed for four years, during which time they defended the same territories.

Four additional species, *C. kleinii*, *C. lineolatus*, *C. reticulatus* and *F. longirostris*, also appeared to form pairs. *Chaetodon unimaculatus* differed from the other corallivores in that individuals inhabited large, overlapping home ranges.

DISCUSSION

Summary by Species:

Trends in the distribution and behavior of butterflyfishes in Hawaii were most apparent when individual species were analyzed separately. Fishes are listed by feeding guild, as planktivores, omnivores and corallivores.

A. Planktivores:

Chaetodon kleinii

The distribution of this species was highly predictable and similar for all sites studied. *Chaetodon kleinii* was always found near the deep, sand-coral interface (Fig. 2.3c). This was the area where pelagic plankton first encountered the reef. Hobson and Chess (1978) observed that many planktivores move to the windward edge of a reef to intercept the plankton when it first comes over the reef. These planktivores can significantly decrease the plankton available. Indeed, most chaetodontid and non-chaetodontid planktivores were most abundant in this habitat (Hayes et al. 1982). Proximity to the reef may provide shelter, while still allowing the fish to reap the richest plankton sources. *Chaetodon kleinii* was not limited to deeper water in other areas of Hawaii where small patch reefs were interspersed with large areas of sand (Pers. obs.). The diet of *C. kleinii* overlaps extensively with the diets of *C. miliaris*, and *Hemitaurichthys* spp. (Hobson 1974, Ralston 1981).

The behavior of C. kleinii differed from that of other Hawaiian planktivores. Rather than schooling, it appeared to form pairs which defended territories along the interface. Reese (1978) suggested that planktivorous butterflyfishes would be unlikely to form pairs, since their food is patchily distributed and unpredictable, and is therefore not economic to defend (sensu Brown 1964). However, the topography at Puako provides some areas of reef at the deep, sand-coral interface, which are probably richer in plankton, and are defendable. Linear territories along the edge of a resource are known for other animals, e.g. dragonflies along the edge of a pond (Davies 1978).

C. miliaris

Chaetodon miliaris was not abundant at Puako. All adults were found near the sand coral interface, probably for the same reasons as C. kleinii. Chaetodon miliaris differed from C. kleinii in that it appeared to be less site attached, often forming aggregations which moved along the sand-coral interface, congregating near pinnacles or points of the reef which jutted out into the sandy areas. Groups moved further out over the sand areas as well as higher in the water column than did C. kleinii. Aggregation may provide protection from large predators, allowing fishes to forage further from cover.

Chaetodon miliaris is endemic to Hawaii (Burgess 1978), and is the most abundant fish at depths between 50m and 100m (Brock and Chamberlain 1968). It feeds on plankton as well as some benthic invertebrates (Hobson 1974, Ralston 1976, 1981, Motta 1980, 1982). It is also very abundant in shallow waters in other areas of the Hawaiian

Islands (Motta, 1980, Ralston 1976, 1981 and pers. obs.). It is not clear why it should be relatively uncommon at Puako.

Ralston (1981) suggested that planktivory by *C. miliaris* may have evolved in Hawaii where there are fewer planktivorous fishes. If so, this may be an example of a change in resource use as a result of the relaxation of competition in Hawaii, as predicted by the resource limitation hypothesis (Hourigan and Reese 1987).

Recently settled juvenile *C. miliaris* were found only in the shallow waters of the surge zone (Table 2.8). These shallow areas are relatively free of larger predators (Fig. 2.7), and are a common habitat for the recruitment of juveniles of many species, including another butterflyfish, *C. lunula* (Hobson 1974). Sale (1968, 1969) showed that the juveniles of the Hawaiian acanthurid, *Acanthurus triostegus*, preferentially chose shallow areas. Although a few *C. miliaris* recruits were noticed in these areas during each year of this study, there was a large influx during 1983. This illustrated the temporally variable nature of larval recruitment, which was also noticeable in peaks of larval settlement in other species in other years. Walsh (1984, 1987) and Schroeder (1985) have documented such patterns for numerous Hawaiian species.

Hemitaurichthys polylepis and *H. thompsoni*

Like the preceding species, both these species occurred near the sand-coral interface. Of the two, *H. polylepis* was the more abundant in the study areas. Although almost identical in morphology, there was no evidence of competitive exclusion, and when *H. thompsoni* was observed, H. polylepis was almost invariably also present. They differed from C. miliaris in that when schooling, they formed much tighter, well coordinated schools, which appeared to travel well out over areas of sand, perhaps to deeper areas. Butterflyfishes of the genus Hemitaurichthys occur in many areas of the Indo-Pacific, and all appear to be planktivores (Allen 1979).

B. Omnivores:

Chaetodon auriga

This species was among the largest of the Hawaiian chaetodontids and although regularly present, it was nowhere abundant. Foraging ranges of individual pairs were very large (Table 2.16) and extended over different habitats. Despite the large size of the foraging ranges, they intraspecifically exclusive, and were defended against conspecific pairs. The behavior of C. auriga resembled that of the other species of butterflyfishes which formed pairs and defended territories. Chaetodon auriga occurs throughout the Indo-Pacific, and is generally observed in pairs (Reese 1975).

Consistent with observations of other researchers (Hobson 1974, Motta 1980), this species fed mostly on large, sessile invertebrates (Table 2.11). Coral feeding was observed on only one occasion, when it fed on the solitary coral Tubastrea coccinea. The large size of the territories may have resulted from the large body size of this fish and the sparse distribution of the food resources, or from a low density of territorial conspecifics, due perhaps to low recruitment. Either or both factors could result in the observed patterns.

C. citrinellus

This species was very rare in all study sites on the Island of Hawaii. It fed primarily on algae and non-coralline invertebrates, with occasional bites on the coral Pocillopora meandrina. Reese (1975) observed this species to be strongly paired at Enewetak, and he classified it as a facultative corallivore.

C. fremblii

Chaetodon fremblii, a Hawaiian endemic, occurred in most habitats, but was nowhere abundant. No habitat preferences were discernible from the present data. In areas around the island of Oahu and in the Northwest Hawaiian Islands, where this species is more abundant, it generally occurs most commonly on reef areas near sand, where it feeds on algae on hard substrata and on polychaetes in the sand (Hobson 1974, Hourigan Chapter IV).

The social behavior of this species was not observed at Puako. Elsewhere in Hawaii, individuals form harems in which one male defends a territory containing one to four females (Hourigan 1986b and Chapter IV). Females defend individual territories against other females within the larger territory of the male.

C. lineolatus

This species was very uncommon at Puako, but when observed, always occurred in pairs. It was the largest Hawaiian species, and appeared to behave in a similar fashion to *C. auriga*. Interestingly, both species reach a larger size in Hawaii than in other areas of the Indo-Pacific (E. Reese, pers. comm. and pers. obs.). At Heron Is., on the Great Barrier Reef small *C. lineolatus* formed groups of 4 to 12 individuals. Recruits of this species were never observed. The rarity of adults, and perhaps their occurrence in pairs rather than larger groups, may have been a result of low recruitment.

C. lunula

Groups of *C. lunula* were often seen near the cliff face. Unlike most other butterflyfishes, individuals of this species were seldom observed to feed during the day. Nocturnal feeding in this species was suggested by Hobson (1974) who collected fish with full guts an hour before sunrise. It is not known why *C. lunula* congregated near the cliff face during the daytime. Large groups were observed traversing the reef at dusk and dawn, indicated that nocturnal or crepuscular feeding may occur at a distance from the diurnal shelters. Such crepuscular "parades" are common among other species (Hobson 1973, 1974, Walsh 1984), but have not been previously reported for a chaetodontid. Sheltering together may facilitate grouping before the initiation of such migrations.

All new recruits to the reef occurred in the shallow surge zone or in tide pools. This area may serve as a refuge from predators as suggested above for *C. miliaris*.

Forcipiger flavissimus

Forcipiger flavissimus was the most abundant omnivore at the study sites. It was most abundant in the deepest habitat, at the sand-coral interface (Fig. 2.3b). Unlike most butterflyfishes, it fed singly or in groups of up to 20 fish during the day, and was often observed at night, sheltering with conspecifics. Cursory observations of its social behavior and feeding were insufficient to reveal the basis of its social structure. Motta (pers. comm.) observed differences in feeding behavior among different habitats at Puako. In shallow areas, it fed primarily on vermetid mollusks, inserting its long mouth into the mollusk's tube. In the deeper areas where vermetids were less abundant, it fed primarily on sedentary polychaetes using a similar feeding method. Without knowledge of the distribution of these food resources, it was not possible to determine their influence on the observed distribution of this fish.

This species was superficially very similar to *F. longirostris* with which it co-occurred. Hobson (1974) showed, however, that these species differ in mouth morphology and diet. The jaw suspension of the two species is very different, indicating greater divergence than would be expected from the external morphology (Motta in prep). Ludwig (1984) studied the morphology of both species where they occurred together, as well as an allopatric population of *F. flavissimus* for evidence of character displacement. Although he did find some minor differences between the populations of *F. flavissimus*, he was unable to relate these differences to competition.

Forcipiger species were the only abundant species for which no new recruits were observed on the reef. Both species appear to spawn later than most other Hawaiian chaetodontids, and have a longer larval period (Ludwig 1984), and consequently, most settlement occurs in September, after the time of our surveys.

F. longirostris

Forcipiger longirostris occurred almost exclusively in the deeper areas below the cliff (Fig. 2.3b). There was no evidence of habitat partitioning or interactions between the outwardly similar *Forcipiger* species. Ludwig (1984) found a similar distribution, and suggested that the more delicate rostrum of *F. longirostris* was endangered by surge when probing in crevices in shallow waters. This seems unlikely, since it appears to use its mouth as a siphon for sucking in plankton (Motta in prep, and pers obs.) rather than for probing in crevices as does *F. flavissimus*. Unlike other planktivores, *F. longirostris* fed on small demersal plankton, usually within 10cm of the bottom, rather than higher in the water column.

Unlike the previous species, *F. longirostris* occurred in pairs which defended home ranges against conspecifics. It was not clear why these species should differ in social behavior. Black morphs of *F. longirostris* at Puako composed around 30% to 40% of the population. The function of this coloration is not known, however, individuals have been observed to change coloration from the black to the yellow form within a few days (Bruce Carlson, pers. comm.).

C. Corallivores:

Chaetodon multicinctus

Chaetodon multicinctus was the smallest butterflyfish, and the most abundant species in most habitats. Adults occurred in male-female pairs which defended feeding territories against conspecific pairs. Chases of other corallivorous butterflyfishes, especially C. ornatissimus and C. trifasciatus, were also observed (Fig. 2.9b). Despite these chases, there was no evidence that adults of these larger species were ever successfully excluded from feeding in the territories of C. multicinctus.

In the field, most feeding bites were directed toward living corals, especially the abundant species, Porites lobata, Porites compressa and Pocillopora meandrina (Table 2.11). Feeding preference tests in the laboratory showed preferences for P. meandrina over P. lobata, which was in turn preferred over P. compressa (Fig. 2.12). Similar feeding preferences were deduced from field feeding observations in the present study (Table 2.14) and by Tricas (1986). Although the abundance of C. multicinctus was correlated with total coral cover (Spearman Rank, $r_s = 0.54$ $p < 0.01$), the correlation was much better when the least preferred coral, P. compressa was excluded (Spearman Rank, $r_s = 0.79$ $p < 0.0001$; Fig. 2.11).

Territorial pairs successfully excluded a number of non-territorial conspecifics. These non-territorial "floaters" fed less than territorial pair mates and were non-reproductive (Hourigan Chapter III). This suggests that intraspecific territoriality limited the number of breeding individuals in this population. When single individuals were removed from their pair mates, mate replacement occurred within one to four days, further indicating the presence of floaters (Hourigan Chapter VI). When an individual or a pair was removed, the area was never taken over by another species as would be predicted by the lottery hypothesis.

Chaetodon multicinctus was the most abundant butterflyfish recruited to the reef in all years (Table 2.8). New recruits occurred in the same areas as the adults, and were vigorously chased by the adults.

Chaetodon multicinctus has recently been the subject of several studies of feeding behavior (Tricas 1985, 1986, Hourigan et al. 1987, Hourigan Chapter III, Motta in prep), morphology (Motta in prep), energetics (Hourigan Chapter V, Tricas in prep), life history (Tricas 1986), territoriality (Tricas 1985, 1986, Hourigan Chapter III) and social behavior (Driscoll and Driscoll in prep; Hourigan Chapter VI). More data have now been accumulated on this species than on any other butterflyfish. In general, its behavior appears to be typical of paired, coral-feeding butterflyfishes.

C. ornatissimus

Although less abundant than the preceding species, *C. ornatissimus* showed similar feeding preferences in the laboratory and in the field, and showed a similar pattern of distribution among habitats (Fig. 2.11). Feeding observations agreed with those of Motta (1980). Adults formed pairs which defended contiguous, intra-specific territories in which all feeding occurred. Four pairs were collected, each consisting of a male and a female. Unlike the preceding species, no non-territorial floaters were observed. Without experimental manipulations, it was impossible to determine whether numbers of territorial adults were limited by resources, or by successful recruitment. The relatively large territory sizes and lack of floaters indicate that population densities were probably below the carrying capacity of the habitat, and pairs expanded their foraging areas until they were limited by the territoriality of conspecific pairs. Population densities of this species are greater, and territory sizes of pairs are smaller, at other areas along the coast of Hawaii (Driscoll and Driscoll in prep.). The social behavior of this species is described by Reese (1975, in prep.) and Driscoll and Driscoll (in prep).

Juveniles occurred in the same habitats as the adults and were chased vigorously by both _C. multicinctus_ and _C. ornatissimus_ adults.

C. quadrimaculatus

The previous two species were considered coral feeding generalists, in that, although they showed distinct feeding preferences, they accepted a wide variety of coral species. _Chaetodon quadrimaculatus_, in contrast, fed extensively on only one coral species, _Pocillopora meandrina_, although it supplemented its diet with algae and polychaetes (Hobson 1974, Hourigan Chapter III). The distribution of adults closely followed the distribution of this shallow-water coral species (Fig. 2.11). _Chaetodon quadrimaculatus_ shows a similar distribution in Moorea, French Polynesia (Bouchon-Navaro 1981).

The number of breeding pairs of *C. quadrimaculatus* appeared to be limited by intraspecific territoriality. Non-territorial floaters were excluded from the shallow habitats which were richest in *P. meandrina*, and occurred in small groups at the border of these territories in the vicinity of the cliff. Small juveniles were found within the areas of the adults. The behavior of adults, sub-adults and juveniles are dealt with in more detail elsewhere (Hourigan 1986a, Chapter III and Chapter VI). As was the case for *C. multicinctus*, when single individuals were removed, mates were quickly replaced, evidently by floaters (Hourigan Chapter VI). When both members of a pair were removed, the area was taken over by neighboring territorial pairs of the same species, excluding floaters. Removed individuals or pairs were never replaced by individuals of another species.

Chaetodon quadrimaculatus was unique in that pairs fed during the day as well as at night (Hourigan 1986a, Chapter III). In the shallow coral-poor zone individuals began to feed when the moon rose and quit when the moon set regardless of the time of day. In the shallow coral-rich zone they fed only during the night. When the territorial pomacentrid *Stegastes fasciolatus* was removed from the coral-rich zone, *C. quadrimaculatus* individuals fed in the same manner as those in the coral poor-zone where the pomacentrid was rare (Hourigan 1986a). This is the only concrete evidence of interspecific effects on butterflyfish behavior. It may constitute an example of temporal partitioning, a relatively rare occurrence among fishes (Ross 1986).

C. reticulatus

Chaetodon reticulatus was rare at all study sites. Adults were almost always observed in pairs. Its feeding behavior was observed only briefly, but it appeared to be similar to that of C. ornatissimus, with which it shares a similar morphology of the feeding apparatus (P. Motta, pers. comm.). These observations differed from the observations of Hiatt and Strasburg (1960) from the Marshall Islands, where algae was the main component of the gut contents of the single individual examined.

C. trifasciatus

Chaetodon trifasciatus formed pairs which defended large, intra-specific territories. Most pairs were observed in shallower areas, a distribution which did not correspond closely to the distribution of corals on which it fed, or to the distribution of the other corallivorous species. This species was uncommon, and it is possible that the population at Puako was severely limited by low recruitment, with pairs ranging over large areas. Little relation would be expected between territory size and coral cover under such conditions. Reese (1975) described this species as "home ranging" rather than territorial at Enewetak. However, home ranges were intra-specifically exclusive, and resembled the territories described here (Reese pers. comm.). Sutton (1985) found that this species defended territories at Heron Island, with the largest territories occurring in the areas of lower coral cover.

The morphological similarity of *C. trifasciatus* to *C. ornatissimus* (Motta 1980, 1985), and their similarities in feeding mode (Motta 1985), diet (Motta 1980; and this study) and food preferences (Reese 1977; Hourigan et al. 1987; and this study) suggest that these two species might compete for food resources. The data from the present study were ambiguous. There was no evidence of differences in diet between *C. trifasciatus* and *C. ornatissimus* (Table 2.15). *Chaetodon trifasciatus* occurred in low densities at which census results were not very accurate. However, it appeared that *C. trifasciatus* was more abundant in the shallower coral-poor areas than in the deeper coral-rich areas where *C. ornatissimus* was most abundant. Since some *C. trifasciatus* pairs occurred in these deeper areas, it did not appear to be a clear case of habitat exclusion. Without experimental removals, it was unclear whether the distribution of one species directly affected the distribution of the other. Individuals of the two species were only observed to approach each other five times, and only one of these interactions appeared to be aggressive.

Habitat separation between these two species may also occur at other localities. In Moorea, *C. trifasciatus* is more abundant on the fringing reef and the barrier reef flat, while *C. ornatissimus* is more abundant on the deeper barrier outer reef slope (Bouchon-Navaro 1981). *Chaetodon trifasciatus* is abundant on the shallow patch reefs of Kaneohe Bay, Hawaii, where *C. ornatissimus* and *C. multicinctus* are rare. Diets of *C. multicinctus* and *C. trifasciatus* overlapped extensively at Puako, where *C. multicinctus* was observed to chase *C. trifasciatus*.

C. unimaculatus

Chaetodon unimaculatus was relatively uncommon at Puako. It was a specialist, feeding primarily on *P. meandrina* and *Montipora* spp. Observations by other researchers (Hobson 1974; Motta 1980, 1985; Cox 1983, 1986) in Hawaii also showed that feeding was predominantly on these corals. The fish's distribution at Puako followed the distribution of *P. meandrina* and *Montipora* spp. (Fig. 2.11).

Unlike most coral-feeding butterflyfishes, *C. unimaculatus* takes small bits of corallite, as well as live coral tissue, and damages the corallite matrix of the coral (Hobson 1974; Motta 1980, 1985; Cox 1983, 1986). The jaws and teeth of this species are functionally well adapted to this mode of feeding (Motta 1980, 1985). Cox (1986) showed that feeding by *C. unimaculatus* on *Montipora verrucosa* in Kaneohe Bay decreased growth rates and reduced the corals competitive abilities versus *P. compressa*. Because of its specialized diet and method of feeding, it may have the most deleterious effect on its preferred coral resources (Hourigan in prep.)

Chaetodon unimaculatus is more abundant in other areas of Hawaii, such as Haunama Bay (Motta 1980), and especially Kaneohe Bay (Cox 1983, and pers. obs.). Corals of the genus *Montipora* are also more abundant in these areas. Greater numbers and larger individuals are found on reefs in Kaneohe Bay with large amounts of *Montipora*, compared to similar reefs with large amounts of *P. compressa* (Cox

1983). All _C. unimaculatus_ observed in this study were small individuals less than 150mm in total length. This is much smaller than the average size elsewhere. It is not clear whether this size difference is due to stunting, perhaps due to the lack of preferred corals, or to death or migration of larger adults.

Chaetodon unimaculatus differed from other corallivores in that it did not form pairs or defend territories. Individuals ranged over large areas and often joined in groups of four or more. This was also the only corallivore which was observed to shelter at night in larger groups. The social structure of this species is not known.

Patterns of butterflyfish recruitment:

The spatial distribution of juvenile butterflyfishes among habitats at Puako appeared to be predictable. Juvenile corallivores were found predominantly in the areas of highest coral cover (Table 2.8), despite vigorous chases by adults which also resided in these areas. These areas provided the most potential food and shelter. In contrast, juveniles of non-coral feeders such as _C. lunula_ and _C. miliaris_ were found in the shallow tide pools or surge zone where corals were rare or absent. It may be that their independence from corals as a food resource allowed exploitation of this relatively predator-free habitat. These patterns indicated either a degree of habitat selectivity by settling larvae, or differential post-settlement mortality in different habitats. Several researchers have found evidence of settlement preferences among coral reef fishes (Sale 1968, 1969; Williams and Sale 1981; Sweatman 1983, 1984a).

Numbers of successful recruits showed a degree of temporal variation. Different species apparently had peaks of recruitment in different years (Table 2.8). Temporal variability in larval recruitment is widely recognized (Doherty 1983; Victor 1983, 1986; Williams 1983; Sale et al. 1984; Walsh 1984, 1987; Schroeder 1985; Shulman 1985c). If numbers of fishes are not otherwise limited, one year of high larval recruitment may provide a cohort which affects the assemblage structure for several subsequent years.

Population densities of many species at Puako may have been limited by larval recruitment or subsequent juvenile survival. This seemed likely for the species which were sparsely distributed and which lacked non-territorial floaters. Compared to some other species, labrids for example, recruitment of butterflyfishes both in absolute numbers and as a fraction of the adult population was low during the years surveyed (Hourigan et al. in prep.). Leis and Miller (1976) found that pelagic butterflyfish larvae were patchily distributed in offshore plankton samples around Hawaii, and less abundant than larvae of many other families of reef fishes. Bell et al. (1985) found differences in species densities of chaetodontids, among geographically separated sites in French Polynesia which they attributed to differences in recruitment.

The abundant species, _C. multicinctus_, _C. ornatissimus_ and _C. quadrimaculatus_ were the species best represented in numbers of successful recruits. Despite annual fluctuations, these species were always observed during censuses of juveniles. Sale (1977, 1978) and Doherty (1982, 1983) assumed that recruitment to any one area of reef was not a function of the numbers of adults in that area. This is undoubtedly true of patch reefs and the small scale at which the early work of Sale was done (100 cm^2 to $5m^2$). It is doubtful that even the extensive reefs at Puako maintained self-recruiting populations. The most abundant species at Puako, however, were also the most abundant species of butterflyfishes elsewhere along the leeward coast of Hawaii (Table 2.5) as well as elsewhere in the Hawaiian Islands. There is oceanographic evidence the set of that populations of reef fishes on the leeward coast of Hawaii may be self recruiting to a large extent (Lobel and Robinson 1986; Hourigan and Reese 1987). Thus, the size of fish stocks along the whole coastline may lead to relatively predictable recruitment at any one geographic site. This would result in a degree of apparent predictability and stability in the local fish assemblage arising from sources other than internal regulation via competition. Positive correlations of recruits to adult stocks are common in the fisheries literature, and should not be surprising (e.g. Everhart and Youngs 1981).

Juvenile butterflyfishes generally did not mature and mate in the same locations where initial settlement occurred. Fricke (1986) studied a Red Sea butterflyfish, Chaetodon chrysurus, and found low juvenile recruitment, in all reef zones. As in the present study, sub-adults subsequently migrated from habitats inhabited by adult pairs. This pattern of post-settlement movement may differ from patterns shown by damselfishes, on which most research has been conducted (Sale et al. 1980; Williams 1980, 1983; Williams and Sale 1981; Doherty 1982, 1983; Sweatman 1983, 1984a). Post settlement movements may be common among other families of fishes (Kock 1982; Shulman 1985b; Hourigan 1986a), and these movements may serve to buffer the unpredictability of initial larval recruitment patterns. This is probably true especially of species with widely ranging, sub-adult floaters.

Nocturnal activity and use of shelters:

Most butterflyfishes appeared inactive at night, sheltering in the same areas used during the day. Although the same shelters were used repeatedly, shelter requirements were general rather than specific. Since fish readily found new shelters when old ones were covered, it was doubtful that numbers of adult butterflyfish were limited by availability of suitable shelters.

Paired individuals usually sheltered alone. Many nocturnal predators such as moray eels use olfactory stimuli to hunt prey (Hobson 1974). Separate shelters may reduce the concentration of stimuli to such predators, thereby reducing the chances of detection.

Hobson (1974) suggested that _C. lunula_ and _C. quadrimaculatus_ fed at night. This was confirmed for the latter species (Hourigan 1986a; Chapter III). The basis of this nocturnal behavior is not known.

Predators, competitors and territorial damselfishes:

The occurrence of piscivory on coral reefs, and its effects on the distribution and abundance of prey species is poorly understood (Sweatman 1984b). The presence of many piscivores on coral reefs undoubtedly has an impact on prey populations (Goldman and Talbot 1976). The present superficial analysis generally showed no negative correlation between numbers of predators and butterflyfishes (Table 2.10; Fig. 2.7), indicating that adult butterflyfishes did not avoid areas of highest predator density.

Butterflyfishes were abundant at Puako, but were uncommon in the guts of predators. During more than 1500 hours of observations of butterflyfishes, no observations of predation have been made (Tricas 1986; pers. obs.). Norris (1985) analyzed gut contents of piscivores from the Northwest Hawaiian Islands in conjunction with data on prey abundances and found that butterflyfishes were disproportionately underrepresented in the diets. Data from other studies (Hiatt and Strasburg 1960, Hobson 1974) support these findings. Gosline (1965) suggested that the high bodies and spiny nature of butterflyfishes caused them to be avoided by predators. Ehrlich et al. (1977) proposed that this morphology evolved as a response to predation. Evidence from trap data, however, indicates that moray eels will eat butterflyfishes when both are confined together in a trap (pers. obs.). The piscivorous wrasse, _Cheilinus_ _unifasciatus_ has been observed to attack bottles containing trapped butterflyfishes (T. Tricas pers. comm.).

If butterflyfishes were not actively avoided by predators, then the apparent lack of predation may have resulted from behavioral mechanisms on the part of these fishes. Active displays against potential predators have been observed in many chaetodontids (Motta 1983). These displays may serve the same function as mobbing of predators by birds. In addition, butterflyfishes appeared to remain relatively aware of their surroundings at night, in contrast to some other fishes such as labrids and acanthurids.

In summary, there appeared to be little evidence of predation on adult butterflyfishes at Puako, or that predation influenced the distribution and abundance of adults. Juvenile fishes are expected to be more susceptible to predation, which may explain their sheltering behavior and the occurrence of some species in shallow areas where predators were rare. Predation on juveniles has been shown to affect the numbers of some reef fishes (Talbot et al. 1978; Kock 1982; Shulman 1985b). Predation on planktonic stages may also be significant. Larvae of chaetodontids are commonly found in the guts of tuna (Brock 1985).

Corallivores of other taxa did not appear to affect the distribution of corallivorous butterflyfishes. There was no evidence of competitive exclusion for any species of corallivore. The only interactions observed between different taxa were chases, primarily by the territorial damselfishes _Plectroglyphidodon johnstonianus_, (a corallivore) and _Stegastes fasciolatus_ (an herbivore). Experimental removals of _S. fasciolatus_ from the shallow coral-rich zone were followed by changes in numbers of one acanthurid, and increased feeding rates by *C. quadrimaculatus* (Hourigan 1986a), indicating that this damselfish may have some effect in limiting access to resources by other fishes. The abundance of butterflyfishes and the abundance of *S. fasciolatus* were negatively correlated. This correlation may, however, have resulted from a negative correlation of algae, the herbivore's food, with depth and/or coral cover rather than from competitive exclusion of butterflyfishes by *S. fasciolatus*.

Patterns of food preferences of corallivores:

All five species of butterflyfishes tested showed predictable feeding preferences for certain coral species. These preferences were similar in laboratory choice tests and in the field (Table 2.14). Two fishes, *C. quadrimaculatus* and *C. unimaculatus*, specialized on corals of the genera *Pocillopora* and *Montipora*, and fed little on the more abundant *Porites* spp.. *Chaetodon multicinctus*, *C. trifasciatus* and *C. ornatissimus* had broader diets, with most bites directed toward *Porites* spp. Nevertheless, both coral-feeding generalists and specialists preferred the same coral species.

These preferences agreed with laboratory tests by Reese (1977) on *C. trifasciatus* and *C. ornatissimus*, and laboratory tests and field observations by Cox (1983) on *C. unimaculatus*. Other studies did not measured coral cover, but nevertheless indicated that that *C. quadrimaculatus* and *C. unimaculatus* feed predominantly on *Pocillopora* and *Montipora* (Hobson 1974; Motta 1980).

Preferences of other chaetodontids for particular coral species have been described by other researchers. *Chaetodon trifascialis* (formerly *Megaprotodon*) feeds almost exclusively on certain species of *Acropora* (Reese 1975, 1981; Motta 1985; Hourigan et al. 1987; Irons in press). Birkeland and Neudecker (1981) found that the Caribbean species, *C. capistratus* showed coral preferences, but these varied in different locations. Gore (1984) investigated the same species and found consistent preferences for some corals both in laboratory choice tests and in the field. *Chaetodon capistratus* also shows distinct preferences for certain gorgonian species (Lasker 1985).

Analyses of the functional morphology of the feeding apparatus of four coral feeding butterflyfishes (*C. ornatissimus*, *C. trifascialis*, *C. trifasciatus*, and *C. unimaculatus*) show specializations associated with their feeding behavior on preferred corals (Motta 1985). Although divergent structures do not prevent food overlap among species, they may place one species at an advantage in obtaining certain foods (Keast and Webb 1966).

All chaetodontid species in the present study preferred the same coral species, suggesting that these preferences were based on intrinsic characteristics of the corals. Similar preferences are shown by the blenny *Exallias brevis* in Hawaii (B. Carlson pers. comm.), and even by the corallivorous starfishes *Acanthaster planci* and *Culcita novaeguineae* (Glynn and Krupp 1986). A survey of the literature on corallivory indicates that corals of the genera *Acropora*, *Pocillopora* and *Montipora* occur most commonly in the diets of coral-feeding fishes (Randall 1974; Hobson 1974; Neudecker 1977;

Motta 1980, 1985; Reese 1977, 1981; Cox 1983, 1986). Coral tissue of preferred species may be more accessible, have a higher energetic content (Hourigan Chapter V), or have fewer and smaller nematocysts (Tricas 1986). Coral feeding selectivity may have consequences for the distribution of butterflyfishes (see below) and for their impact on the coral community (Neudecker 1979; Wellington 1982; Cox 1986).

Reese (1981) suggested that obligate corallivores may serve as indicators of environmental stress, such as pollution, on corals. The occurrence of consistent coral preferences suggests that butterflyfishes may respond differentially to changes in the quality of preferred and non-preferred corals (Hourigan et al. 1987).

Use of space, territoriality, and interactions with other fishes.

Most species in this study formed pairs which inhabited large, intra-specifically exclusive territories. These observations agreed with previous observations (Reese 1973, 1975, 1981; Barlow 1984; Ludwig 1984; Sutton 1985; Tricas 1985, 1986; Fricke 1986; Hourigan 1986a; Driscoll and Driscoll in prep.). These pairs were probably heterosexual, as was found in all previous studies (see also Hourigan Chapter VI, Hourigan et al. 1987). Reese (1975, 1978) noted a correlation between corallivory and pair-bonding, and planktivory and schooling. These trends are supported by my study, with the exception of C. unimaculatus and C. kleinii.

Territory sizes determined the number of territorial pairs in a habitat, and were related in part to the abundance of food resources in the habitat. Territory sizes of corallivores were larger in habitats with less coral. When the abundance of _P. lobata_ within the territory of a _C. multicinctus_ pair is reduced, the pair attempts to expand their territory size, and this expansion is resisted by neighboring individuals (Tricas 1985, 1986; Hourigan et al. 1987; Hourigan Chapter III, VI). This indicates that the areas are feeding territories. Tricas (1986) also found territory contraction in some cases when the preferred coral, _P. meandrina_ was added to a territory. Adjustment of territory size to the abundance of preferred food resources was consistent with observed differences in fish densities in habitats with different coral densities.

In addition to food resources, territoriality by neighboring conspecific pairs appeared to be a major factor limiting territory size. When coral abundances were reduced within territories of _C. multicinctus_, agonistic encounters with neighbors increased (Hourigan Chapter III, IV). This competition apparently prevented pairs from expanding their territories to compensate for all resources lost. When both members of a pair of _C. multicinctus_ or _C. quadrimaculatus_ were removed, the area was taken over by neighboring conspecific pairs which expanded their territories, rather than by new individuals (Hourigan Chapter VI). These increases in territory size occurred in the absence of changes in coral resources. This indicates that the major proximate factor limiting territory size is competition by neighboring territory holders. When competitor densities are low, pairs may defend larger areas than are necessary for their present food requirements (Tricas 1986). This appeared to be the case for less abundant species such as C. ornatissimus, C. trifasciatus and C. auriga.

In no case were territories inter-specifically exclusive. This differs from many territorial pomacentrids (Sale 1980), which are solitary and exclude other species from small territories. Competitive equality, assumed by the Lottery Hypothesis, may occur among such damselfishes, but seems unlikely for butterflyfishes with large differences in body size and territory size.

Non-territorial individuals, or floaters, occurred among the most abundant territorial species, C. multicinctus and C. quadrimaculatus. These floaters were usually smaller than territory holders and were not reproductive (Hourigan Chapter V). Pair formation and territoriality may be prerequisites for successful breeding in these species. The formation of transitory pairs and small groups at the edge of adult areas resembled the behavior of small, non-resident C. capistratus in the Caribbean as described by Gore (1983).

General patterns of the assemblage structure of chaetodontids at Puako.

Seven general patterns were discerned in the distribution and abundance of butterflyfishes:

1. The distribution of butterflyfishes among contiguous habitats was not random, but instead followed the distribution of preferred food resources (Table 2.3; Fig. 2.3, 2.11)

The planktivorous butterflyfishes were found in areas where pelagic plankton first crossed the reef and was probably most abundant. Corallivorous butterflyfishes were also distributed among habitats in relation to their food resources. Coral-feeding specialists were most abundant in those areas where the preferred corals were most abundant. Coral-feeding generalists were more broadly distributed, but population densities did not appear to be influenced by the occurrence of the abundant, but least preferred coral <u>Porites</u> <u>compressa</u>. The distribution of omnivorous butterflyfishes among habitats did not appear random, but insufficient data on the distribution of food resources prevented similar comparisons. The among-habitat trends in butterflyfish distribution were the same at all sites investigated. There was some evidence for differential distributions of juvenile butterflyfishes among habitats, perhaps resulting from larval settlement preferences. The patterns of adult distribution however, appeared to result from movements by sub-adults. Post-settlement movements may be common for many species on large reefs (McFarland 1981; Kock 1982; Shulman 1985b).

Previous studies have compared butterflyfish distributions with total coral cover, rather than the distribution of the corals which the fish preferred as food (Harmelin-Vivien and Bouchon-Navaro 1983, Findley and Findley 1985; Bell et al. 1985). This has led to poor correlations (Hourigan et al. 1987). Reese (1981) noted the importance of dietary specialization in the case of C. trifascialis, which feeds almost exclusively on corals of the genus Acropora. Its distribution throughout the Pacific closely follows the distribution of these corals. Neudecker (1985) suggested that the generalist diet of C. capistratus may explain its broad distribution among many habitats. Coral-feeding generalists at Puako also had broader distributions than the specialists.

2. Population densities of abundant species of butterflyfishes within habitats were similar over time (Table 2.7; Fig. 2.4).

Censuses in the same habitat conducted in different seasons and years revealed similar numbers of individuals of abundant species. Three separate factors, or some combination thereof, may result in constant population densities over time (Schoener 1985):

1. There may be little turnover of individuals during the periods sampled. Butterflyfishes are long lived, with adults of at least two species residing in the same territories over seven years (Reese 1981). Many of the same pairs of C. quadrimaculatus and C. multicinctus were observed in the same territories during all four years of this study.

2. Populations may be in a state of equilibrium, with mortality balanced by recruitment. This does not imply that they will remain in this state indefinitely.

3. Populations may be stable, and if perturbed, will return to the same equilibrium. This implies an aspect of internal regulation of population numbers.

Establishing the existence of population equilibrium requires the observation of populations for time periods equal to, or greater than the time necessary for complete population turnover (Connell and Souza 1983). Comparisons of my census data with data collected in 1974 (Kimmerer and Durbin 1975), probably do not meet this criterion, considering the longevity of butterflyfishes. Determination of population stability requires observation of the responses of populations to experimental field manipulations (Connell 1974; Colwell and Fuentes 1975; Schoener 1983). These experiments have not been done. Nevertheless, there was evidence of some internal regulation in breeding population sizes in two species (see below).

3. Densities of breeding individuals of the abundant species _C. multicinctus_ and _C. quadrimaculatus_ within a habitat appeared to be limited by intra-specific territoriality.

In each of these species, adult males and females occurred in pairs which defended feeding territories, and excluded other conspecifics. There was also a pool of non-territorial individuals or floaters. These floaters had lower feeding rates than territorial individuals and were non-reproductive (Hourigan Chapter III). For these butterflyfishes, recruitment to the breeding population may be limited by the ability to form a pair and defend a territory. Non-territorial individuals were only observed to gain a territory when a territorial individual's pair mate died or was experimentally removed (C. multicinctus: N=20; and C. quadrimaculatus N=12; Hourigan Chapter VI). Thus, competition appeared to regulate the number of breeding pairs. The minimum territory size, and therefore the maximum number of territorial pairs, was probably limited by the abundance of preferred food corals (see above). Total population density (i.e. territorial pairs, non-territorial floaters and juveniles) may also be food limited, but appropriate data to determine this are lacking.

4. Population densities of abundant species of butterflyfishes were similar for comparable habitats in different geographic areas (Table 2.7; Fig. 2.3, 2.4).

At geographically separated sites A and B at Puako, habitats matched by depth, relief, and percent coral composition and abundance had similar numbers of individuals of each of the abundant butterflyfish species. This may have resulted from either: 1) Similar numbers of successful recruits below the carrying capacity of the environment at both sites, or 2) Recruitment levels above the carrying capacity of the environment, with subsequent survival limited by similar resource levels at both sites. The present sampling methods were not sensitive enough to discriminate between these two alternatives. Once recruited to a site, individual fish of each species would be expected to distribute themselves among the habitats at that site according to the availability of preferred resources as noted in Pattern 1.

These results differed from observations of Bell et al. (1985) in French Polynesia. They found differences in species densities among geographically separated sites with similar coral cover. They attributed these differences to differences in recruitment. They did not, however, measure either the abundance of individual coral species, or butterflyfish coral-food preferences.

5. Population densities of breeding individuals of less abundant species of butterflyfishes did not appear to be limited by intraspecific territoriality.

Populations of territorial species other than C. multicinctus and C. quadrimaculatus did not appear to have a pool of non-territorial individuals. The lack of floaters remains to be confirmed by removal experiments. Elsewhere in Hawaii, there are areas of similar coral resources with higher densities of these fishes (e.g. C. ornatissimus, Driscoll and Driscoll in prep.; C. unimaculatus, Cox 1983). This suggests that population densities of these species at Puako during the four years reported here, were limited by low recruitment or post-recruitment survival, rather than by food resources. These results are in agreement with the sparse and variable nature of recruitment observed for these species. These would be the species most likely to exhibit differences in population densities among sites, and fluctuations within sites over time.

The occurrence of territoriality alone is not sufficient evidence that some resource is presently limiting population sizes (Doherty 1983). Tricas (1986) found that territory sizes of C. multicinctus pairs expanded to three times their original size when neighboring territorial pairs were removed. Territory sizes also contracted when the density of conspecifics was increased. There were no changes in resource levels during these experiments. He concluded that conspecifics were a major determinant of territory size. If recruitment of territorial species is sparse, pairs may expand their territories to fill available space until resisted by another pair (Krebs 1971). This would explain the large, but intraspecifically exclusive areas held by pairs of C. trifasciatus, C. ornatissimus, C. auriga, and possibly other species. Once established, intraspecific territories of butterflyfishes are defended largely with displays, and without overt aggression (Reese 1975; Ehrlich et al. 1977; Sutton 1985; Fricke 1986; Tricas 1986; Hourigan Chapter III). The costs of maintaining an intra-specifically exclusive area under conditions of low population density may be small compared to the costs of establishing a new territory under conditions of high population density.

6. Each species of butterflyfish appeared to be distributed among contiguous habitats independent of other species (Fig. 2.11).

The feeding preferences and the distribution of food resources were known or measured for planktivores and corallivores. Among these, the distribution of any one species could be predicted on the basis of the distribution of the preferred food resources alone. This pattern was conspicuous among the corallivores. Despite dietary overlap, there was little evidence of spatial segregation or competitive exclusion. Only *C. multicinctus* occassionally chased other butterflyfishes (Fig. 2.9b), and these chases were not successful in excluding adults of other species.

Chaetodon ornatissimus and *C. trifasciatus* had the greatest overlap in diet (Table 2.15) and morphology (Motta 1985), and provided the only suggestion of possible competitive exclusion. Although evidence for disjunct spatial distributions was weak, this species pair deserves further attention, since there are few documented cases of competitive exclusion among marine fishes (Ross 1986). The two clearest cases are for California rockfish (Larson 1980) and surfperches (Hixon 1980). Both cases involved very closely related species pairs.

If breeding populations of some species, e.g. *C. multicinctus* and *C. quadrimaculatus* were limited by food resources, then the presence of other species of corallivores would further limit food resources. Competition need not result in either resource partitioning or competitive exclusion. One species may indirectly affect the territory size and therefore the population density of another species, by reducing the cover of coral on which both feed. If coral reduction occurs, either through feeding by other species or by some other cause such as storm damage (e.g. Walsh 1983), individuals would be expected to increase the size of their intraspecific territories.

Such increases would be resisted by conspecific neighbors. This response was found in coral reduction experiments with C. multicinctus (Tricas 1986; Hourigan Chapter III). Likewise, if populations are limited by recruitment, territory sizes should expand until they are resisted by other conspecifics or until travel costs exceed foraging gains. Thus the chaetodontid assemblage would be structured by resources which determine minimum territory sizes, and by recruitment which determines the number of conspecifics and the occurrence of non-territorial individuals. Fish could compensate for more heterospecific competitors by defending larger intraspecific territories, rather than by interspecific exclusion. Robertson (1984) described a similar situation among territorial damselfishes in the Caribbean. The larger species, Microspathodon chrysurus is able to superimpose its territory over the territories of the smaller species Eupomacentrus dorsopunicans.

Coping with interspecific competition by adjusting intraspecific territories, rather than by defending interspecific territories has several advantages: 1) The costs of defending an interspecifically exclusive territory will rise more quickly with increasing territory size than the costs of defending an intraspecific territory. Interspecific territories of reef fishes are invariably smaller than the intraspecific territories of any of the butterflyfishes in the present study. 2) Interspecific territoriality may be difficult when fishes of greatly differing sizes, morphologies and habits (especially considering non-chaetodontid corallivores as well) compete for similar resources (e.g. the same preferred corals). 3) The evolution of intraspecific feeding territoriality would be facilitated if territories also serve an intraspecific function other than feeding. Paired spawning by butterflyfishes occurs within the territory (Fricke 1986), and territoriality probably also serves a reproductive function (Hourigan Chapter VI, VII).

Vance (1985) proposed a theoretical model for the coexistence of two or more species feeding on the same resource. He showed that coexistence can occur if members of two species interfere with the foraging behavior of conspecifics (e.g. via intraspecific territoriality) more than they interfere with the foraging behavior of the other species. The situation that occurs among corallivorous butterflyfishes appears to fit these criteria (Fig. 2.9b).

7. The composition of chaetodontid assemblages was similar at different geographic sites, and at the same sites over different years (Table 2.4; Fig. 2.5 and 2.6).

The relative proportion of the total number of individual chaetodontids in each habitat, comprised by individuals of each species, was similar at the same site over time and at different sites along the leeward coast of Hawaii. This followed from the similarities in population density for each individual species at different sites over time which were detailed in Patterns 1 through 4 listed above, and the lack of competitive exclusion noted in Pattern 6. Although various factors may have contributed to these observed similarities, the similarities indicated a degree of spatial and temporal predictability in the chaetodontid assemblage along the leeward coast of Hawaii over the four to six year time scale of this study.

Fricke (1986) censused butterflyfishes in three habitats in the Red Sea over different seasons in 1970 and again in 1980. He found no differences in relative seasonal or annual abundance. Absolute abundances of the two most numerous species did not differ in similar habitats at two different geographic locations.

Comparison of observed patterns to assumptions and predictions of major hypotheses:

The observations in the present study can be compared to predictions from the three major hypotheses concerning the mechanisms structuring reef fish assemblies: The Resource Limitation Hypothesis, the Lottery Hypothesis, and the Non-Equilibrium Hypothesis (Table 2.17). These are only preliminary comparisons, and should not be construed as tests of the predictions of the hypotheses. Such tests require controlled field experiments. In addition, comparisons to predictions from the hypotheses suffer from three major problems:

1. Definitions of terms such as "habitat" and "similarity" are interpretations of the author.

Table 2.17 Assumptions and predictions of the three major hypotheses proposed to explain the structure of reef fish assemblages. Table modified from Table 1. in Doherty (1983).

Hypothesis	Assumptions, and Predictions, given stable resources	Mechanisms by which densities are limited
Resource Limitation	Assumption: 1. Population densities limited by resources. Prediction: 1. Population densities of each species are stable leading to a stable density and composition of guilds.	Recruitment, and/or postrecruitment survival of each species is inversely related to the densities of conspecifics and superior competitors.
Lottery	Assumption: 1. Space is limiting. 2. Larval pool is sufficient to replace all fishes which disappear. Predictions: 1. Population densities of each species are unstable 2. The collective density, comprised of all guild members, is stable, but the species composition of the guild is unstable.	Recruitment of each species is inversely related to the collective density of all guild members. Postrecruitment survival is not determined by differential competitive abilities among recruited fishes.
Non-Equilibrium	Assumption: 1. Population densities of each species are not limited by resources. Predictions: 1. Population densities of each species are unstable 2. The collective density, comprised of all guild members, and the species composition of the guild are unstable.	Recruitment and post-recruitment survival of each species is independent of all other species because low recruitment or some external disturbance such as predation or storms is preventing resource saturation.

2. Predictions of each hypothesis are highly assumption dependent. These assumptions are not often stated explicitly, and when they are, the extent to which deviations from these assumptions will affect predictions is not given.

3. Predictions from the three hypotheses are not mutually exclusive. For example, similarities among assemblages over time may result from different causes (Schoener 1985).

A. Resource Limitation Hypothesis:

Assumption: Population densities of each species are resource limited and are at the carrying capacity of the habitat.

Shelter did not appear to be limiting for any butterflyfish species. There was no evidence of microhabitat partitioning among species, and no interspecific exclusive use of space.

There was evidence that food was potentially limiting. Population densities of each species were positively correlated with preferred food resources. Breeding populations of two abundant species, _C. multicinctus_ and _C. quadrimaculatus_ may have been limited by food resources. Access to these food resources within species, but not among different species was mediated by territorial defense. The absence of non-territorial floaters in less abundant species, suggested that population densities of these species were not similarly limited.

Prediction 1: Population densities of individual species are stable and predictable, leading to stable and predictable assemblages.

Again a dichotomy existed among abundant and rarer species. Population densities of each of the abundant species were similar in different geographic sites, perhaps as a result of either: 1) similar levels of recruitment and mortality, but still leaving populations below the carrying capacity of the environment; or 2) internal regulation of population densities. Densities of these species at individual sites also showed a degree of constancy over the course of the study. This may reflect the longevity of the residents, population equilibrium, or population stability (Schoener 1985). The numbers of breeding pairs of _C. quadrimaculatus_ and _C. multicinctus_ appeared to meet the criteria of stability, since when a population was perturbed by removal of a breeding individual, it returned to equilibrium quickly as the individual was replaced.

Less abundant species could not be analyzed statistically. However, numbers of recruits varied among years (Table 2.8), suggesting that if these recruits survived, adult densities might vary over time. Sale and Steel (1986) also found that the occurrence of all but eight species on patch reefs could be accounted for by postulating random colonization by recruits. The remaining eight species which did not conform to this simple hypothesis included some of the most abundant species present.

In addition to this major prediction, resource partitioning is often considered an integral part of the Resource Limitation Hypothesis. It is predicted that fishes in the same guild are highly specialized, and when they coexist will either exhibit differences in diet, or they will segregate by differences in microhabitat preferences and feeding time, or one species will exclude the other.

Dietary overlap among the coral-feeding generalists was extremely high, and the coral-feeding specialists fed almost exclusively on the coral species which were most preferred by the generalists as well as other, non-chaetodontid corallivores. Foraging ranges of all corallivores overlapped, and there was no evidence of microhabitat partitioning or competitive exclusion. Both dietary overlap and habitat overlap were higher than among Caribbean holocentrids where similar measures were used (Gladfelter and Johnson 1983). The lunar periodicity of feeding by C. quadrimaculatus was a possible example of temporal partitioning. Reduction of interspecific competition among coral-feeding butterflyfishes may be mediated by intraspecific territoriality as suggested by theoretical competition models of Vance (1985).

B. Lottery Hypothesis:

Assumption 1. Space is limiting.

As indicated above, there was no evidence to support this prediction. Sale (1977) originally envisioned equal competitors excluding other species from space. This may occur among territorial damselfishes, but did not occur among Hawaiian butterflyfishes.

Assumption 2. Fish larvae are present in sufficient numbers to saturate the environment.

There was evidence that the less abundant butterflyfish species were recruitment limited. Even juveniles of the more abundant species occurred within the territories of adults, suggesting that initial recruitment was not limited by the presence of adults of the same or different species.

The Lottery Hypothesis was based on three additional assumptions concerning reef fishes (Sale 1977):

a. Fishes are generalists in their use of space and food resources. This appeared to be true of many of the butterflyfishes in this study.
b. Fishes are generally sedentary, and once recruited to a space will remain there until they die. Adult butterflyfishes restricted their movements to permanent home ranges. There was good evidence however that juveniles of several species left the areas where they were initially recruited. Initial recruitment may be stochastic, but post-settlement movements may be limited by intraspecific competition.
c. Larval recruitment is assumed to be unrelated to the numbers of adults at any site. This assumption was also proposed by Doherty (1983) for the Non-Equilibrium Hypothesis. In the present study, the most abundant species at Puako were also most abundant along the whole coast of Hawaii, and had the highest numbers of recruits.

Prediction 1. Population densities of each species are unstable.

There was some evidence of stability in numbers of breeding pairs of abundant species.

Prediction 2. The total density of all members of a guild is stable.

Since there were no great fluctuations in the densities of individual species in a guild, this prediction could not be discriminated from Prediction 1 of the Resource Limitation Hypothesis. Experimental removal of single individuals or pairs of _C. multicinctus_ and _C. quadrimaculatus_ did not result in changes of numbers or behavior of other species of corallivores. When individuals were removed, they were always replaced by members of the same species. This indicated that there was no simple multi-species guild stability as originally envisioned by Sale.

C. Non-equilibrium Hypothesis:

Assumption 1. Population densities of each species are not resource limited and are below the carrying capacity of the habitat.

As described above, this appeared to be the case for all but the most abundant species of butterflyfishes. There appeared to be low recruitment of the less abundant species, but I could not rule out post-recruitment mortality. There was no reason to suspect that these species were less abundant than other species because of differential juvenile mortality, so numerical differences among species probably reflected basic differences in initial recruitment rates.

Prediction 1. Population densities of each species are unstable.

The results here are the same as for Prediction 1 of the Lottery Hypothesis.

Prediction 2. The collective density comprised of all members of a guild is unstable.

The results here are the same as for Prediction 2 of the Lottery Hypothesis.

In summary, no single theory appeared able to account for the observed structure of the chaetodontid assemblage. Numbers of most species could be accounted for by simple recruitment limitation and subsequent movement to areas of preferred food. Sale and Steel (1986) have argued that recruitment limitation is the simplest and most parsimonious explanation for the number of fishes observed on a reef. Other mechanisms of population density control, such as competition should only be invoked in cases where recruitment limitation appears to fail. Population densities of breeding individuals of more abundant species may have been limited by intraspecific competition for food resources. Hawaii has a depauperate butterflyfish and coral fauna compared to other areas in the Indo-Pacific. It is not known to what extent the patterns shown here can be generalized to other areas or to other guilds of fishes.

CONCLUSIONS

1. The abundance of butterflyfishes on a reef was a function of the number of larvae which recruited to and survived on that reef. In general, each year the more abundant species were best represented in the recruitment, with rarer species subject to sparse and fluctuating recruitment.

2. The distribution of adult planktivorous and corallivorous butterflyfishes among contiguous habitats was correlated to the distribution of preferred food resources.

3. Population densities of most species were kept below carrying capacity by low levels of recruitment and were not food limited. However, for the abundant territorial species, C. multicinctus and C. quadrimaculatus, the number of breeding pairs was probably limited by intra-specific territoriality, which was a function of limited food resources. Shelters did not appear to be a limiting resource for butterflyfishes.

4. Interspecific competition among species in the same guild was not a major factor which directly affected the structure of the assemblage. However, resource depletion by one species, especially depletion of preferred corals, may have indirectly affected the intraspecific territory sizes and thereby densities of other corallivores. The territorial damselfish, Stegastes fasciolatus chased butterflyfishes,

and numbers of the damselfish were negatively correlated with numbers of butterflyfishes.

5. Predation was not a major factor affecting the distribution of adult butterflyfishes.

6. Neither the Resource Limitation Hypothesis, the Lottery Hypothesis, nor the Non-equilibrium (Recruitment Limitation) Hypothesis alone could explain the patterns of abundance and distribution of all species, since each species showed different levels of recruitment compared to food resource levels.

CHAPTER III

THE FEEDING ECOLOGY AND FORAGING BEHAVIOR OF TWO SPECIES OF HAWAIIAN BUTTERFLYFISHES: *CHAETODON MULTICINCTUS* AND *CHAETODON QUADRIMACULATUS*

INTRODUCTION

Foraging behavior is a major component of the behavioral repertory of most animals. An individual's fitness depends on acquiring food resources, since these resources provide energy and organic materials for growth, maintenance and reproduction. Current theory predicts that natural selection acts to maximize fitness - defined as lifetime reproductive success. To the extent that fitness depends on food intake, foraging behavior should also approach optima, given the constraints of other factors related to fitness (reviewed by Pyke et al. 1977; Krebs 1978; Krebs et al. 1983; Krebs and Mc Cleery 1984).

Several factors may affect the balance of costs and benefits of the foraging behavior of an animal. First, the energetic needs of the individual determine the profitability of certain prey and of certain foraging strategies (Magurran 1986). Males and females may have different time constraints and energetic requirements due to differences in reproductive costs and behavior (Schoener 1971). These costs may vary between the reproductive and non-reproductive seasons. Likewise, different age classes might be expected to differ in foraging behavior. Second, the nutritional and energetic content of different food types, as well as the prey's anti-predator mechanisms will determine the benefits and costs respectively of feeding on different prey items and will therefore influence prey selection. The abundance, distribution and stability of food resources in time and space will also affect costs and benefits of foraging. Finally, foraging may be constrained by the behavior of conspecific and heterospecific competitors as well as by the risks of predation (Hart 1986).

Many of the field studies of the foraging behavior of marine fishes deal with the feeding territoriality of herbivorous fishes (e.g. Nursall 1977, 1981; Robertson et al. 1979; Ebersole 1980; Norman and Jones 1984; Robertson 1984; Robertson and Gaines 1986). Most of the remaining literature is based on gut content analyses. Such studies provide valuable ecological data, but say little about how the food was acquired.

Many species of butterflyfishes (family: Chaetodontidae) feed on living tissues of corals (Hiatt and Strasburg 1960; Randall 1970; Hobson 1974; Reese 1975, 1977; Harmelin-Vivien and Bouchon-Navaro 1981, 1983; Anderson et al. 1981; Motta 1985) and therefore may be of great ecological importance to tropical reef ecosystems (Harmelin-Vivien and Bouchon-Navaro 1983; Hourigan et al. 1987). The foraging behavior of these fishes is easily observed in the field (Reese 1975; Birkeland and Neudecker 1981; Motta 1980, 1985; Cox 1983, 1986; Gore 1984; Tricas 1986, Hourigan et al. 1987), and several species display distinct feeding preferences for certain coral species in laboratory and field experiments (Reese 1977; Cox 1983; Gore 1984; Hourigan et al. 1987; Hourigan Chapter II). Many species are territorial, excluding conspecifics and sometimes other corallivores from feeding territories (Reese 1975; Sutton 1985; Tricas 1985, 1986; Fricke 1986; Hourigan 1986a, Chapter II). Long term defense of exclusive feeding territories entails benefits and costs to the territory holder in terms of foraging behavior (Brown 1969).

The present study compared the foraging behavior of two closely related species of coral-feeding butterflyfishes. *Chaetodon multicinctus*, the banded butterflyfish, and *Chaetodon quadrimaculatus*, the fourspot butterflyfish, both feed on live scleractinian corals (Hobson 1974; Hourigan et al. 1987; Hourigan Chapter II), which allowed quantification of their feeding behavior through field observations. In addition, *C. quadrimaculatus* feeds on algae and noncoralline invertebrates. The major areas of emphasis in this study were:

a. Differences in foraging behavior between different classes of individuals (males vs. females, juveniles vs. adults).

b. Prey selection.

c. Diel, lunar and seasonal periodicity in feeding behavior.

d. Use of space, including foraging paths and territoriality.

These observations allowed a description of the foraging behavior of these two species. In addition, two experiments investigated the effects upon foraging behavior of reduction of food abundance within territories and the reduction in the abundance of territorial pomacentrids.

METHODS

Study site and observation techniques.

Field observations of the feeding behavior of *C. multicinctus* and *C. quadrimaculatus* were conducted on the coral reefs of Puako, on the leeward coast of the island of Hawaii (lat. 19°58'N, lon. 155°51'W). This extensive fringing reef can be divided into several distinct habitats (Hayes et al. 1982; Hourigan Chapter II): a surge zone, two shallow water (depth < 5m) habitats, designated the coral-rich and coral-poor habitats, and several deeper, coral-rich habitats. The shallow habitats were separated from the deeper habitats by a 3m to 5m cliff. The shallow, coral-rich habitat was characterized by large mounds of the coral *Porites lobata* with occasional sand and rubble filled gullies. The shallow, coral-poor habitat was exposed to greater surge and consisted primarily of a flat basalt reef platform with occasional small heads of the coral *Pocillopora meandrina* and some encrusting *P. lobata*. Below the cliff was an area of boulders, a rich cover of *P. lobata*, and some finger coral, *Porites compressa*. From this point the bottom sloped gently, with increasing amounts of *P. compressa* in a deep, coral-rich habitat. At depths between 20m and 30m, the coral reef ended and a steep sandy slope began.

Observations on both butterflyfish species were conducted by scuba divers in the shallow coral-rich and coral-poor habitats (depth < 5m), while observations of *C. multicinctus* were also made in the deeper coral-rich areas where *C. quadrimaculatus* did not occur.

Additional observations were conducted on eight pairs of C. multicinctus in similar habitats on the island of Oahu, Hawaii. Four pairs were observed in shallow waters (depth < 7m) at Kahe Pt. (lat. 21°21'N, lon. 158°8'W) and four pairs in deeper water (depth - 10-20m) at Hanauma Bay (lat. 21° 16'N, lon. 157°42'W). These habitats were similar, respectively, to the shallow coral-poor habitats and deep coral-rich habitats at Puako.

The basic design of the study was to identify individuals of each species in the field, record their feeding behavior, and map their home ranges and movements. Individuals of each species were identified using natural markings, and followed, recording the number of bites on species of corals and other substrata. Following an initial 10 min acclimatization period, feeding data were recorded during 5 min intervals. Repeated observations were made on the same individuals for a minimum of twenty 5 min intervals. Five minute observation intervals were alternated between pair mates. The occurrence of feeding, as well as other behaviors such as sheltering, chasing and posing for cleaning was recorded during five 1 min subsets within each 5 min interval. Observers usually maintained a distance of at least 2 m from the fish, and this did not appear to influence the fish's foraging activity or movements.

a. Differences in foraging behavior between the sexes and among different age classes.

Observations of individuals of both species were conducted during four consecutive summers from 1980 through 1983. Sexes of adult pair mates were determined by behavioral differences in territorial defense. After a minimum of twenty 5 min observation intervals on each member of twenty pairs of *C. multicinctus* and 15 pairs of *C. quadrimaculatus*, both members of each pair were collected by spearing in order to confirm their sexes. In an additional ten cases, for each species, only one member of a pair was removed. Fishes were collected in concert with experiments described in Chapter V and VI and were used for stomach content analyses. In all cases the actual sex agreed with the sex predicted from behavioral observations. Feeding observations were conducted on a total of 30 adult pairs of *C. multicinctus* and 28 adult pairs of *C. quadrimaculatus*.

Juveniles of both species first appeared on the reef in March. During the summer, juveniles of both species measured less than 40mm in length and occurred singly. Feeding observations were conducted on six juveniles of each species. Additional feeding observations were conducted on six non-territorial sub-adults of each species.

b. Prey availability and prey selection.

To determine prey selection, the number of bites by individual fish on different species of corals and other substrata was recorded.

During feeding observations of twenty adult pairs of C. multicinctus and 10 pairs of C. quadrimaculatus, the grouping of feeding bites in bouts on coral colonies, or patches, was examined. The number of consecutive bites per coral colony was counted. Different colonies were defined operationally as coral patches which were not continuous. Since most coral species can reproduce by fragmentation, several adjacent patches might be genetically identical. The coral polyps in one colony would not respond, however, to feeding which was directed toward its neighbor.

The bottom cover of different substrata in each habitat was estimated by quadrat sub-sampling. A 1/4 m^2 grid with 50 intersections was placed on the bottom at regular 5 m intervals along a 50 m line set within the habitat. The type of substratum or coral species beneath each intersection was recorded and percent cover computed.

An electivity index E, (Gore 1984, modified from Ivlev 1961) was used to compare the number of bites on corals to the abundance of each species of coral within each habitat:

$$E = (b_i - c_i)/(b_i + c_i)$$

where b_i is the proportion of bites on a coral species, and c_i is the proportion of the total coral cover made up by that coral species. Positive values show a preference for that particular species, while negative values show that it is fed upon less than would be expected by chance given, its occurrence in the environment.

Stomach contents of individuals of both species were examined to confirm feeding observations. Contents were sorted into general taxonomic categories, and their wet weight measured. Stomach contents of ten C. multicinctus from the shallow coral-poor habitat and ten from the deep coral-rich habitat were examined. Twenty-one C. quadrimaculatus from the shallow coral-poor habitat were collected at different times of the day and lunar month, and their stomach contents were examined.

c. Diel and seasonal foraging patterns.

During the summer, observations of six pairs of C. quadrimaculatus and four pairs of C. multicinctus were conducted at different times of the day to determine diel changes in foraging behavior. Observations were conducted during 2 hr intervals, from first light to dusk, e.g. 0700-0900, 0900-1100, 1100-1300, 1300-1500, 1500-1700 and 1700-1900. Evidence from gut content analyses of fish caught before dawn (Hobson 1974) suggested that C. quadrimaculatus fed at night as well as during the day. Divers used red lights to observe the nocturnal activity of both species at different times of the lunar cycle. Five individual C. quadrimaculatus were speared in the shallow coral-poor habitat before dawn on the morning following the new and full moon, and stomach contents were analyzed for evidence of nocturnal feeding. Similar collections were made in the shallow coral-rich habitat on the same days.

To determine seasonal patterns, feeding observations of the same six pairs of _C. quadrimaculatus_ were conducted in spring (March 1980, 1981), summer (July 1980, 1981, 1982, 1983) and Fall (Nov. 1979, 1980). The four pairs of _C. multicinctus_ were observed during the same months in spring (1982, 1983), summer (1980, 1981, 1982, 1983) and Fall (1981, 1982).

d. Foraging areas and foraging paths.

To determine the foraging areas of individuals of each species, numbered nails with colored flagging tape were dropped in order at the points where the animals fed. Using the method of Odum and Kuenzler (1955) it was determined that 95% of the foraging area was delineated following two to three 1 hr observation periods for pairs of _C. multicinctus_ and four to five 1 hr periods for pairs of _C. quadrimaculatus_ (N=5 for each species). Following this initial determination, colored tags were dropped during a minimum of four and six hour observations for these species respectively.

Maps of these foraging areas were drawn on underwater paper. A line marked off in meter intervals was set through the center of the marked area, and the distance from this line to each flag was measured and marked on the map. In addition, major features, such as shelters, large coral heads and boulders were marked. Subsequent movements outside the previous boundaries, as well as positions where agonistic encounters occurred, were then marked directly on the maps. The foraging areas of the six _C. quadrimaculatus_ and four _C. multicinctus_ pairs were first mapped in 1979/1980, and re-mapped every summer through 1983. Areas of four additional pairs of each species were mapped during the summer of 1982 and re-mapped in 1983. Areas of 10-15 pairs of each species were mapped only once.

To determine how different portions of the foraging area were used, the foraging paths of C. multicinctus and C. quadrimaculatus were mapped by recording the positions of individuals at 30 sec intervals on a previously drawn map of their foraging area. Replicate maps were made for four pairs of each species in the morning and afternoon on three consecutive days. This procedure was repeated at least three times during different months of the year.

e. Food reduction experiments for C. multicinctus.

Food reduction experiments were conducted during the summer of 1983 to determine the effects of changes in coral cover on the foraging behavior of individual C. multicinctus. Six pairs (three experimental and three control) in the deep coral-rich habitat were observed for four consecutive days, during which territories were mapped and feeding behavior was recorded. During a minimum of twenty 5 min feeding intervals, the number of consecutive bites on each patch of coral was counted as well as the total feeding rate. For three of these pairs, 12 to 24 m^2 of the coral Porites lobata was covered with cloth material, limiting access to this species of coral, but leaving other corals, primarily P. compressa, available as food. Tricas (1986) showed that similar covers over substrata other than live coral did not affect territorial defense or feeding behavior. During four days following the covering of the corals, feeding observations on all six pairs were repeated and territory sizes were re-measured. After two weeks, territory sizes were measured again to determine any longer term changes.

f. Pomacentrid removal experiment for C. quadrimaculatus.

Initial observations indicated that individual C. quadrimaculatus remained sheltered during the day in the shallow coral-rich habitat at times when pairs were foraging actively in the shallow coral-poor habitat. A major difference between these habitats was the presence of large numbers of the territorial damselfish Stegastes fasciolatus in the coral-rich habitat. The damselfish was observed to chase C. quadrimaculatus on numerous occasions (Hourigan Chapter II). Since C. quadrimaculatus fed extensively on algae as well as coral polyps and other benthic invertebrates, it was a potential competitor of the damselfish. The damselfish was removed to determine if the absence of diurnal foraging by C. quadrimaculatus in the shallow coral-rich habitat was due to chases by S. fasciolatus.

To test the effect of the presence of the territorial damselfish, a 25m x 10m site in the shallow coral-rich habitat was chosen for removal of S. fasciolatus. Similar control sites were chosen in the shallow coral-rich and coral-poor habitats, located 100m and 400m respectively from the experimental site. In June 1980, replicate visual censuses of the damselfish were conducted at each site by one diver on three consecutive days (Hourigan Chapter II). Four, 10 min observations were made on each of four focal individual *C. quadrimaculatus* per site, during which feeding bites, chases by *S. fasciolatus*, and time spent sheltered were recorded.

On the following four days, a total of 119 *S. fasciolatus* were speared and removed from the experimental area. Each day, new intruding individuals were also removed. Mock spearings were conducted, in which a diver swam through the control areas releasing a spear at rocks but spearing no fishes. Beginning on the second day, the three replicate visual censuses of damselfish and observations of *C. quadrimaculatus* were repeated. Spearings were conducted in the mornings, and observations and censuses in the afternoon. At ten and twenty days, after the completion of the experiment, numbers of *S. fasciolatus* in the experimental area were counted to document any recolonization that might have occurred. In summary, the basic structure of the experiment consisted of three days of observation, four days of pomacentrid removal, during which observations were repeated, with two later spot checks, ten and twenty days following the experiment.

h. Statistical Analyses.

All distributions of data were tested for normality using the Kolmogorov-Smirnov D test with a rejection level of 5% (i.e. at least a 5% probability that the sample came from a population with a normal distribution). Most data were counts and were normalized using a standard square root transformation and analyzed using parametric statistical tests. Data presented as a proportion or percentage were normalized using an arcsine transformation. Simultaneous comparisons of multiple means were conducted using the Waller-Duncan K-Ratio t-test. Those data which could not be normalized were analyzed using standard non-parametric tests.

RESULTS

1. *Chaetodon multicinctus*

Chaetodon multicinctus was the smallest and the most abundant butterflyfish in all habitats at Puako. Adults occurred in male-female pairs with individuals spending 74% (SD 34%) of their time swimming and feeding within 2 meters of their pair-mate. Feeding occurred in 97.3% of all 1 min feeding intervals (Table 3.1). In timed observations (Table 3.2), individuals spent 56.4% of the time either inspecting corals or actively feeding on them, and spent 42.5% of the time travelling between corals. Small amounts of time during the day were spent in non-feeding activities including agonistic encounters, sheltering and posing for cleaning.

a. Differences in foraging behavior between the sexes and among different age classes.

Adult fish were always found in male-female pairs which defended feeding territories and fed continuously during the day. Adult females fed significantly more than their pair-mates in 27 out of 30 cases (Independent Wilcoxon's signed-ranks tests, $p<0.05$ to $p<0.005$; when means for all pairs are pooled, $p<0.005$; Fig. 3.1). Pair-mates often fed together on the same coral colony with no observed agonistic behavior. There were no significant differences in mean feeding rates within sexes among different habitats (1 way ANOVA of square root transformed feeding rates, $p > 0.5$).

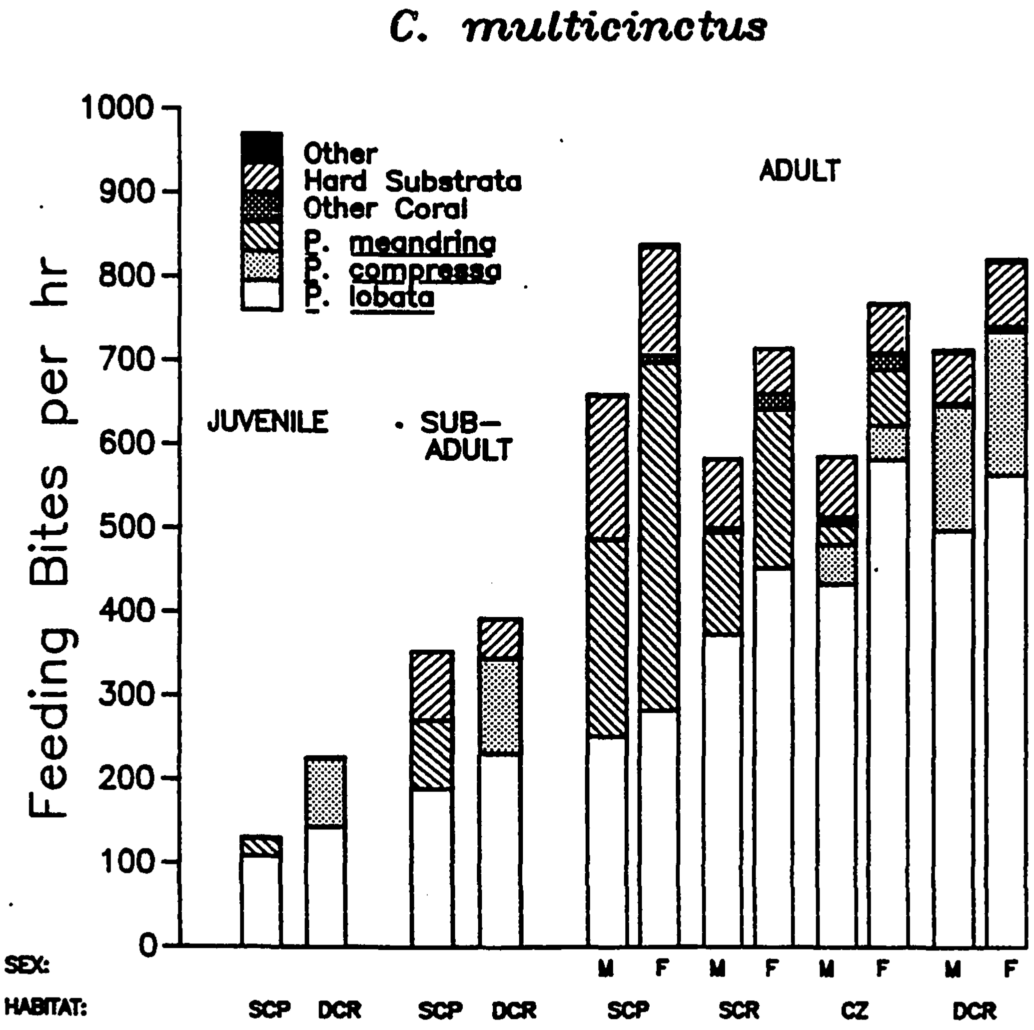
Table 3.1. Activity budgets for *C. multicinctus* and *C. quadrimaculatus* at Puako. Feeding, sheltering and posing for cleaning are expressed as the percent of all 1 min observation intervals during which that behavior occurred, and may sum to more than 100%. Data for *C. multicinctus* were collected during daylight hours in all habitats, while data for *C. quadrimaculatus* refer to observations in the coral-poor habitat and neighboring cliff area during daylight hours after the moon had risen (see text).

ACTIVITY	BUTTERFLYFISH SPECIES							
	C. multicinctus				*C. quadrimaculatus*			
	Male	Female	Sub-Adult	Juvenile	Male	Female	Sub-Adult	Juvenile
Fish Observed N =	30	30	6	6	28	28	6	6
Total Hours Observed	58	58	10	10	50	50	10	10
Feeding (% of all 1 min intervals)	96.2%	98.4%	88.2%	72.1%	91.3%	96.5%	53.7%	62.3%
Sheltering (% of all 1 min intervals)	0.03%	0.03%	16.1%	37.0%	8.9%	3.8%	24.5%	46.8%
Posing for cleaning (% of all 1 min intervals)	1.4%	0.8%	0.4%	0%	1.4%	0.7%	0.5%	0%
Agonistic displays per hr	1.45	0.71	0	0	0.99	0.28	0.21	0.0
Chases per hr	6.77	2.45	0	0	3.51	0.52	0.11	0.0

Table 3.2 Timed observations of activity of adult C. multicinctus at Kahe Pt. and Hanauma Bay (combined).

	Male (N=4)	Female (N=4)
Total hours observed	8	8
Feeding (% of total time)	53.7	59.0
Mean feeding bout duration (in sec)	8.2 (SD 13.4)	9.0 (SD 10.2)
on corals:		
Porites lobata	7.9 (SD 9.4)	9.1 (SD 9.8)
Porites compressa	5.0 (SD 4.0)	6.3 (SD 5.0)
Pocillopora meandrina	15.0 (SD 19.6)	16.0 (SD 15.5)
on hard substata:	5.2 (SD 6.1)	3.2 (SD 4.0)
Traveling (% of total time)	45.0	40.2
Mean travel time between feeding bouts (in sec)	7.6 (SD 6.7)	7.3 (SD 5.5)
Chasing (% of total time)	1.28	0.05
Mean duration of chases (in sec)	26.2	12.7
Posing for cleaning (% of total)	0.03	0.77
Mean duration of posing (in sec)	1.1	7.2

Figure 3.1. Mean feeding rates of juveniles (N = 6; each observed for 100 min), non-territorial sub-adults (N = 6; each observed for 100 min), and territorial adults (N = 30 pairs; each individual observed for at least 100 min) of the banded butterflyfish, C. multicinctus in different habitats at Puako, Hawaii. Feeding rates are subdivided by major coral species and other substrata on which feeding occurred.


C. multicinctus
1000
900
800
700
600
500
400
300
200
100
0
Feeding Bites per hr
Other
Hard Substrata
Other Coral
P. meandrina
P. compressa
P. lobata
JUVENILE
SUB-ADULT
ADULT
SEX:
M
F
M
F
M
F
M
F
HABITAT:
SCP
DCR
SCP
DCR
SCP
SCR
CZ
DCR

Feeding rates of recently settled juveniles were lower than those of adults (t-test of square root transformed feeding rates, $p<0.05$; Fig. 3.1). Recently settled juveniles occurred in all habitats from March through August, but were most abundant in the deeper coral-rich habitats. In this smallest size class (SL<40mm), individuals were mostly solitary, and usually sheltered. Feeding by juveniles was often interrupted by the chases of adult fish.

Larger sub-adults were also seen occasionally in both shallow and deep habitats. These fish did not defend territories, but instead were sheltered in corners between territories, or traversed large areas, feeding alone or in twos or threes around the peripheries of adult territories. Sub-adults were often chased by territorial adults. Sub-adults responded to chases by giving way. The feeding rates of these individuals were also significantly lower than the feeding rates of territorial adults (t-test of square root transformed feeding rates, $p<0.05$; Fig. 3.1).

b. Prey availability and prey selection.

Adult _C. multicinctus_ in all habitats directed most feeding bites toward the surface of living scleractinian corals (Fig. 3.1) especially the most abundant species, _Porites lobata_, _Porites compressa_ and _Pocillopora meandrina_. A smaller number of bites were taken on corals of the genera _Cyphastrea_, _Montipora_, _Pavona_, and _Leptastrea_. In addition, some bites were directed toward other hard substrata. Examination of the areas of other hard substrata where bites took place revealed occasional small polychaete tubes, but more commonly, fine filamentous algae. Solitary juveniles fed almost exclusively on corals, with few or no feeding bites directed toward other hard substrata.

Male and female *C. multicinctus* fed on the same foods. In all habitats except the coral-poor habitat, there were no significant differences in the proportion of bites on different substrata by males and females of the same pair (Wilcoxon's signed-ranks test, $p>0.05$). In the coral-poor habitat, females directed a significantly greater proportion of their total feeding bites toward the coral *P. meandrina* than did males (49.7% vs. 35.7% respectively, Wilcoxon's signed-ranks test, $p<0.05$; Fig. 3.2). In contrast, males directed a significantly greater proportion of their total feeding bites toward algae and invertebrates on the hard substratum than did females (26.0% vs. 15.4% respectively, Wilcoxon's signed-ranks test, $p<0.05$; Fig. 3.2). There were no consistent differences in food preferences between pair mates for the most abundant coral species, *P. lobata*. Similar trends occurred in the shallow coral-rich habitat and the cliff zone, but these were not significant at the 95% confidence level.

The number of feeding bites on different coral species as a function of the abundance of those corals in the habitat is shown in Table 3.3. In all habitats, *P. meandrina* was fed on more than expected by chance feeding, given the abundance of each coral species (i.e. positive electivity scores). *Porites compressa* was fed on relatively less than expected, and *Porites lobata* was fed on in nearly

Figure 3.2. Percent of feeding bites on different substrata in the shallow coral-poor habitat by adult female and male C. multicinctus belonging to six pairs. Each point below the 45° line signifies that the male of that pair fed more on that substratum than his pair-mate, and each point above the line signifies that the female fed more on that substratum than her pair-mate.

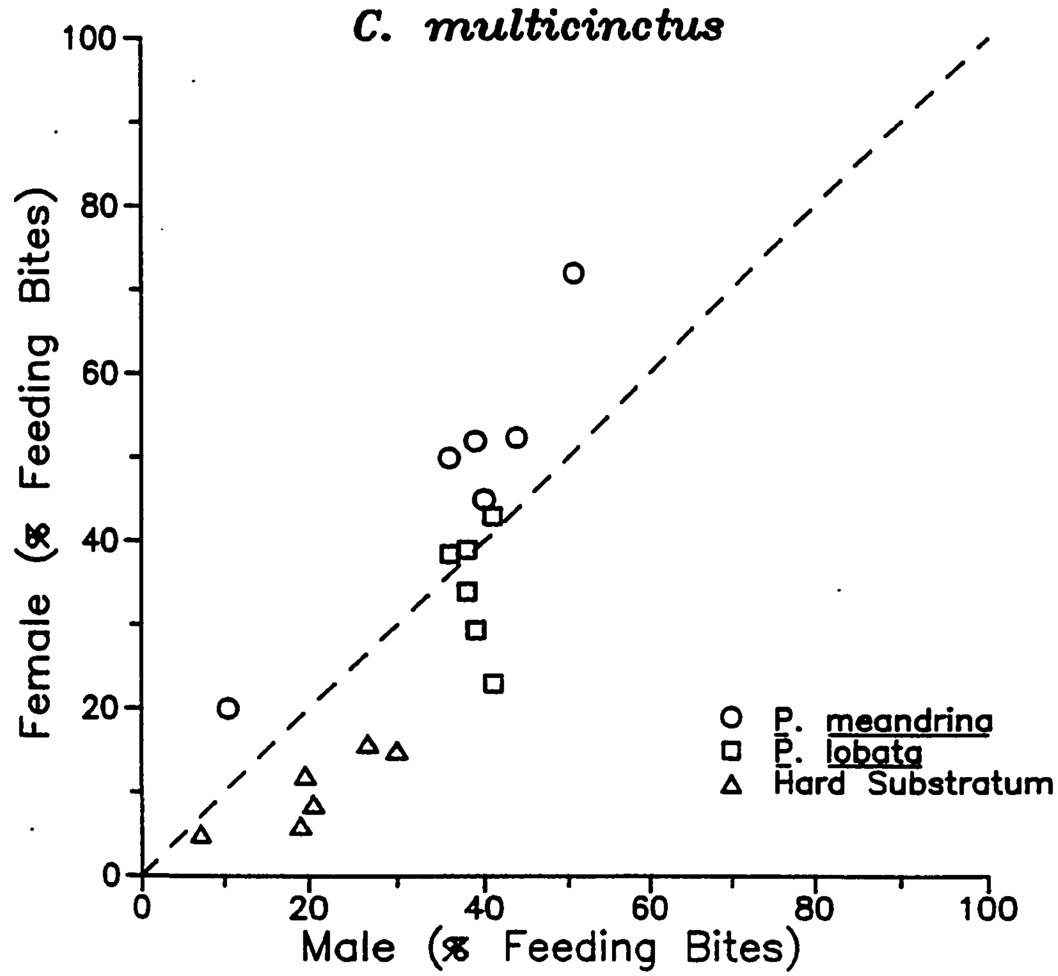

C. multicinctus
Female (% Feeding Bites)
Male (% Feeding Bites)
0
20
40
60
80
100
0
20
40
60
80
100
○ P. meandrina
□ P. lobata
△ Hard Substratum

Table 3.3 Feeding bites on different substrata, and electivity indices for male and female *C. multicinctus* in different habitats at Puako, Hawaii.

SHALLOW CORAL-RICH HABITAT

(4 Pairs; each fish observed 100 min)

SUBSTRATUM	% CORAL[a] COVER	BITES PER HR		ELECTIVITY	
		Male	Female	Male	Female
P. lobata	87.6	373	452	-0.08	-0.12
P. compressa	0	0	0	-	-
P. meandrina	11.6	122	189	0.36	0.42
Other corals	0.8	5	19	0.11	0.57
Hard substratum		82	54	-	-
Crevices		0	0	-	-
Other		0	0	-	-
All corals[b]	31.9	500	660	0.46	0.49
Total Bites		582	714	-	-

SHALLOW CORAL-POOR HABITAT

(6 Pairs; each fish observed at least 100 min)

SUBSTRATUM	% CORAL[a] COVER	BITES PER HR		ELECTIVITY	
		Male	Female	Male	Female
P. lobata	79.4	251	282	-0.21	-0.33
P. compressa	0	0	0	-	-
P. meandrina	19.8	235	415	0.42	0.50
Other corals	0.8	1	9	-0.59	0.23
Hard substratum		171	129	-	-
Crevices		0	0	-	-
Other		1	3	-	-
All corals[b]	14.6	487	706	0.67	0.70
Total Bites		659	838	-	-

Table 3.3 (cont.)

CLIFF BASE HABITAT

(4 Pairs; each fish observed 100 min)

SUBSTRATUM	% CORAL[a] COVER	BITES PER HR		ELECTIVITY	
		Male	Female	Male	Female
P. lobata	85.3	433	581	-0.01	-0.02
P. compressa	7.4	47	41	0.11	-0.12
P. meandrina	2.8	24	67	0.25	0.54
Other corals	4.5	9	20	-0.44	-0.23
Hard substratum		72	58	-	-
Crevices		0	0	-	-
Other		0	1	-	-
All corals[b]	53.7	513	709	0.24	0.26
Total Bites		585	768	-	-

DEEP CORAL-RICH HABITAT

(16 Pairs; each fish observed at least 100 min)

SUBSTRATUM	% CORAL[a] COVER	BITES PER HR		ELECTIVITY	
		Male	Female	Male	Female
P. lobata	60.9	497	563	0.11	0.11
P. compressa	37.1	149	171	-0.24	-0.23
P. meandrina	0.1	2	3	0.51	0.60
Other corals	0.6	2	5	-0.32	0.06
Hard substratum		61	77	-	-
Crevices		1	1	-	-
Other		2	2	-	-
All corals[b]	57.7	650	742	0.23	0.22
Total Bites		711	819	-	-

---

a. Coral cover determined from ten .25 m^2 quadrats within each habitat.

b. All corals = total % bottom cover which was live coral.

the same proportion as it occurred in the habitat. Differences in prey selection between male and female pair mates in the shallow coral-poor habitat are reflected in the differing values for the electivity indices. A test of independence between coral abundance in the habitat and abundance in the diet showed that fish did not feed on corals in proportion to their abundance (Pooled G-test for all pairs: df = 3, $p < 0.001$).

Feeding-bite behavior differed for bites on different substrata. Bites on P. meandrina were forceful and direct. Bites on Porites spp. in contrast were usually slower and less forceful. Often bites on P. compressa appeared preferentially directed toward the tips of the branches. Finally, bites on hard substrata were often accompanied by a sideways jerking of the head.

The distribution of feeding bites in bouts on different species of corals is shown in Fig. 3.3. Colonies or patches of corals differed in size, from a few polyps to occasional large colonies of P. lobata, 2m to 3m in diameter. Porites lobata and P. compressa had the greatest variance in patch size. Pocillopora meandrina colonies were much more uniform in size. Numbers of bites per coral colony (i.e. bites per patch) were distributed in a Poisson fashion, with most bouts containing only one bite. Feeding bouts on preferred corals (as revealed from electivity indices, Table 3.3) such as P. meandrina, had fewer bouts with only one bite, and more bouts with two or more bites than did feeding bouts on less preferred corals (e.g. P. compressa).

Analysis of the stomach contents of male and female fish revealed that 95% of the contents by weight were composed of coral tissue

Figure 3.3a. Distribution of the number of feeding bites by *C. multicinctus* per feeding bout on each coral colony, as a percent of all bites on that coral species (N = 10 pairs; each observed for 100 min). 3a. Frequency distribution of bites directed toward individual colonies of the corals *Porites lobata* and *Pocillopora meandrina* in the shallow coral-poor habitat (N = 6 pairs; each observed for 100 min).

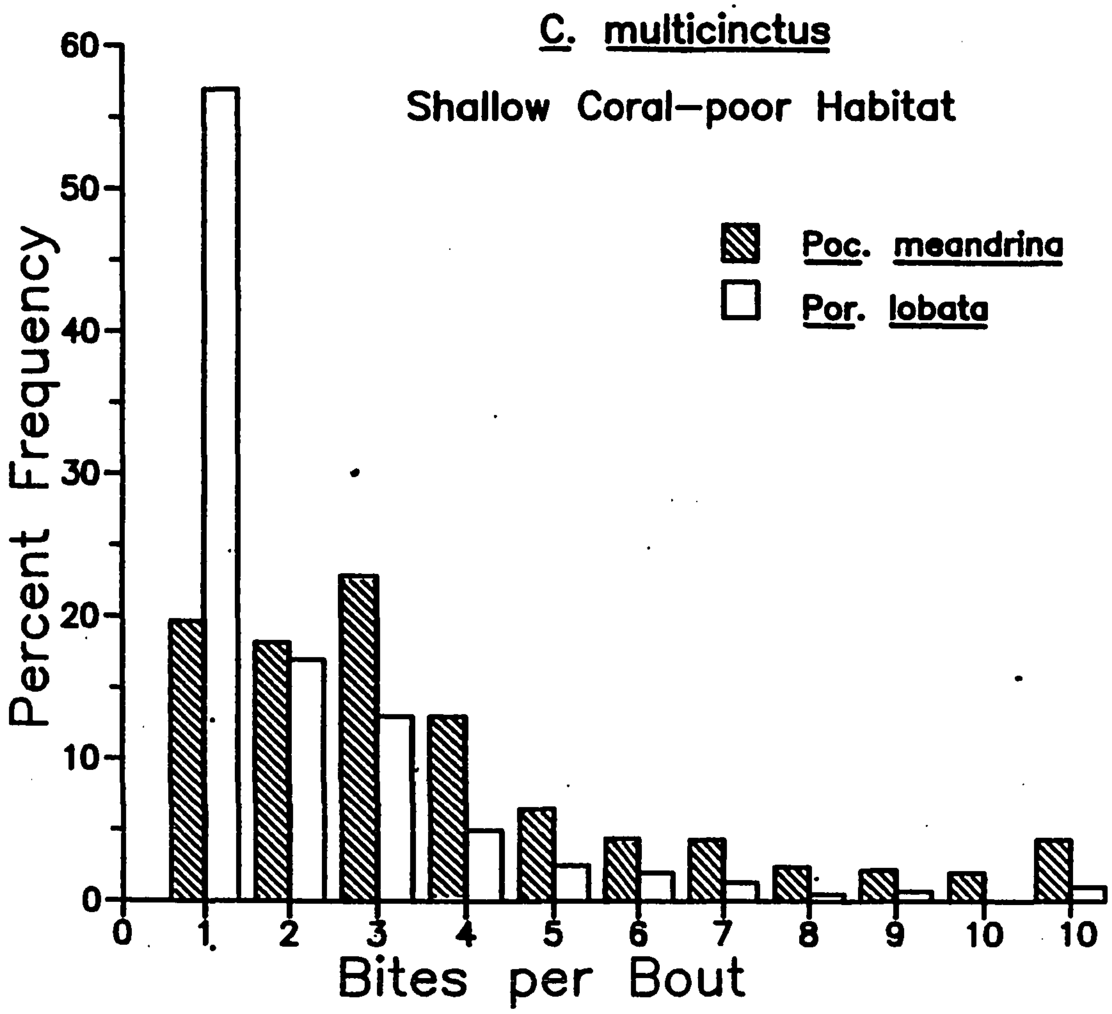
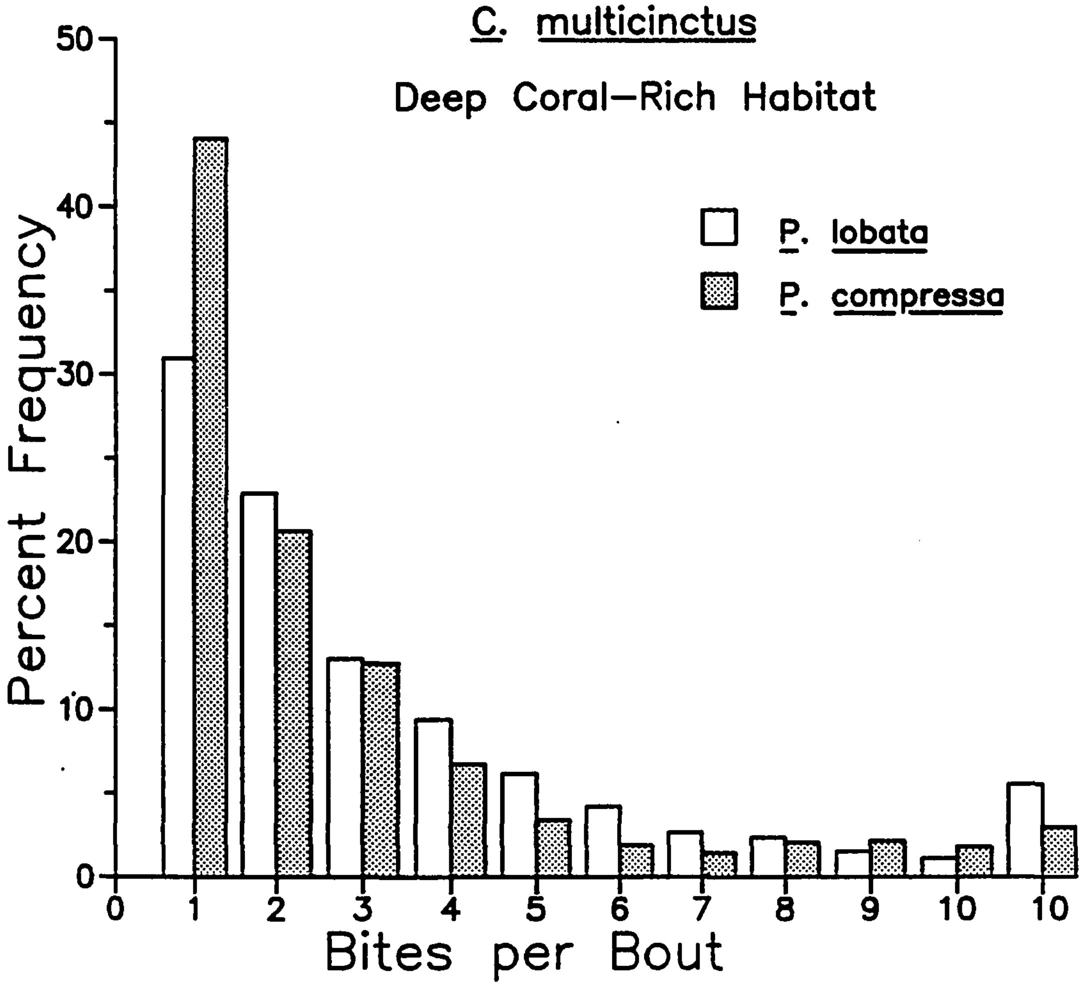

C. multicinctus
Shallow Coral–poor Habitat
Poc. meandrina
Por. lobata
Percent Frequency
60
50
40
30
20
10
0
0
1
2
3
4
5
6
7
8
9
10
10
Bites per Bout

Figure 3.3. Distribution of the number of feeding bites by C. multicinctus per feeding bout on each coral colony, as a percent of all bites on that coral species (N = 10 pairs; each observed for 100 min). 3b. Frequency distribution of bites directed toward individual colonies of the corals Porites lobata and Porites compressa in the deep coral-rich habitat (N = 10 pairs; each observed for at least 100 min).

b



C. multicinctus
Deep Coral–Rich Habitat
P. lobata
P. compressa
Percent Frequency
50
40
30
20
10
0
0
1
2
3
4
5
6
7
8
9
10
10
Bites per Bout

Table 3.4 Stomach contents of *C. multicinctus* collected in the shallow coral-poor and deep coral-rich habitats at Puako, Hawaii.

SHALLOW CORAL-POOR HABITAT (Sample of 10 fish)

Food Item	Per cent by wet weight	Number of Fish with Item
Coral tissue	94.2%	10
Polychaetes	2.1%	7
Algae	2.7%	10
Amphipods	0.9%	4
Other	0.1%	1

DEEP CORAL-RICH HABITAT (Sample of 10 fish)

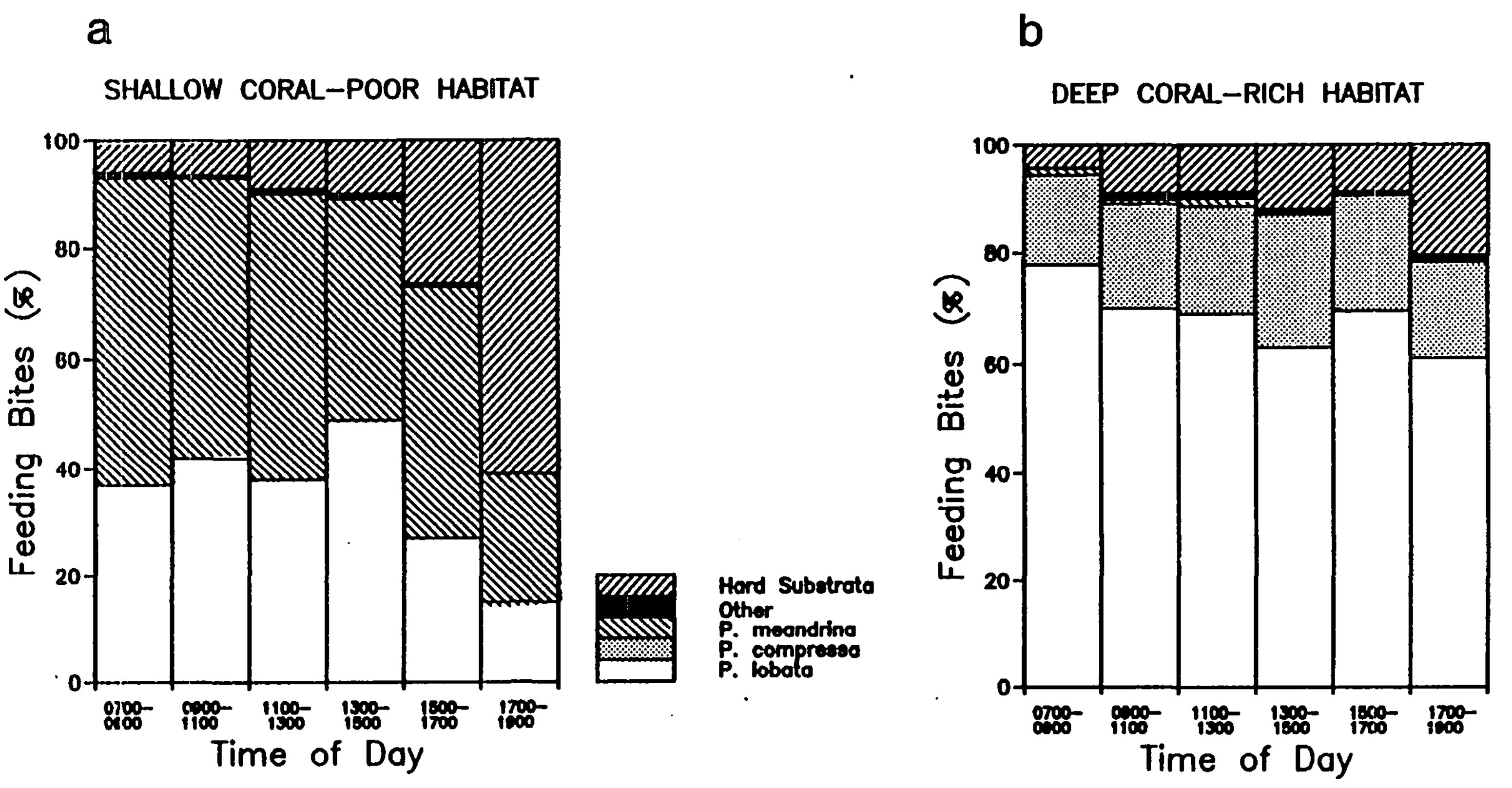
Food Item	Per cent by wet weight	Number of Fish with Item
Coral material	97.3%	10
Polychaetes	1.3%	8
Algae	0.7%	6
Amphipods	0.4%	3
Other	0.3%	1

(Table 3.4). Zooxanthellae and both discharged and intact nematocysts were common. Small amounts of filamentous algae and occasional small polychaete worms and amphipods were also present in the stomachs (Table 3.4). On the average, the dry weight of stomach contents of a male was 88% of that of its female pair-mate (paired t-test $p<0.001$), even though males were usually slightly larger than their mates (mean difference in standard length = 2 mm; paired t-test, $p < 0.05$).

c. Diel and seasonal foraging patterns.

Chaetodon multicinctus were among the first fish to begin foraging on the reef in the morning. Fish left their individual sleeping shelters at first light, about 20 min before actual sunrise. Pair-mates then came together and began to feed. Pairs foraged almost continuously throughout the day, with no significant differences in feeding rates at different times of the day (One-way ANOVA of square root transformed feeding rates; $p > 0.30$). The only major breaks in foraging occurred when the fish posed for cleaning, or engaged in chases with other fish. In the coral-rich habitat, there were no differences in food choice throughout the day. In contrast, in the shallow coral-poor habitat, individuals increased the mean proportion of feeding bites directed toward hard substrata during the last four hours of feeding (1500-1900 hrs; Fig. 3.4; One-way ANOVA of arcsin transformed proportions; Waller-Duncan $p<0.05$). Chaetodon multicinctus was among the last fishes actively feeding on the reef,

Figure 3.4. Percent of feeding bites on different substrata by C. multicinctus at different times of the day at Puako, Hawaii (N = 4 pairs; data were gathered over a period of 1 year, with at least 100 min of observation for each member of the pair during each 2 hr time interval). 4a. Shallow coral-poor habitat. 4b. Deep coral-rich habitat.

a
SHALLOW CORAL-POOR HABITAT
Feeding Bites (%)
100
80
60
40
20
0
0700-0900
0900-1100
1100-1300
1300-1500
1500-1700
1700-1900
Time of Day
Hard Substrata
Other
P. meandrina
P. compressa
P. lobata
b
DEEP CORAL-RICH HABITAT
Feeding Bites (%)
100
80
60
40
20
0
0700-0900
0900-1100
1100-1300
1300-1500
1500-1700
1700-1900
Time of Day

and foraged up to 40 min after the sun had set. At night, individuals were found inactive in separate shelters within their territories.

There were no significant differences in the feeding rates of the same individuals in four pairs measured during different seasons (Two-way ANOVA of square root transformed feeding rates, $p>0.1$). During all seasons, females fed more than the males with whom they were paired (Wilcoxon's signed-ranks test $p<0.05$).

d. Territoriality and foraging paths.

Adult pairs defended territories against conspecifics. The borders of these defended areas were the same as the borders of the feeding ranges. Other coral feeding butterflyfishes, particularly *Chaetodon ornatissimus* and *Chaetodon trifasciatus* were occasionally chased from these territories. A total of 44 territories were mapped. Territory sizes ranged from $44m^2$ in the coral-rich zone below the cliff, to the largest territory in the shallow coral-poor habitat which measured $171m^2$. Average territory sizes were $73m^2$ (N=29, SD=21) in the deep coral-rich habitat, and $107m^2$ (N=15, SD=29) in the shallow coral poor habitat. The sizes of most territories remained constant over the 3 years observations were conducted (Fig. 3.5). Of the four territories that were repeatedly mapped, two expanded when a neighboring pair disappeared (Fig. 3.5). A similar expansion occurred in one of the other four territories that was mapped during two consecutive summers.

Figure 3.5. Territories of four adult pairs of C. multicinctus (A,B,C,D) in the deep coral rich habitat at Puako, Hawaii, mapped during three consecutive summers: 1981, 1982, 1983. Territorial expansion occurred in two of the territories (A and B) between 1982 and 1983, when a neighboring pair (E) disappeared.

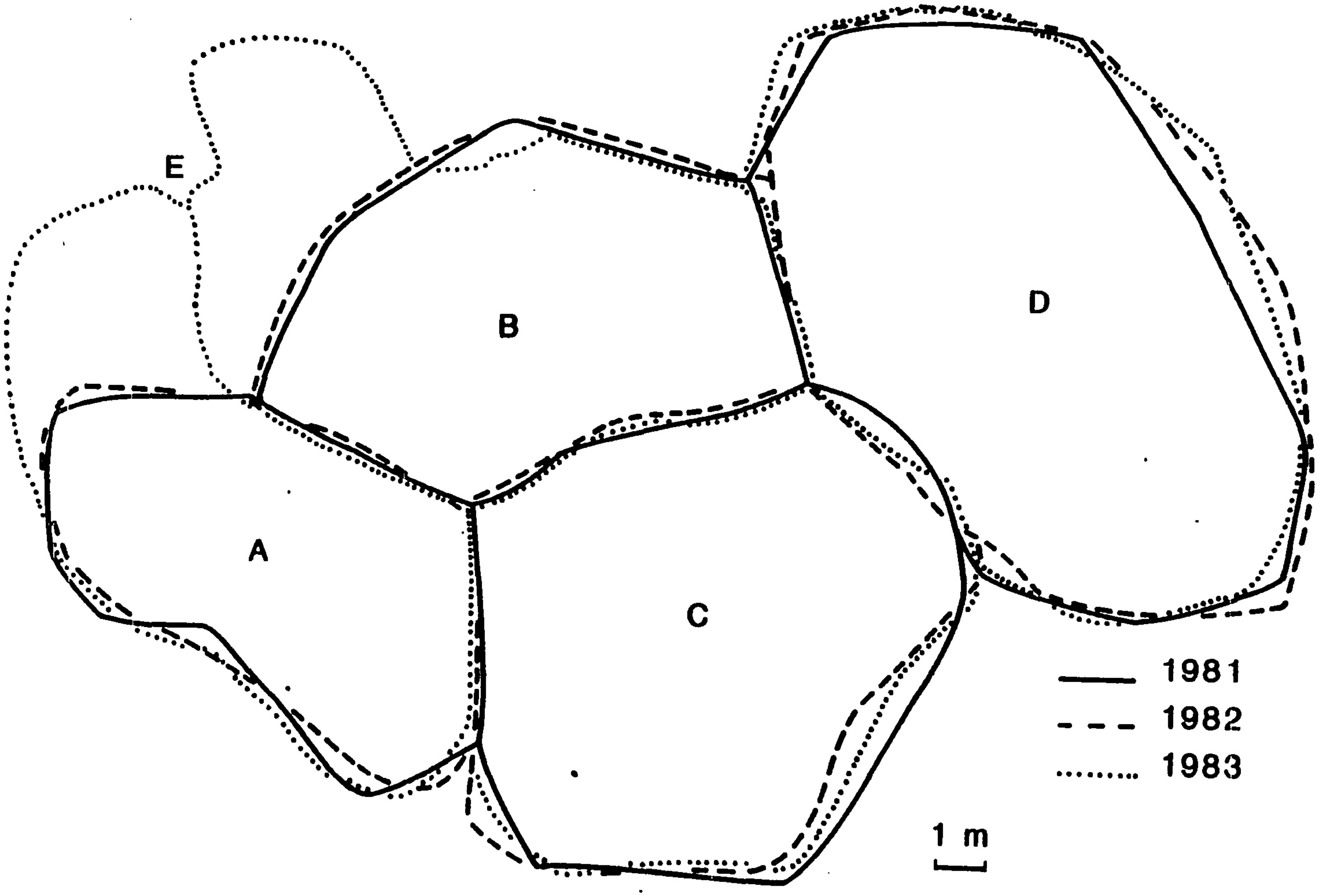
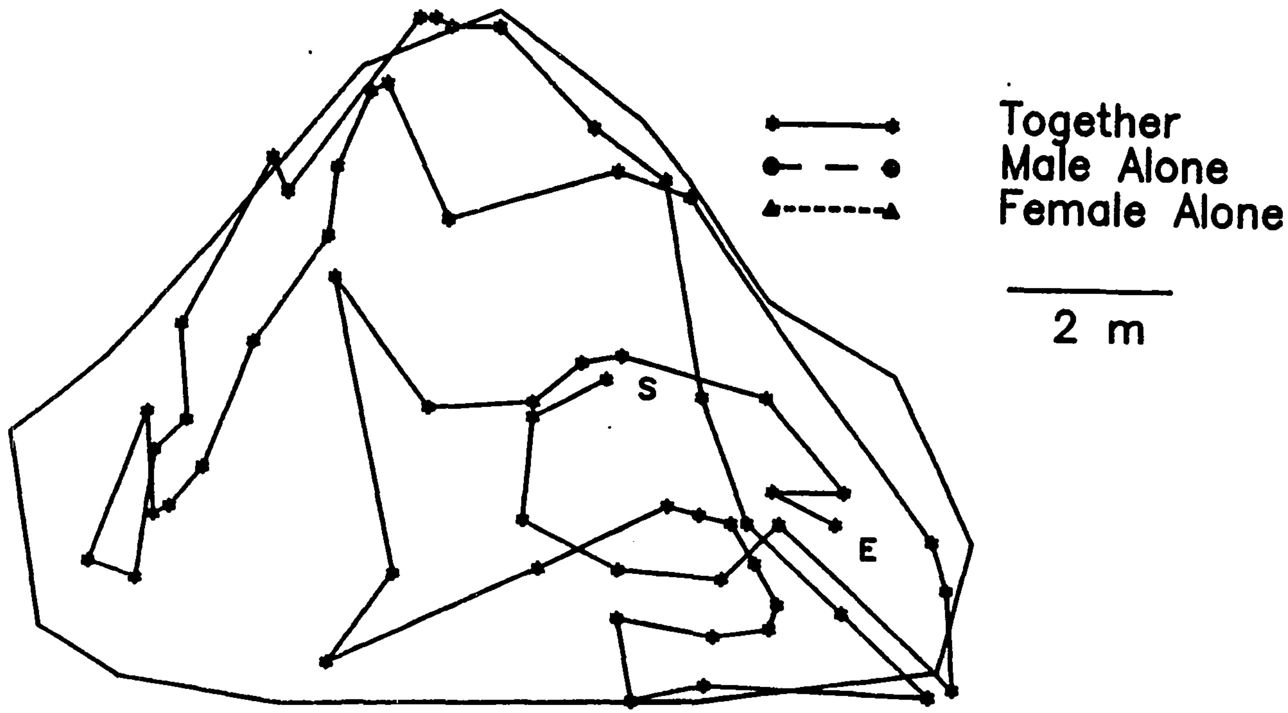

E
B
D
A
C
1981
1982
1983
1 m

Figure 3.6. Sample map of the foraging paths of a pair of _C. multicinctus_ during the afternoon. S- Start of observations, E- End of observations. Positions of each individual were marked at 30 second intervals for a total observation period of 30 min; movements between these positions is approximate. Open circles and dashed lines are those periods when members of a pair were separated; closed circles and solid lines are those periods when pair-mates were foraging within one meter of each other.

C. *multicinctus*



Sample foraging paths of a pair of C. multicinctus in the deep coral-rich habitat are shown in Fig. 3.6. Foraging paths were similar in the morning and afternoon. Most movements within the territory occurred with the male and female moving together as a pair. Some paths between coral heads were used repeatedly, and many individual coral heads were visited several times during an observation period. Boundaries of the territory were visited once or twice every 30 min, usually by both members of the pair. Areas containing several large heads of P. lobata, were used most intensively, although almost all areas of the territory were visited during the day. Foraging paths and areas of maximum use were consistent over different seasons of the year (Fig. 3.7).

e. Food reduction experiments:

Coral abundance within the territories of three pairs of C. multicinctus in the deep coral-rich habitat was reduced by covering 25% to 35% of the territory. Porites lobata was covered preferentially, with greater than 70% of its original surface area unavailable for feeding. Results are shown in Table 3.5 and Fig. 3.8. In all three cases, territorial expansion occurred. There was also an increase in territorial encounters and chases with neighboring pairs as the experimental pair intruded into neighboring territories (Table 3.5). Chases were analyzed as the proportion of observation periods in which at least one chase occurred. Differences between means were tested by generating 95% confidence limits for a binomial proportion

Figure 3.7. Territory use by a sample pair of _C. multicinctus_ in the deep coral-rich habitat during different seasons: November 1982; March 1983; and June 1983. Each map was constructed by noting the positions of individuals at 30 sec intervals during 30 min periods on the morning and afternoons of three consecutive days (see Figure 3.6) and calculating the percent of all observations which occurred in each 1 m^2 quadrat. Major areas of use were the same during each season and corresponded to large colonies of the coral _Porites lobata_.

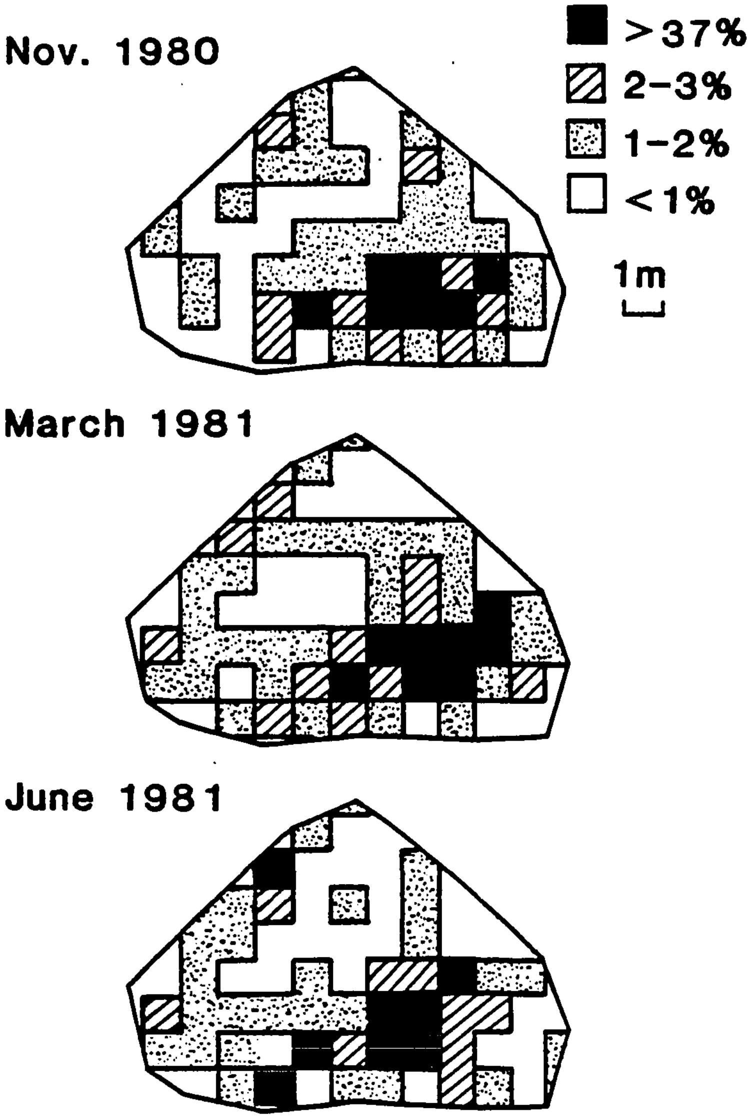
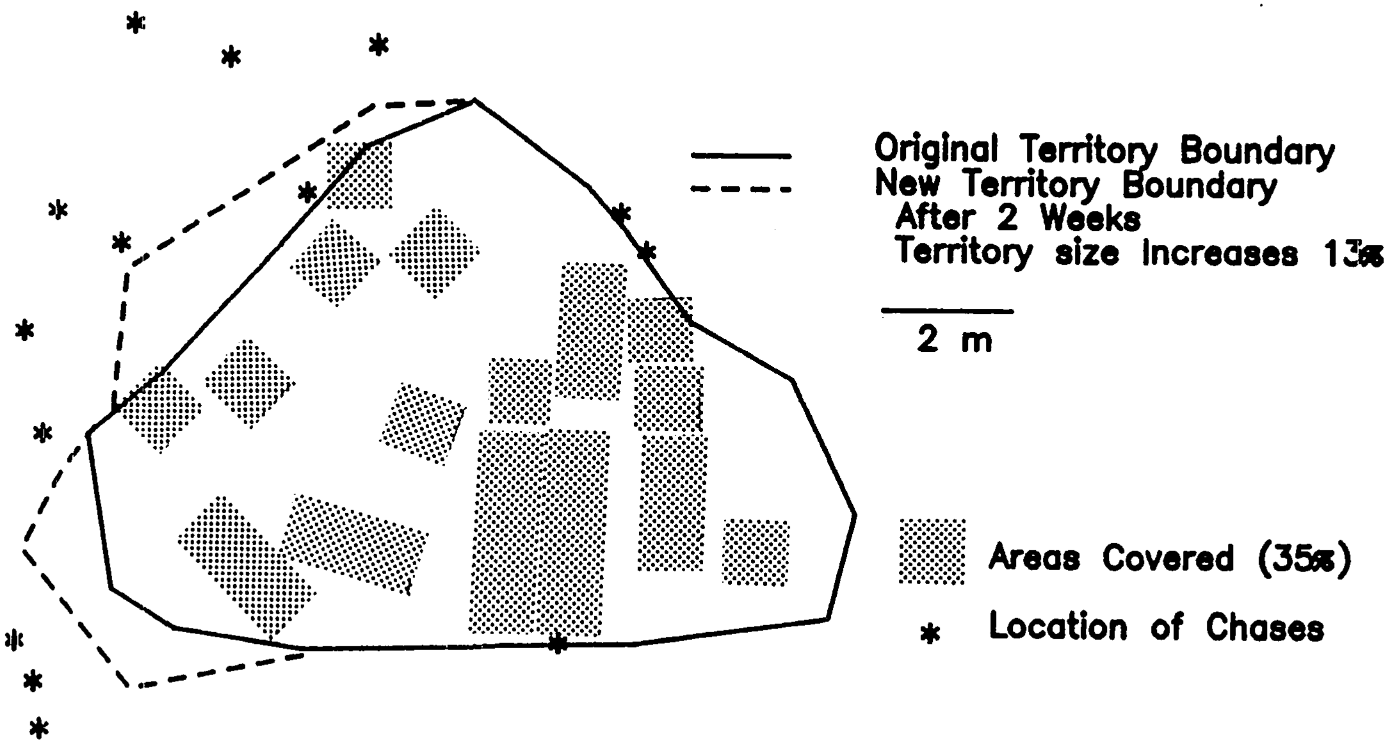

Nov. 1980
March 1981
June 1981
>37%
2-3%
1-2%
<1%
1m

Table 3.5 Coral reduction experiment conducted on three pairs of Chaetodon multicinctus in the deep coral-rich habitat at Puako. * signifies a significant difference ($p<0.05$) after coral reduction compared to before (see text for statistical tests).

	% Territory covered	% Change in territory size	Chases per hr		Feeding Rate (bites/hr)		% Bites on: P. lobata		% Bites on: P. compressa		% Bites on: Hard Substratum	
			Before	After	Before	After	Before	After	Before	After	Before	After
EXPERIMENTAL												
Pair #1.	25%	+7%	0.84	3.00 *	M 691 F 928	504 * 829 *	79.4%	49.9% *	14.9%	20.2%	5.6%	29.8% *
Pair #2.	35%	+13%	0.30	5.40 *	M 699 F 868	464 * 810	78%	28.3% *	18.7%	19.5%	3.3%	52.2% *
Pair #3.	30%	+14%	0.18	4.70 *	M 580 F 689	461 * 566 *	65.7%	47.4%	25.3%	31.2%	9.0%	21.3% *
CONTROLS												
Pair #4.	0	0	0.24	0.00	M 607 F 892	658 847	80.9%	76.7%	15.0%	11.5%	4.1%	7.4%
Pair #5.	0	0	0.00	0.12	M 601 F 780	647 794	65.2%	65.9%	22.4%	28.8%	9.3%	5.1%
Pair #6.	0	+0.5%	0.42	0.60	M 508 F 642	572 680	74.1%	68.9%	19.7%	21.2%	6.2%	9.9%

Figure 3.8. Territorial expansion after coral-food reduction within the territory of one of three pairs of C. multicinctus in the deep coral-rich habitat. Large colonies of Porites lobata were covered preferentially. Dotted lines mark stable boundaries achieved two weeks after coral reduction. * marks positions where agonistic encounters with neighboring pairs were observed during territorial expansion.

C. multicinctus



(Tate and Clelland 1957), and found to be significant for each experimental pair.

In all three cases, the feeding behavior of the experimental pair also changed. A greater proportion of feeding bites were directed toward hard substrata, probably feeding on algae, during the four days following coral reduction (t-test of arcsine transformed proportions, $p<0.05$; Table 3.5). In addition, for each fish, the average number of bites in each feeding bout on the remaining exposed heads of P. lobata increased (Chi^2 test $p<0.05$). With the increase in chases there was a concomitant decrease in the overall feeding rate of five out of six of the experimental individuals (Table 3.5). During 5min intervals when no chases occurred, feeding rates were slightly higher due to rapid feeding bites on hard substrata. There were no significant changes in territory sizes, numbers of chases or feeding rates for the unmanipulated control pairs.

2. Chaetodon quadrimaculatus

Chaetodon quadrimaculatus attained a larger size than C. multicinctus. Adult pairs defended contiguous territories in the shallow habitats. Occasional pairs and small groups of sub-adult fish were seen just below the cliff, but unlike C. multicinctus, the species was rare or absent in the deeper coral-rich habitats. Adults in the shallow coral-poor habitat had lower feeding rates than did C. multicinctus (667 vs. 838 feeding bites per hr for females, and 502 vs. 659 bites per hr for males; Mann-Whitney U-test, $p<0.001$). Fish in the shallow coral-poor habitat were active during the lunar day, rather than during the solar day (Hourigan 1986a). When active during daylight hours, individuals fed continuously, feeding during 91.3% of all 1 min intervals, with only small amounts of time spent in other activities (Table 3.1). Pair mates spent 50% (SD 37%) of their active period within 2 m of each other. In the shallow coral-rich habitat, individuals were generally sheltered during the day and apparently fed at night. Unless otherwise noted, the data presented below are for fish in the shallow coral-poor habitat only.

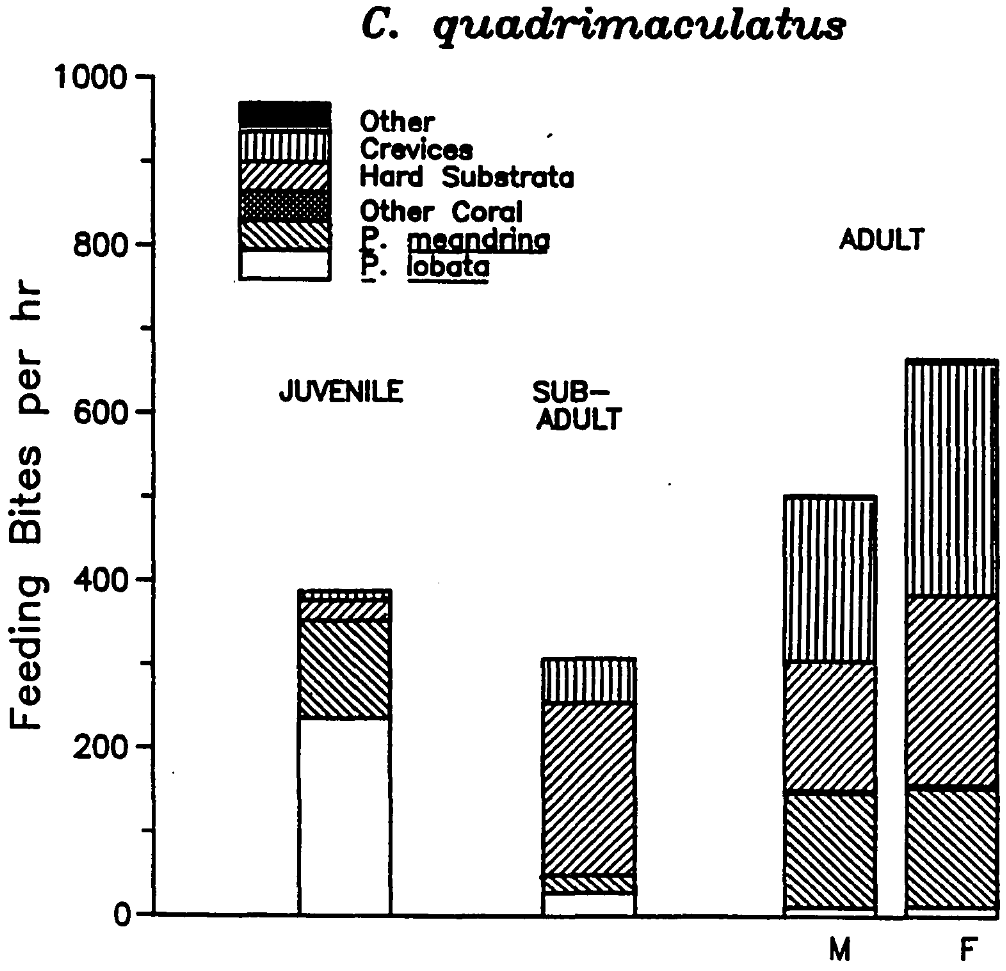
a. Differences in foraging behavior between the sexes and among different age classes.

Adult females fed more than the males with whom they were paired (Independent Wilcoxon's signed-ranks tests, $p<0.05$ to 0.005, N=25; Fig. 3.9). The mean difference between male and female feeding rates within a pair was greater than for C. multicinctus (t-test $p< 0.05$).

Feeding rates of juveniles were lower than those of adult pairs (Mann-Whitney U test, $p<0.05$; Fig. 3.9). Juvenile C. quadrimaculatus less than 40mm in total length were found sheltered in the territories of adult pairs. Juveniles fed in a 1 to $2m^2$ area, never straying far from shelter, and were chased vigorously and repeatedly by the resident pair.

Sub-adults larger than 40mm occurred in loose groups of 2 to 20 individuals which swam below the edge of the cliff, along the border

Figure 3.9. Feeding rates of juveniles (N = 6; each observed for 100 min), non-territorial sub-adults (N = 6; each observed for 100 min), and territorial adults (N = 25 pairs; each individual observed for 100 min), of the fourspot butterflyfish, *C. quadrimaculatus* in the shallow coral-poor habitat at Puako, Hawaii. Feeding rates are subdivided by major coral species and other substrata on which feeding occurred.


C. quadrimaculatus
Feeding Bites per hr
1000
800
600
400
200
0
Other
Crevices
Hard Substrata
Other Coral
P. meandrina
P. lobata
JUVENILE
SUB-ADULT
ADULT
M
F

of the adult territories. Groups appeared to be of unstable composition, often breaking up into smaller groups, pairs or singles, or joining other groups. These fish occasionally invaded the territories of adults, feeding until they were chased away. Inspection of the gonads of 10 members of a group revealed both immature females and immature or marginally mature males. Sub-adult individuals had very low feeding rates compared to territorial adults, (Mann-Whitney U test $p<0.05$; Fig. 3.9). These individuals were often seen feeding under overhangs on the cliff face.

b. Prey availability and prey selection.

Prey choice by _C. quadrimaculatus_ differed from that of _C. multicinctus_. Only 27.1% of all bites were directed toward living corals, predominantly toward _Pocillopora meandrina_ (Fig. 3.9). Fish fed infrequently on the most abundant coral _Porites lobata_ and the less abundant corals of the genera _Montipora_, _Leptastrea_, _Pavona_ and _Cyphastrea_. Electivity indices showed a strong preference for _P. meandrina_ (Table 3.6). The remaining bites were mostly directed toward other hard substrata, or towards crevices, especially the crevices in _P. lobata_ produced by alpheid shrimp. A test of independence between coral abundance in the habitat and abundance in the diet showed that fish did not feed on corals in proportion to their abundance (Pooled G-test for all pairs: df = 3, $p< 0.001$), in agreement with the results of the electivity indicies.

Table 3.6 Feeding bites on different substrata, and electivity indices for male and female *C. quadrimaculatus* in different habitats at Puako, Hawaii.

SHALLOW CORAL-RICH HABITAT[a]

(4 Pairs)

SUBSTRATUM	% CORAL[c] COVER	BITES PER HR		ELECTIVITY	
		Male	Female	Male	Female
P. lobata	87.6	4	7	-0.62	-0.64
P. compressa	0	0	0	-	-
P. meandrina	11.6	15	31	0.72	0.72
Other corals	0.8	<1	1	0.01	0.24
Hard substratum		70	129	-	-
Crevices		144	297	-	-
Other		0	0	-	-
All corals[d]	31.9	19	39	-0.60	-0.60
Total Bites		233	465	-	-

SHALLOW CORAL-POOR HABITAT[b]

(25 Pairs; each fish observed at least 100 min)

SUBSTRATUM	% CORAL[c] COVER	BITES PER HR		ELECTIVITY	
		Male	Female	Male	Female
P. lobata	79.4	13	13	-0.80	-0.82
P. compressa	0	0	0	-	-
P. meandrina	19.8	134	150	0.68	0.69
Other corals	0.8	<1	1	-0.59	0.00
Hard substratum		154	231	-	-
Crevices		199	269	-	-
Other		1	2	-	-
All corals[d]	14.6	148	164	0.34	0.25
Total Bites		502	667	-	-

---

a. Data from the shallow coral-rich habitat are from a few daylight observation periods during which the normally sheltered fish did some feeding (N = 17 observation periods for each sex).

b. Data from the shallow coral-poor habitat were all taken during daylight hours after the moon had risen.

c. Coral cover determined from ten .25 m^2 quadrats within each habitat.

d. All corals = total % bottom cover which was live coral.

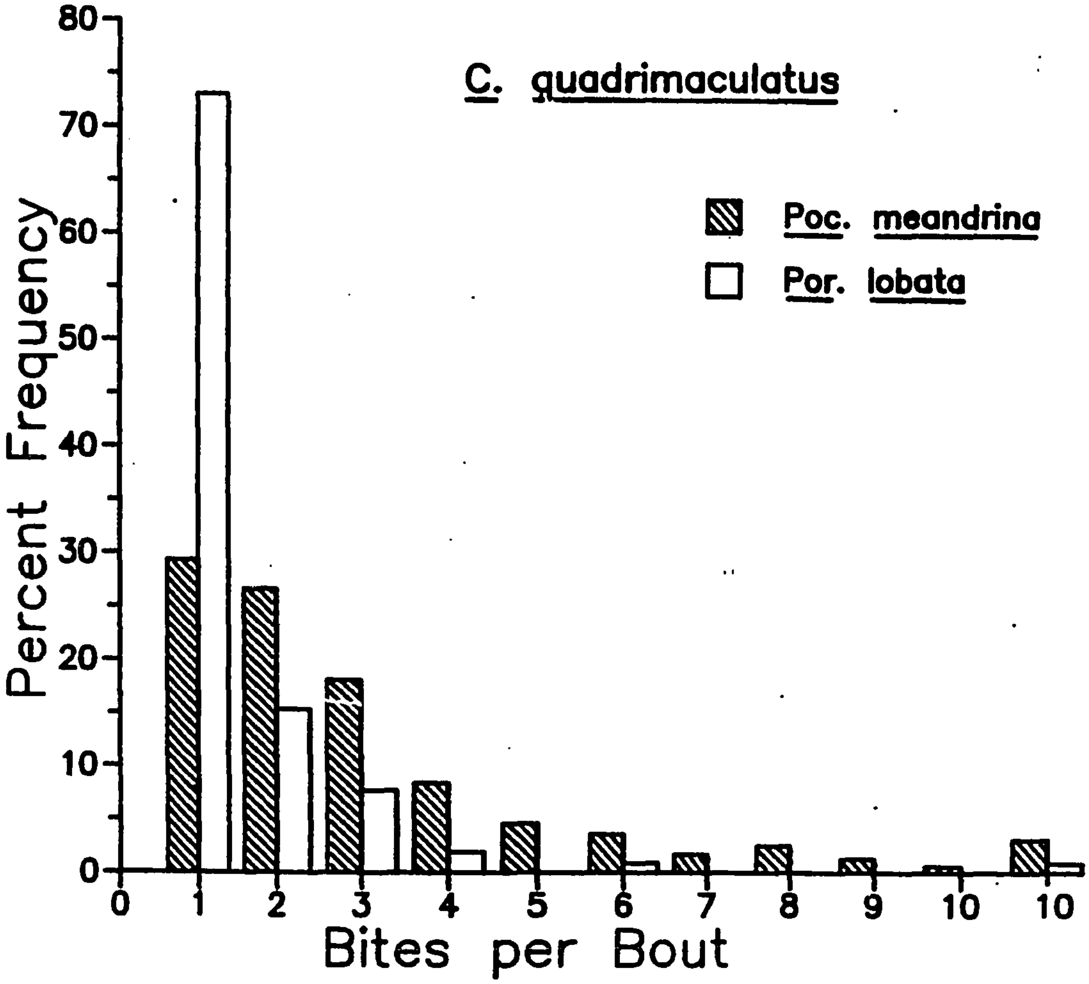
There were no consistent differences in the proportion of feeding bites on different substrata by adult male and female pair-mates (Wilcoxon's signed-ranks test, $p>0.4$). Pair-mates often fed together on the same coral head with no observed aggression.

Prey choice by juveniles and sub-adults differed significantly from that of adults (Fig. 3.9). Juveniles fed almost exclusively on corals. Proportions of bites on *P. lobata* were much higher for juveniles (54%) than for adults in the same habitat (2-3%; t-test of arcsin transformed proportions, $p<0.001$). Non-territorial sub-adults directed most bites toward hard substrata and crevices, with fewer feeding bites on coral than either territorial adults or juveniles (t-test of arcsin transformed proportions, $p<0.01$).

Feeding-bite behavior differed on different substrata. Bites on *P. meandrina* were forceful and direct. Feeding bites on hard substrata were often accompanied by a sideways jerk of the head. *Chaetodon quadrimaculatus* differed from *C. multicinctus*, in that it fed deeper between the branches of *P. meandrina* and more often turned on its side to reach polyps beneath the edges of the lower branches.

The distribution of feeding bites in bouts on coral colonies (patches) is shown in Fig. 3.10. When feeding on the preferred coral, *P. meandrina*, there were fewer bouts with a single bite, and more bouts with two or more bites than when feeding on *P. lobata*. *Chaetodon quadrimaculatus* also fed extensively in crevices, usually with more than one bite in each crevice.

Figure 3.10. Distribution of the number of feeding bites by *C. quadrimaculatus* per feeding bout on each coral colony, expressed as a percent of all bites on that coral species. Frequency distribution of bites directed toward individual colonies of the corals *Porites lobata* and *Pocillopora meandrina* in the shallow coral-poor habitat (N = 10 pairs; each observed for at least 100 min).


C. quadrimaculatus
▨ Poc. meandrina
☐ Por. lobata
Percent Frequency
0
10
20
30
40
50
60
70
80
Bites per Bout
0
1
2
3
4
5
6
7
8
9
10
10

Analysis of stomach contents revealed that polychaetes comprised the largest percentage (52%-63%) of the wet weight of food material collected at mid-day and at dusk (Table 3.7). Other benthic invertebrates including sipunculids and small amphipod crustaceans comprised 10%-15% of the wet weight. Coral tissue, including oral disks, nematocysts and zooxanthellae comprised 8%-13% of stomach contents by wet weight. The final major food item was filamentous algae, which constituted 8% of the stomach material at noon, and significantly more (25%) at dusk (t-test of arcsin transformed proportions, $p<0.05$). Sample sizes from different times of the day were small, and the results must be viewed with caution. Gut fullness differed at different times of the day, depending on the phase of the moon (Table 3.7).

c. Diel and seasonal foraging patterns.

1. Diel foraging patterns.

Changes in the foraging behavior of C. quadrimaculatus during the day were conspicuous. Feeding rates in the late afternoon were higher than in the morning (Kruskal-Wallace test, $p<0.05$). The proportion of feeding bites on hard substrata increased as the day progressed (Kruskal-Wallace test, $p<0.05$; Fig. 3.11). The increased proportion of algae found in the stomachs of fish speared at dusk indicated that this increase in feeding on hard substrata probably reflected feeding on algae. Feeding on corals, as a proportion of total feeding, was highest during the morning, and gradually decreased.

Table 3.7. Stomach contents of *C. quadrimaculatus* collected in the shallow coral-poor habitat at Puako, Hawaii, during different times of the day, at the time of the new and full moon.

First Light - Full Moon (Sample of 5 fish)

Food Item	Per cent by wet weight	Number of Fish with Item
Coral tissue	87.5%	5
Polychaetes	11.1%	5
Algae	0.9%	4
Other	0.5%	2

First Light - New Moon (Sample of 6 fish)

Food Item	Per cent by wet weight	Number of Fish with Item
Coral tissue	-	0
Polychaetes	-	0
Algae	-	0
Other*	100%	6

*small amount of mucous and unidentifiable material

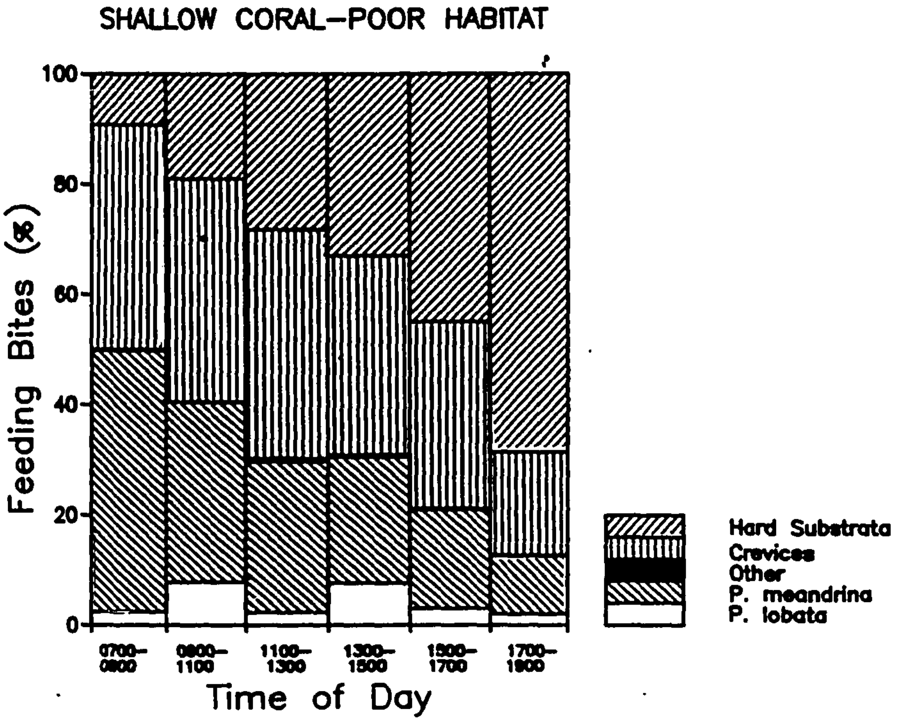
Mid-day - New Moon (Sample of 6 fish)

Food Item	Per cent by wet weight	Number of Fish with Item
Coral tissue	13.3%	6
Polychaetes	63.2%	6
Algae	7.6%	6
Other invertebrates	15.3%	5
Other	0.6%	5

Dusk - New Moon (Sample of 4 fish)

Food Item	Per cent by wet weight	Number of Fish with Item
Coral tissue	8.6%	4
Polychaetes	52.1%	4
Algae	24.6%	4
Other invertebrates	9.5%	4
Other	5.2%	3

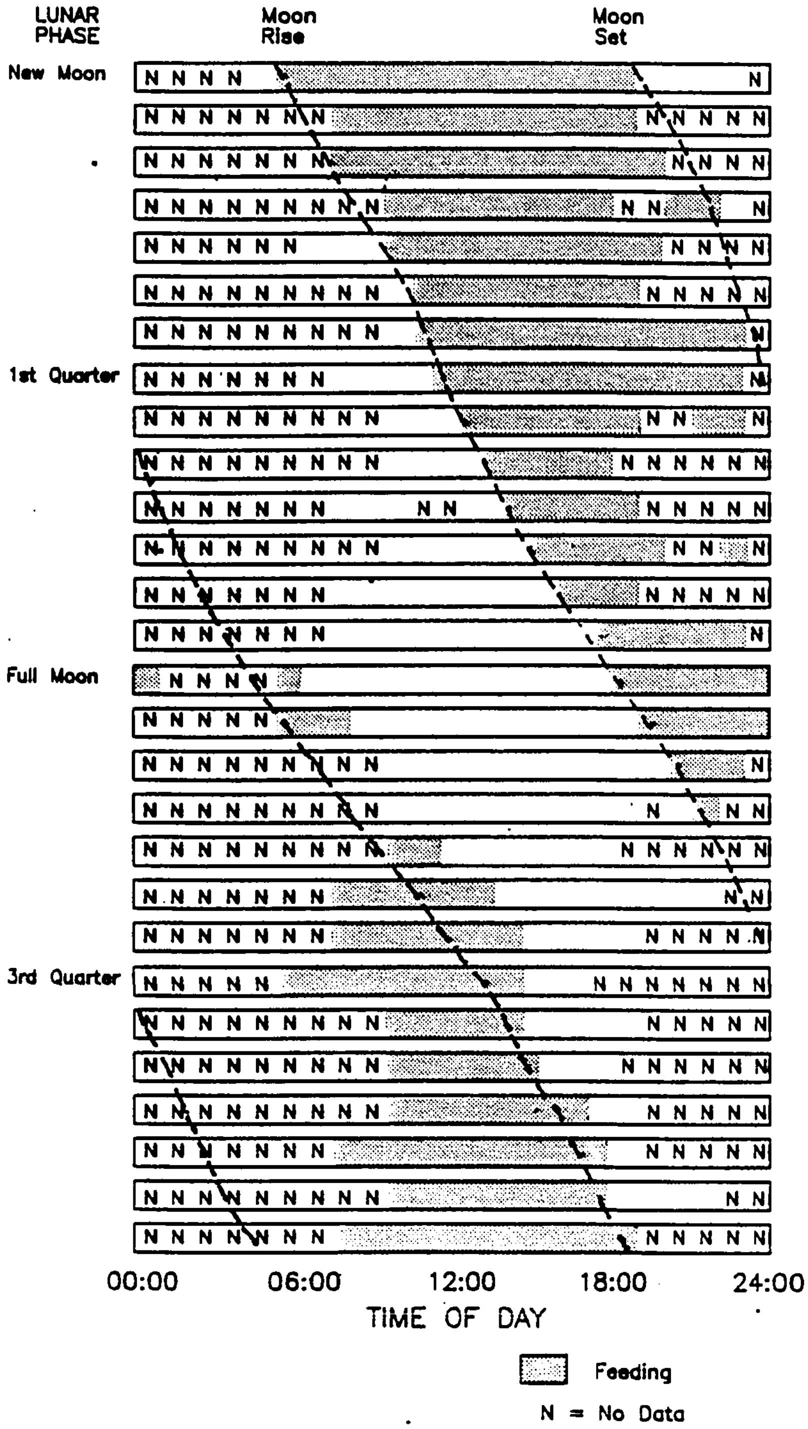
Figure 3.11. Percent of feeding bites on different substrata by *C. quadrimaculatus* at different times of the day in the shallow coral-poor habitat at Puako, Hawaii (N = 6 pairs; data were gathered over a period of 1 year, with at least 100 min of observation for each member of the pair during each 2 hr time interval).


SHALLOW CORAL-POOR HABITAT
Feeding Bites (%)
100
80
60
40
20
0
0700–0800
0800–1100
1100–1300
1300–1500
1500–1700
1700–1900
Time of Day
Hard Substrata
Crevices
Other
P. meandrina
P. lobata

Feeding activity differed between the shallow coral-rich and coral-poor habitats. In both areas individuals formed male-female pairs which inhabited intra-specifically exclusive feeding ranges. In the coral-rich habitat, individuals remained in separate shelters most of the day and were chased by the territorial damselfish Stegastes fasciolatus when they attempted to feed. On night dives conducted near the time of the new moon, individuals in the coral-poor habitat were observed sheltered, while individuals in the coral-rich habitat were observed out of their shelters, apparently foraging. Chaetodon quadrimaculatus was frightened even by dive lights with red light, so actual observations of feeding could not be made on these moonless nights. All individuals speared in the coral-rich habitat on the morning of both the new and full moon had guts full of food.

Feeding schedules of C. quadrimaculatus in the coral-poor areas were more complicated. Observations on individuals at all hours of the day during the four years of this study revealed a distinct lunar periodicity. Each day, feeding began at moonrise and continued until moonset (Fig. 3.12). Thus on days of the new moon, feeding began at dawn and continued until dusk. On subsequent days, feeding began and ended approximately 50 min later each day until the time of the full moon when feeding began at dusk. Active feeding was observed on several occasions at different times of the night by the light of full moon. On these nights, feeding ended near dawn, and fish remained sheltered during the daylight hours of the subsequent day. The feeding period continued to track the lunar day throughout the lunar

Figure 3.12. Observations of feeding by <u>Chaetodon</u> <u>quadrimaculatus</u> on each day of the lunar month in relation to moonrise and moonset (dashed lines). Data are compiled from observations conducted on different days during four years. Data from night dives assume that fish are feeding if known individuals were observed feeding or actively swimming within their territory, or if they were absent from their usual nocturnal shelters. N - Hours during which no data were collected.


LUNAR PHASE
Moon Rise
Moon Set
New Moon
1st Quarter
Full Moon
3rd Quarter
00:00
06:00
12:00
18:00
24:00
TIME OF DAY
Feeding
N = No Data

month (Fig. 3.12). Occassionally near the end of feeding periods, females fed up to an hour after males had finished thier feeding period and retired to their shelters. All individuals speared on the morning following the full moon had guts full of coral tissue, including recognizable polyps of P. meandrina (Table 3.7). In contrast, all individuals speared on the morning of the new moon had empty guts.

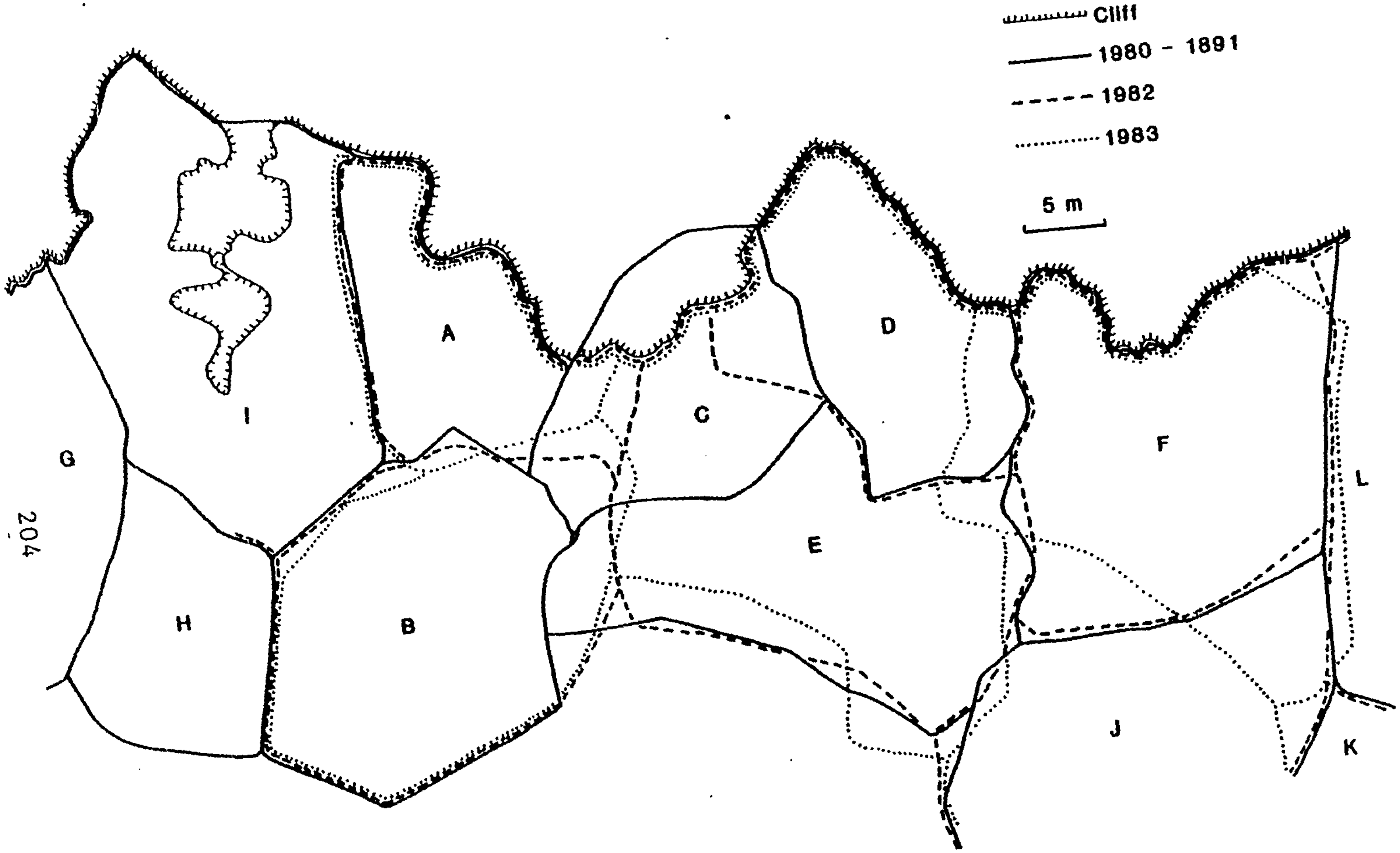
2. Seasonal changes in foraging behavior.

Chaetodon quadrimaculatus females fed more during March in two consecutive years, than during July or November (Two-way ANOVA of square root transformed feeding rates; Waller-Duncan $P<0.05$). March corresponded to the height of the breeding season, which began in December or January and ended around July (Hourigan Chapter V). No comparable differences were observed in the feeding rates of males. There were also changes in foraging paths over different months, but these did not appear to show seasonal periodicity.

d. Territoriality and foraging paths.

Adult pairs of C. quadrimaculatus defended territories against conspecifics, including neighboring pairs, sub-adults and juveniles. As was the case for C. multicinctus, territories were contiguous and the borders of the defended areas were the same as the borders of the feeding ranges (Fig. 3.13). No feeding was observed more than 1m outside the territories. Unlike C. multicinctus, no chases of

Figure 3.13. Territories of six adult pairs (A,B,C,D,E,F) of _C. quadrimaculatus_ in the shallow coral-poor habitat at Puako, Hawaii, mapped during four consecutive summers: 1980, 1981, 1982, and 1983. Territorial expansion occurred in 1982 when one pair (C) disappeared, and again in the following year when a second pair (D) disappeared. Additional territories (G,H,I,J,K,L) were mapped during the summer of 1981.


Cliff
1980 - 1891
1982
1983
5 m
A
B
C
D
E
F
G
H
I
J
K
L

heterospecifics were observed. Territory borders were often located along gullies or other physical landmarks, and ended abruptly at the cliff.

Mean territory size in the shallow coral-poor zone was 276m^2 (SD=116, N=24), with territory size ranging from 105m^2 to 558m^2. The territories were larger than those of C. multicinctus (t-test $p<0.001$) with which they overlapped completely. Territory size was negatively correlated to the coral cover of Pocillopora meandrina within each territory (Pearson's correlation coefficient, r = 0.78, N = 12, $p<0.001$). Territory borders remained stable from year to year, except when a pair disappeared (two cases shown in Fig. 3.13). After such disappearances, neighboring pairs expanded their territories to fill the available space.

The spatial pattern of foraging paths of C. quadrimaculatus within territories differed from the patterns of C. multicinctus. Pairs remained together only 50% of the time, and visits to the borders of the territory were more common for the male than the female (Fig. 3.14). During the morning, most feeding was concentrated in a core area of the territory, which contained a large number of P. meandrina coral heads and crevices. A pair fed primarily in the same core areas for several months, then established a new core area in a different part of the territory (Fig. 3.15). Males made tours of the periphery of the territory about once every half hour. During the late afternoon, feeding occurred more evenly over the whole territory.

Figure 3.14. Foraging paths of a sample pair of C. quadrimaculatus. S- Start of observations, E- End of observations. Positions of each individual were marked at 30 second intervals during 30 min; movements between these positions is approximate. Open circles and dashed lines are those periods when members of a pair were separated; closed circles and solid lines are those periods when pair-mates were foraging within one meter of each other.

C. quadrimaculatus

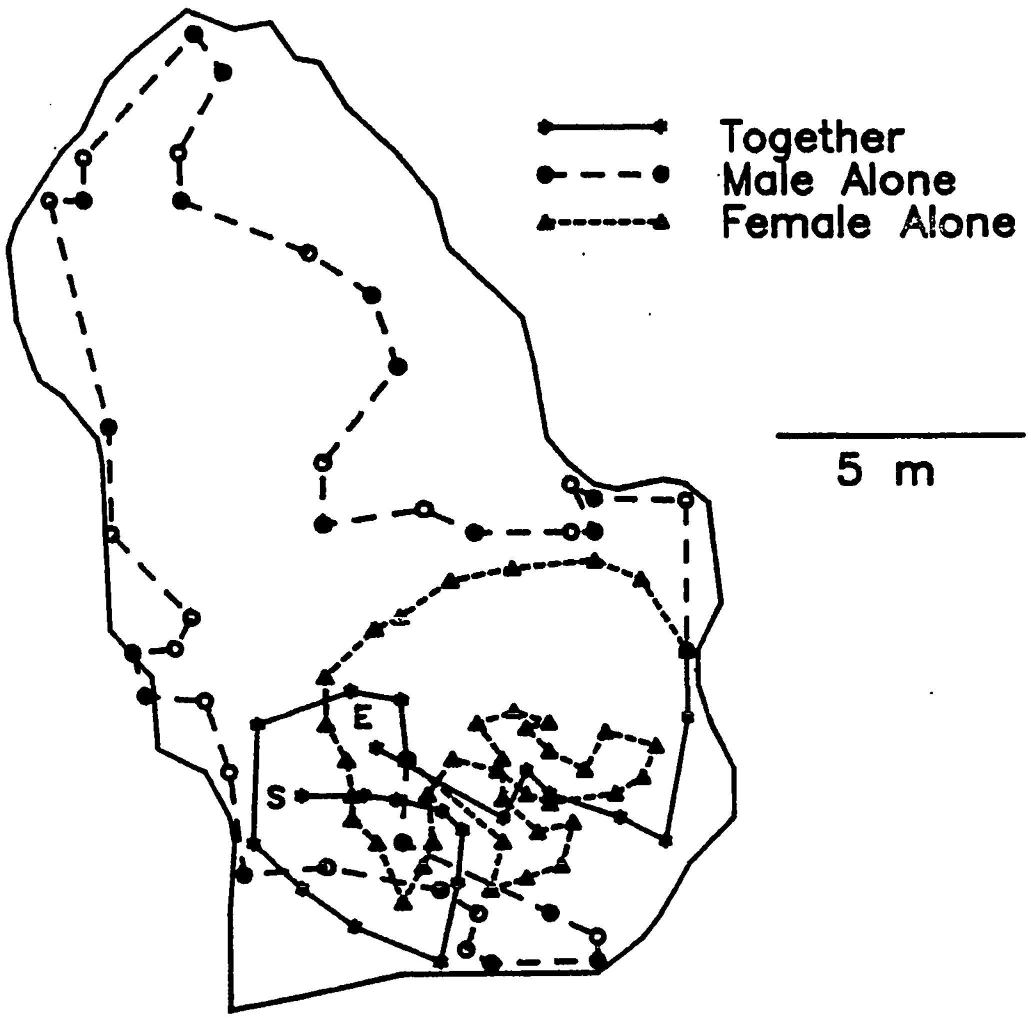
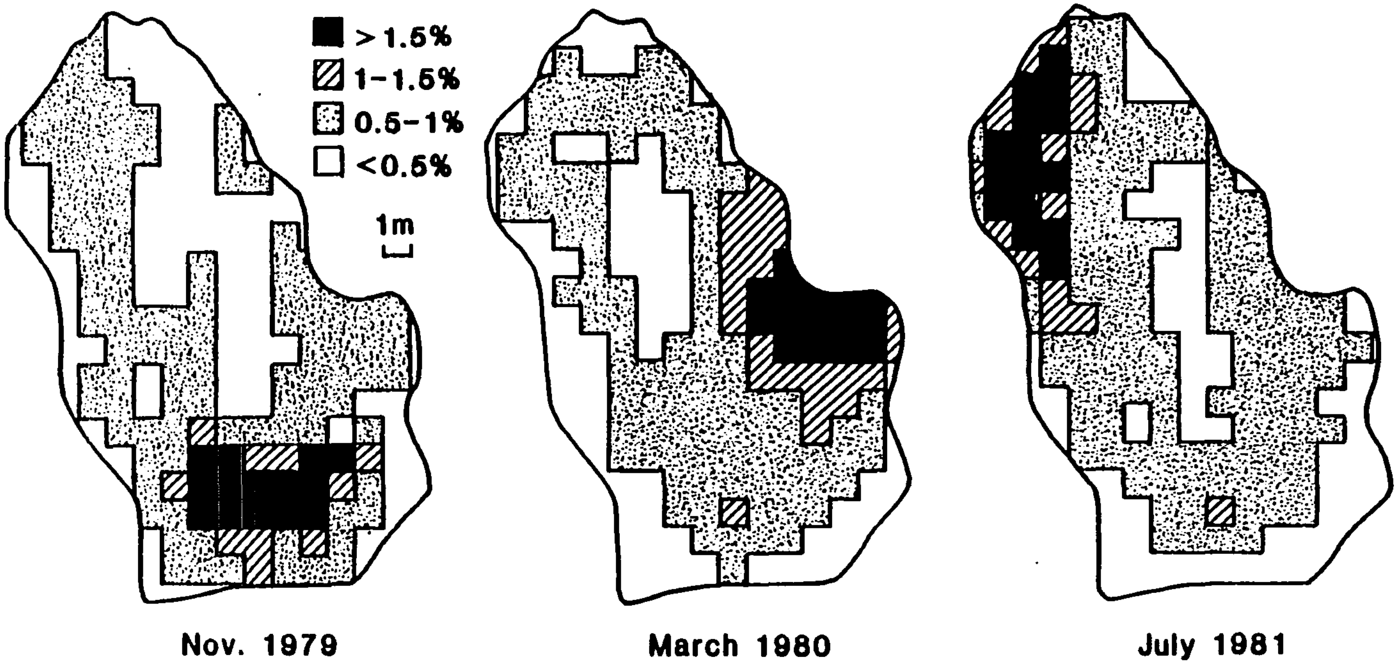


Figure 3.15. Territory use by a sample pair of C. quadrimaculatus during different seasons: November 1979; March 1980; and July 1980. Each map was constructed by noting the positions of individuals at 30 sec intervals during 30 min periods on the morning and afternoon of three consecutive days (see Figure 3.14), and calculating the percent of all observations which occurred in each 1 m^2 quadrat.



Nov. 1979

March 1980

July 1981

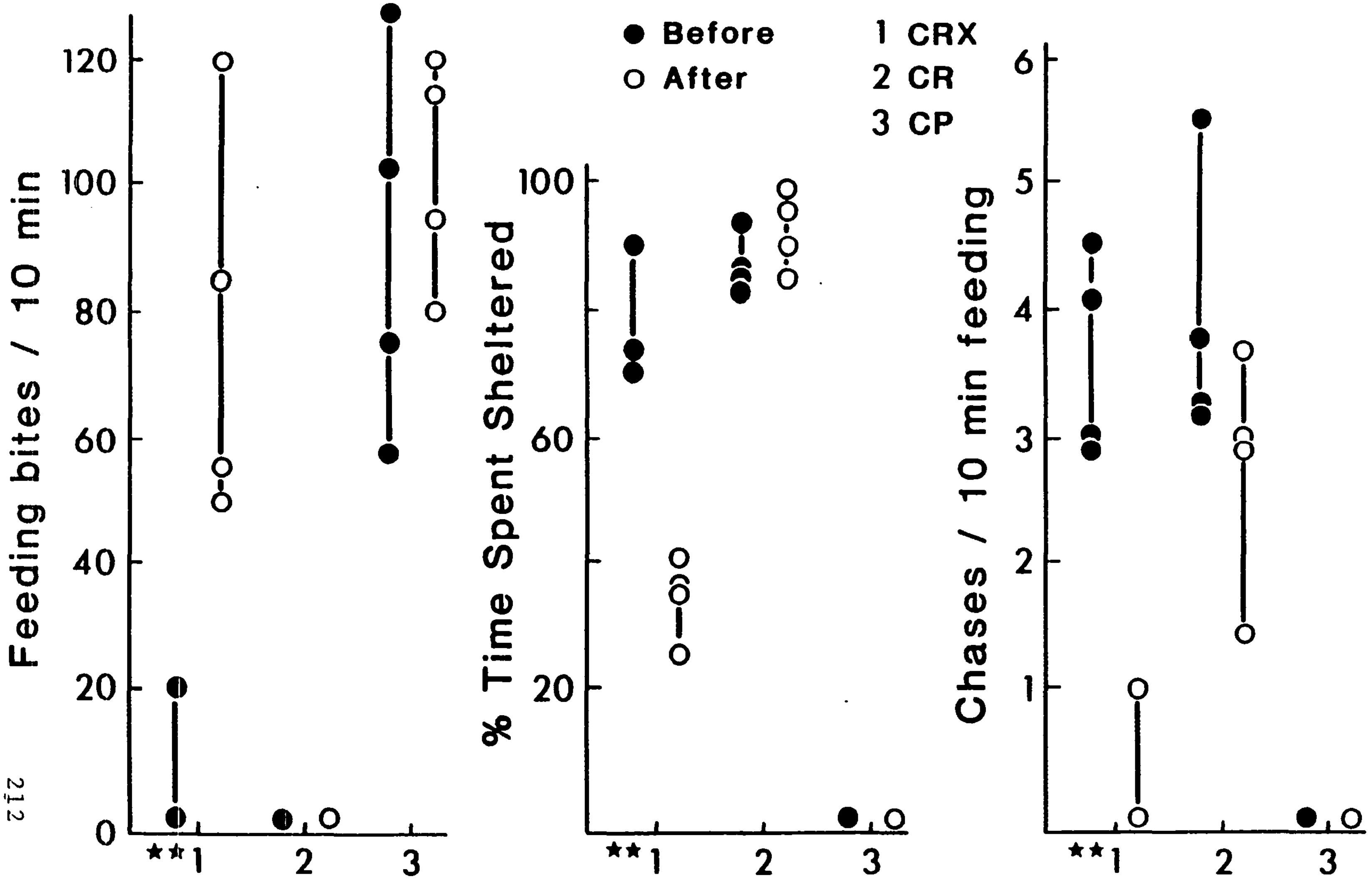
f. Effects of pomacentrids: an experimental removal.

Large numbers of the territorial damselfish, Stegastes fasciolatus occurred in the shallow coral-rich habitat and were nearly absent in the shallow coral-poor habitat. Individual damselfish defended well defined algal "mats" and were observed to chase C. quadrimaculatus.

Observations were conducted near the time of the new moon. At this time, the four focal C. quadrimaculatus in the experimental area and the four control fish, in another area of the coral-rich habitat were sheltered throughout the day. Before pomacentrid removal, the four focal individuals in the coral-poor habitat fed continuously during the day.

Pomacentrids were removed to determine if these differences in feeding behavior by C. quadrimaculatus were due, in part, to chases by S. fasciolatus. Removal reduced the average number of S. fasciolatus in the experimental area from 67 individuals to seven. Feeding bites by C. quadrimaculatus per 10 min increased significantly in the experimental area after pomacentrid removal (Fig. 3.16, $p<0.01$, Median test in two-way classification with four observations per cell: Tate and Clelland, 1957), with a concomitant decrease in time spent sheltered. The number of chases by S. fasciolatus per time spent feeding (i.e. time not sheltered) also decreased significantly (Median test, $p<0.01$). There were no significant changes in the control areas. The behavior of other herbivorous fishes also changed as a result of the pomacentrid removal (Hourigan 1986a).

Figure 3.16. Chaetodon quadrimaculatus: Feeding rates, sheltering behavior and chases by pomacentrids before and after removal of S. fasciolatus. a. Median number of feeding bites (N=4) observed for each of four C. quadrimaculatus individuals in the coral-rich experimental (CRX), coral-rich control (CR), and coral-poor control (CP) areas, before and after pomacentrid removal. b. Median time spent sheltered by each individual C. quadrimaculatus before and after pomacentrid removal. c. Median number of chases by S. fasciolatus directed toward each individual C. quadrimaculatus per ten min foraging (i.e. not sheltered), before and after pomacentrid removal. Data were analyzed using a non-parametric median test in two-way classification, with four observations per cell (**=$p<0.01$).


Feeding bites / 10 min
0
20
40
60
80
100
120
**1
2
3
● Before
○ After
1 CRX
2 CR
3 CP
% Time Spent Sheltered
20
60
100
**1
2
3
Chases / 10 min feeding
1
2
3
4
5
6
**1
2
3

After three days of spearing, fewer than ten _S. fasciolatus_ were observed in the experimental area. On the tenth day following removal, 40 adult or subadult damselfish were observed, and after twenty days, a total of 51 were observed. Following this rapid recolonization, the two pairs of _C. quadrimaculatus_ in the experimental area were again found sheltered at times when other individuals in the coral-poor area were feeding.

DISCUSSION

This study investigated the foraging behavior of the butterflyfishes, C. multicinctus and C. quadrimaculatus in the field. Adults of both species formed male-female pairs which defended feeding territories. Foraging was the major daily activity of these fishes. The observed differences in patterns of foraging by the same individuals over time, and among different individuals and species, indicate that the needs of individuals of different classes (e.g. species, sexes or age classes) or the constraints on their feeding, must also differ or change with time. The major trends in foraging behavior shown by the two species are summarized in Table 3.8.

a. Sex and age class differences in foraging.

Adult females of both species fed more than the males with whom they were paired. This occurred despite the fact that males were generally larger (Hourigan Chapter V) and more active in territorial defense, and might therefore be expected to have higher metabolic needs. Since both members of a pair foraged in the same territory without apparent intra-pair competition for resources, these differences in feeding rates probably reflect different energetic strategies.

Females of both butterflyfish species followed a strategy of energy maximization (sensu Schoener 1971) in comparison to males. They fed almost continuously, and spent longer periods inspecting and nipping at food and had stomachs filled with more food than did males.

Table 3.8 Summary of the foraging behavior of *C. multicinctus* and *C. quadrimaculatus*.

FEEDING BEHAVIOR	SPECIES	
	C. multicinctus	*Chaetodon quadrimaculatus*
a. Feeding Rates (bites/hr)		
Mean for Females	805	667
Mean for Males	650	502
Sex Differences	Females fed more than males.	Females fed more than males.
Age Differences	Adults fed more than subadults or juveniles.	Adults fed more than subadults or juveniles.
b. Prey Selection		
Diet:		
Adults	Mostly coral.	Coral, algae and polychaetes.
Juveniles	" "	Mostly coral.
Coral preference	*P. meandrina* > *P. lobata* > *P.compressa*	*P. meandrina* > *P. lobata*
Prey selection	Changes with habitat.	Distribution of fish limited to habitats with preferred coral.
Time in patch	More time spent feeding on patches (colonies) of preferred coral species.	More time spent feeding on patches (colonies) of preferred coral species.
c. Temporal Periodicity		
Diel periodicity	Feed continuously during daylight hours. More bites on algae during the afternoon.	Feed continuously for 12 hrs, beginning feeding period at moonrise. More bites on algae during the afternoon.
Lunar periodicity	None observed.	Feeding occurs during lunar day rather than solar day.
Seasonal periodicity	None observed.	Female feeding rates are higher during the spawning season.

Table 3.8 (cont.)

FEEDING BEHAVIOR	SPECIES	
	C. multicinctus	Chaetodon quadrimaculatus
d. Territoriality and Foraging Paths		
Who defends?	Joint defense by pair of mature male and female. Male contributes most to territorial defense.	Joint defense by pair of mature male and female. Male contributes most to territorial defense.
Against whom?	Conspecifics and other species of corallivores.	Conspecifics only.
Mean territory size	Shallow: 107m^2 Deep: 73m^2	Shallow: 276m^2
Foraging paths:	Most areas of territory visited, with most time spent in areas with most cover of preferred coral.	Most feeding limited to a core area which changes location within the territory over a period of months.
Diel patterns:	Paths similar during morning and afternoon.	Paths in the late afternoon are more evenly distributed over territory.
Patrolling of borders:	By both male and female.	Usually by male only.

Energy gained by feeding in excess of daily maintenance needs could be directed toward reproduction. The fitness of female butterflyfishes is probably limited primarily by their lifetime production of eggs (Hourigan Chapter V). In contrast, the fitness of males is often limited by the availability of mates, rather than food (Wilson 1975). Females invested 13 to 16 times more energy into reproductive tissues than did their similarly sized male pair mates (Chaetodon multicinctus and C. quadrimaculatus respectively: Hourigan Chapter V). Compared to females, males behaved as foraging "time minimizers" (Schoener 1971), minimizing their feeding time to allow more time for other activities. The primary difference between male and female feeding rates appeared to be a function of increased time spent by males in chases and surveillance. Tricas (1986) also found that female C. multicinctus fed more and chased less than did males.

Differences in male-female foraging rates are found among numerous fishes. Females of two species of territorial labrids (Bodianus rufus and B. diplotaenia) spend more time feeding than do males (Hoffman 1983). When individual females undergo sex change to become males, they reduce the time they spend foraging. Territorial males of other labrid species, e.g. Thalassoma duperrey (Ross 1983) and Tautoglabrus adspersus (Green et al. 1984), reduce their feeding rates when courting and spawning occurs. Females and non-territorial males feed significantly more during this time. Among monogamous fishes, such as butterflyfishes (Hourigan 1985, Chapter VII; Fricke 1986), or the surgeonfish Acanthurus leucosternon (Robertson et al.

1979), higher female feeding rates may be facillitated by the male pair-mate assuming the majority of the territorial defense activities. It appears likely that female energy maximization in comparison to males is the rule among many fishes.

Juveniles and sub-adults had lower feeding rates than did adults. Juveniles which occurred within the territories of adult pairs were chased vigorously. As a result, they spent large amounts of time sheltered, leaving less time for feeding. Since juveniles of both species fed on some of the same corals as the adults, chases may have been a response to feeding competition. Sheltering may also be important for small fish which are more subject to predation.

Juveniles apparently resided within the territories of adults until they were too large to shelter effectively, and were then chased out by the adult pair. The lower feeding rates of juveniles and sub-adults were probably a result of the chases by territorial pairs. This provides evidence for the feeding advantage of territoriality in these species. Adult C. multicinctus pairs defended contiguous feeding territories over most areas of the reef. Sub-adults were found either sheltered in interstitial areas between territories, or travelling long distances while skirting the borders of adult territories. This behavior probably reduced chases, since the borders of territories had a narrow "no man's land" between neighboring pairs. Nursall (1977) found that adult red-lipped blennies, Ophioblennius atlanticus, excluded juveniles from feeding territories. These juveniles occurred in small interstitial areas between adult territories.

The distribution of C. quadrimaculatus sub-adults differed from that of C. multicinctus sub-adults. The contiguous territories of adult C. quadrimaculatus ended abruptly at the cliff, and all sub-adults were found near this interface. The rarity of the most preferred coral, Pocillopora meandrina, in this habitat was reflected in the low occurrence of that coral in the diet of sub-adults. The habitat discontinuity caused by the underwater cliff allowed a a concentration of sub-adult fish in this area and the formation of larger groups. The behavior of sub-adults resembled the behavior of small Chaetodon capistratus observed by Gore (1983) in the Caribbean. Those smaller individuals also formed temporary pairs and groups of varying compositions in shallower areas where larger, resident individuals did not occur.

Groups of subadult C. quadrimaculatus were observed to intrude on adult territories next to the cliff. Grouping by sub-adult C. quadrimaculatus may increase their chances of successfully invading the territories of adults. This tactic has been shown in parrotfishes, where sub-adults school to circumvent the territoriality of larger adults (Robertson et al. 1976). Other herbivorous species may school to invade the algal patches of territorial pomacentrids (Barlow 1974; Itzkowitz 1975; Robertson et al. 1976; Hourigan 1986a). Exclusion of non-territorial, usually younger animals from optimal territories is a common phenomenon among terrestrial vertebrates. Among fishes, exclusion of small males from the spawning territories of large males is common among species with lek-like spawning (Loiselle and Barlow 1978).

b. Prey selection.

Chaetodon multicinctus fed primarily on scleractinian corals. *Chaetodon quadrimaculatus* also fed extensively on corals, although algae and non-coralline invertebrates also occurred prominently in the diet. These results agree with previous gut content analyses (Hobson 1974) and observations (Reese 1975, Tricas 1986, Hourigan et al. 1987). Coral tissues contain lipid and protein, but also have a large water content (Tricas 1986, Hourigan Chapter V). In addition, *C. multicinctus* and *C. quadrimaculatus* appeared unable to digest the cell walls of symbiotic zooxanthellae in the coral (Hourigan Chapter V). This resulted in a low net energy intake per bite, and may explain why coral-feeding butterflyfishes spent almost all available time in foraging activities. Nursall (1981) reviewed time budgets of four fish species, each of which spent only 8 to 20 percent of its time feeding, considerably less than the time spent by butterflyfishes.

Chaetodon multicinctus fed on most of the coral species available, but exhibited distinct preferences among the major coral species. *Pocillopora meandrina* was the preferred coral in all habitats. *Porites lobata* was fed on in nearly the same proportion that it occurred in the habitat, while *Porites compressa* was fed on less than would be expected by chance. These preferences exhibited in the field paralleled preferences indicated by choice tests in which two corals were simultaneously presented to fish in the laboratory (Hourigan Chapter II). *Chaetodon quadrimaculatus* also preferred *P. meandrina* over *P. lobata* in both the field and the laboratory.

The proximate basis of these feeding preferences is still unclear. They do not appear to be a result of resource partitioning due to interspecific competition for food resources, since other sympatric corallivores show the same preferences (Reese 1977, Hourigan Chapter II). Preferences may be based on some desirable quality of the preferred corals themselves. Possible factors include the nature of defense mechanisms (e.g. nematocysts and secondary compounds), morphology of the coral, or the energetic return per unit time. These factors are reviewed by Hourigan (Chapter II and V) and Tricas (1986).

The choice of foods by C. multicinctus differed among habitats. Chaetodon multicinctus appeared to be a generalist that accepted a large variety of corals. Individuals changed their foraging tactics depending on the availability of preferred corals. When P. lobata was covered in the food reduction experiment, individuals were able to change their foraging tactics. They increased their consumption of less preferred prey and fed more intensively on the remaining exposed P. lobata. This generalist strategy probably accounted for the occurrence of this species in almost all habitats where there were corals (Hourigan Chapter II). Other coral-feeding generalists had similar distributions (Hourigan et al. 1987, Hourigan Chapter II). Neudecker (1985) has similarly explained the wide distribution of the Caribbean butterflyfish Chaetodon capistratus on the basis of its generalized diet.

In contrast, C. quadrimaculatus fed mostly on only one species of coral, P. meandrina. The distribution of adult territories was correlated to the distribution of this coral (Hourigan Chapter II), and the size of these territories was inversely related to the cover of this coral. The distribution of this fish in Hawaii is similar to its distribution in other areas (Bouchon-Navaro 1981). It is probable that similar causal factors are responsible for the preferences for *P. meandrina* by *C. quadrimaculatus*, *C. multicinctus*, and other corallivorous butterflyfishes (Reese 1977, Hourigan et al. 1987, Hourigan Chapter II). Adult *Chaetodon quadrimaculatus*, however, differed from the coral-feeding generalists in that they did not readily accept the less preferred coral species.

Chaetodon quadrimaculatus attained a larger size than *C. multicinctus*, but had a lower feeding rate. This is consistent with its larger mouth (resulting in a larger bite size), and its reliance on additional food sources such as polychaetes, which may have a higher energy or nutrient content than corals. In laboratory and field tests, *C. quadrimaculatus* ingested more energy per bite than did *C. multicinctus* (Hourigan Chapter V). These factors may also explain the greater difference between male and female feeding rates observed for *C. quadrimaculatus* as compared to *C. multicinctus*. If females maximized their feeding, while males minimized feeding time, then the species with the greatest energy intake per bite would show the greatest male-female difference in feeding rates. Polychaetes are more cryptic than corals, and may require greater search time. This may have contributed to the lower overall feeding rates of *C. quadrimaculatus*.

Both _C. quadrimaculatus_ and _C. multicinctus_ supplemented their diets with algae and polychaetes. These items were major portions of the diet only for _C. quadrimaculatus_. Omnivory of this type has been observed in other butterflyfishes (Hobson 1974, Birkeland and Neudecker 1980), angelfishes (Hourigan et al. in press), and other fishes. These fishes may require additional nutrients available only from a varied diet. This does not explain why _C. multicinctus_ and several other closely related species, - even juvenile _C. quadrimaculatus_ - fed almost entirely on corals, while adult _C. quadrimaculatus_ fed extensively on other foods.

Inclusion of large portions of algae and non-coralline invertebrates in the diet of _C. quadrimaculatus_ may have allowed specialization on the preferred coral _P. meandrina_. The mouth of _C. quadrimaculatus_ has a large gape and generalized morphology and dentition well suited to sideways tearing motions which are used in feeding on algae and polychaetes (Motta in prep.). _Chaetodon quadrimaculatus_ may have a greater latitude of coral choice if polychaetes are nutritious and included frequently in the diet. This may allow it to feed only on the most preferred corals. The morphology of the feeding apparatus of _Chaetodon multicinctus_, on the other hand, is functionally very well adapted for sucking and scraping on coral polyps (Motta in prep.). If constrained to feeding on corals, a pair of _C. multicinctus_ would have to defend a much larger area in order to feed exclusively on preferred coral species.

Juvenile _C. quadrimaculatus_ fed almost exclusively on corals, dividing their feeding between the two most abundant species, _P._

lobata and P. meandrina, rather than specializing on P. meandrina. Differences in juvenile and adult food choice are known in cases where different size classes live in different habitats (not the case for C. quadrimaculatus: Hourigan Chapter II), or where limitations of the feeding apparatus lead to choosing prey of different sizes (Liem 1984). Laboratory preference tests show that both juveniles and adults prefer the coral P. meandrina over P. lobata, although juveniles eat the latter more readily than do adults in single species presentations (Hourigan unpubl. data). This suggests that the threshold for accepting less preferred species rises as the fish mature. Newly settled fish restricted their movements to small home ranges. If there is little chance of finding a colony of a less abundant, but preferred species of coral within that range, then specialization on P. meandrina would limit larval settlement to habitats where that coral was abundant. Therefore there will be an advantage for the juvenile to accept less preferred species. As the individual matures and its home range expands, it can afford to specialize on less abundant but preferred coral species.

c. Diel and seasonal foraging patterns, and temporal periodicity.

1. Diurnal patterns:

Both species directed significantly more feeding bites toward non-coralline hard substrata during the late afternoon than at other times of the day. This behavior was most pronounced in C.

quadrimaculatus, where feeding on hard substrata increased from less than 10% of total feeding in the morning to nearly 70% in the evening (Fig. 3.11). Sample sizes of gut content analyses were small, however they indicated that most of this feeding was directed toward algae (Table 3.7).

This change in food choice may be related to temporal changes in the energy content of the algae. Unlike corals and other invertebrates, these small algae have little storage capability. Carbon fixation by photosynthesis occurs primarily between 1000 hrs and 1800 hrs (Doty et al. 1967), and the protein and storage products increase during this time (Edmonds 1965). These products reach a peak during the late afternoon and are used up during the night in metabolism and growth, returning the tissues to a lower energy content by morning.

Fishes which feed on algae will receive a higher return in energy and nutrients per bite by feeding in the late afternoon than by feeding in the morning. If algae are needed to supplement the nutrition of these fishes, then the optimal tactic would be to concentrate algal feeding during the afternoon. Algae may only attain energy levels which make them profitable to feed upon during these times. A similar feeding periodicity has been found in the herbivorous Mediterranean blenny Blennius sanguinolentus (Taborsky and Limberger 1980). This species fed almost exclusively on green algae, and feeding increased significantly during the afternoons. The herbivorous blenny, Ophioblennius atlanticus (Nursall 1981) and the damselfishes Stegastes planifrons, Stegastes dorsopunicans, Microspathodon chrysurus (Robertson 1984) and Stegastes fasciolatus (M. Hixon pers. comm.), show the same feeding periodicity, indicating that this pattern may be a common one among reef herbivores.

2. Lunar Periodicity.

Both species fed an average of 12 to 14 hrs per day, however the feeding of C. quadrimaculatus in the coral-poor habitat showed a distinct lunar periodicity. Rather than feeding during the solar day, as do most diurnal fishes, C. quadrimaculatus began feeding at moonrise and finished near moonset. Since moonrise at these latitudes occurs 45-55 minutes later every day, the time of feeding changed accordingly. At the new moon, feeding occurred only during the day, while at the full moon, feeding occurred only at night. This resulted in a diurnal cycle which was nearly 25 hrs long, rather than 24 hrs. This time period corresponds closely with the natural circadian periodicity of many organisms in the absence of external cues. This periodicity in general activity was also shown by several pairs of C. quadrimaculatus caught in the field and kept in aquaria where they were isolated from tidal cues (Hourigan unpubl. data).

The lunar periodicity in feeding and activity of C. quadrimaculatus is unique among fishes thus far described. Although females sometimes fed for longer than 12 hours, there were nevertheless long periods of daylight when neither sex fed. True energy maximizers might have been expected to utilize this time for further feeding. Apparently the 10 to 12 hr resting period served some function in these fishes.

Gut content analysis revealed that C. quadrimaculatus fed at night on the coral P. meandrina. Many corals extend their polyps at night and retract them during the day (Jokiel in press). This behavior may be a response to increased nocturnal plankton or to decreased risk from diurnal predators. Such behavior may make polyps more accessible to a nocturnal corallivore. Pocillopora meandrina has very small polyps, and attempts to observe polyp extension in the field at night were inconclusive. However, if its polyps are extended at night, the peculiar feeding periodicity of C. quadrimaculatus may be more understandable. Like most butterflyfishes, C. quadrimaculatus is a visual predator, and may need some moonlight to feed efficiently. During nights of the full moon, even when overcast, there is considerable available light in the shallow waters where C. quadrimaculatus lives (Hobson 1972). A second possiblity is that the lunar periodicity in feeding by C. quadrimaculatus is timed to coincide with some lunar periodicity in the corals. Many corals show lunar periodicity in spawning or planulation. The congener, Pocillopora damicornis reproduces during the full moon (Richmond and Jokiel 1985), and has a higher energy content at the time of reproduction (Richmond 1982).

Most butterflyfishes are diurnal predators (Hobson 1974). It is perhaps significant that C. quadrimaculatus exhibits permanent coloration consisting of a darkened dorsal area with two bright white spots, similar to the nocturnal coloration of several other species of chaetodontids, specifically Chaetodon citrinellus, C. melanotus, C. tinkeri and C. trifascialis (Fricke 1973b; Burgess 1978). Such color patterns increase visibility at night (Hailman 1977), and may help pair-mates find each other in the dim moonlight. Chaetodon lunula also shows permanent coloration of contrasting black and white areas, and has been implicated in nocturnal feeding (Hobson 1974).

3. Seasonal periodicity.

There were no significant seasonal differences in feeding rates of male or female C. multicinctus. This might be expected if females maximized their food intake during all seasons, while males did not change their activities and thereby their energy needs. Food gathered during the non-breeding season (July to December) in excess of metabolic needs is probably stored as fat. Fat tissues were observed to increase after the breeding season and then drop sharply during the next breeding season (Tricas 1986; Hourigan Chapter V) in both sexes.

Feeding rates of female C. quadrimaculatus, however, were higher during the spring than at other times of the year. This time corresponded to the height of the breeding season (Hourigan Chapter V). Males showed no seasonal changes in feeding rates. During the breeding season, females may be expected to have greater energy expenditures than during other times of the year due to the energy requirements of egg production. This suggests that for this species, females were not feeding at full potential during the non-breeding season. Chaetodon quadrimaculatus acquires more energy per bite than C. multicinctus, perhaps allowing the former to depend less on fat reserves during the breeding season.

d. Territoriality and foraging paths.

Adult pairs of both species defended territories against both juvenile and adult conspecifics. The borders of the defended areas were the same as the feeding ranges and size varied inversely with preferred coral cover. This indicated that the function of these territories was, in part, protection of food resources. Tricas (1985, 1986) also concluded that defended areas of *C. multicinctus* were feeding territories. Feeding territoriality has been observed in several species of coral feeding butterflyfishes (Reese 1975, 1981; Sutton 1985; Fricke 1986; Hourigan Chapter II and pers. obs.). Coral is a stable and predictable resource, factors which make it economically feasible to defend (Brown 1964). Territoriality apparently allowed increased feeding rates by the residents as compared to non-territorial individuals. It may also have allowed the resident pair to forage in a more efficient manner, since they were the exclusive users of their species in that area. It has not been shown that the occurrence of territoriality, or of different territory sizes or qualities affects reproductive success. However, such a result would be consistent with the observation that the behavior of pairs maximizes the energy intake of females.

Chaetodon multicinctus also defended territories against other species of corallivores, supporting the conclusion that territories served a feeding function. *Chaetodon quadrimaculatus* inhabited much larger territories, which were perhaps not economical to defend against other corallivores. The larger size of *C. quadrimaculatus* territories may have been a function of limiting most of its coral feeding to one species of coral, P. meandrina. The distribution of food resources other than corals was not measured.

Food resources were not distributed evenly within the territories of butterflyfish pairs. It follows that certain foraging paths were more efficient than others for exploiting resources. Individual pairs resided in the same territories for many years (at least 4 years for the present study and more than six to seven years for congeners: Reese 1981; Fricke 1986). Since coral colonies may also survive for many years, fish may learn the locations of corals, and foraging paths may optimize long term returns rather than allowing the overexploitation of resources for short term gains.

The foraging paths of C. multicinctus and C. quadrimaculatus reflect different foraging tactics. Both spent a major portion of their foraging time in one area, interspersed with occasional tours of the borders. Chaetodon multicinctus pair mates usually performed both these behaviors together. In contrast, male C. quadrimaculatus usually toured the borders of the territory alone. This suggests that the primary function of these tours of outlying areas was to patrol territorial borders rather than to forage per se.

The areas of maximum use by C. multicinctus pairs changed throughout the day, but some large coral heads appeared to be favored during most observation periods. Pairs of C. quadrimaculatus also had areas of heavy use within each territory. These core areas were used for several months, after which the pair shifted to other areas within the territory. These differences between the species may result from their different diets. Coral polyps retract soon after a fish begins to feed on a coral head. If the fish moves on, the polyps usually come out again within the hour. This behavior of corals may allow fish to graze on the same coral heads with only short intervals between feeding bouts. Coral regeneration is also relatively quick, with 1 cm^2 areas on most common Hawaiian species regenerating within two weeks (Hourigan unpubl. data). Pairs of C. quadrimaculatus, however, fed on other prey items whose recovery was probably slower. Concentrated feeding in one area may be the effective harvesting method under these circumstances.

Both species moved from coral to coral, taking only a few bites from each individual coral head. Laboratory experiments (Hourigan Chapter II, V) and changes in patch use during the food reduction experiment in the field, showed that C. multicinctus was capable of feeding continuously for long periods of time on individual coral heads. Such concentrated feeding did not occur under natural conditions, perhaps preventing overgrazing. Cox (1983, 1986) showed that one corallivorous butterflyfish, Chaetodon unimaculatus negatively affected the growth and competitive abilities of its preferred food-coral under natural conditions. It is perhaps significant, that C. unimaculatus is not territorial, and ranges over very large home ranges. Alternately, moving from coral to coral after only a few bites may reflect short term changes in profitability, such as decreased return per bite once coral polyps have retracted.

Not all foraging patterns could be explained as optimal tactics. In each species, pairs often followed the same paths, in the same directions. Such behavior may not exploit all available food resources in the most efficient manner. Reese (pers. comm.) has noted similar patterns of "habit formation" in individuals of two other species of butterflyfishes. The advantages of such learned behavior, as opposed to following a set of optimal decision rules, may be that the fish follows paths which have proven safe (e.g. from predators) in the past and is feeding on corals or food patches of "known" quality or return. Thus, for fish which are long term residents of an area, foraging problems become deterministic as opposed to probabilistic. Foraging behaviors therefore may not conform to probabilistic optimal foraging models.

e. Food reduction experiment.

Several authors have applied models of feeding territoriality to fishes (e.g. Dill 1978; Ebersole 1980; Hixon 1980). These models depend on certain crucial assumptions, and may give different results if these assumptions are violated (Schoener 1983; Hixon 1987). Two predictions concerning the effects of food reduction experiments, however, are shared by most models. First, if pairs attempt to maximize food available for females, they should defend the largest area possible which does not reduce the female's feeding rate by increased travel or defense costs. Therefore, if food is reduced within the territory, territorial expansion to regain food resources is expected, but only at the expense of increased defense costs. Second, if feeding is time limited, the increased defense costs should be translated into decreased time available for foraging.

When food within the territory was reduced, experimental pairs successfully expanded their territorial borders, confirming the first prediction. This expansion was not equal to the area covered, and was accompanied by increased agonistic encounters and decreased feeding rates. This indicated that fish responded to changes in food, but the magnitude of territorial expansion was limited by the aggression of neighboring conspecific pairs. Results from this experiment must be viewed with caution, however, since the sample size of the experiment (N=3 pairs) was very small.

Tricas (1986) performed similar food reduction experiments on three pairs of C. multicinctus at a nearby site. He covered 19% to 24% of the territory area, placing squares of material randomly over the corals as opposed to covering a particular coral species. He found that food reduction was accompanied by territorial expansion in all cases. Unlike the present experiment, chase rates of pairs did not increase significantly (the chase rate of one female decreased), and feeding rates of one male and two females increased. Tricas measured feeding and chase rates two to four weeks after food reduction, whereas in the present study, feeding and chase rates were measured during the four days following food reduction, as territorial expansion was in progress. Chase rates were much lower for the pairs he observed than recorded in the present study, perhaps indicating that new, stable territorial boundaries had been reached and dominance relationships established. Increased feeding rates may have resulted from an increased reliance on algae as a food resource, with shorter inter-bite intervals. In the present study, during 5 min observation periods when no chases occurred, feeding rates for two of the pairs increased. These increases were due to increased feeding rates on hard substratum, not corals.

Tricas (1986) also increased coral resources within territories of _C. multicinctus_, and manipulated numbers of conspecific competitors. Although pairs attempted to modify their territory size in relation to changes in food density, he found that the abundance of competitors was the major factor limiting territory size in this species. This is in agreement with the present experiments showing that pairs subjected to food reduction were unable to expand their territories to regain areas equal to the areas covered. Such competition would also explain why pairs in the present study greatly increased their territory sizes when a neighboring pair disappeared. Tricas concluded that both food supply and the abundance of other territorial pairs influenced territory size in _C. multicinctus_.

f. Pomacentrid removal experiment.

This experiment showed that the common territorial damselfish, _Stegastes fasciolatus_ influenced the foraging behavior of individual _C. quadrimaculatus_. Following the removal of pomacentrids there was an increase in diurnal feeding and a decrease in sheltering by _C._

quadrimaculatus concomitant with decreases in the number of chases by *S. fasciolatus*. Effects of pomacentrid removal on the behavior of other species of fishes are documented in Hourigan (1986a).

Chaetodon quadrimaculatus, is typical of many butterflyfishes, in that pairs inhabit the same territory for several years, and defend this area against conspecific intrusion. Pairing and permanent territoriality constrain the options available to individuals in response to the pomacentrids. They probably cannot adopt the schooling strategy shown by many acanthurids, scarids and others (Barlow 1974; Robertson et al. 1976; Hourigan 1986a). Instead, individuals must find some alternate means of responding to the territoriality of pomacentrids if they are to co-exist in the same area. *Chaetodon quadrimaculatus* apparently solved this problem by flexibility in the time when it fed.

CONCLUSIONS

This study revealed patterns of unexpected complexity in the foraging behavior of two species of coral reef fishes, *Chaetodon multicinctus* and *C. quadrimaculatus*. Foraging patterns varied depending on the age and sex of the individual, its experience, resource distribution, time of day, lunar month or season, and the behavior of other fishes. These patterns indicate that foraging behavior depends on the distribution of food resources as well as the age, sex, and social environment of individual fish. These complexities raise questions about simplistic descriptions or generalizations about the feeding behavior of "species" or simplified theoretical models, and point out the need for information on the age and sex of fish studied. Despite these complexities, a picture emerges for both species of foraging behavior which tends to maximize food intake for different individuals with changing needs in a changing but predictable environment. The extent to which animals are successful in maximizing energy intake is constrained by the territorial behavior of conspecifics. The relationship of differing energy needs of males and females to the social systems of reef fishes will be analyzed in the following chapters.

CHAPTER IV

THE SOCIAL ORGANIZATION OF THE HAREMIC BUTTERFLYFISH CHAETODON FREMBLII

INTRODUCTION

In haremic social systems, a single male mates and maintains exclusive social contact with two or more females. Most studies of harem polygyny have concentrated on birds and mammals. Based on the assumptions that female reproduction is limited by access to resources, often food, while male reproduction is limited by the number of females with which he can mate, Emlen and Oring (1977) identified two major conditions under which harem polygyny should occur: resource defense polygyny and female-defense polygyny.

In resource-defense polygyny, males defend resources necessary for females, and female choice of males is based in part on the resources he controls. Males with territories containing more resources mate with more females than do males defending sparser territories. This appears to be the most common mating system among polygynous birds (Emlen and Oring 1977; Oring 1982). The point at which it becomes more advantageous for a female to mate bigamously with an already mated male in a rich territory in preference to mating monogamously with a single male in a poorer territory is called the polygyny threshold (Verner and Willson 1966; Orians 1969). If resources necessary for females are distributed unevenly among males territories, the polygyny threshold will be low, and haremic polygyny will be favored.

The second case, female-defense polygyny, occurs when males aggressively exclude other males from groups of females. Male monopolization of multiple females is enhanced if environmental factors result in the aggregation of females. This may occur either because of an uneven distribution of resources necessary for females, or because grouping of females is advantageous for some other reason such as protection from predators. This case has most often been studied among mammals.

Haremic social systems occur in several families of reef fishes (reviewed by Kuwamura 1984; Thresher 1984). Harem formation is most common among protogynous hermaphrodites (fishes which change sex from female to male), and has been reported for wrasses (Labridae: Robertson 1972; Roede 1972; Moyer and Shepard 1975; Robertson and Hoffman 1977; Warner and Robertson 1978; Thresher 1979; Kuwamura 1984; Thresher 1984), parrotfishes (Scaridae: Choat and Robertson 1975; Robertson and Warner 1978; Hoffman 1984), angelfishes (Pomacanthidae: Moyer and Nakazono 1978; Moyer et al. 1983; Aldenhoven 1984, 1986; Moyer and Zaiser 1984; Hourigan and Kelley 1985; Hourigan 1986b; Moyer, in press) and damselfishes (Pomacentridae, genus Dascyllus: Fricke 1977, 1980a; Shpigel and Fishelson 1986). Other species with haremic social systems have been assumed to be gonochoristic (fishes with separate male and female sexes which do not change sex), although this remains to be demonstrated in most cases. These fishes include surgeonfishes (Acanthuridae: Barlow 1974; Robertson pers. comm.), triggerfishes (Balistidae: Fricke 1980b; Thresher 1984), sharpnosed puffers (Tetraodontidae, genus Canthigaster: Kobayashi 1986) and boxfishes (Ostraciidae: Moyer 1979). The basis of these harems is often assumed to be females grouping around spatially clumped resources, and male defense of these resources, or male defense of females. The identity of these resources and the detailed structure of most harems have not been investigated (Hourigan 1986b).

Individuals of most butterflyfish species (family: Chaetodontidae) form long lasting, apparently monogamous, heterosexual pairs (Reese 1975, 1981; Allen 1979; Thresher 1984; Barlow 1984, 1986; Fricke 1986; Hourigan Chapter VII), an unusual social system among reef fishes. A conspicuous exception to this rule are the planktivorous butterflyfishes which generally occur in large aggregations or schools, and appear to spawn in groups (Reese 1978; Ralston 1981; Fricke 1986). Butterflyfishes are sexually monochromatic, consistent with low levels of sexual selection found in monogamous or promiscuous mating systems (Burgess 1978). Reese (1975) surveyed 19 species of Indo-Pacific chaetodontids, and found that 13 species, mostly corallivores, occurred in pairs. Three species of planktivores occurred in larger groups or schools. The remaining species, mostly small omnivores, were more difficult to classify. They were observed as solitary individuals, or in pairs, or in small groups. The social structure of these small omnivorous species has not been studied.

The bluestripe butterflyfish, Chaetodon fremblii is endemic to Hawaii. It is an omnivore, feeding on polychaetes, other invertebrates and algae (Hobson 1974), and is among the most abundant butterflyfishes in Hawaii (Hobson 1974; Hourigan and Reese 1987). Reese (1975) noted that this species is observed most often as single individuals. Subsequent observations have revealed a haremic social system (Hourigan 1986b). In the present study, the feeding behavior and use of space by males and females in a natural population of C. fremblii were documented in relation to their social behavior. Interactions within and between sexes were observed under natural conditions and in response to experimental field manipulations of food and mates.

METHODS

The bluestripe butterflyfish was studied on coral reefs at Kahe Pt. on the leeward coast of the Island of Oahu, Hawaii. Seventeen *C. fremblii* were captured, sexed underwater by cannulation (Hourigan and Kelley 1985), marked by fin clipping, and released. An additional 29 butterflyfish were identified by individual markings without being captured, and subsequently sexed based on behavioral observations followed by selective spearing and gonad analysis. After a minimum of twenty, 5 min observation intervals on each of twenty fish, each individual was collected by spearing in order to confirm its sex. In all twenty cases, gonad analysis revealed that the presumed sex was the same as the actual sex. Fishes collected in this manner were utilized for energetic and reproductive studies reported in Chapter V.

The basic design of this study was to identify individuals, record their feeding behavior, and map their home ranges and movements. Food resources were reduced to assess their importance to the spacing behavior of residents. Individuals of either sex were selectively removed to observe changes in social structure.

Foraging Behavior

Field observations of the feeding behavior of *C. fremblii* were conducted during the years 1982 to 1984, mostly during the Spring, Summer and Fall. Observations were primarily conducted during the the mid-morning and early afternoon (0900 - 1500 hrs) with occasional observations at dawn and dusk. Observations of feeding were conducted as described in Chapter III: individuals were followed, recording the number of bites which were directed toward different substrata. Following an initial 10 min acclimatization period, feeding data were recorded during four, 5 minute intervals for a total observation period of 20 min per fish. Repeated observations were made on the same individuals for a minimum of twenty, 5 min intervals. A cursory examination of stomach contents was conducted on 10 speared individuals, to determine the major types of prey items.

Feeding Ranges and Territoriality.

To determine the feeding ranges of each sex, numbered nails with colored flagging tape were dropped in order at the points where the animals fed. New tags were dropped when the animal fed outside the previously marked area. Using the method of Odum and Kuenzler (1955) it was determined that 95% of the feeding area was delineated following three 1 hour observation periods for females (N=5) and four to five 1 hour periods for males (N=3). Following this initial determination, colored tags were dropped during a minimum of four and six hour observations for each sex respectively.

Maps of the foraging areas of the individual fishes were drawn on underwater paper. A line marked off in meter intervals was set through the center of the marked area, and the distance from this line to each flag was measured and marked on the map. In addition, major features, such as shelters, large coral heads and boulders or sand patches were marked. Subsequent movements outside the previous boundaries were then marked directly on the maps. The feeding ranges of the 12 males and 30 associated females were mapped. The positions of agonistic encounters were marked on the same maps.

To determine how different areas of the feeding ranges were used, the foraging paths of males and females were mapped by recording the positions of individuals at 30 sec intervals on a previously drawn map of their feeding range. Replicate maps were made for three males and four females.

Male-Female Interactions.

The occurrence of intraspecific interactions was recorded during each minute of observation. These included displays, chases, and presence in close proximity of another individual. Whenever possible, the identity of the other fish with whom the interaction took place was noted.

Food Reduction Experiment

In order to assess the importance of food resources to male and female butterflyfish, access to food resources was restricted. The male and one female from two non-contiguous harems were observed for five days as described above, and the areas within the female's territory where most feeding occurred were marked. For one of these females, $20 m^2$ of the preferred feeding areas were covered with 1 m^2

squares of cloth material. Changes in feeding rates, encounters rates with conspecifics and territory sizes were measured as above for both the focal female and her harem master during the following three weeks. A transect line was placed in the territory of the female in the second harem. This constituted some disturbance, but did not restrict access to food resources. This second harem served as a control and was monitored as above. Three replicate food manipulations using different harems were conducted sequentially, each with a concurrent control.

Mate Removal Experiments.

In order to simulate mortality within a harem, a male or female was removed from a harem. Data were collected on all individuals from two non-contiguous harems. Each individual was observed for a minimum of 100 min, and territory areas were mapped. These observations were conducted over a period of three months. Thereafter, one individual (either a male or a female) from one of the two harems was removed. The second harem served as a control. During each day of the following week, observations were conducted on the male and one female from the control harem, as well as on the remaining members of the experimental harem. Changes in space use by each of the remaining individuals in the experimental harem were mapped and compared to the unmanipulated control harem during the following weeks. Three male removals and three female removals from six separate harems were conducted.

RESULTS

Foraging Behavior

Extensive observations were conducted on 6 male *Chaetodon fremblii* and 14 associated females. Additional observations were made on another six males and 16 females. *Chaetodon fremblii* began foraging shortly before sunrise and fed almost continuously until shortly after sunset. Feeding occurred during 96.5% of all 1 min observation intervals for females and 91.3% of all 1 min observation intervals for males. Male and female *C. fremblii* directed feeding bites toward the same substrata (Table 4.1). Most feeding bites were directed toward prey on hard substrata, in the sand and in crevices, with additional bites directed toward the surface of the sea urchin *Tripneustes gratilla*. Gut content analyses revealed that fish fed primarily on algae, polychaetes, and other invertebrates (Table 4.2).

Feeding rates varied dependent on the substratum fed on and the time of day. The feeding rate of fish feeding in the sand was lower than that of the same fish feeding on prey on hard substrata. Therefore, fish with large sand areas within their territories had lower feeding rates (e.g. Harem #5). Feeding rates increased as the day progressed (ANOVA of square-root transformed feeding bites, $p < 0.05$; Fig. 4.1). This increase was accompanied by an increased proportion of feeding bites on hard substratum, reaching a peak during the last two hours before sunset (ANOVA of arcsine transformed feeding bites, $p < 0.05$; Fig. 4.2).

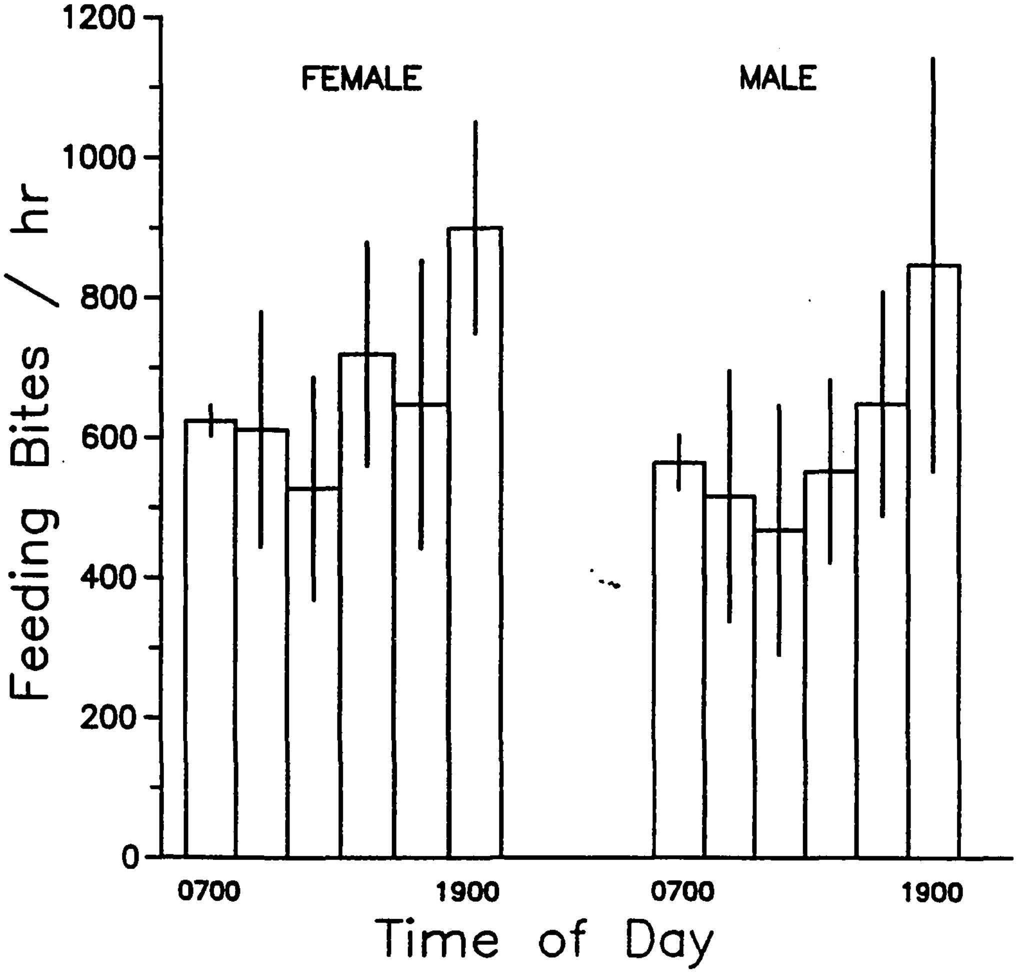
Table 4.1. Male and female feeding rates (bites per hr) of C. fremblii. Values are means (± standard deviation).

	SEX	
	Male	Female
N =	12	30
Hard Substratum	495 (± 223)	582 (± 251)
Sand	46 (± 78)	51 (± 56)
Crevices	18 (± 27)	6 (± 13)
Sea Urchin Pedicillaria	8 (± 8)	7 (± 12)
Eggs	1 (± 5)	< 1
Plankton	1 (± 4)	< 1
TOTAL	568 (± 179)	646 (± 224)

Table 4.2. Stomach contents of ten *C. fremblii*.

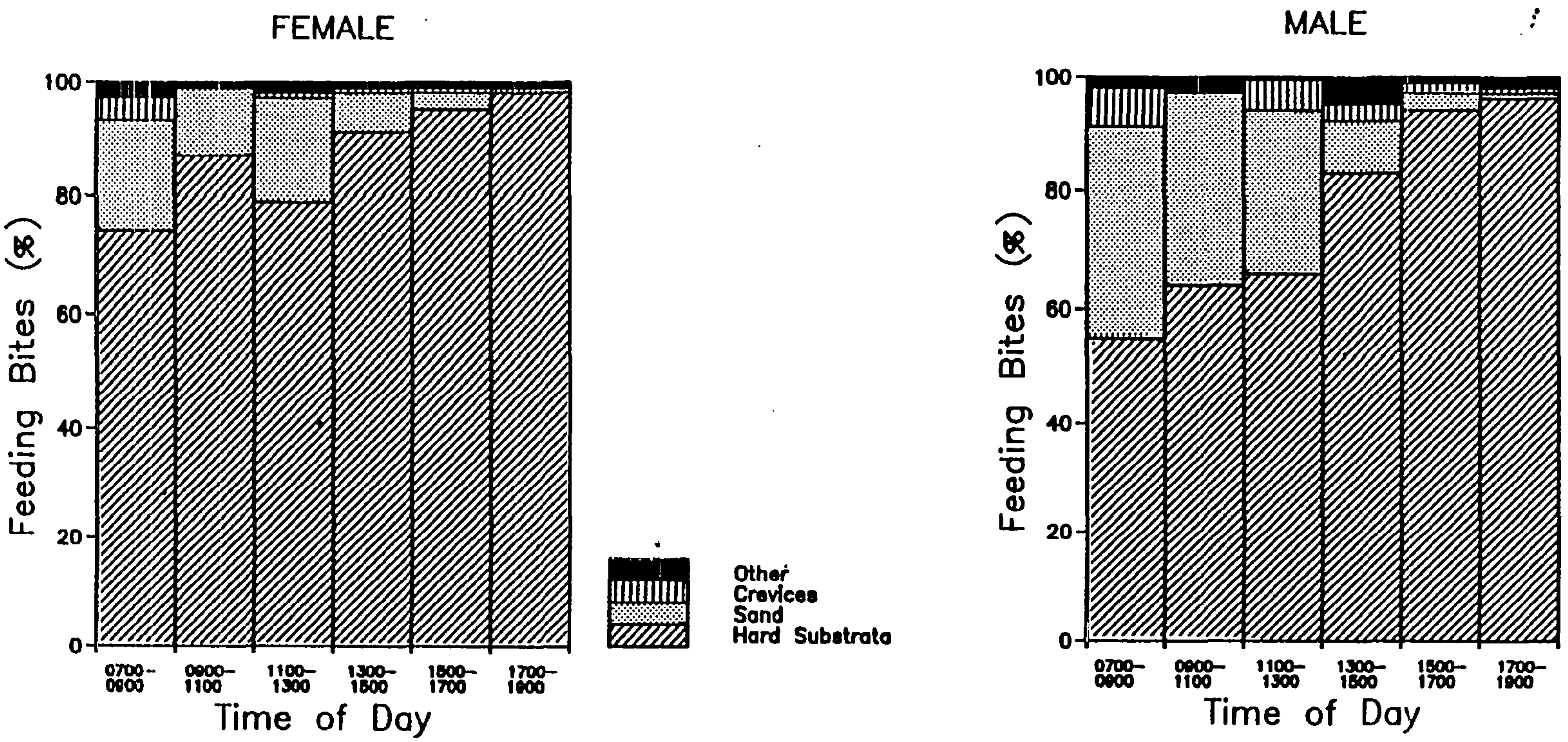
FOOD ITEM	No. of Fish with Item	Rank by Wet Weight
Algae	10	2
Sabellid polychaete fragments	9	1
Sea urchin pedicillaria	9	5
Terebellid polychaete fragments	8	3
Amphipods	7	4
Other small crustaceans	4	7
Other invertebrates	7	6
Eggs	3	8

Figure 4.1. Mean feeding rates (bites per hr, ± SD) of male and female *C. fremblii* at different times of the day.



FEMALE
MALE
Feeding Bites / hr
1200
1000
800
600
400
200
0
0700
1900
0700
1900
Time of Day

Figure 4.2. Percent of feeding bites on different substrata by male and female C. fremblii at different times of the day.


FEMALE
MALE
Feeding Bites (%)
100
80
60
40
20
0
0700–0900
0900–1100
1100–1300
1300–1500
1500–1700
1700–1900
Time of Day
Other
Crevices
Sand
Hard Substrata

The feeding rates of males were lower than the feeding rates of the females which fed in the same area (Independent Wilcoxon's signed-ranks tests for 6 males and each of their mates, observations matched by the same time of day: $0.05 > p > 0.005$; Combined Wilcoxon's signed-ranks test for mean feeding rates of 6 males and 14 associated females: $p < 0.005$; Table 4.3).

Feeding Ranges and Territoriality

The foraging areas of 6 male Chaetodon fremblii and 14 associated females are shown in Figure 4.3. Females inhabited exclusive home ranges in which all feeding and sheltering occurred. These ranges were defended vigorously from other females and were therefore considered to be territories (mean territory size - $269m^2$ SD - $112m^2$). The border of the defended area was the same as the border of the feeding range. These territories were roughly oval shaped and contiguous with the territories of other females. Females normally did not stray more than a few meters from their territories.

Individual males had a large home ranges (mean male area - 756 m^2 SD - $359m^2$) which overlapped and completely enclosed the territories of one to four females (Fig 4.4; Table 4.3). Male ranges were territories defended against other males, but not against females. Male territories conformed to the shape of the territories of their females (Fig. 4.3). Small, non-territorial males occurred in outlying areas and between male territories. They associated with no females and were aggressively excluded by the larger territorial

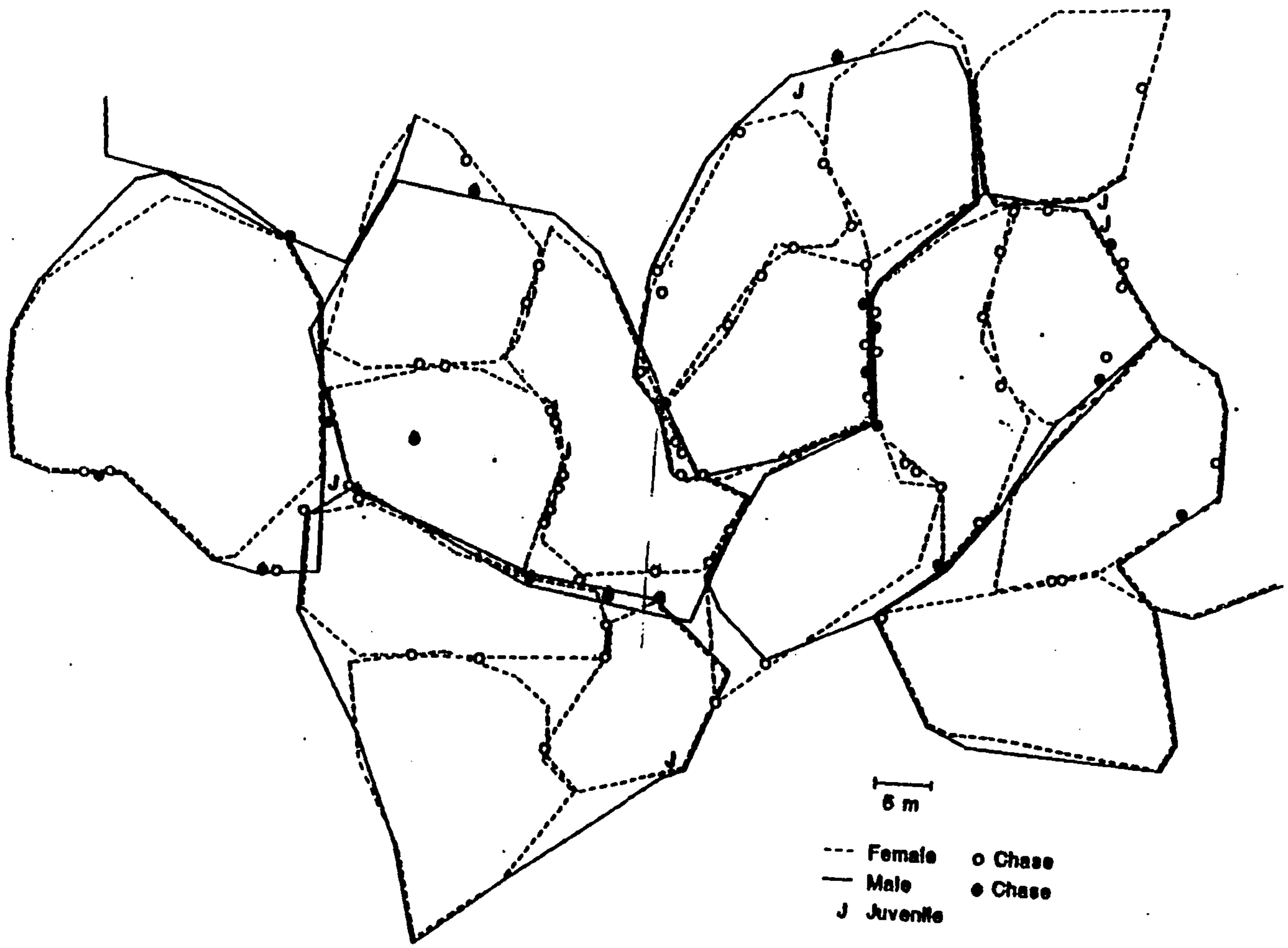
Table 4.3. Activity budgets of male and female *C. fremblii* from each of six harems.

Harem	Sex	Time Observed min		Time Together %	Number of		Feeding Bites per hr
					Chases per hr	Displays per hr	
1	Male	100	Mean	22.6	1.8	0	519
			SD	(27.2)	(3.1)	-	(87)
1	Female	100	Mean	19.3	4.1	0.25	569
			SD	(22.6)	(3.5)	(2.1)	(132)
1	Female	60	Mean	7.2	3.3	0	611
			SD	(13.4)	(6.9)	-	(99)
2	Male	225	Mean	37.2	2.9	0	449
			SD	(30.4)	(7.3)	-	(137)
2	Female	100	Mean	9.5	6.4	0.7	689
			SD	(15.5)	(9.6)	(2.9)	(197)
2	Female	130	Mean	3.1	6	0.9	551
			SD	(9.3)	(11.4)	(3.2)	(189)
2	Female	100	Mean	28.3	12.9	0	613
			SD	(42.7)	(20.8)	-	(104)
3	Male	100	Mean	35.3	4	3.2	539
			SD	(30.4)	(9.8)	(8.4)	(172)
3	Female	100	Mean	10.7	4.2	0	665
			SD	(19.1)	(9.4)	-	(145)
3	Female	80	Mean	6.5	4.5	0	719
			SD	(8.1)	(8.2)	-	(112)
3	Female	100	Mean	16.3	4.8	0	511
			SD	(28.3)	(6.6)	-	(105)
4	Male	285	Mean	27.7	0.8	0.2	627
			SD	(27.0)	(3.8)	(1.6)	(190)34
4	Female	100	Mean	3.9	8	0.7	606
			SD	(8.5)	(13.7)	(2.8)	(144)
4	Female	100	Mean	16.6	1.2	0	767
			SD	(32.2)	(2.8)	-	(184)
4	Female	100	Mean	8.4	2.4	0	649
			SD	(18.6)	(5)	-	(134)

Table 4.3. (cont.) Activity budgets of male and female *C. fremblii* from each of six harems.

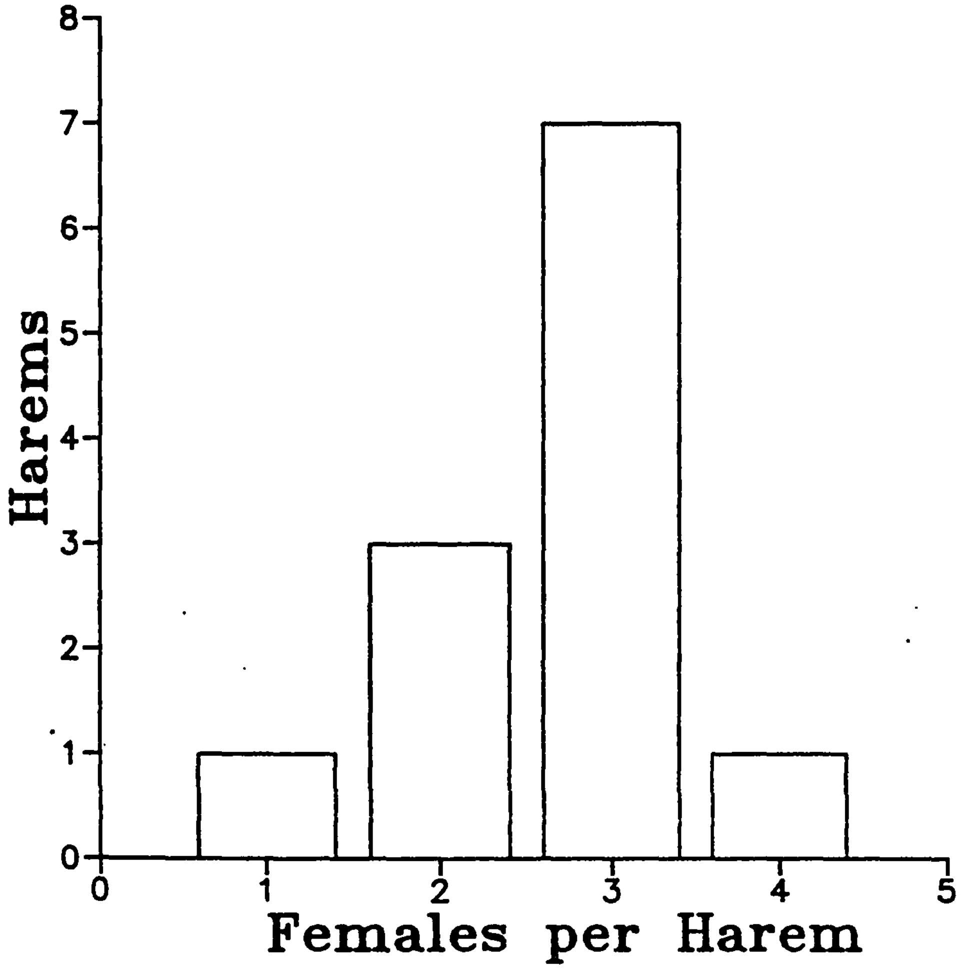
Harem	Sex	Time Observed min		Time Together %	Number of Chases per hr	Number of Displays per hr	Feeding Bites per hr
5	Male	100	Mean	41.1	0.1	0	285
			SD	(34.7)	(0.2)	-	(91)
5	Female	60	Mean	7.2	2.9	0	358
			SD	(9.3)	(5.3)	-	(98)
5	Female	100	Mean	24.6	3.9	1.9	494
			SD	(35.2)	(6.5)	(4.5)	(170)
6	Male	100	Mean	6.6	2.1	0	516
			SD	(17.3)	(8.9)	-	(127)
6	Female	100	Mean	16.8	3.7	0	672
			SD	(25.8)	(7.5)	-	(147)
TOTAL	Male	910	Mean	28.4	1.95	0.57	489
	Female	1430	Mean	13.9	4.96	0.32	660
		Combined Wilcoxon's Signed-Ranks Test			p<0.001	NS	p<0.001

Figure 4.3. Foraging areas of six males and the 14 females in their harems.



J
5 m
--- Female
— Male
J Juvenile
o Chase
● Chase

Figure 4.4. Frequency distribution of the number of females per harem.


8
7
6
5
4
3
2
1
0
Harems
0
1
2
3
4
5
Females per Harem

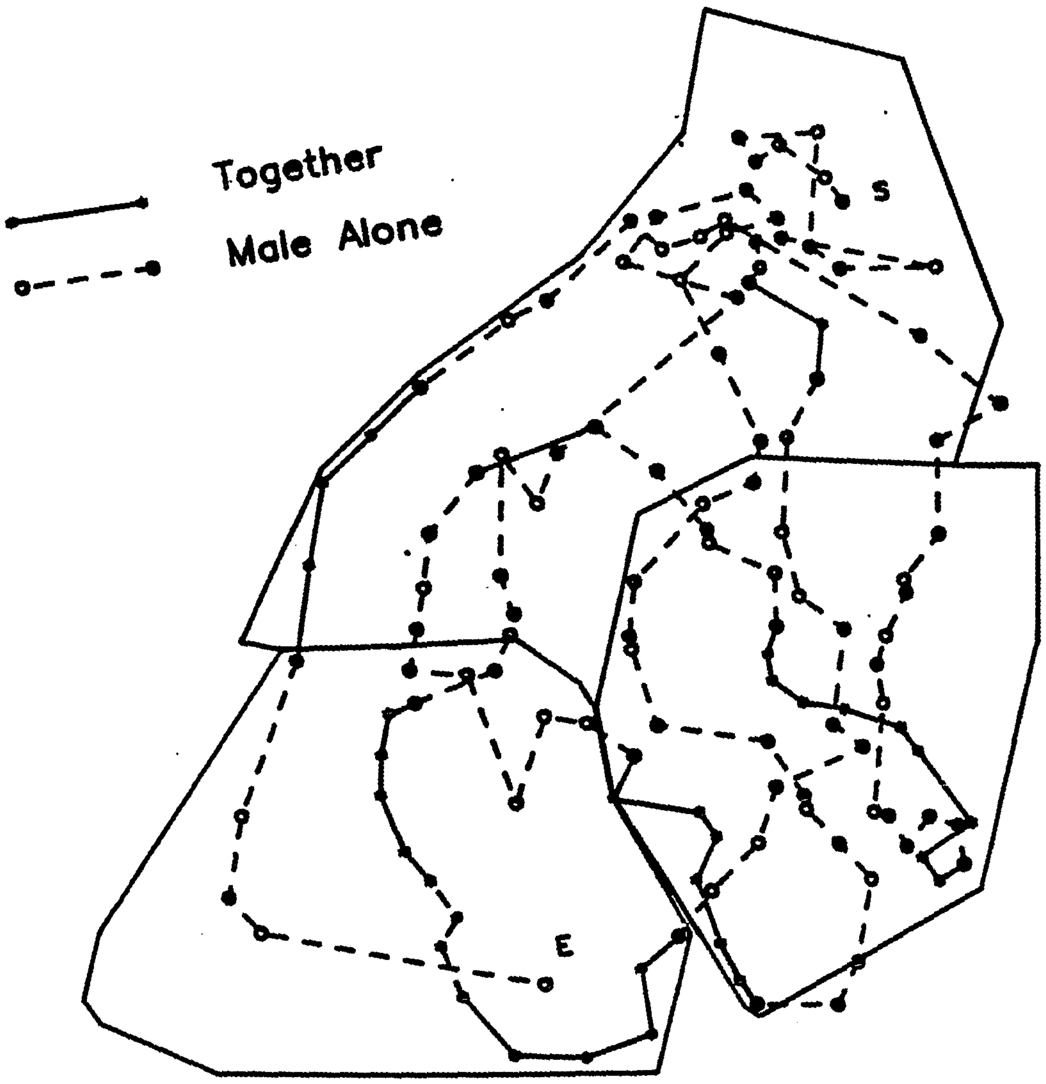
males. Observations on six additional males and 10 females revealed similar patterns of space use.

Territorial borders of both males and females remained remarkably stable over the two year period of observation. Only one change in territory borders was observed. This occurred when a female disappeared. The exact time of disappearance was not known, but within one to seven days, her area had been taken over by two neighboring females from the same harem.

Male-Female Interactions.

Time budgets showed that males spent an average of 9.3 min per hour in the vicinity (separated by less than 2 m) of each individual female whose territory they overlapped (Table 4.3; Fig. 4.5). When the male entered the female's foraging area, the female would usually swim to the male and follow him. Occasionally, the male hovered about 2 m above the bottom, head up, until the female joined him. After the male and female came together, they fed side by side with no aggression and few or no displays. There was great variance in the time that males spent with females, and it was not clear if they spent more time with particular females. When males and females were together, it was possible to compare sizes and colors of mates. In all cases, males were larger than their mates. In addition, the body of the male appeared to be a darker yellow hue than that of the female. This dichromatism may have been temporary, as no differences were discernible among speared specimens.

Figure 4.5. Sample foraging path of a territorial male C. fremblii. S - Start of observations, E - End of observations. Positions of the male were marked at 30 sec intervals over a period of 30 min; movements between positions are approximate. Open circles and dashed lines are those periods when the male swam alone; closed circles and solid lines are those periods when the male was within two meters of a female.


Together
Male Alone
S
E

Occasionally (less than 2% of all minutes observed), males would swim over to neighboring females from other harems, while the resident male was occupied elsewhere. Females in these harems showed no differences in behavior toward these neighbor males compared to their own harem masters. Chases between males occurred most often when the resident male discovered these interlopers. Chases between females usually occurred when a neighboring female was discovered near or within the border of the feeding territory of the resident female.

On one occasion in May 1984, a female was seen with a swollen abdomen typical of females containing hydrated eggs (see Fricke 1986). The male whose territory overlapped the area of that female spent 95% of all 1 min intervals during the following 90 min in close proximity to the female. This was a much larger percentage of time than that spent by any other male with a female (Table 4.3). Spawning was not observed, however on the following day, the swelling had disappeared and the male divided his time more evenly among all four females in his area.

Chases among territorial adults were always directed toward members of the same sex (based on 55 chases where the identities of both fish were known). Chases were infrequent occurrences, and were analyzed by generating 95% confidence limits for a binomial proportion based on the proportion of 5 min observation periods in which at least one chase occurred (Tate and Clelland 1957). Females chases occurred in a significantly greater proportion of all 5 min intervals than did male chases. When mean numbers of chases by males and females within the same harems were compared, female chases were observed significantly more often than male chases (Combined Wilcoxon's signed-ranks test for the means of males and females from six harems: $p < 0.005$; Table 4.3). Agonistic displays were directed only toward individuals of the same sex. These displays consisted of short rushes in the direction of the opponent. Other displays, including circling and frontal or lateral displays with raised dorsal fins were noted occasionally between fish of the same sex, but were not quantified. During agonistic encounters, one fish often exhibited a temporary brown coloration of the head and anterior portion of the body. This coloration was never observed during intersexual interactions, but did occur when individuals posed for cleaning by the cleaner wrasse *Labroides phthirophagus*. Agonistic encounters with other species were rare, and were limited to occasional chases of *Chaetodon miliaris* by *C. fremblii*, and chases of *C. fremblii* by damselfish, primarily *Stegastes fasciolatus*.

Sheltering was generally observed only at night. Males and females had separate shelters, usually consisting of a simple overhanging coral head.

Juveniles recruited to the study area from April through June. Newly recruited juveniles fed beside adult males or females with no observed agonism. After the first three months, however, chases of juveniles by both males and females were observed. Juveniles fled from these chases to shelters. About this time (July, August), juveniles moved out of the territories of females, into the interstices between territories.

Food Reduction Experiment

In all three cases, when $20m^2$ of preferred feeding areas within the territories of female C. fremblii were covered, the resident female attempted to feed in areas beyond the former borders of her territory. This expansion was resisted by neighboring females, and chase rates with these neighbors increased significantly (95% confidence limits for a binomial proportion based on the proportion of 5 min observation periods before and after food reduction in which at least one chase occurred did not overlap; Table 4.4). During this period of expansion, the resident female's feeding rate decreased (Table 4.4). Feeding rates and chase rates of the male associated with the experimental female did not change, although he had previously fed in the area which was covered. The proportion of all 1 min intervals which males spent with the experimental female decreased slightly but not significantly (95% confidence limits for a binomial proportion based on the proportion of 1 min observation intervals in which male was near female overlapped; Table 4.4).

One to two weeks following food reduction, territorial borders had stabilized, and territory sizes of the manipulated females had increased $2m^2$ to $6m^2$. No changes in chase rates or territory sizes were observed in males of the experimental harems, or in males or females of three concurrent controls whose territories were not covered. The stability of territorial borders over time at both the control territories and other territories monitored over two years,

Table 4.4. Food reduction experiment conducted on three harems of *C. fremblii*. * signifies a significant difference ($p < 0.05$) after food reduction compared to before (see text for statistical tests).

	% Territory Covered	% Change in[a] Territory Size	Chases[b] per hr		Feeding Rate[b] (Bites/hr)	
			Before	After	Before	After
EXPERIMENTAL						
Harem #1						
Female	9%	+3%	3.6	24.0 *	658	319 *
Male	3%	0	0.9	0	526	479
Harem #2						
Female	8%	+1%	7.9	18.2 *	667	468
Male	3%	0	1.3	0.5	552	581
Harem #3						
Female	13%	+4%	2.4	48.6 *	740	391 *
Male	2%	0	0.6	0.2	592	677
CONTROL						
Harems # 1,2,3						
Female	0	0	No Change		No Change	
Male	0	0	No Change		No Change	

a. Territories remeasured after 3 weeks.

b. Feeding and chase rates were measured before food reduction and during the week immediately following food reduction.

indicated that changes in territory size were due to the experimental manipulations.

Mate Removal Experiment:

In all three harems from which a male was removed, neighboring males quickly expanded their territories to include the ranges of the females from the experimental harem. Intense aggressive encounters and chases occurred among neighboring males in the area of the removed male. The frequency of chases was significantly greater during the week following removal, than that observed before removal (95% confidence limits for a binomial proportion based on the proportion of 5 min observation periods before and after removal in which at least one chase occurred did not overlap). These new males were quickly accepted by the females with no unusual displays observed. After two weeks, territorial boundaries had stabilized, and the boundaries of the males followed the boundaries of the females from the experimental territory. There were no changes in female chase rates or feeding rates before and after male removal. There were no changes in the behavior of individuals of either sex in control harems.

In the three cases where a female of a harem was removed, the area was quickly occupied by neighboring females. Chase rates by these females increased significantly (95% confidence limits for a binomial proportion based on the proportion of 5 min observation periods before and after removal in which at least one chase occurred did not overlap). Over 90% of the territory area of the removed female was taken over by females from the same harem, even when there were extensive borders with females from other harems. The reason for this was not clear, although the male from one experimental harem directed one weak chase toward a female from an adjoining harem. Males did not increase the proportion of time spent with each female in their harems, even though there was one female fewer (95% confidence limits for a binomial proportion based on the proportion of 1 min observation intervals in which male was near female overlapped). There were no changes in unmanipulated control harems.

DISCUSSION

The social organization of Chaetodon fremblii was distinguished by female defense of individual feeding territories, and male defense of larger territories containing one to four females. This indicated a haremic social system. Spawning of C. fremblii was not observed, but it is likely that it occurs among harem masters and their females. This was supported by the observation of a male escorting a female in his area which appeared ready to spawn. This is the first report of haremic polygyny in any butterflyfish.

Emlen and Oring (1977) proposed that a major basis for haremic social systems lies in the spatial distribution of females. If females are aggregated, some males may be able to defend groups of females, resulting in a haremic social system. Uneven distribution of resources necessary for females may be the basis of such female grouping. Food is often a limiting resource determining the distribution of females (Wilson 1975), and for this reason, the foraging behavior of C. fremblii was investigated.

The distribution of female C. fremblii appeared to be determined by food resources. Perimeters of defended areas were the same as the boundaries of the feeding areas and were contiguous with the boundaries of other females. In addition, territories expanded when food resources were covered. These data indicate that female home ranges were feeding territories. When neighboring females were removed, females expanded into these newly opened areas and fed there.

They continued to shelter in their old areas, indicating that food, not shelter, was the limiting resource which was being defended, and that female-female defense limited feeding territory size. Females foraged continuously throughout the day, further evidence that female fitness may be food limited.

Both sexes showed increased feeding rates on hard substrata near the end of the day. This foraging pattern is also found in two other butterflyfishes, Chaetodon multicinctus and Chaetodon quadrimaculatus (Hourigan Chapter III). This increase probably represents increased feeding on algae near the end of the day. The nutritional and energetic return from algal feeding is probably greatest during the afternoon, when protein and storage products reach their peak (Edmonds 1965; Hourigan Chapter III). Similar feeding patterns are found among herbivorous fishes (Taborsky and Limberger 1980; Nursall 1981; Robertson 1984; M. Hixon pers. comm.) and may be widespread.

The distribution of food resources was not measured. Feeding observations and stomach contents indicated a varied diet. The results of the preliminary stomach content analyses were similar to those of Hobson (1974). A varied diet will have the effect of increasing the evenness of the distribution of food resources. Two other observations indicated that on the large scale of female territories, food resources for females were relatively evenly distributed. Females foraged relatively evenly over most of their territories; and female territories were similar in size, contiguous and evenly distributed throughout the available habitat. This would seem to contradict Emlen and Oring's (1977) conditions favoring harem formation by resource defense polygyny.

In contrast, male territories were much larger than those of females, although they fed less than females. Male home ranges conformed to the shapes of female territories, and males defended these areas from other males. Male territory boundaries did not expand when food resources within the territory were reduced. Male territories did expand when neighboring males were removed, although food resources remained unchanged. New territory boundaries followed the boundaries of female territories. This indicated that the function of male territoriality was the defense of females, not food.

Only three replicates of each experiment were conducted, and inferences made from this small sample size must be viewed with caution. In particular, any response by males to food reduction may not have been noticeable, due to the small proportion of their foraging areas affected. Nevertheless, it appeared unlikely that food resources were limiting to male _C. fremblii_.

The social system of _C. fremblii_ exemplified aspects of both female-defense polygyny and resource-defense polygyny (Emlen and Oring 1977). Although male territories contained resources essential for females, i.e. food, male territory boundaries conformed to female territories, not resources. There was no evidence that males established territories before females. Neighboring males were immediately accepted by haremic females after mate removal, indicating that females did not actively select males or male territories as would be expected in classical resource-defense polygyny. Harem sizes appeared to be limited by the number of site-attached females a male was able to defend.

In spite of a degree of habitat homogeneity, there was uneven partitioning of females among male butterflyfish. I cannot discount the possibility that this resulted from skewed sex ratios. Haremic males were larger than both females and non-territorial males, however, suggesting that large males were excluding smaller males. Butterflyfishes are long lived animals, with adults of some species residing in the same home ranges for four to seven years or more (Reese 1981; Tricas 1986; Fricke 1986; Hourigan Chapter III). Since males defend areas throughout the year, old males may be able to gradually acquire females as neighboring males die, while still excluding new males. In this manner, a haremic social system may develop over time, even under conditions of an initially equal sex ratio and an even distribution of resources.

This hypothesis presumes either differential male and female mortality, or a greater probability of new females entering established harems than of new males taking over areas with females. Territories from which females were removed were filled by other females from the same harem, not from neighboring harems. Remaining females in these harems had expanded territories, perhaps larger than needed for foraging. Such harems may be more likely to allow the immigration of a new female. This patchwork of permanent territories, determined by intrasexual defense and the pattern of mortality and recruitment over many years differs from the structure of most tetrapod harems (Emlen and Oring 1977).

Harems in which females defend individual territories are rare among fishes (Kuwamura 1984). Such harems have been described in the gonochoristic Lake Tanganyika cichlid, *Lamprologus brichardi* (Taborski and Limberger 1981), and the dwarf cichlid, *Apistogramma trifasciatum* (Burchard 1965). In both these species, females defend small, spawning territories within a male's larger territory. Kobayashi (1986) observed harems of a small puffer, *Canthigaster punctatissima*, in which an individual male would interact exclusively with more than one female. Females had very small territories, but there was no evidence of female aggregation or female choice of males. The rarity of such mating systems may be caused by the difficulty of controlling more than one female given female dispersion and strong competition from other males (Turner 1986)..

Harem polygyny in marine fishes is usually, but not always, associated with protogynous hermaphroditism (see references in the introduction). Several lines of evidence indicate that *C. fremblii* is not protogynous (1) A range of both small and large males occurs in the population. (2) When males were removed experimentally, females did not begin to show male behavior. (3) Finally, preliminary histological observations of the gonads of males revealed no atretic oocytes or membrane lined ovarian lumen as occurs among many secondary males (Hourigan Chapter V). As noted by Sadovy and Shapiro (1987), none of these observations alone can exclude protogyny, and more extensive histological examinations are planned. Nevertheless, taken together they suggest that *C. fremblii* may be gonochoristic. No other protogynous butterflyfishes have been reported (Thresher 1984; Tricas 1986), and it is conceivable that functional protogyny has not evolved in this family, despite favorable situations such as may occur in C. fremblii. The structure of harems in this species, where females defend large, exclusive territories, may also reduce the selective advantage of sex change. When a male disappears, a female from his harem would have to be able to change sex and take over territories of neighboring females before they were taken over by neighboring haremic males or non-territorial males. In contrast, in most haremic systems of fishes, females have overlapping home ranges, with the largest female already controlling access to several smaller females (Robertson 1972; Kuwamura 1984; Hourigan 1986b).

The social behavior of C. fremblii differed from that of other butterflyfishes. Males and females rarely showed coordinated swimming and spent little time together, much less than in paired, monogamous species (Reese 1975; Tricas 1986; Fricke 1986; Hourigan Chapter II and III). Even when a male C. fremblii had only a single female in his area, he did not spend any more time with her than did other males with any one of their females. When a male of a monogamous pair is removed from his mate, the territory size and feeding rate of the remaining female decrease, and chase rates with neighbors increase (Fricke 1986; Hourigan Chapter VI). Removal of female pair-mate also results in increased chase rates by the remining male (Fricke 1986; Hourigan Chapter VI). The remaining individual of either sex vigorously courts new individuals of the opposite sex (Hourigan Chapter VI). This was not the case for C. fremblii. The haremic mating system of _C. fremblii_ appears to be qualitatively different from the monogamous system of other butterflyfishes. The monogamous social systems are not merely cases of harems which have not reached the polygyny threshold, but derive from different behavioral repertoires of males and females.

CHAPTER V

ENERGETICS OF FEEDING AND REPRODUCTION FOR MALES AND FEMALES OF THREE SPECIES OF HAWAIIAN BUTTERFLYFISHES

INTRODUCTION

An animal's fitness depends on acquiring energy by feeding, and partitioning this energy between reproduction and other metabolic demands (Calow 1985). Many foraging models use energy intake from feeding as the major currency in the determination of fitness (Pyke et al. 1976). These analyses assume a relationship between energy intake and reproductive fitness. Each animal, however, must partition usable energy among the demands of current reproduction, maintenance activities, growth, and storage for future survival and reproduction. In addition, there is an unavoidable loss of energy in the form of heat and unutilized waste products. If energy is a limited resource, then energy budgets of animals will be sensitive to natural selection (Anderson 1967; Calow 1984).

Animals can meet their energy budgets by adjusting their energy intake by changes in foraging behavior, or by adjusting how this energy is partitioned. An individual animal's activity levels, foraging behavior, and partitioning of energy may all differ between the reproductive and non-reproductive seasons (Elliot 1979; Soofiani and Hawkins 1985; Wootton 1985). The energetic trade-off between current reproduction and growth and survival for future reproduction is a basic premise of life history theory (Williams 1966; Stearns 1976).

Energy budgets may also differ between the sexes. Females are expected to contribute more energy into each reproductive effort than a male (Bateman 1948; Trivers 1972), a situation resulting from anisogamy, where the female's energy investment in ova is greater than the male's investment in sperm. Although males may contribute significant amounts of energy to offspring in terms of parental care, it is the initial inequality of anisogamy which is considered to be the basis of many social systems (Trivers 1972; Wilson 1975; Emlen and Oring 1977). In situations without parental care, such as occurs in broadcast spawning reef fishes, the inequality of male vs. female investment in offspring is expected to be a predominant factor affecting mating systems.

Schoener (1969, 1971, 1983) broadly categorized animal foraging strategies as lying along a continuum from foraging "time minimizers" to "energy maximizers". Time minimizers limit their feeding time to the minimum necessary to meet their daily metabolic requirements. This maximizes the time available for other activities. Ebersole (1980) has termed this an energy maintenance strategy. In contrast, energy maximizers forage to maximize their daily rate of energy intake. Energy in excess of that needed for metabolic maintenance may be channeled into increased reproduction or stored for future use.

Schoener (1971) proposed that in many species, males tend to be foraging time minimizers, while females tend to be energy maximizers.

Finally, different species with different energy budgets are expected to have differing patterns of energy intake and partitioning. These differences may be reflected in different social systems.

Studies of energy budgets in fishes have concentrated on freshwater species, predominantly salmonids, under hatchery or laboratory conditions (Elliot 1976, 1979; Brett and Groves 1979; Brafield 1985). Field studies of several temperate freshwater fishes reveal seasonal differences in energy intake and partitioning (reviewed by Soofiani and Hawkins 1985). Evidence for sexual differences in energy budgets is less common (Newsome et al. 1975; Diana 1983; Wootton 1985). Very few studies of reef fishes have measured energy intake and partitioning from an ecological perspective (Muir and Niimi 1972; Brett and Groves 1979). For several reef fish species, where sexual differences in foraging behavior are known, females feed more than males: e.g. acanthurids (Robertson et al. 1979), pomacentrids (Ebersole 1980), labrids (Ross 1983; Green et al. 1984) and scarids (Warner and Downs 1977). Hoffman (1983) found that in protogynous Bodianus spp. females reduced their foraging time when they changed sex to become males.

It is generally assumed that additional energy intake by female fish is channeled into increased egg production. This assumption has rarely been tested (Wootton 1985). Hirshfield (1980) showed that increased food rations led to higher female fecundity in the Japanese medaka (Oryzias latipes). In the stickleback, Gasterosteus aculeatus, fecundity per spawn was limited by female size, however, food ration was the most important factor determining the number of spawnings per breeding season (Wootton 1977, 1985).

The present study compares energy intake and energy partitioning by males and females of two coral-feeding butterflyfishes, *Chaetodon multicinctus* and *Chaetodon quadrimaculatus*, during the reproductive and non-reproductive seasons. *Chaetodon multicinctus* feeds almost exclusively on live coral tissue, while *C. quadrimaculatus* feeds on coral and supplements its diet with algae and polychaetes (Hobson 1974; Hourigan Chapter III). These species have similar social systems, consisting of long term, apparently monogamous pairs in which both sexes defend a shared feeding territory (Tricas 1985, 1986; Hourigan 1986a, Chapter III). The findings from these two species are compared to data collected during the breeding season of a third butterflyfish, *Chaetodon fremblii*, which exhibits a haremic social system (Hourigan 1986b, Chapter IV). It is an omnivore which feeds primarily on polychaetes and algae (Hobson 1974, Hourigan Chapter IV). All three species are broadcast spawners, which release gametes into the water column and show no parental care. A series of eight experiments were conducted to determine seasonal and sexual differences in energy intake and absorption efficiencies, and the partitioning of this energy between somatic, storage, and reproductive tissues. These results are compared to field observations of feeding and activity in these species.

METHODS AND RESULTS

I. Study sites and field collections:

Methods:

Field observations of the feeding behavior of C. multicinctus and C. quadrimaculatus, and collections of specimens were conducted on the coral reefs at Puako, Hawaii (Lat 19° 58'N, Lon 155° 51'W; for a complete description of the habitats and observation methods see Hayes et al. 1982; and Hourigan Chapter II and III). The third species, Chaetodon fremblii was rare at Puako. Therefore, observations and collections were conducted in similar habitats at Kahe Pt. (Lat 21° 21'N, Lon 158° 8'W) off the leeward coast of the island of Oahu (Hourigan Chapter IV). Additional collections of C. multicinctus were made at Kahe Pt. and at coral poor areas at Portlock, Oahu (Lat 21° 16'N, Lon 157° 4'W).

Male-female pairs of C. multicinctus and C. quadrimaculatus were collected by spearing at Puako during three times of the year: the non-breeding season in fall (November 1980), the height of the breeding season in spring (March 1981), and the end of the breeding season in summer (July, 1981). Individual C. fremblii were collected at Kahe Pt. Oahu during the spring (March 1981). Additional collections of C. multicinctus were made at Kahe Pt. and Portlock in November 1983. Each fish was either dissected immediately, or labeled, double bagged and frozen for later analysis.

In the laboratory individual fishes were thawed, and standard length (SL) and wet weight were measured. Fishes were then dissected, and the liver, gonads, and fat deposits surrounding the intestine removed and weighed. Three small sub-samples from each ovary were removed, weighed, fixed in 10% formalin and preserved in 70% alcohol. Numbers of vitellogenic eggs were counted and staged according to the methods of Hourigan and Kelley (1985). The remaining tissues as well as food material from the pouchlike stomach, and portions of feces from the rectal region were saved to be utilized in the experiments described below.

Results:

A sample of 24 pairs of adult, territorial C. multicinctus, 24 pairs of adult, territorial C. quadrimaculatus, and ten male and 12 female C. fremblii was collected. Pairs were composed of one male and one female, both reproductively mature. Length-weight relationships for males and females of the same species were similar, indicating similar growth patterns (Fig. 5.1). Chaetodon multicinctus was the smallest species, while C. quadrimaculatus reached the largest mean size. In both paired species, males were usually larger than their pair-mates (paired t-tests, $p<0.05$ for both species). The mean size difference, however, was small: 2mm and 0.94g for C. multicinctus and 2mm and 2.7g for C. quadrimaculatus. The haphazard collection of C. fremblii precluded similar comparisons. Observations of harems

Figure 5.1a Length-weight relationship for males and females of three species of Hawaiian butterflyfishes: a) *C. multicinctus*. b) *C. quadrimaculatus*, and c) *C. fremblii*.

a

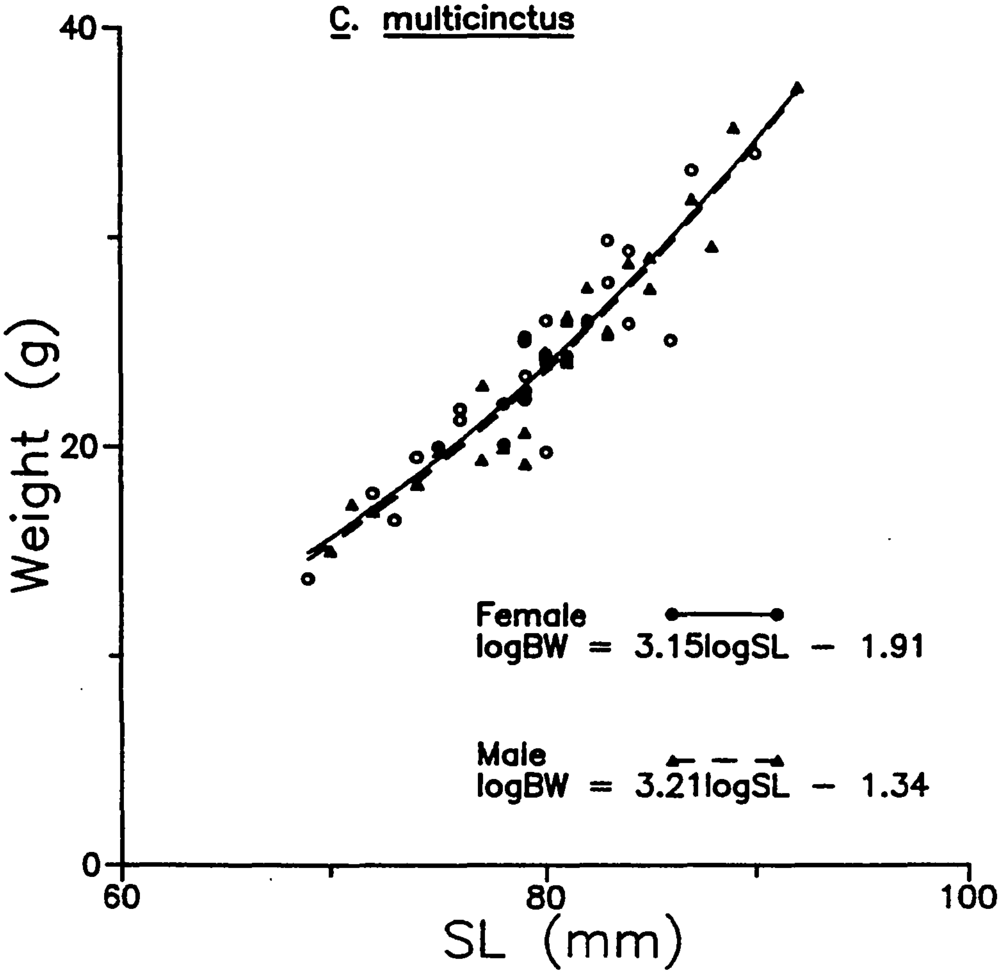

C. multicinctus
40
20
0
Weight (g)
60
80
100
SL (mm)
Female
logBW = 3.15logSL − 1.91
Male
logBW = 3.21logSL − 1.34

Figure 5.1b Length-weight relationship for males and females of three species of Hawaiian butterflyfishes: b) *C. quadrimaculatus*.

b

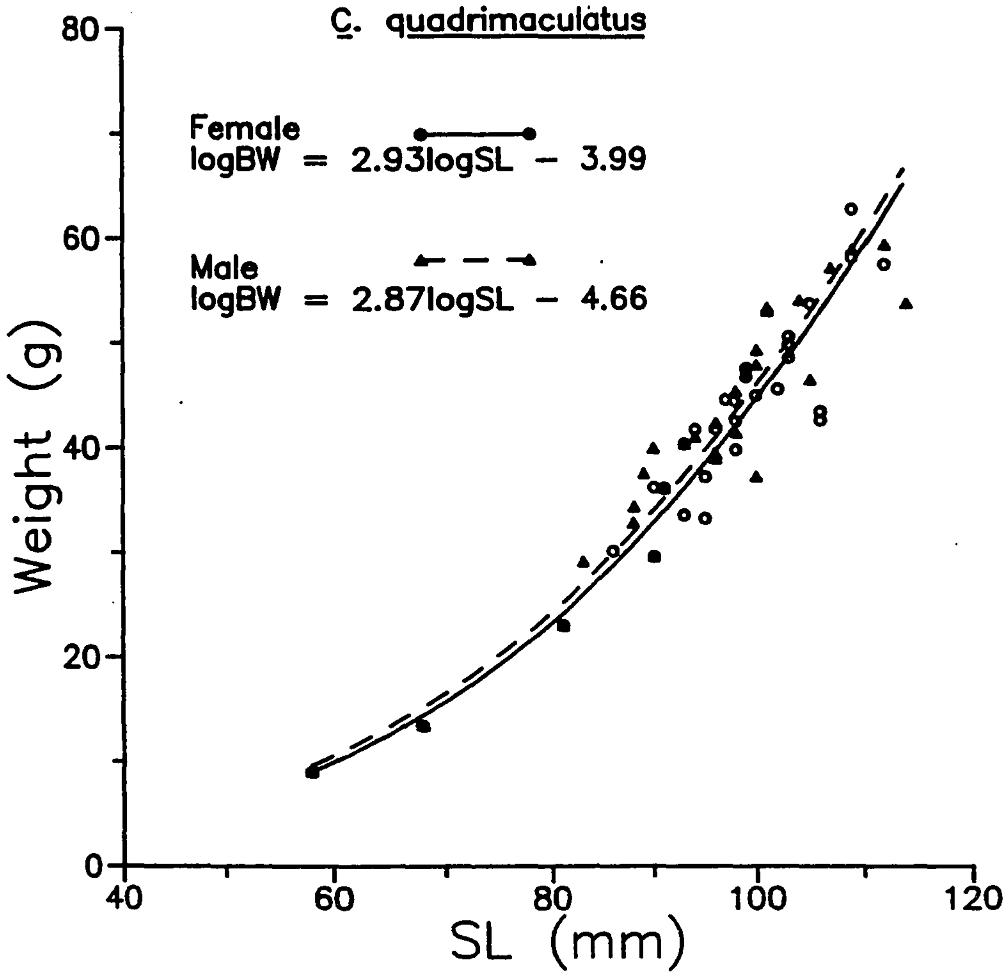
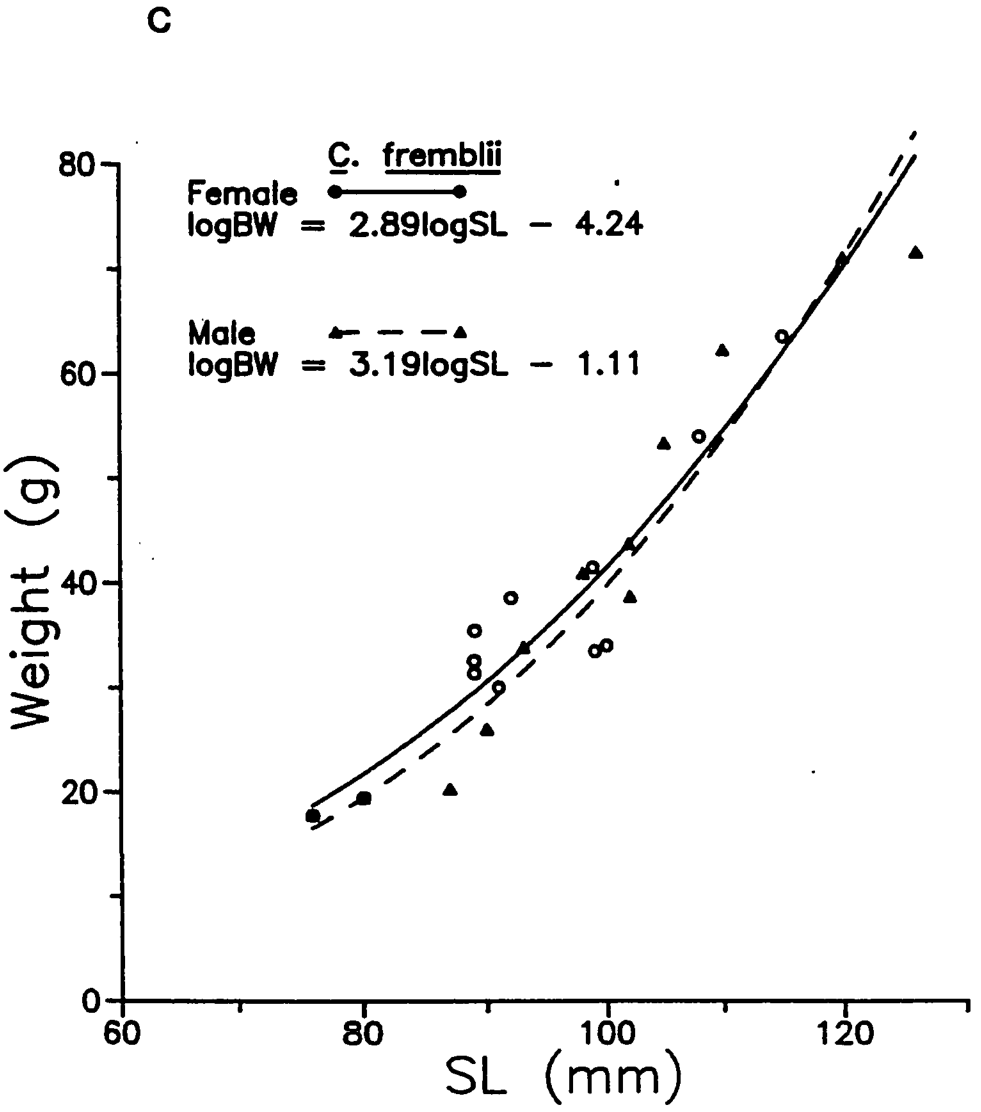

C. quadrimaculatus
Female
logBW = 2.93logSL − 3.99
Male
logBW = 2.87logSL − 4.66
Weight (g)
0
20
40
60
80
40
60
80
100
120
SL (mm)

Figure 5.1c Length-weight relationship for males and females of three species of Hawaiian butterflyfishes: c) *C. fremblii*.


C
C. fremblii
Female
logBW = 2.89logSL − 4.24
Male
logBW = 3.19logSL − 1.11
Weight (g)
0
20
40
60
80
SL (mm)
60
80
100
120

indicated that males were visibly larger than their associated females.

Gonosomatic indices (GSI = 100 X ratio of wet weight of gonad to total wet weight of body) of both males and females of the paired species were highest during the spring (Table 5.1). Comparisons of GSIs of fish with very different body sizes are difficult due to associated body-gonad allometries (deVlaming et al. 1982). There were, however, no significant differences within each species among the body sizes of fish in the three seasonal samples (Independent one-way ANOVAs, $p>0.5$). Fecundity, defined as the the total number of vitellogenic oocytes (yolked eggs) contained in the ovary of a female, was also highest in spring, as was the median ova diameter (Table 5.1). Almost all vitellogenic oocytes were of a similar size and stage of development. Hydrated eggs were only found on two occasions, among C. multicinctus speared in spring, on an evening seven days prior to the new moon. Spawning was also observed on that occasion. Examination of the two ovaries containing hydrated eggs showed that 77% to 82% of large vitellogenic eggs had undergone hydration synchronously. This allowed estimation of the batch fecundity, defined as numbers of eggs spawned at one time, estimated as 79.5% of the total number of vitellogenic eggs (Table 5.1), assuming that the two remaining species spawned a similar proportion of all vitellogenic oocytes. Chaetodon fremblii had the largest estimated batch fecundity of the three species, followed closely by C. quadrimaculatus.

Preliminary histological observations of the testes of all three species revealed no evidence of protogynous sex change. Testes

Table 5.1 Gonadosomatic index (GSI), fecundity and ova diameters of the three species of butterflyfishes during three seasons.

	Chaetodon multicinctus			*Chaetodon quadrimaculatus*			*Chaetodon fremblii*
	Spring	Summer	Fall	Spring	Summer	Fall	Spring
GSI (%)[a]							
Male Mean:	0.268	0.208	0.201	0.215	0.179	0.187	0.198
SD:	(0.061)	(0.105)	(0.069)	(0.216)	(0.088)	(0.105)	(0.111)
Female Mean:	2.365	1.284	1.246	3.319	1.548	1.295	3.756
SD:	(1.366)	(1.123)	(0.569)	(1.013)	(0.573)	(0.584)	(1.699)
Female Fecundity[b]							
Mean:	11079	3081	636	25344	8544	6024	27223
Range:	9754-15220	542-6393	108-2471	21958-28440	1204-17540	90-16754	22361-32164
Median Ova Diameter[c] (mm)	0.3-0.4	0.1-0.2	0.1-0.2	0.2-0.4	0.1-0.2	0.1-0.2	0.3-0.4
Estimated Batch Fecundity (in Spring)[d]	8810			20150			21640

a. GSI is expressed as the percent wet body weight comprised by the gonad.
b. Estimated total fecundity is the mean number of vitellogenic eggs.
c. Ova diameters are expressed as the range of median diameters of all vitellogenic eggs in subsamples from each ovary.
d. Estimated batch fecundity is those eggs of the largest mode which are expected to be spawned.

contained no atretic oocytes, nor was a membrane lined ovarian lumen remnant present.

In addition to the adult fishes, six non-territorial _C. multicinctus_ and eight non-territorial _C. quadrimaculatus_ were collected in March 1981. These fish were significantly smaller than territorial individuals of the same species (independent t-tests for males and females, $p<0.01$). Both males and females were represented, but neither were sexually mature (i.e. ovaries did not contain vitellogenic oocytes, and testes did not contain live sperm).

II. Field and Laboratory Experiments.

The following experiments were designed to estimate rates of energy intake in the field, in order to determine how this energy was partitioned, and to estimate spawning rates of females.

Experiment #1.: Energy intake per feeding bite.

Methods:

Individual _C. multicinctus_ and _C. quadrimaculatus_ were captured in the field by divers using hand nets. These fishes were transported to the Hawaii Institute of Marine Biology in aerated buckets and placed in large (200 l) tanks with flow-through filtered seawater and plastic tubes for shelter. Live coral colonies (coral heads) were placed in each tank for food, and the fish were left undisturbed for at least 24 hrs. All coral colonies used in these experiments were collected from Kahe Pt. and different locations in Kaneohe Bay. Individual, healthy colonies were removed and transported back to the laboratory where they were kept in an outdoor water table with free flowing sea water. Fresh corals were collected on the day before each experiment.

Prior to the experiment, an individual was transferred to a 40 l aquarium along with a freshly collected coral colony of a particular species. Only fish which fed on the offered coral colony were used. After 30 min the coral colony was removed, and the fish starved for 24 hrs to allow gut clearance and acclimatization to the test aquarium.

On the following day, a new coral colony of the same species previously offered, was placed in the test aquarium, separated from the fish by a clear partition. After one hour, the coral polyps had expanded and the partition was removed. Each experimental fish was observed for 30 min following its first bite on the coral. All feeding bites were counted by an observer sitting quietly 2 m from the aquarium, or recorded on videotape for subsequent counting. The behavior of fishes did not appear to differ during early trials of these two recording methods, so all subsequent observations were conducted with an observer present. Eight replicate trials with C. multicinctus were conducted, with each of the three most abundant Hawaiian coral species Porites lobata, Porites compressa and Pocillopora meandrina, for a total of 24 trials. Eight trials with C. quadrimaculatus were conducted using only Pocillopora meandrina.

After 30 min, the experimental fish was removed from the aquarium, sacrificed immediately, weighed and measured (SL). The fish was dissected, its sex determined, and stomach contents were removed. The length of the gut was measured, and the distance cleared by food from the previous day was measured. The stomach contents were inspected, weighed, then dried to constant weight in a 60°C oven.

Each sample of dried stomach contents was ground and homogenized using a mortar and pestle. The homogenate was further subdivided into sub-samples which were formed into pellets, weighed, and either ashed at 500°C and re-weighed to determine ash free dry weights (AFDW), or combusted in a Phillipson^R oxygen microbomb calorimeter, as described by Paine (1971), to determine caloric content. In general, four sub-samples of each dried tissue were analyzed for AFDW, and four to five sub-samples (5 to 20 mg each) were analyzed for caloric content. In this manner, dry weights, ash-free dry weights and caloric values were obtained for the samples. These were then calculated on a per-bite basis.

Results:

Chaetodon multicinctus fed readily on the coral colonies introduced to the aquarium. The amounts of each coral ingested are summarized in Table 5.2. More than 95% of the material ingested in 30 min remained in the pouchlike stomach. Organic content and caloric content (cal/mg AFDW; 1 cal = 4.81 joules) were slightly higher for stomach contents of fish feeding on P. meandrina than for those of

Table 5.2 The mean amount of coral material ingested by C. multicinctus and C. quadrimaculatus. Lines connect those means which do not differ at the 95% confidence level (ANOVA, Waller-Duncan K-ratio t-test for multiple comparisons).

	C. multicinctus			C. quadrimaculatus.
	P. meandrina N=8	P. lobata N=8	P. compressa N=8	P. meandrina N=8
Calories/mg AFDW	5.76 (SD=0.29)	5.28 (SD=0.35)	4.99 (SD=0.45)	5.01 (SD=0.23)
% Organic content	81.7% (SD=2.3)	75.6% (SD=2.4)	71.8% (SD=4.2)	82.1% (SD=3.1)
Dry weight/bite (in mg)	0.0528 (SD=0.0119)	0.047 (SD=0.0092)	0.036 (SD=0.0125)	0.192 (SD=0.056)
Calories/bite	0.25	0.19	0.13	0.70
Est. Caloric intake per day from that coral (in calories)[a]	3 - 1248	572 - 1284	0 - 267	1126-1260

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a. Caloric intake per day for each coral is estimated from the average number of bites on that species of coral per day times the average caloric return per bite. Since feeding bites on different corals differed between sexes and among different habitats, a range is given.

fish feeding on the two *Porites* spp. Net intake in calories per bite was higher for fish feeding on *P. meandrina* than those feeding on either *Porites* species. *Chaetodon quadrimaculatus* ingested more energy per bite than did *C. multicinctus* (Table 5.2). *Chaetodon quadrimaculatus* adults presented with either *Porites* species did not feed.

Examination of the stomach contents of fishes feeding on *P. meandrina* showed complete oral disks with tentacular rings. Only a few such rings were visible in the stomachs of fish feeding on *Porites* spp.. No calcareous material was ingested. Examination of the corals themselves revealed that most polyps on *Porites* spp. were still intact with perhaps only portions of one polyp removed per bite. After a single bite, polyps in a 10-15 mm radius of the bite retracted completely into the calyces within 15 seconds. Additional polyps were partially retracted in a radius of 20-30 mm around the bite. If left undisturbed, polyps would come out after 3 to 6 min.

Experiment #2. Energy intake per feeding bite: Field observations.

Methods:

To determine energy intake per feeding bite in the field, two male and two female *C. fremblii*, *C. multicinctus* and *C. quadrimaculatus* were discovered in shelters before dawn, and subsequently followed for 30 min after they had begun feeding. The number of feeding bites by each fish on different substrata were counted. The fishes were then speared, placed in plastic bags and returned to the laboratory on ice. Fishes were weighed and measured, and their stomach contents removed, dried and processed as in Experiment #1. These energetic values could then be compared to values from Experiment #1 and field observations of feeding.

Results:

Male and female C. multicinctus fed almost exclusively on corals, especially Porites lobata and P. compressa. Chaetodon quadrimaculatus fed on the coral Pocillopora meandrina as well as in crevices and on the hard substratum. There was some feeding on P. lobata. The third species, C. fremblii fed on the hard substratum, in crevices, in the sand, and on pedicillaria of the sea urchin Tripneustes gratilla.

After 30 min of feeding, 95% of the newly ingested food remained in the stomach. Inspection of stomach contents revealed that C. multicinctus fed nearly exclusively on coral tissue, and stomach contents included large numbers of zooxanthellae and both intact and discharged nematocysts. Stomach contents of C. quadrimaculatus contained coral material as well as polychaetes, small crustaceans and algae. The stomach contents of C. fremblii contained only polychaetes, crustaceans, algae and sea urchin pedicillaria. Females of all three species had more material in their stomachs, and a greater calculated energy intake than did males (Table 5.3).

Table 5.3 Caloric content of the diets of butterflyfishes captured in the morning after 1/2 hr of feeding.

	C. multicinctus		*C. quadrimaculatus*		*C. fremblii*	
	Males N=2	Females N=2	Males N=2	Females N=2	Males N=2	Females N=2
Bites per 1/2hr	323-364	391-425	182-264	366-387	262-302	301-323
Mean cal/stomach	66.5	81.3	173.9	316.3	108.5	185.4
Mean cal/bite	0.19	0.20	0.78	0.84	0.38	0.59
Caloric intake[a] est. cal/day	1596	1951	4175	7590	2604	4450

a. Daily caloric intakes for the fishes were estimated by averaging feeding over 12 hrs.

Experiment # 3. Rate of food clearance through the gut.

Methods:

Energy absorption from food intake depends in part on the time that food remains in the gut. A rough measure of the rate of food clearance through the gut was determined by sacrificing fish at 6, 12, 24 and 48 hrs after they were fed, and measuring the amount of the stomach and intestine which was cleared of food material. Two male and two female *C. multicinctus* were sacrificed at each time interval. The guts were removed, the length of the intestine was measured, and the portion which was cleared of food was recorded.

Results:

After 6 hrs, the stomach was empty, as well as the first 32% (SD 4.6%) of the intestine. After 12 hours, 82% (SD 8.5%) of the intestine had been cleared of food. After 24 hrs 88% (SD 2.3%) of the intestine was cleared. Some fecal material was still retained in this last 12% even after 48 hrs. There were no consistent differences between males and females. Sample sizes in this experiment were small (N - 4), however, guts from both *C. multicinctus* and *C. quadrimaculatus* from experiment 1 and all three species from experiment 2 had similar percentages of cleared areas corresponding to the last time they had fed.

Experiment #4. Estimation of caloric intake and absorption.

Methods:

In this experiment, the caloric intake and relative absorption (assimilation) efficiency of male and female fishes were determined. Food in the stomachs of teleosts is subjected to the action of HCl and peptidases, but little or no absorption occurs there (Kapoor et al. 1975). Thus as feeding is relatively continuous (Hourigan Chapter III) and food moves at a constant rate through the gut (Experiment #3), the energy content of the diets of fishes can be estimated by analyzing the energy content of the stomach contents (Talbot 1985). In butterflyfishes, the stomach is followed by a very long intestine where most absorption of nutrients occurs. At the distal end of this intestine is a short rectal region. The energy content of material in this region probably approximates that voided in the feces.

Eight male-female pairs of C. multicinctus and C. quadrimaculatus were collected by spearing in November 1980, March 1981 and in July 1981, at Puako, for a total sample of 48 fish of each species. Pair-mates were collected at the same time, but different pairs were collected at different times of the day. Six individual male and six female C. fremblii were collected in the afternoon on several different days in March 1981 at Kahe Pt.. Fishes were frozen immediately, and subsequently partially thawed before analysis. This allowed removal of the stomach contents and feces with little contamination by material from the remaining portion of the intestine (Talbot 1985). Samples of stomach contents and feces from each fish were dried and analyzed as in Experiment #1. In this manner the organic content and caloric content of the food and feces was estimated.

Results:

Female *C. multicinctus* and *C. quadrimaculatus* had more material in their stomachs than did the males with whom they were paired. The dry weight of stomach contents of male *C. multicinctus* averaged 88% of the weight of stomach contents of their mates, speared at the same time ($N = 24$; Paired t-test $p<0.001$). Stomach contents of male *C. quadrimaculatus* averaged 68% of the dry weight of stomach contents of their mates ($N = 24$; Paired t-test $p<0.001$). This was true even though males were on average larger than their mates. Because male and female *C. fremblii* were not collected at the same time, similar comparisons of stomach content weights could not be made.

Stomach contents were of similar composition to those in Experiment #2. For the paired species there were no significant differences between pair members in the percent organic content of the stomach contents (=organic density: 100 X AFDW/dry weight) or in the energetic content per gram (=caloric density expressed as cal/mg AFDW; paired t test $p > 0.5$; Table 5.4). This is in accordance with observations that both males and females fed on similar foods. There were no differences between male and female *C. fremblii* in the organic or caloric densities of stomach material (t-test $p > 0.25$).

Table 5.4 Organic and energetic content of the diet of three species of butterflyfishes, and associated per-cent absorption (assimilation) efficiencies. Means and standard deviations (SD) refer to all seasons combined.

	Chaetodon multicinctus		*Chaetodon quadrimaculatus*		*Chaetodon fremblii*	
STOMACH CONTENTS	Male N = 24	Female N = 24	Male N = 24	Female N = 24	Male N = 6	Female N = 6
Organic Density[a] (%)	83.1 (SD=4.2)	82.9 (SD=3.7)	80 (SD=5.7)	81.6 (SD=5.1)	85.2 (SD=3.1)	84.3 (SD=2.5)
Caloric Density[b] cal/mg dry wt.	4.2 (SD=0.5)	4.1 (SD=0.6)	4.4 (SD=0.6)	4.8 (SD=0.4)	4.6 (SD=0.7)	4.4 (SD=0.6)
Caloric Density cal/mgAFDW	5 (SD=0.6)	4.9 (SD=0.5)	5.5 (SD=0.6)	5.9 (SD=0.3)	5.4 (SD=0.5)	5.2 (SD=0.6)
FECES						
Organic Density (%)	66.2 (SD=7.2)	66.3 (SD=6.1)	70.6 (SD=5.6)	72.6 (SD=5.6)	49.7 (SD=8.9)	50.31 (SD=8.4)
Caloric Density cal/mg dry wt.	3.3 (SD=0.7)	3.1 (SD=0.4)	3.8 (SD=0.4)	4 (SD=0.5)	2.7 (SD=0.6)	2.5 (SD=0.7)
ABSORPTION EFFICIENCY						
Organic Material (%)	20.3 (SD=9.1)	23.7 (SD=8.5)	11.4 (SD=7.5)	11.1 (SD=5.2)	41.5 (SD=11.7)	40.3 (SD=10.1)
Calories (%)	21.5 (SD=8.8)	23.3 (SD=8.1)	12.9 (SD=9.1)	16.1 (SD=5.3)	40.3 (SD=10.1)	43.8 (SD=14.5)

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a. Organic density is the ash free percent of the stomach or fecal contents.
b. Caloric density is given in cal/mg dry weight and cal/mg ash-free dry weight (AFDW).

All three species had very long intestines. The ratio of body length (SL) to intestine length (measured from the pyloric sphincter to the anus) was 1:8.64 (SD = 0.99) for C. multicinctus, 1:7.23 (SD = 0.96) for C. quadrimaculatus, and 1:6.67 (SD = 1.31) for C. fremblii. Within each species, there were no differences in these ratios between the sexes (Independent t-tests, $p > 0.8$), nor did there appear to be differences in the shapes of male and female guts. The fecal material at the end of the gut had very little recognizable material except for large numbers of apparently undigested zooxanthellae in the guts of the two coral-feeding species. Again, for each species there were no significant differences between males and females in the percent organic content of the feces.

A coefficient of absorption efficiency (assimilation efficiency) of organic material, A_o was calculated using the equation (adapted from Fange and Groves 1979):

$$A_o = 100 \times \left[1 - \frac{\text{\% organic content of feces}}{\text{\% organic content of stomach contents}} \right]$$

A similar equation gives the caloric absorption efficiency, A_c:

$$A_c = 100 \times \left[1 - \frac{\text{Calories per mg dry wt. of feces}}{\text{Calories per mg dry wt. of stomach contents}} \right]$$

There was no difference between males and females within the same species in either measure of efficiency (Table 5.4). For the two paired species there were no significant differences in energy density of the food intake or in absorption efficiencies between seasons.

There was, however, a great difference in the absorption efficiencies of C. fremblii compared to the the remaining two species (One way ANOVA, p<0.01). Chaetodon fremblii appeared to absorb two to three times as much organic material from its diet than did the other species, resulting in a higher net energy intake.

Experiment #5. Estimation of caloric partitioning among different tissues by males and females of the three species.

Methods:

In this experiment, the energetic content of the body tissues of the fishes of all three species used in Experiment #4 (N = 48 C. multicinctus, 48 C. quadrimaculatus, 12 C. fremblii) was analyzed. After the guts were removed, the remaining tissues were divided into gonads, liver, gut mesenteries with attached fat deposits, and the remaining carcass. A tissue sample from the dorsal musculature was also removed. The remaining carcass was dried, weighed, then ashed for a determination of the ash-free dry weight. Each of the other tissues was dried, weighed, homogenized and formed into pellets as described above.

Ash-free dry weights and caloric contents were determined from 5 sub-samples of each tissue as described in Experiment #1. Because of the small size of testes, fewer sub-samples (2-5) were used. Since the fat deposits yielded liquids when dried, the ash-free portions were assumed to be lipid, and were given a value of 9.45 cal/mg AFDW for comparative purposes. This value is the energy physiologically available in lipids (Brett and Groves 1979).

Results:

Tissues were divided into three major categories: reproductive tissues (the ovaries and testes), storage tissues (the fat stores of the intestinal membranes and the liver), and other somatic tissues (represented by the sample of muscle tissue and the rest of the body). The distribution of organic content and energy among these different tissues is shown in Table 5.5 and 5.6. Organic density is represented as a percentage ratio of ash-free dry weight (AFDW) to total dry weight of the tissue, and represents the percent of organic material in the tissue. Caloric density is presented as cal/mg AFDW and represents the energy content of organic material in the tissue. In addition, the percentage of the total organic content of the animal which is comprised by that tissue (Fig. 5.2) provides a rough approximation of the percent of net organic intake devoted to that tissue. In the case of reproductive tissues, this provides a first approximation of reproductive effort (RE) for comparative purposes.

Chaetodon multicinctus

Reproductive tissues showed the greatest difference between the sexes in tissue energy content. The ovaries of females contained 8 to 15 times as many calories as did the testes of males, even though male

Table 5.5 Organic and energetic content of the gonads of C. multicinctus and C. quadrimaculatus. Means and standard deviations (SD) are given for each season. Significance level for F statistic from standard one-way ANOVAs (d.f. 2/21) are presented for between season comparisons. Comparisons between sexes for all seasons are paired t-tests comparing differences between pair-mates. $*=p<0.05$, $**=p<0.01$, $***=p<0.001$, NS = $p > 0.05$.

5.5a. GONAD

			Chaetodon multicinctus			Chaetodon quadrimaculatus		
Sex	Season		Organic[a] Density %	Caloric[b] Density cal/mgAFDW	Total[c] Calories	Organic Density %	Caloric Density cal/mgAFDW	Total Calories
Male	Spring	Mean	91.5	6.01	78	87.9	6.08	73
		SD	(2.5)	(0.06)	(24)	(2.2)	(0.07)	(23)
	Summer	Mean	89.3	6.08	59	88.6	6.02	96
		SD	(3.7)	(0.03)	(36)	(3.2)	(0.05)	(52)
	Fall	Mean	89.9	6.10	50	89.2	5.98	97
		SD	(2.9)	(0.05)	(7)	(4.5)	(0.04)	(22)
	Between Seasons	F	NS	NS	NS	NS	**	NS
Female	Spring	Mean	93.1	6.23	1144	93.5	6.28	2101
		SD	(2.1)	(0.10)	(531)	(1.3)	(0.08)	(212)
	Summer	Mean	90.4	6.11	480	91.2	6.18	1041
		SD	(1.5)	(0.11)	(506)	(1.2)	(0.13)	(410)
	Fall	Mean	89.9	6.06	419	92.5	6.05	1264
		SD	(1.1)	(0.05)	(119)	(1.9)	(0.09)	(244)
	Between Seasons	F	*	*	***	*	**	***
	Between Sexes	Paired t-test	*	**	***	***	***	***

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a. Organic density is the ash free percent of the tissue.
b. Caloric density of the tissue is given in cal/mg ash-free dry weight (AFDW).
c. Estimate of the total caloric content of the whole tissue in the fish.

Table 5.5 (cont.). Organic and energetic content of fat deposits of *C. multicinctus* and *C. quadrimaculatus*. Means and standard deviations (SD) are given for each season. Significance level for F statistic from standard one-way ANOVAs (d.f. 2/21) are presented for between season comparisons. Comparisons between sexes for all seasons are paired t-tests comparing differences between pair-mates. *=$p<0.05$, **=$p<0.01$, ***= $p<0.001$, NS = $p > 0.05$. NM = Not measurable because fat was not visibly present.

5.5b. FAT

Sex	Season		*Chaetodon multicinctus* Organic Density %	*Chaetodon multicinctus* Caloric Density cal/mgAFDW	*Chaetodon multicinctus* Total Calories	*Chaetodon quadrimaculatus* Organic Density %	*Chaetodon quadrimaculatus* Caloric Density cal/mgAFDW	*Chaetodon quadrimaculatus* Total Calories
Male	Spring	Mean	NM	NM	0	NM	NM	0
		SD	NM	NM	(0)	NM	NM	(0)
	Summer	Mean	91.3	9.45	110	90.1	9.45	161
		SD	(2.7)	NM	(93)	(3.8)	NM	(82)
	Fall	Mean	94.0	9.45	479	93.6	9.45	1573
		SD	(3.5)	NM	(385)	(2.9)	NM	(1641)
	Between Seasons	F	***	-	***	***	-	***
Female	Spring	Mean	NM	NM	0	NM	NM	0
		SD	NM	NM	(0)	NM	NM	(0)
	Summer	Mean	NM	NM	0	NM	NM	0
		SD	NM	NM	(0)	NM	NM	(0)
	Fall	Mean	93.2	9.45	1024	92.6	9.45	3404
		SD	(3.7)	NM	(311)	(2.3)	NM	(2509)
	Between Seasons	F	***	-	***	***	-	***
	Between Sexes	Paired t-test	Dependent on Season			Dependent on Season		

Table 5.5 (cont.). Organic and energetic content of the liver of *C. multicinctus* and *C. quadrimaculatus*. Means and standard deviations (SD) are given for each season. Significance level for F statistic from standard one-way ANOVAs (d.f. 2/21) are presented for between season comparisons. Comparisons between sexes for all seasons are paired t-tests comparing differences between pair-mates. *=p<0.05, **=p<0.01, ***= p<0.001, NS = p > 0.05.

5.5c. LIVER

			Chaetodon multicinctus			*Chaetodon quadrimaculatus*		
Sex	Season		Organic Density %	Caloric Density cal/mgAFDW	Total Calories	Organic Density %	Caloric Density cal/mgAFDW	Total Calories
Male	Spring	Mean	90.9	5.97	162	91.6	5.91	345
		SD	(0.9)	(0.20)	(22)	(1.1)	(0.22)	(56)
	Summer	Mean	91.5	5.81	157	91.6	5.70	268
		SD	(1.6)	(0.15)	(46)	(1.8)	(0.17)	(56)
	Fall	Mean	92.1	5.95	151	91.1	6.01	213
		SD	(1.3)	(0.21)	(31)	(1.4)	(0.13)	(194)
	Between Seasons	F	NS	NS	NS	NS	NS	NS
Female	Spring	Mean	90.2	6.01	186	91.1	5.97	567
		SD	(1.4)	(0.15)	(14)	(1.1)	(0.07)	(92)
	Summer	Mean	91.4	5.79	174	91.9	5.51	345
		SD	(1.3)	(0.11)	(43)	(1.4)	(0.24)	(121)
	Fall	Mean	91.8	6.10	202	91.7	6.04	490
		SD	(0.9)	(0.13)	(40)	(1.4)	(0.11)	(211)
	Between Seasons	F	NS	*	NS	NS	**	*
	Between Sexes	Paired t-test	NS	NS	***	NS	NS	***

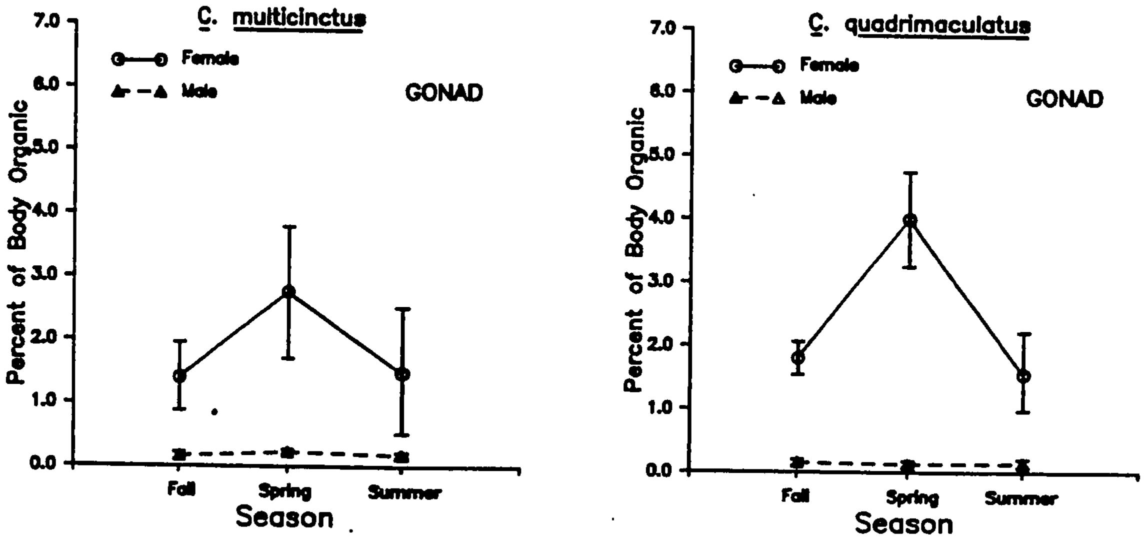
Table 5.5 (cont.). Organic and energetic content of muscle tissue of C. multicinctus and C. quadrimaculatus. Means and standard deviations (SD) are given for each season. Significance level for F statistic from standard one-way ANOVAs (d.f. 2/21) are presented for between season comparisons. Comparisons between sexes for all seasons are paired t-tests comparing differences between pair-mates. *=$p<0.05$, **=$p<0.01$, ***= $p<0.001$, NS = $p > 0.05$. Total calories of all muscle was not measured.

5.5d. MUSCLE

			Chaetodon multicinctus			Chaetodon quadrimaculatus		
Sex	Season		Organic Density %	Caloric Density cal/mgAFDW	Total Calories	Organic Density %	Caloric Density cal/mgAFDW	Total Calories
Male	Spring	Mean	92.1	4.89	-	90.7	4.94	-
		SD	(1.2)	(0.23)	-	(2.4)	(0.15)	-
	Summer	Mean	91.7	4.92	-	92.2	5.01	-
		SD	(2.5)	(0.22)	-	(2.2)	(0.21)	-
	Fall	Mean	91.8	4.97	-	91.4	4.98	-
		SD	(2.3)	(0.25)	-	(2.4)	(0.20)	-
	Between Seasons	F	NS	NS	-	NS	NS	-
Female	Spring	Mean	92.0	4.90	-	91.3	4.99	-
		SD	(2.4)	(0.21)	-	(1.2)	(0.18)	-
	Summer	Mean	90.0	4.96	-	91.0	4.90	-
		SD	(1.6)	(0.17)	-	(2.1)	(0.26)	-
	Fall	Mean	93.2	5.00	-	92.3	4.95	-
		SD	(2.3)	(0.23)	-	(1.5)	(0.14)	-
	Between Seasons	F	NS	NS	-	NS	NS	-
	Between Sexes	Paired t-test	NS	NS	-	NS	NS	-

Figure 5.2. Partitioning of organic material in different tissues of male and female C. multicinctus and C. quadrimaculatus, during the fall, spring, and summer. Values represent the mean percent (± 95% confidence limits) of the total organic content of the body which is comprised by the organic content of a particular tissue. The organic content of the tissues was determined from their ash-free dry weights. The tissues are: a) the gonads, b) the viceral fat. For each season, the sample for each species consisted of eight fish of each sex.

a


C. multicinctus
Female
Male
GONAD
Percent of Body Organic
7.0
6.0
5.0
4.0
3.0
2.0
1.0
0.0
Fall
Spring
Summer
Season
C. quadrimaculatus
Female
Male
GONAD
Percent of Body Organic
7.0
6.0
5.0
4.0
3.0
2.0
1.0
0.0
Fall
Spring
Summer
Season

b

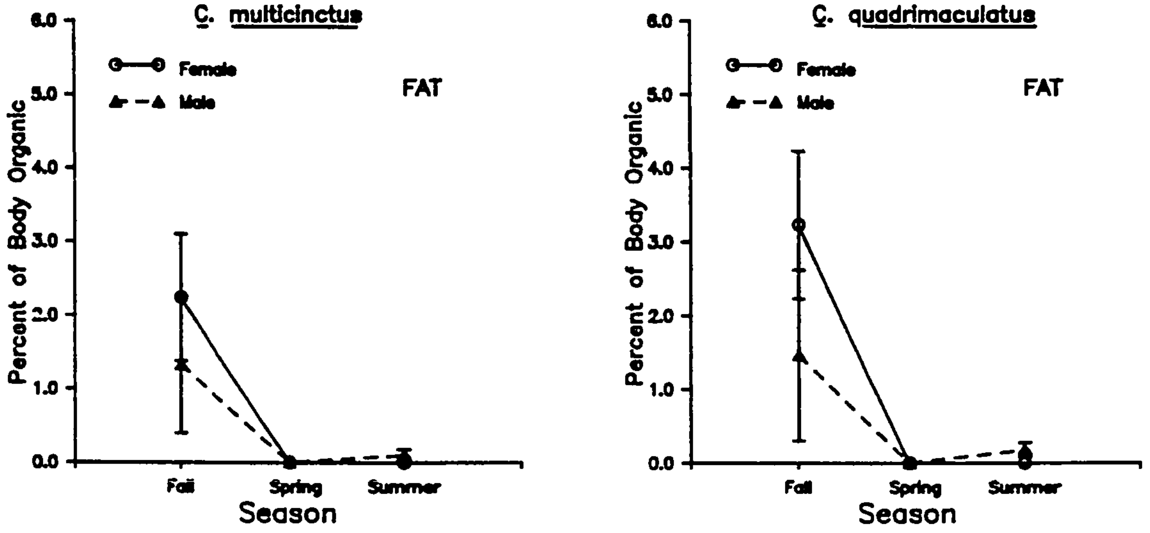
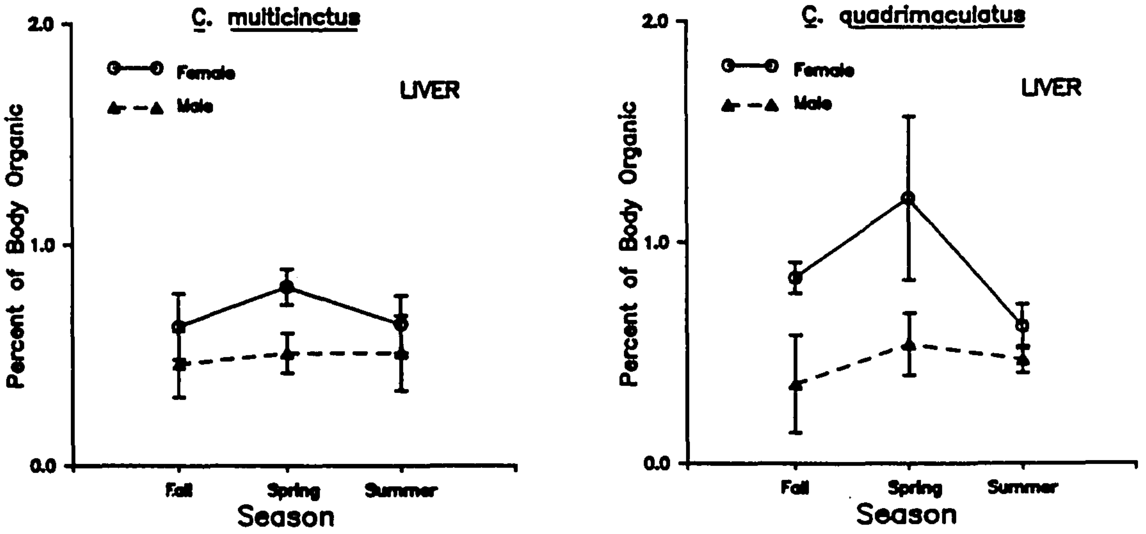
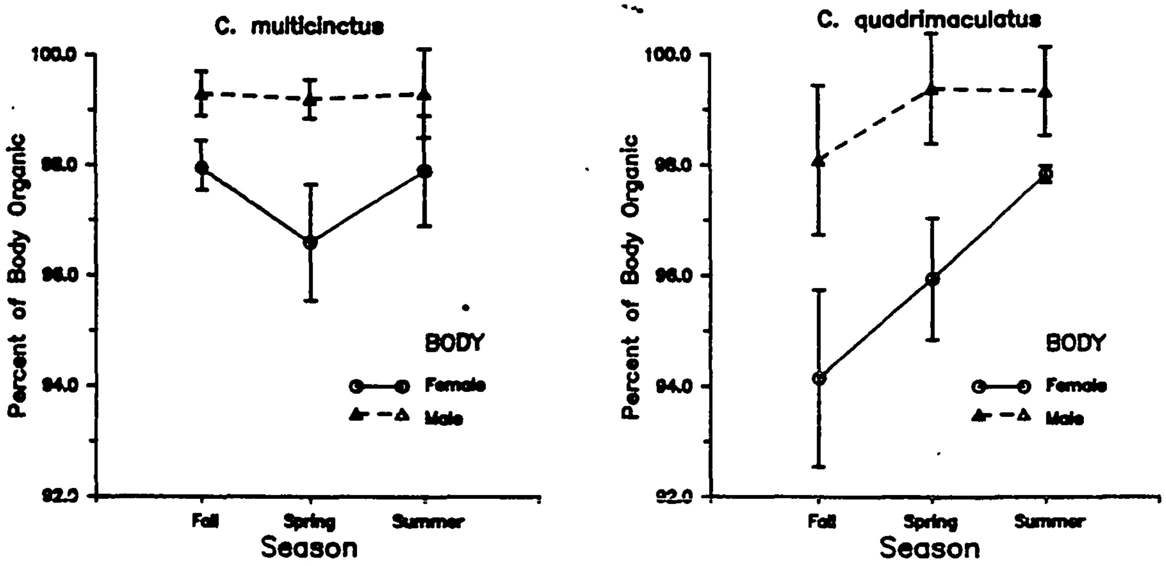

C. multicinctus
Female
Male
FAT
Percent of Body Organic
6.0
5.0
4.0
3.0
2.0
1.0
0.0
Fall
Spring
Summer
Season
C. quadrimaculatus
Female
Male
FAT
Percent of Body Organic
6.0
5.0
4.0
3.0
2.0
1.0
0.0
Fall
Spring
Summer
Season

Figure 5.2(cont.) Partitioning of organic material in different tissues of male and female C. multicinctus and C. quadrimaculatus, during the fall, spring, and summer. Values represent the mean percent (± 95% confidence limits) of the total organic content of the body which is comprised by the organic content of a particular tissue. The organic content of the tissues was determined from their ash-free dry weights. The tissues are: c) the liver, and d) the remaining body tissues. For each season, the sample for each species consisted of eight fish of each sex.

c


C. multicinctus
Female
Male
LIVER
Percent of Body Organic
2.0
1.0
0.0
Fall
Spring
Summer
Season
C. quadrimaculatus
Female
Male
LIVER
Percent of Body Organic
2.0
1.0
0.0
Fall
Spring
Summer
Season

d


C. multicinctus
Percent of Body Organic
100.0
98.0
96.0
94.0
92.0
BODY
Female
Male
Fall
Spring
Summer
Season
C. quadrimaculatus
Percent of Body Organic
100.0
98.0
96.0
94.0
92.0
BODY
Female
Male
Fall
Spring
Summer
Season

body size was on the average larger than female body size. Paired comparisons showed that ovaries contained both a greater organic density and a greater caloric density (cal/mg AFDW) than the testes of the pair-mate (Table 5.5a).

One-way ANOVAs showed a significant seasonal factor in the organic density of the ovaries, but not of the testes (Table 5.5a). The percent of the total organic content of females devoted to reproductive tissues was higher in the spring (Fig. 5.2a). The caloric density of ovaries was also higher during this time. Subsamples of the ovaries showed an average of 11,000 vitellogenic oocytes per ovary during the spring (Table 5.1). These oocytes represented an average investment of 0.104 calories per egg, including the investment in associated follicle, previtellogenic oocytes and gonad structure.

Energy storage in the liver and fat deposits also showed seasonal trends. Females had no appreciable fat deposits in the intestinal mesenteries except during the fall (Table 5.5b). During this season, females had greater amounts of fat and a greater proportion of their total organic content devoted to fat (Fig. 5.2b) than did males (Paired t-test $p<0.001$). In spring, neither sex had visible fat reserves. In late summer however, males began to accumulate fat, while females still had none. An additional area of fat storage was found surrounding the brain in the cranial cavity in all three species. Although this was not measured, its occurrence was correlated with the occurrence of fat in the body cavity.

Organic density and caloric density of the liver did not differ significantly between males and females (Table 5.5c). Females, however, devoted a greater percentage of their total organic content to the liver than did males (Fig. 5.2c). The liver showed no significant seasonal differences in either sex (Table 5.5c), although females appeared to invest a greater percentage of their total organic content into the liver in spring, compared to other seasons (Fig. 5.2c).

Dorsal muscle tissue showed no seasonal differences or differences between sexes in organic or caloric density (Table 5.5d). When the remaining carcass was analyzed, the percent of the total organic content of the fish partitioned into these somatic tissues was significantly higher for males (Paired t-test $p<0.001$; Fig. 5.2d). No attempt was made to analyze the total caloric content of the remaining body.

Chaetodon quadrimaculatus

Patterns of energy partitioning by C. quadrimaculatus were roughly similar to those of C. multicinctus (Table 5.5). Reproductive tissues showed the greatest difference between sexes in energy content. The ovaries of females averaged 10 to 20 times more calories than did the testes of males. Paired comparisons showed that ovaries contained both a greater organic density and a greater caloric density than the testes of the pair-mate (Table 5.5a). A greater percent of the total organic content of females was devoted to reproductive tissues during the spring than during the other seasons (Fig. 5.2a). Organic density and caloric density of the ovary were also highest at this time. Sub-samples of the ovaries indicated an average of 25,000 vitellogenic eggs per ovary during the spring (Table 5.1). These eggs represented an average investment of 0.081 calories per egg, including the investment in associated follicle, previtellogenic oocytes and gonad structure.

Energy storage in the liver and fat deposits followed the same trends as for C. multicinctus (Table 5.5b & 5c). Females had fat deposits in the intestinal mesenteries only in the fall. During this season, females had greater amounts of fat and greater proportions of their total organic content in fat than did males (Fig. 5.2b). In spring, neither sex had visible fat reserves, and in late summer only males had accumulated fat. Organic density and caloric density of liver tissue did not differ significantly between males and females. Females, however, devoted a greater percentage of their total organic content to the liver (Fig. 5.2c). The liver of females also showed significant seasonal differences, with greater caloric density as well as a greater percentage of total organic material devoted to the liver during the spring (Table 5.5c, Fig. 5. 2c).

Dorsal muscle tissue showed no differences between sexes in organic or caloric density. When the remaining carcass was analyzed for organic content, males had a slightly higher organic density in these somatic tissues (Paired t-test $0.1 > p > 0.05$) but the proportion of the total organic content of the fish partitioned into these somatic tissues was significantly higher for males (Paired t-test $p < 0.02$; Fig. 5.2d). Attempts to homogenize the complete carcass to determine caloric densities were not very successful, but for the two pairs from the spring collection for which this was attempted, there were no significant differences in cal/mg AFDW between the male and female of a pair.

Chaetodon fremblii

Ovaries of female C. fremblii had a greater caloric density than the testes of males, and composed a greater proportion of the total organic content of the fish (Table 5.6). This was similar to the trend found in the previous two species. Sub-samples of the ovaries revealed an average of 27,000 vitellogenic oocytes per ovary (Table 5.1). These oocytes represented an average investment of 0.088 calories per egg, including the investment in associated follicle, previtellogenic oocytes and gonad structure.

Fat stores were found in two out of six males and in no females. This constituted a difference from the previous two species in which neither sex had accumulated fat reserves in the spring. The liver composed a greater proportion of the total organic content of females than did the liver of males. There was, however, no significant difference between males and females in the organic or caloric density of the livers. Finally, there was no difference in the caloric density of muscle tissue and no difference in the total percent organic content devoted to the remaining somatic tissues. In the latter respect, C. fremblii also differed from the previous two species.

Table 5.6 Organic and energetic content of tissues of *C. fremblii*. N = 6 individuals of each sex.

			Chaetodon fremblii			
Sex			Organic[a] Density %	% of Body[b] Organic	Caloric[c] Density cal/mgAFDW	Total[d] Calories
GONAD						
Male	Spring	Mean	94.3	0.21	5.77	236
		SD	(1.5)	(0.12)	(0.42)	(73)
Female	Spring	Mean	92.8	4.07	6.21	2386
		SD	(0.5)	(3.03)	(0.17)	(1102)
	Between[e] Sexes	t-test	NS	**	*	***
FAT[f]						
Male	Spring	Mean	97.1	1.86	9.45	2774
		SD	(0.2)	(2.11)	-	(3832)
Female	Spring	Mean	NM	0	NM	0
		SD	NM	0	NM	0
	Between Sexes	t-test	***	***	-	***
LIVER						
Male	Spring	Mean	91.4	0.49	5.76	321
		SD	(1.4)	(0.12)	(0.39)	(122)
Female	Spring	Mean	91.0	1.47	5.81	572
		SD	(0.7)	(0.48)	(0.22)	(113)
	Between Sexes	t-test	NS	**	NS	*
MUSCLE & BODY			muscle	body	muscle	
Male	Spring	Mean	92.3	96.36	4.66	-
		SD	(1.0)	(4.68)	(0.08)	-
Female	Spring	Mean	92.5	94.35	4.71	-
		SD	(1.2)	(3.19)	(0.07)	-
	Between Sexes	t-test	NS	NS	NS	-

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a. Organic density is the ash free percent of the tissue.

b. % of Body Organic is the percent of the total organic content of the fish which is partitioned into that tissue.

c. Caloric density of the tissue is given in cal/mg ash-free dry weight (AFDW).

d. Estimate of the total caloric content of the whole tissue in the fish. Total calories of all the remaining body tissues was not measured.

e. Differences between sexes were determined using the Students t-test; *=$p<0.05$, **=$p<0.01$, ***= $p<0.001$, NS=$p>0.05$.

f. NM = Not measurable because fat was not visibly present.

Experiment #6. Energy partitioning in C. multicinctus pairs from food-rich vs. food-poor habitats.

Methods:

Four pairs of C. multicinctus were collected in November 1983 in a coral-rich habitat at Kahe Pt. Four additional pairs of similar size were collected in a coral-poor habitat at Portlock at the same time on the following day. Fish were measured and dissected, and prepared as in Experiment #5. Ash-free dry weights were determined for tissues, but caloric contents were not. Coral cover in the two areas where the fish were collected was visually estimated on subsequent dives.

Results:

Coral cover was much greater at Kahe Pt. than at Portlock. Large mounds of P. lobata covered approximately 50% of the bottom, with P. compressa (10%), Pocillopora meandrina (2.5%) and Montipora spp. (5%) also common. Coral cover at Portlock was very sparse, predominantly composed of small patches of P. lobata covering less than 10% of the bottom. Other coral species comprised less than 1-2% of the bottom cover. Cursory observations of C. multicinctus pairs in the coral-poor habitat showed more feeding on hard substratum and larger territory sizes than in the coral-rich habitat. Stomachs of fish caught in the coral-poor habitat were less full than those caught at the same time on the previous day in the coral-rich habitat.

Ovaries of females from the coral-rich habitat were larger than those from females caught in the coral-poor habitat and comprised a greater percent of the total organic content of the body (Table 5.7). Females from the coral-rich habitat also had more vitellogenic oocytes per dry weight of body than did those from the coral-poor habitat. Livers of both males and females had a higher organic density and comprised more of the total organic content in the coral-rich habitat than did livers of fish from the coral-poor habitat. All differences in values for the liver and gonad were consistent for all fish from the two habitats, however sample sizes were small (N = 4 for each sex) and must be viewed with caution. Finally, both males and females from the coral-rich habitat had significant fat stores, while none of the fish from the coral-poor habitat had stored fat.

Experiment #7. Estimated resting metabolism rate of C. multicinctus.

Methods:

Four naturally occurring male-female pairs of C. multicinctus were captured as in Experiment #1 in November 1983 at Kahe Pt. and isolated in 40 l tanks, one pair to a tank. These tanks had free flowing, filtered sea water and shelters, but no food. After 24 hrs, each fish was removed from the tank, blotted dry with a paper towel, weighed, and then returned to its tank. The fish showed no ill effects from this treatment. During the following six weeks, the fishes were starved, and weighed as above at seven day intervals, always at the same time of the day. Water temperatures were measured

Table 5.7 Organic content of tissues of eight *C. multicinctus* captured in the coral-rich habitat at Kahe Pt. Oahu, compared to tissues of eight individuals captured on the following day in the coral-poor habitat at Portlock, Oahu. Mann-Whitney U-test: * = $p < 0.05$.

			Coral-Rich Habitat		Coral-Poor Habitat	
			Organic Density %	% of Body Organic Content	Organic Density %	% of Body Organic Content
GONAD						
	Male	Mean	92.4 *	0.20	88.1	0.15
		SD	(3.1)	(0.08)	(2.8)	(0.06)
	Female	Mean	91.3 *	1.51 *	90.1	0.78
		SD	(1.7)	(0.43)	(1.2)	(0.28)
LIVER						
	Male	Mean	91.7	0.51	91.1	0.48
		SD	(1.4)	(0.17)	(1.8)	(0.21)
	Female	Mean	91.5	0.66 *	90.9	0.42
		SD	(1.4)	(0.15)	(1.5)	(0.09)
FAT						
	Male		Present		Absent	
	Female		Present		Absent	
FECUNDITY[a]						
		Mean	1020 *		60	
		Range	360 - 3150		0 - 250	

a. Fecundity of females is the number of vitellogenic oocytes present in the ovary.

sporadically during the experiment and remained at 26°±1°C. Average weight loss per day was calculated and converted to a rough estimate of metabolism rate (plus ammonia excretion) in terms of calories per day. When an individual showed the first signs of poor health, it and its pair-mate were sacrificed and examined internally for comparison to fish from Experiment #6 captured at the same time, but not starved. Ash-free dry weights and caloric contents of the gonads and ash-free dry weights of the livers were determined.

I have called the estimate of metabolism rate measured here, the resting metabolism rate (Brett and Groves 1979). This rate is probably higher than the theoretical standard metabolism rate, but lower than the metabolism rate of feeding fish (feeding metabolism rate = resting metabolism rate plus specific dynamic action, SDA), and much lower than the normal active metabolism rate of fish in the field.

Results:

Starved fish survived from 19 to 41 days (Mean = 32 days) without food. Males and females lost similar amounts of weight during the experiment: 0.439% (SD 0.074%) of wet body weight per day for males vs. 0.402% (SD 0.143%) of wet body weight for females. Since the body tissues averaged 70-75% water (see Experiment #4) and the loss was assumed to be of organic material, this was equivalent to 1.1 to 1.3 mg AFDW/g wet body wt./day for males and 1.0 to 1.2 mg AFDW/g wet body wt./day for females. The conversion to calories depends on the substrate which was metabolized, ranging from 4.8 cal/mg for protein to 9.45 cal/mg for lipid (Brett and Groves 1979). The average caloric content of body tissues ranged from 5.8 to 6.1 cal/mg AFDW (Experiment #4). Using this range, and further assuming that the decrease in weight was organic tissue metabolized for energy, then the average metabolic loss was 6.38 to 7.93 cal./g wet body wt./day for males (0.27-0.33cal/g/hr) and 5.80 to 7.32 cal/g wet body wt./day (0.24-0.31cal/g/hr) for females. These are necessarily very rough estimates, however resting metabolism rates for males and females of this species appeared similar.

Analysis of the caloric content of the tissues of these fish revealed that both males and females had no fat, and they had smaller livers and gonads relative to dry body weight than the control individuals captured at the same time (Table 5.8). The organic densities of the testes and especially of the ovaries of the starved individuals were lower than those of the controls.

Experiment #8. Induced spawning of C. multicinctus.

Methods:

Because of the difficulty of observing spawning of butterflyfishes in the field, an attempt was made to artificially induce spawning in C. multicinctus in the laboratory. Six females were injected with human chorionic gonadotropin (10 IU HCG/g body weight) in April during the week prior to the new moon. This treatment induced hydration of oocytes in three individuals. After

Table 5.8 Organic content of gonads and liver of eight *C. multicinctus* after starvation, compared to controls caught at the start of the experiment. Mann-Whitney U-test: * = $p < 0.05$.

		STARVED			CONTROL[a]	
		Organic Density %	% of Body Organic Content	Caloric Density cal/mg AFDW	Organic Density %	% of Body Organic Content
GONAD						
Male	Mean	89.1 *	0.15 *	5.11	92.4	0.20
	SD	(3.2)	(0.13)	(0.12)	(3.1)	(0.08)
Female	Mean	85.0 *	0.58 *	4.17	91.3	1.51
	SD	(2.1)	(0.39)	(0.51)	(1.7)	(0.43)
LIVER[b]						
Male	Mean	90.1	0.33 *	-	91.7	0.51
	SD	(1.7)	(0.12)	-	(1.4)	(0.17)
Female	Mean	91.0	0.36 *	-	91.5	0.66
	SD	(1.8)	(0.11)	-	(1.4)	(0.15)
FAT						
Male		Absent			Present	
Female		Absent			Present	

a. Controls are the same individuals used in Experiment #7 (Table 7).
b. Caloric density of the liver was not measured.

32hr the ovulated eggs were stripped by hand and mixed with 200ml sea water. Numbers of eggs in ten 1ml aliquots were counted and the proportion of viable eggs estimated by dividing the number of eggs which were clear and floating by the total number of eggs.

Results:

The three females which were artificially spawned had 10520 (SD 1290), 11360 (SD 1740) and 12490 (SD 1830) eggs respectively. Approximately 90% to 95% of these were viable, and when mixed with sperm, most began to undergo cleavage and development.

DISCUSSION

This study investigated several aspects of male and female energetic strategies in three species of butterflyfishes. Differences between the sexes were found in energy ingested and in the way this energy was partitioned in different seasons among reproduction, growth, and storage for future survival and reproduction. The general relationship between energy intake and partitioning can be expressed as follows:

$$E_i = E_l + E_m + E_g + E_s + E_r$$

where:

E_i = Energy intake from feeding.

E_l = Energy loss. This consists mainly of energy excreted in the feces, but also includes energy excreted by other means e.g. as ammonia at the gills and in urine, and sloughing off of mucus and other tissues.

E_m = Energy of metabolism. This includes standard metabolism, plus increases in metabolism due to activity (routine metabolism and active metabolism) and increases following feeding, known as specific dynamic action (SDA).

E_g = Energy diverted to somatic growth.

E_s = Energy stored.

E_r = Energy diverted to reproduction (i.e. gonad growth and gamete production), upon which an animal's fitness ultimately depends.

Table 5.9 Activity budgets and feeding rates of the three species of butterflyfishes. Data are summarized from (Hourigan Ch III, IV).

ACTIVITY BUDGETS[a]

	C. multicinctus		*C. quadrimaculatus*		*C. fremblii*	
	Males	Females	Males	Females	Males	Females
Fish observed	N = 30	N = 30	N = 28	N = 28	N = 12	N = 30
Hours observed	58	58	50	50	18	24
Time spent foraging	96.2% *	98.4%	92.5% *	98.1%	91.3% *	96.5%
Time spent sheltered	0.03%	0.03%	8.9%	3.8%	0.8%	0.4%
Time with mate(s)	74.0%	74.0%	50.0%	50.0%	28.4%	13.9%
Time spent posing for cleaning	1.4%	0.8%	1.4%	0.7%	0.4%	1.1%
Chases/hr. of						
Adults	2.84 *	0.66	1.89 *	0.33	1.95	4.96 *
Juveniles	2.53 *	1.79	1.26 *	0.19	0.75	0.40
Other species	1.40 *	0.00	0.36 *	0.00	0.00	0.00
Agonistic displays/hr.	1.45 *	0.71	0.99 *	0.28	0.57	0.32

FEEDING RATES in bites/hr

	Males		Females		Males	Females	Males	Females
	Shallow	Deep	Shallow	Deep	Shallow	Shallow	Shallow	Shallow
Coral	487	649	706	741	148	165	0	0
P. lobata	251	497	283	563	13	13	0	0
P. compressa	0	149	0	171	0	0	0	0
P. meandrina	235	1	416	2	134	150	0	0
other coral	1	2	7	5	1	2	0	0
Hard Substratum	171	61	129	77	154	231	495	582
Crevices	1	0	3	0	199	269	18	6
Sand	0	0	0	0	0	1	46	52
Sea urchins	0	0	0	0	0	0	8	7
Other	0	1	0	1	1	1	1	0
Total	658 *	711 *	837	819	502 *	667	568 *	647

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[a] Activity budgets are expressed in the percent of all 1 min observation intervals in which a particular behavior occurred. Observations are during all daylight hours, during which feeding occurred. Since *C. quadrimaculatus* feeds on a lunar day, the occurrence of feeding and sheltering represents only those observations when the fish were normally feeding (Hourigan 1986a). Values are means for all individuals observed. * signifies a significant difference between sexes at the 95% confidence level or higher (tests were Wilcoxon's signed-rank tests between males and females sharing a territory i.e. pair mates, or in the case of *C. fremblii*, males and their female harem mates.

The primary purpose of this study was not the construction of a complete energy budget, however the experiments do shed light on ways in which these components may differ over time, between, sexes and among species. In order to complete these comparisons, information from field observations of feeding and activity rates for these three species has been summarized in Table 5.9 (Hourigan Chapter III, IV). These observations were made in the same areas and during the same seasons as the collections reported above. Calculated energy budgets are for sexually mature, territorial adults. The behavior and growth of juveniles and sub-adults differ greatly from those of adults (Hourigan Chapter III, IV) and their energy budgets are probably also different in most respects.

Energy Intake (E_i), Energy Absorption, and Energy Loss (E_l):

Feeding was the major activity of males and females of each species in this study. Feeding observations and stomach contents indicated that females and males fed on the same prey items (Table 5.9), but females had higher feeding rates than males and thereby ingested more energy and nutrients. These observations support the prediction that females are energy maximizers with respect to males (Schoener 1969, 1971). Since absorption efficiencies and gut transit times did not differ between sexes, females must be obtaining more usable energy from their diets. In the comparisons between pair-mates, both fish shared a feeding territory, and had access to the same resources. Differences in energy intake between pair-mates must therefore be due to differences in behavior between the sexes.

The rate of energy ingestion by fishes in the field was estimated in Experiment #2. The rate of energy intake by C. multicinctus derived from laboratory feeding rates (Experiment #1), agreed generally with the rates obtained for that species in the field. The coral species with the greatest energy return per bite was Pocillopora meandrina, the species preferred by both C. multicinctus and C. quadrimaculatus both in the field and in laboratory preference tests (Hourigan Chapter II and III). This coral is also preferred by other butterflyfish species (Hourigan et al. 1987). Tricas (1986) found that P. meandrina had a higher caloric density than the two Porites spp. This coral contains high energy lipid bodies just below the oral disk which may be accessible to coral predators (Stimson, in press). Polyp retraction also appeared to be more successful in the perforate corals such as Porites spp. than in Pocillopora spp., where the polyps sit in shallow depressions. Fish were more successful at removing whole polyps from the latter species, further increasing the profitability of feeding on it. Polyp retraction, and the time necessary for polyps to come out after attack may explain why butterflyfishes in the field feed only a few bites at a time on each coral colony (Hourigan Chapter III).

The average wet weight of stomach contents of C. multicinctus and C. quadrimaculatus was two to three times the weight of material ingested during 30 min of feeding in the laboratory or in the field. Since both species fed continuously for 12 to 13 hrs per day (Hourigan

Chapter III), this indicates that they filled their stomachs 9 to 13 times per day. Harmelin-Vivien and Bouchon-Navaro (1983) examined gut contents of corallivorous butterflyfishes in French Polynesia, and suggested that individuals filled their guts approximately twice a day. They presented no supporting evidence for this assertion. They estimated that corallivores had only a minor impact on reef corals. These conclusions deserve re-analysis in light of the present findings. Cox (1983, 1986) found that feeding by the the corallivorous butterflyfish, Chaetodon unimaculatus had a significant impact on at least one coral species in Hawaii.

The energy absorbed by a fish is the energy ingested minus the unabsorbed energy remaining in the feces (Brett and Groves 1979). Since food appeared to move continuously through the gut, with no major differences in clearance rates between males and females (Experiment #3), energy absorption or assimilation efficiencies could be calculated. Among the three butterflyfish species, C. fremblii had the highest absorption efficiency (42.1%; Table 5.10a). The two corallivorous species were very inefficient in energy absorption. Mean absorption efficiencies of 22.4% for C. multicinctus and 14.5% for C. quadrimaculatus were low compared to average values from the literature of 80% to 85% absorption of energy from the diets of carnivores, and 58% to 60% absorption of the dietary energy for herbivores (Brett and Groves 1979, Pandian and Vivekanadan 1985). Most literature values were based on laboratory experiments of fishes fed artificial diets. While useful for aquaculture studies, these

Table 5.10 Summary of calculated energy intake and expenditures of the three species of butterflyfishes in this study. Unless otherwise noted, all values are in units of cal/fish/day.

5.10 a. DAILY NET ENERGY INTAKE = ENERGY INTAKE (Experiment 2) - ENERGY IN FECAL EXCRETION.

	C. multicinctus		*C. quadrimaculatus*		*C. fremblii*	
	Males	Females	Males	Females	Males	Females
Total Intake	1596	1951	4175	7590	2604	4450
Absorption efficiency	21.5%	23.3%	12.9%	16.1%	40.3%	43.8%
Net Intake	343	455	539	1222	1049	1949

Table 5.10 (cont.). Summary of calculated energy intake and expenditures of the three species of butterflyfishes in this study. Unless otherwise noted, all values are in units of cal/fish/day.

5.10 b. ESTIMATED ENERGY LOSS DUE TO AMMONIA EXCRETION.

	C. multicinctus		*C. quadrimaculatus*		*C. fremblii*	
	Males	Females	Males	Females	Males	Females
Ammonia excretion[a]	10 - 31	14 - 41	16 - 49	37 - 110	31 - 94	58 - 175
Net Energy available to fish	312 - 333	414 - 441	490 - 523	1112 - 1185	955 - 1018	1774 - 1891

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[a] Estimated as 3% to 9% of net energy intake (range given by from Brett and Groves 1979).

Table 5.10 (cont.) Summary of calculated energy intake and expenditures of the three species of butterflyfishes in this study. Unless otherwise noted, all values are in units of cal/fish/day.

5.10 c. ENERGY EXPENDED IN METABOLISM.

	C. multicinctus		*C. quadrimaculatus*		*C. fremblii*	
	Males	Females	Males	Females	Males	Females
Mean weight of fish	24g	23g	45g	44g	44g	41g
RMR[a]	153 - 190	133 - 168	287 - 357	255 - 322	281 - 349	238 - 300
Net Energy - RMR	122 - 180	246 - 308	133 - 236	790 - 930	606 - 737	1474 - 1653
SDA[b]	16 - 100	21 - 132	25 - 157	56 - 356	48 - 305	89 - 567
FMR (1)[c] =	169 - 290	154 - 300	312 - 514	311 - 678	329 - 654	327 - 867
FMR (2) =	184 - 494	160 - 437	344 - 928	306 - 837	337 - 907	286 - 867
Net Energy - FMR[d]	-182 - 164	23 - 287	-438 - 211	275 - 879	48 - 689	907 - 1605

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a. RMR = Daily Resting Metabolism Rate. Calculations assume males and females of average weight, and that metabolism rates per gram body weight are similar for all three species.

b. SDA = Specific Dynamic Action. Estimated as 5% to 30% of Net energy absorbed for metabolism of carbohydrates or proteins respectively (Jobling 1985). Actual values will lie within this range, depending on the proportion of different constituents in the diet.

c. FMR = Daily Feeding Metabolism Rate. This rate is given as a range based on two independent estimates:

1. Resting Metabolism Rate (RMR) - Specific Dynamic Action (SDA).
2. By estimating that the feeding metabolic rate is 1.2 to 2.6 times the resting metabolic rate (Brett and Groves 1979).

d. Net Energy - FMR = Estimate of daily energy available for growth, storage or reproduction.

Table 5.10 (cont.). Summary of calculated energy intake and expenditures of the three species of butterflyfishes in this study. Unless otherwise noted, all values are in units of cal/fish/day.

5.10 d. ENERGY COST OF REPRODUCTION.

	C. multicinctus		*C. quadrimaculatus*		*C. fremblii*	
	Males	Females	Males	Females	Males	Females
Ave. # eggs per spawn[a]	-	8810	-	20150	-	21640
Energy per spawn[b] (cal)	78	570[1] - 920[2]	73	1050[1] - 1630[2]	236	1190[1] - 1900[2]
Stored Energy per Spawn[c] (g lipid)	0.008	0.06 - 0.10	0.008	0.11 - 0.17	0.023	0.13 - 0.20
Days to spawn[d]	1 - ?	2 - 40	1 - ?	2 - 6	1 - 5	1 - 3
Reproductive Effort[e]		4.2% - 7.3%		2.9% - 4.8%		2.1% - 3.5%

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a. Average number of eggs per spawn estimated by assuming that 79.5% of all vitellogenic oocytes are spawned.

b. Energy per spawn (in calories):

Males: Estimated by assuming that the total contents of the testes are used in a single spawning effort.

Females: Two estimates of calories per spawn are calculated:

1. Assuming that 50% of the energetic content of the ovary is expelled in each spawn (Hunter and Leong 1981).
2. By multiplying the # of eggs spawned by the average caloric content per egg.

c. Stored energy per spawn is the grams of stored lipid reserve necessary to fuel a spawn are calculated assuming the energy physiologically available is 9.45 cal/mg lipid.

d. The days necessary to store enough energy to spawn are calculated based on the net energy available minus the resting or feeding metabolism rates calculated in Table 10c. This will be an underestimate, since the costs of active metabolism are not included.

e. Reproductive effort is calculated as a percent of net energy available (Table 10b) per year based on 2 spawnings per month during a 6 month spawning season.

values may overestimate what fishes absorb from natural diets in field situations. A large portion of the energy unutilized by corallivores may reside in the zooxanthellae, which apparently resisted digestion and were excreted in the feces. Many of these are still viable after passing through the digestive tract of a butterflyfish (Mueller-Parker 1984). Corals are low in energy content and high in water content, and the low absorption efficiencies compound these problems for corallivorous butterflyfishes. This may explain why butterflyfishes, especially the corallivores, feed continuously throughout the day (Hourigan Chapter III). The amount of time spent feeding was higher than for most other fishes for which such data have been recorded (reviewed by Nursall 1981). This may also help explain why corallivory is a relatively uncommon feeding strategy among tropical fishes.

Fishes also lose energy by the excretion of nitrogen compounds (primarily ammonia and urea), which are produced by the deamination of proteins in the diet and the metabolism of proteins for energy. Literature values for mean ammonia excretion range from 2% of total energy intake for herbivores to 7% for carnivores (Brett and Groves 1979). This ranges from 3% to 9% of the energy absorbed by these fishes after fecal energy is subtracted. Although excretion of ammonia represents an energy loss which was not measured in the present study, there was no reason to expect differences between the sexes in its excretion as a proportion of ingested energy. Net energy available to the fish is equal to the energy absorbed minus the energy lost in nitrogenous compounds. The estimated daily net energy available to males and females of the three species is calculated in Table 5.10b. These values range from 312 cal/day for male C. multicinctus to 1891 cal/day for female C. fremblii. The major differences among species are based on differences in absorption efficiencies rather than on the amount of energy ingested (Table 5.10a.).

The feeding behavior of these species was more complex than is suggested by the simple observations presented here. Food choice and feeding rates differed among habitats, as well as among different times of the day, and for C. quadrimaculatus, they also differed among different times of the lunar cycle (Hourigan 1986a, Chapter III, IV). The use of average values for feeding rates was therefore a simplification which may have introduced additional errors. Absorption efficiency values may also have been biased, since the material which was in the feces might not have had the same original composition as the food in the stomach at the time of capture. This was not a problem for the paired comparisons, since the male and female of a pair were collected at the same time, however it would bias absolute comparisons among species.

Energy Partitioning:

1. Energy of metabolism (E_m)

Females of all three species had more usable energy at their disposal than did males. This additional energy could fuel increased metabolism rates, or go into storage, growth or reproduction. The estimated resting metabolism rates of C. multicinctus were probably somewhere between the standard and routine metabolism rates (Brafield 1985) and showed no great differences between males and females. Energy budget balances for starving fish are often poor due to invalid assumptions about the energy value of the fish tissues being metabolized (Brafield 1985). Nevertheless, resources are apparently used during starvation following the same set of physiological priorities that operate during gamete formation, and may shed light on these processes (Calow 1984). The present method of estimation was crude, however, there was no a priori reason to suppose that metabolism rates should differ between the sexes. Resting metabolism rates for males and females of average weight of all three species were calculated (Table 5.10c), assuming that resting metabolism rates per gram body weight for the three species were similar to those of C. multicinctus and did not vary with the size of the specimen. This may have overestimated resting metabolism rates of the larger species, since energy requiring processes should scale in proportion to body weight to a power between 0.67 and 1.00, rather than always linearly (Winberg 1961; Jobling 1985). Calculated resting metabolism rates for these fishes ranged from 13% to 73% of net energy intake. Metabolism rates represent a large proportion of the energy budget, and errors in these determinations will greatly bias the estimated energy budgets.

Calculated values reflected resting metabolism rates of starving animals and were probably much lower than actual metabolism rates of fish in the field (Soofiani and Hawkins 1985). Butterflyfishes foraged continuously for at least 12 hours a day, continually swimming between food patches around their large territories. Records of metabolism rates of feeding fishes range from 1.2 to 2.6 times the average daily routine metabolism rate (Brett and Groves 1979). A portion of these increases is due to increased metabolism rates associated with food intake, termed specific dynamic action or SDA. This increase in metabolism rate after feeding is usually considered to be the metabolic cost of digestion, converting food resources to compounds for storage and production, and the deamination of amino acids and synthesis of nitrogenous waste products (Jobling 1985). The value of SDA for a growing fish will vary depending on the composition of the diet, ranging from 5% of the net energy absorbed in a diet of pure carbohydrates to 30% of net energy of a diet of pure protein (Jobling 1985). Two estimates for feeding metabolism rates of the butterflyfishes are calculated in Table 5.10c, using the extreme ranges of the estimates of Jobling 1985) and Brett and Groves (1979).

In addition to routine feeding costs, territorial defense probably constituted a significant energetic cost. Brett and Sutherland (1965) found that metabolism rates in the pumpkinseed sunfish, Lepomis gibbosus rose by about 50% during peaks of attack and defense. Similar metabolism rate increases were found during aggressive encounters among young sockeye salmon (Brett 1973). This does not include energy released during maximum bursts, which is almost entirely anaerobic but creates an oxygen debt which must be repaid. Brett and Groves (1979) have suggested that just a few bursts of attack or escape each day would be equivalent to doubling the standard metabolism rate. Since the males of both paired species were involved in more chases and chases of longer duration than females (Table 5.9 and Hourigan, Chapter III), it seems reasonable that they would have higher active metabolism rates. This would further increase the difference in net energy available to males and females of the same species.

It is clear from this analysis that daily energy intake for C. multicinctus and C. quadrimaculatus was not far above the daily energy needs of the active fish (Net energy - Feeding Metabolism Rate, Table 5.10c). This was especially true for males, which fed less than females, but were involved in more chases (Table 5.9). Males appeared to follow a strategy of energy maintenance (Ebersole 1980) or feeding time minimization (Schoener 1983) in comparison to their mates. The increased efficiency of energy absorption by C. fremblii provided more usable energy for individuals of that species and may have made possible the defense of larger territories by males as well as the large number of chases engaged in by females of that species. Larger male territories contained more than one female, providing the basis for the haremic social structure exhibited by this species.

2. Energy devoted to somatic growth (E_g)

Energy which is not required by metabolism may be further partitioned between growth, storage and reproduction. Growth rates during the first two years of life are known for two butterflyfishes, *Chaetodon miliaris* (Ralston 1976) and *C. multicinctus* (Tricas 1986). During the first year, *C. multicinctus* grow quickly, and fish attain 76% of their average maximum adult length. Sexual maturity occurs after the first year, and thereafter growth is very slow, suggesting that energy is shunted to other processes, perhaps to reproduction. By the end of the second year, fish had reached 94% of average maximum length (Tricas 1986). Although fish live longer than four years, aging by otolith microincrements was difficult after two years. Growth rates for *C. miliaris* were similar (Ralston 1976).

Length-weight relationships in the present study suggested that males and females grew and gained weight in a similar fashion. Tricas (1986) measured a larger sample of *C. multicinctus* and found that females were slightly heavier for a given length. *Chaetodon fremblii* exhibited the greatest differences in size between the sexes, with males reaching a larger size than females.

The organic and caloric content of muscle tissue did not vary between sexes or among seasons. In the paired species, males devoted more of their total organic material to somatic tissues. This was consistent with lower investment in storage and reproduction, and did not indicate a pattern of more rapid somatic growth. Among paired butterflyfishes, pair-mates are often closely matched in size (Reese 1981; Tricas 1986; Hourigan et al. 1987), and both may benefit from large size (Reese 1981). Large size may be most important for male *C. fremblii*. If larger males can defend larger areas, they may be able to include more females in their harems. This may help explain the more pronounced size difference between males and their harem mates in this species compared to the species which form pairs. Such size differences are common among animals with haremic social systems (Wilson 1975).

3. Stored energy (E_s)

In all three species there were pronounced differences between the sexes in energy partitioned into storage tissues. A primary storage area was fat tissues in the gut mesenteries. Both sexes of the paired species accumulated fat reserves during the non-breeding season. Females at this time had greater fat reserves than males, probably related to higher female feeding rates and lower chase rates. During the spring, fat reserves were at a minimum in both sexes. This suggested that fat reserves accumulated during the non-breeding season were mobilized for reproduction. In the case of females this was probably related to the production of eggs. Alternately, lipids may have been used in metabolism during the reproductive season, with current food intake and protein reserves used for egg production (Cowey and Sargent 1979).

Males evidently also mobilized fat reserves to meet increased energy requirements during the spawning season. The production of sperm is probably not as costly as the production of eggs (but see Ursin 1979; Baylis 1981), however male activity levels were probably higher during the reproductive season. Observations of spawning in _C. multicinctus_ showed that neighboring males were attracted to females with hydrated eggs which were ready to spawn. The female's pair-mate made repeated, and apparently successful efforts to chase away two to six such invading males before spawning with its mate (Hourigan Chapter VII). Following the breeding season, males appeared to build back their fat reserves more quickly than females. The presence of fat reserves in males showed that at least during the non-breeding season, they did not follow a strict energy maintenance or feeding time minimization strategy. Comparable samples were not available from different seasons for *C. fremblii*. However, as in the other two species, females had no fat reserves in spring. Two males, however, did have significant fat reserves. The latter occurrence may be another result of the greater net energy available to individuals of this species.

The seasonal trends in visceral fat are consistent with the pattern found by Tricas (1986) in lipid content of the viscera of 630 *C. multicinctus* collected weekly or biweekly over 18 months. As in the present study, lipid content of both males and females was inversely correlated with gonad development. MacDonald (1981) found similar trends in qualitative estimates of the fat content of a coral feeding pomacentrid, *Plectroglyphidodon johnstonianus*. Visceral fat was deposited during the non-spawning season, and mobilized during gonad development. Similar alternating cycles of fat deposition and reproduction have been observed in other fishes (Shul'man 1974; Wootton and Evans 1976; Diana and MacKay 1979, Delhunty and deVlaming 1980; Hunter and Leong 1981).

The liver is also a major energy storage area for most fishes. In females of all three species the liver composed a greater percentage of the body's energy content than it did in males. Energy storage in the livers of female *C. quadrimaculatus* showed seasonal trends, with most energy devoted to the liver during the spring. This may result from the liver's function in the production and storage of vitellogenin which is later transported to the gonad and incorporated into oocytes as yolk. Rates of protein synthesis of isolated liver cells of female *Trematomus hansoni* during the reproductive season are 50% higher than rates of cells from males or non-reproductive females (Haschmeyer and Mathews 1983).

5. Energy of reproduction (E_r)

The energy investment by females in the ovaries was highest during the spring. This period corresponds to the breeding season of *C. multicinctus* as well as other butterflyfishes (Lobel 1978; Ralston 1981; Tricas 1986; Walsh 1987). Egg production, median size of vitellogenic oocytes, and the proportion of vitellogenic oocytes were highest during this season. Growth of the ovaries apparently occurred at the expense of energy stored as fat. Similar trends have been found in other fishes, including the perch (Craig 1977), stickleback (Wootton 1985) and largemouth bass (Adams et al. 1982).

Reproductive effort by females, defined as the percent of energy intake devoted to reproduction (Williams 1966; Wootton 1985), depends on the number of eggs per spawn (batch fecundity) and the frequency of spawning. The number of eggs released when spawning was artificially induced (Experiment #7) corresponded to most of the vitellogenic eggs present in the ovary of C. multicinctus of that size. This indicated that most vitellogenic oocytes matured synchronously and were spawned at the same time, a conclusion consistent with the observation that for all three species, most vitellogenic eggs were of a similar size and stage of development. In the two gonads of C. multicinctus which contained hydrated oocytes, 79.5% of all vitellogenic oocytes had undergone hydration. Tricas (1986) estimated that 76% of all vitellogenic oocytes of C. multicinctus, undergo hydration synchronously, and sequential clutches are spawned at least two days apart. This allowed the estimation of the number of eggs per spawn (Table 5.10d). Spawning frequency for butterflyfishes is problematic, since few observations have been made (Thresher 1984). Spawning or the presence hydrated eggs in C. multicinctus was observed on the week prior to the new moon (Lobel 1978; Tricas 1986; Hourigan Chapter VII) and on the week prior to the full moon (Tricas 1986). This suggests that spawning may occur once every two weeks or once a month. Ralston (1981) also suggested synchronous spawning for the Hawaiian butterflyfish C. miliaris, although he was unable to determine any lunar periodicity.

The energy investment by females in spawning is probably large. Hunter and Leong (1981) estimated that 50% of the energy of the ovary was expelled in each spawn of the northern anchovy, Engraulis mordax. A second estimate of the energetic cost of spawning was calculated based on an individual's average energy investment in vitellogenic oocytes and the batch fecundity, i.e. the number of eggs spawned (Table 5.10d). Using these two estimates the average cost per spawn ranged from 570 cal for *C. multicinctus* to 1900 cal for *C. fremblii* (Table 5.10d). These ranges represent a reproductive effort per spawn of 2 to 40 times the daily net energy available to *C. multicinctus*, and 2 to 6 times the daily net energy available to *C. quadrimaculatus* females after feeding metabolism rates have been subtracted. These estimates indicate the minimum number of days between spawning events if the fishes were not otherwise active, did not use energy for somatic maintenance or growth, and did not use stored energy reserves. Similar calculations for *C. fremblii* indicate a much shorter interval of one to two days needed between spawnings. If spawning occurred every two weeks over a six month breeding season, the annual reproductive effort of a female would range from 2.1% of net energy available to *C. fremblii* to 7.3% of net energy available to *C. multicinctus*. These values are useful only for making comparisons of the relative reproductive effort of the different species. They are underestimates, since they do not incorporate active metabolism rates. Female *C. fremblii* invested more energy in eggs and spawned more eggs than did female *C. quadrimaculatus*, although the mean size of *C. fremblii* females was smaller. This indicates that the batch fecundity of female *C. quadrimaculatus* was limited, not by the size of the body cavity, but perhaps by energy available.

Males invested less energy in gametes than did females. Testicular tissue represented only 0.12% to 0.24% of the total organic content in the body compared to 1.43% to 4.07% for ovaries. The actual energy investment will depend on how frequently spawning occurs. It is probable that in the paired species, on average, males spawn the same number of times as their mates, or slightly more if occasional attempts are made to sneak spawnings with neighboring females. In the haremic species males should spawn at least one to four times as often as females, depending on the size of the harems. This may explain why the testes of C. fremblii were larger than the testes of the paired species. Even if the total contents of the gonads were expelled with each spawn, the investment by males in gametes would be extremely small compared to the investment of females (Table 5.10d). It appears that the principle of anisogamy applies to these species.

Few studies have compared the reproductive effort of males and females. Northern pike, Esox lucius show similar patterns of somatic growth for both sexes, but females ingest more energy, and have higher estimated reproductive efforts (14% to 16%) than males (7% to 10%) (Diana 1983). The energy requirements for ovarian growth are also higher than those for testicular growth in the stickleback (Wootton 1985) and the largemouth bass (Adams et al. 1982).

The present study suggests that differences in male and female energy intake and partitioning were related to the differences in investment in reproduction. Observations of female C. multicinctus from coral-rich and coral-poor habitats (Experiment #7) supported the conclusion that additional energy from food was channeled into female reproduction. Although observations were made during the non-breeding season, the females in the food-poor area fed less and had significantly smaller gonads, fewer vitellogenic oocytes and less stored fat. The largest decrease in energy content in the starved fish (Experiment #8) occurred in the reproductive tissues, indicating that when energy budgets are negative, energy is channeled from the gonads to maintenance. Together, these factors indicated that reproduction of female C. multicinctus and C. quadrimaculatus is likely food limited. Females of several other species of reef fishes also feed more than males (Robertson et al. 1979; Ebersole 1980; Ross 1983; Hoffman 1982; Green et al 1984). Energy maximization by females compared to males, with this excess energy channeled into increased reproduction, may be a general trend among fishes, as has previously been suggested for birds (Schoener 1971).

CONCLUSIONS

This study compared the bioenergetics of males and females of three species of butterflyfishes. In all three species, females differed from males both in their energy intake, and in how that energy was partitioned among activity, storage and reproduction. Females fed more than males, gaining additional energy which was apparently channeled into reproduction or into storage for future reproductive effort, depending on the season of the year. Females appeared to maximize their energy intake, while males spent less time foraging. The two paired, corallivorous species, C. multicinctus and C. quadrimaculatus had relatively low absorption efficiencies and hence low net available energy compared to their energy needs. Reproduction in females of these two species was probably food limited. The haremic species, C. fremblii showed a greater efficiency of absorption of food eaten than the other two species. This provided it with more available energy, perhaps contributing to the observed higher activity rates, female fecundity and haremic social system.

CHAPTER VI

PAIR-BOND FORMATION AND RECRUITMENT TO THE BREEDING POPULATION IN TWO SPECIES OF BUTTERFLYFISHES

INTRODUCTION

Heterosexual pair-bonds have been documented in many species of butterflyfishes, Family Chaetodontidae (Reese 1973, 1975, 1981; Burgess 1978; Allen 1979; Barlow 1984; Fricke 1986; Hourigan 1986a; Hourigan et al. 1987). Such bonds may persist for seven years or more, with members of a pair remaining together throughout the year (Reese 1981; Fricke 1986). In most cases both members of the pair share in the defense of a permanent feeding territory on a coral reef (Sutton 1985; Tricas 1985, 1986; Fricke 1986; Hourigan Chapter II, III). Spawning occurs between pair-mates in a territory (Neudecker and Lobel 1982; Thresher 1984; Fricke 1986; Hourigan Chapter V), indicating that these pair-bonded fishes are monogamous in having essentially exclusive social associations and mating relationships (Wittenberger and Tilson 1980; Wickler and Seibt 1983).

The formation of stable pair-bonds and the establishment of a feeding territory may be prerequisites for breeding, or may allow fish to breed more successfully. Permanent residency, territorial defense, and high adult survival may restrict the opportunity of new individuals to enter the breeding population. Recruitment or entrance into the breeding population could occur in several ways. Fish may be able to secure small areas on the reef when young, hold on to these areas until they grow to maturity, and then mate with a neighbor, as has been observed in pomacentrids (Sale et al. 1980; Doherty 1982, 1983) and blennies (Nursall 1977). Alternatively, juveniles may be excluded from adult areas, and have to compete for territories or mates as adults. The latter appears to be the case for butterflyfishes (Hourigan Chapter II). The alternatives for these fish are: 1) To forcibly supplant a territory holder and subsequently pair with its mate (as occurs in tropical house wrens - Freed 1986). 2) To form a pair-bond first with a member of the opposite sex, and then take over a territory or begin to defend a new area (Freed 1987). 3) Wait until an individual of the same sex dies and then mate with the remaining fish. Subsequent to pairing, already mated individuals may improve their reproductive success by switching mates and moving to a more favorable territory. Many studies of the ecology of reef fishes have concentrated on the initial recruitment of juveniles to the reef (reviewed by Sale 1980; also: Doherty 1983; Shulman et al. 1983; Sale and Douglas 1984; Shulman 1985a; Victor 1986). The factors controlling recruitment into the breeding population of fishes which form pair-bonds are likely to differ from conditions affecting initial larval recruitment. Both sets of factors are important, since both recruitment steps are essential to the fitness of the individual.

This paper presents the results of field experiments designed to investigate how new pair-bonds are formed, and how different population structures of two species of butterflyfishes affect the entrance of new fish into the breeding population. Chaetodon multicinctus, the banded butterflyfish, and Chaetodon quadrimaculatus, the fourspot butterflyfish, each form long-term heterosexual (i.e. male-female) pair-bonds (Hourigan et al. 1987, Hourigan Chapter III). Both species feed on live coral polyps, and are among the most abundant Hawaiian chaetodontids (Hobson 1974; Hourigan Chapter II). Adult pair-mates share a feeding territory which they defend against conspecifics (Tricas 1985, 1986; Hourigan 1986a, Chapter III). Pair-mates remain together throughout the year, and pairs have been observed in the same territories for four years. Spawnings are with pair-mates within the pair's territory. Non-reproductive juveniles and sub-adults are non-territorial, feed less than adults, and are excluded from territories by chases from mature pairs (Hourigan Chapter III).

The two butterflyfish species differ in their distribution among different habitats in the coral reef environment in Hawaii (Hourigan et al. 1987; Hourigan Chapter II). Chaetodon multicinctus pairs hold contiguous territories over most areas of the reef, and the sub-adults occur as single individuals, temporary pairs, or threesomes, sheltered in the "no-man's land" corners where territories meet, or occasionally skirting the boundaries of adult territories. In contrast, adult C. quadrimaculatus territories are restricted to the shallows where their preferred food-coral, Pocillopora meandrina is concentrated (Hourigan 1986a). Sub-adult C. quadrimaculatus form groups of up to 20 individuals which swim over large distances along the boundaries of the adult territories.

Field experiments were performed to promote the formation of new pair-bonds by the removal of one or more residents, and to test the effect of food abundance on pair-mate choice. Most of these experiments were specifically designed to test predictions of an hypothesis concerning feeding advantages accrued by females which form permanent pair-bonds, and these results are reported elsewhere (Hourigan 1985, Chapter VII).

METHODS AND RESULTS

Study site and baseline observations:

Methods:

All observations and experiments were conducted during the summers of 1980 through 1983, on the coral reefs of Puako along the leeward coast of the island of Hawaii, lat. 19°58'N, lon. 155°51'W. Observations were conducted in shallow areas (< 5m depth) of low coral cover, as well as deeper areas (8m to 20m depth) where live coral cover reached nearly 100%. Three species of corals, *Porites lobata*, *Porites compressa* and *Pocillopora meandrina* dominated the substratum. All observations were conducted by divers using scuba.

Individual butterflyfish of each species were identified using natural markings (Reese 1973). After allowing fish ten minutes to habituate to the diver, individual members of a pair were followed, and colored markers were dropped along the perimeter of the foraging area for home range determination. On subsequent dives this procedure was repeated, and the number of feeding bites per 5 min on different corals and on other prey items was recorded. Feeding observations of each member of a pair were alternated, for a total of four or five feeding observations on each member of a pair per dive. All agonistic interactions were recorded, as well as the time which the pair-mates spent together (within 2m of each other). Feeding ranges were mapped by measuring the distance of each perimeter marker from a central line bisecting the home range.

Sexes of pair-mates were determined behaviorally (Hourigan Chapter III) and verified by collecting both members of 20 pairs of C. multicinctus and 15 pairs of C. quadrimaculatus, after a minimum of twenty 5 min observations on each member of the pair. In all cases pairs were heterosexual and predictions of the sex of each fish based on behavioral criteria were confirmed. In another ten cases, only one individual was removed, and the pair-mate was assumed to be of the opposite sex.

Results:

Chaetodon multicinctus:

Feeding observations were conducted on 30 pairs of Chaetodon multicinctus. In 27 out of 30 cases, females fed significantly more than their male pair-mates (Table 6.1). Males were involved in more territorial chases directed toward neighboring conspecifics than were females, and also exhibited more territorial displays than females (Table 6.1). Intraspecific territorial displays consisted of quick rushes in the direction of an intruder, and head down displays, facing the opponent with soft dorsal and anal fins fully extended. When neighboring individuals intruded into a territory, or when two pairs came together at a boundary, there was significant agreement between the sex of the intruder and the defender, showing that males primarily chased males, and females primarily chased females (Table 6.2; Agreement: K = 0.66, 95% confidence interval (C.I.) = 0.46 0.87;

Table 6.1. Activity budgets of male and female *C. multicinctus* (N = 30 pairs) and *C. quadrimaculatus* (N = 25 pairs).

			C. multicinctus		
	MEAN (SD)		WITHIN-PAIR[a] COMPARISONS		ALL PAIRS[b] COMBINED
	Male	Female	Male > Female	Female > Male	
FEEDING RATE (Bites/hr.)	685 (230)	835 (255)	0/30	27/30	Female > Male ***
CONSPECIFICS:					
Chases/hr	2.84 (8.26)	0.66 (2.62)	12/30	0/30	Male > Female **
Displays/hr	1.45 (4.59)	0.71 (3.59)	9/30	0/30	Male > Female *
HETEROSPECIFICS:					
Chases/hr	1.40 (4.59)	0.00 (0.00)	14/30	0/30	Male > Female ***
			C. quadrimaculatus[c]		
	MEAN (SD)		WITHIN-PAIR COMPARISONS		ALL PAIRS COMBINED
	Male	Female	Male > Female	Female > Male	
FEEDING RATE (Bites/hr.)	502 (207)	667 (249)	0/25	25/25	Female > Male ***
CONSPECIFICS:					
Chases/hr	1.89 (4.63)	0.33 (1.55)	11/25	0/25	Male > Female **
Displays/hr	0.99 (3.32)	0.28 (1.47)	8/25	0/25	Male > Female **

a. Within pair comparisons: Individual Wilcoxon's signed-ranks tests for each pair, $p < 0.05$.

b. All pairs combined: Combined Wilcoxon's signed-ranks test for means from all pairs.

c. No chases by *C. quadrimaculatus* of heterospecifics were observed.

Table 6.2. Intraspecific chases by male and female butterflyfishes in intact pairs during agonistic encounters with neighboring pairs. Data are included for all cases where the sexual identity of both the intruder and the defender were known.

		C. multicinctus				*C. quadrimaculatus*			
		INTRUDER				INTRUDER			
		Male Alone	Female Alone	Pair		Male Alone	Female Alone	Pair	
DEFENDER				Male	Female			Male	Female
Male Alone		4	3	8	1	9	7	4	0
Female Alone		0	0	0	1	0	1	0	0
Pair	Male	14	2	26	0	5	2	5	0
	Female	2	1	0	9	1	1	0	4

Bishop et al. 1975). Chases by males were longer in duration (mean duration: 12.7 sec for females, 26.2 sec for males; Combined Wilcoxon's signed-ranks test for 8 pairs, $p<0.05$), and appeared to cover greater distances and to be more vigorous than female chases. Males also appeared to spend more time hovering above the bottom than females. Interspecific chases were uncommon, and were nearly always initiated by the male pair mate (Table 6.1). These chases were always directed toward other coral-feeding fishes, especially *Chaetodon ornatissimus* and *Chaetodon trifasciatus*.

In observations of more than 30 pairs during the four summers (1980 to 1983), only one natural disappearance of an individual - a female - occurred. The male which remained, formed a pair-bond with a new female within three days. Although the complete sequence of pair formation was not observed, the behavior of the male appeared similar to that of a male when its female pair-mate was removed experimentally (see below). Two pairs disappeared during the periods between the summers, and their areas were taken over by neighboring pairs which expanded their territories (see Hourigan Chapter III).

Chaetodon quadrimaculatus

Feeding observations were conducted on 25 pairs of *Chaetodon quadrimaculatus*. The behavior of males and females was similar to the behavior of each sex of *C. multicinctus*. Females fed significantly more than their male pair-mates in all cases (Table 6.1). Males were involved in more territorial chases and territorial displays directed toward neighboring pairs than were females (Table 6.1). As was the case for C. multicinctus, males primarily chased males and females chased females (Table 6.2; Agreement: K = 0.28, 95% C.I. = 0.17 to 0.39). Chases by males were not timed, but they were clearly longer in duration, more vigorous, and covered greater distances than female chases. Chases of other species of fishes by C. quadrimaculatus were not observed.

There were no observations of natural disappearances or territory takeovers by C. quadrimaculatus. Two pairs disappeared during the periods between the summers, and their areas were taken over by neighboring pairs which expanded their territories (see Hourigan Chapter III).

Experiment 1. Removal of single individuals.

Methods:

Since the natural disappearance of territorial individuals was rare, single individuals were experimentally removed to observe the process of mate replacement. Two non-adjacent pairs in similar habitats were observed as described above for at least four consecutive days. Observations on the two pairs were conducted concurrently by two divers, or less often, sequentially on the same dive by one diver. After these initial observations, the male or female of one pair (the experimental pair) was removed, while the second pair (the control pair) was was left intact. Observations were then repeated, and territory sizes re-mapped for a minimum of six subsequent days. A total of twelve male C. multicinctus and six male C. quadrimaculatus, and six female C. multicinctus and five female C. quadrimaculatus were removed from their respective mates. Six of the experimental pairs of C. multicinctus (four male removals and two female removals) were located in the low population density areas of the shallow coral-poor habitat, with the remaining pairs located in the deeper, coral-rich habitat which had a higher density of C. multicinctus. All experiments on C. quadrimaculatus pairs were conducted in the shallow coral-poor habitat where this species was most abundant.

Results:

Chaetodon multicinctus:

Male Removal:

Following the removal of males from their territories, single females showed significant reductions in territory size and feeding rate. Within hours after male removal, neighboring conspecific pairs began to intrude successfully upon the area previously occupied by the pair. Chases of neighbors by experimental females increased from a mean of 0.7 (SD=0.72) chases per hour before removal, to 26.4 (SD=31.2) chases per hour by the second day after removal - more than a 37 fold increase (Combined Wilcoxon's signed-ranks test of mean chase rates for all 12 females, $p<0.001$). In all cases, females whose males were removed had higher chase rates than the concurrently monitored controls (Independent Wilcoxon's signed-ranks tests for each female, $p<0.01$ to 0.001). Attacks were also more violent than in normal territorial encounters. In two cases, the female defender rammed an intruder in the side with extended dorsal spines, dislodging scales from the intruder. Females chased both male and female neighbors when they intruded as a pair.

Lone females appeared to be unable to exclude the neighbor pairs without male assistance, and their feeding ranges decreased by an average of 65% (Fig. 6.1 and 6.2a). In three cases, females were unable to defend an exclusive area at all. In only one of these three cases did the female regain her territory, and in that case, only several days after forming a new pair-bond.

Concomitant with the increased chase rates, all solitary females fed significantly less after male removal than before (Mean reduction 30%, Mann-Whitney U-Test, $p<0.05$; Fig. 6.3). After mate removal, experimental females fed significantly less than the concurrent control females in intact pairs (Independent Wilcoxon's signed-ranks test for each female, $p < 0.05$ to 0.005), although there was no significant difference before male removal ($p>0.05$; Fig. 6.3). There was an inverse relationship between chase rates and feeding rates for females during a given 1hr observation period (Pearson coefficient $r = -0.47$ $N=50$; Fig. 6.4). Responses of females were similar in both the shallow coral-poor territories and the deeper coral-rich territories. There were no significant changes in territory sizes, chase rates or feeding rates for the females in the concurrent control pairs.

Figure 6.1. Territory size of a female C. multicinctus before and after (shaded area) removal of her pair-mate. Dotted lines show the areas where neighboring conspecific pairs encroached upon her territory following male removal.

Male Removal

C. multicinctus

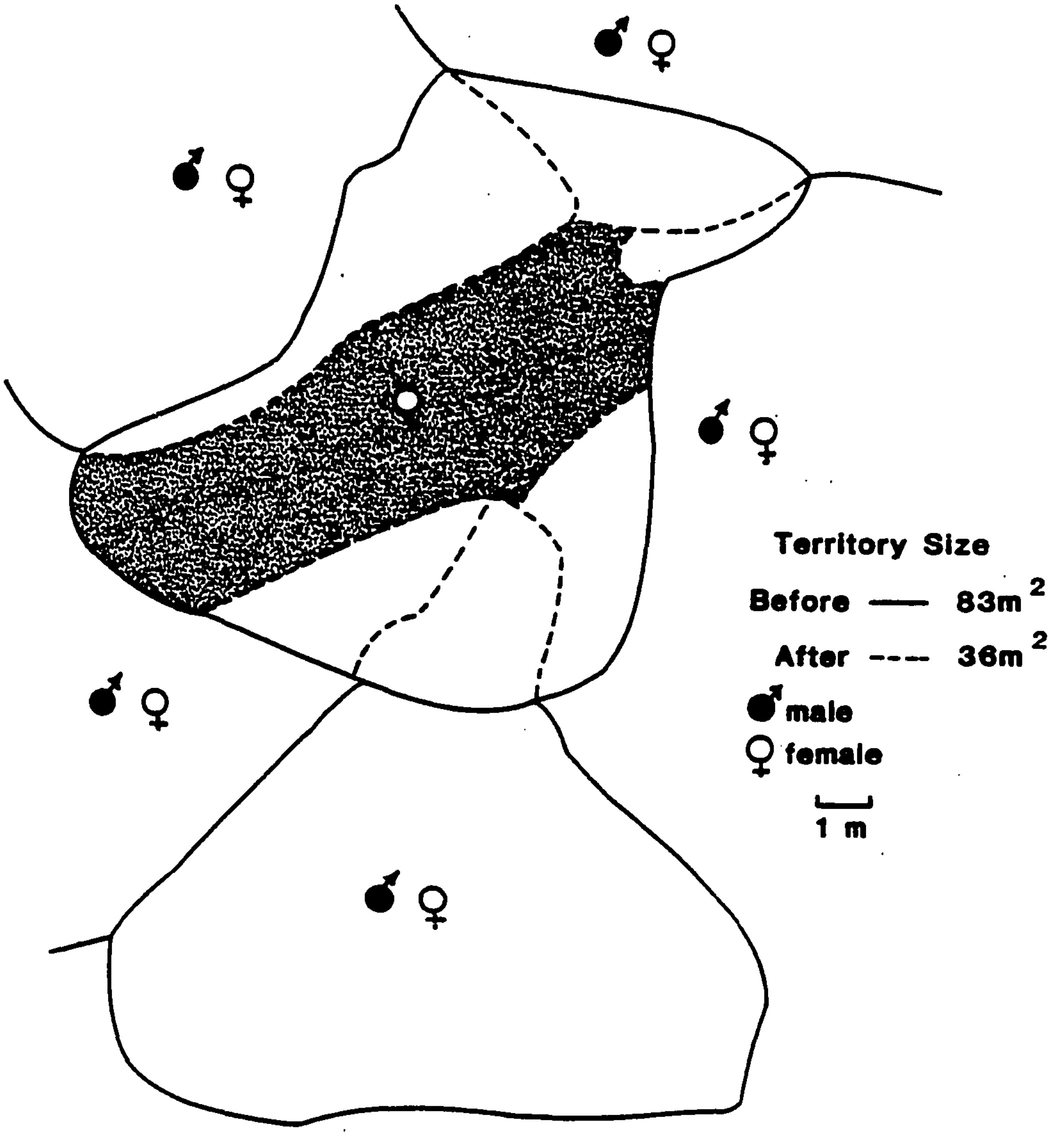


Figure 6.2. Changes in territory size following pair-mate removal for male and female butterflyfishes, and for control pairs in which no fish were removed. Points falling below the 45° line signify territories which decreased in size.

a. C. multicinctus: Combined Wilcoxon's signed-ranks test, females ($N=12$): $p<0.005$; males ($N=6$): NS.

b. C. quadrimaculatus: Combined Wilcoxon's signed-ranks test, females ($N=6$): $p<0.05$; males ($N=5$): NS.

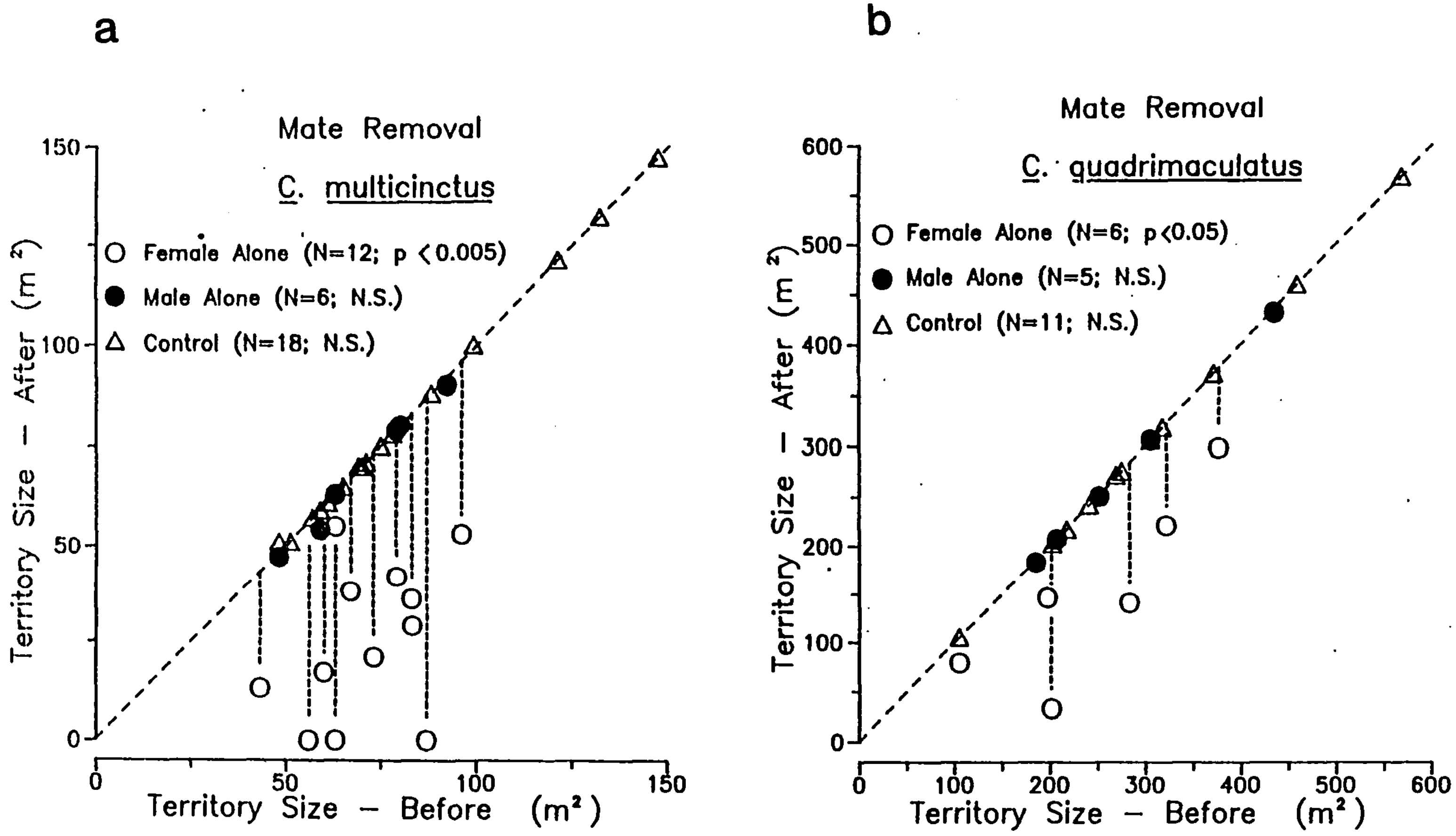

a
Mate Removal
C. multicinctus
○ Female Alone (N=12; p < 0.005)
● Male Alone (N=6; N.S.)
△ Control (N=18; N.S.)
Territory Size – After (m²)
Territory Size – Before (m²)
0
50
100
150
b
Mate Removal
C. quadrimaculatus
○ Female Alone (N=6; p<0.05)
● Male Alone (N=5; N.S.)
△ Control (N=11; N.S.)
Territory Size – After (m²)
Territory Size – Before (m²)
0
100
200
300
400
500
600

Figure 6.3. Mean feeding rates (± 95% confidence limits) of female (12 experimental and 12 control) and male C. multicinctus (6 experimental and 6 control) before (B) and after (A) removal of the pair-mate. Shaded bars show feeding rates of each experimental individual whose mate was removed, while the unshaded bars show concurrent feeding rates of the individual of the same sex in the unmanipulated control pair. (Mann-Whitney U- test: * = $p < 0.05$; ** = $p < 0.01$; *** $p < 0.001$; N.S. = not significant, i.e. $p > 0.05$).

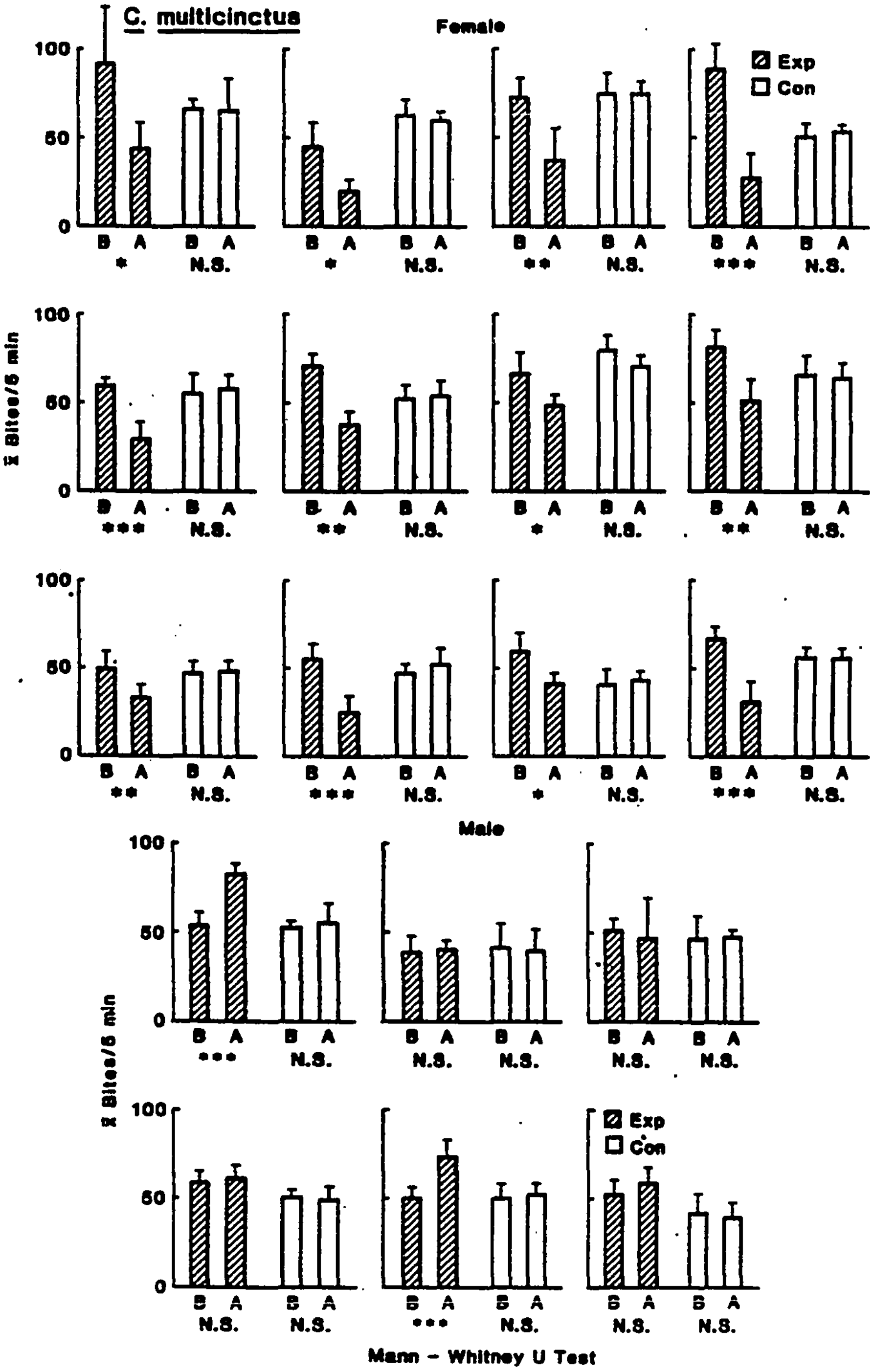
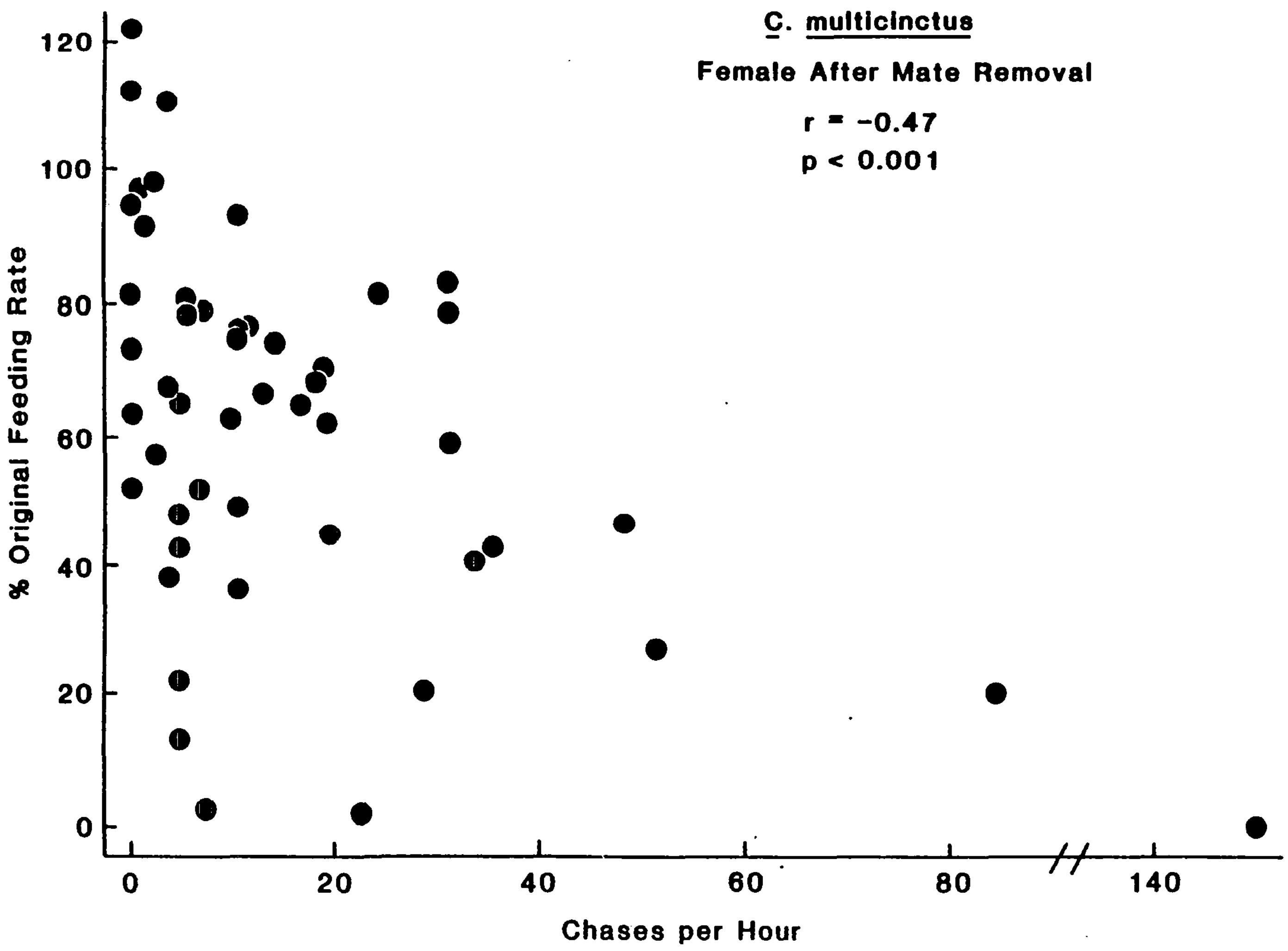

C. multicinctus
Female
▨ Exp
☐ Con
100
50
0
x̄ Bites/5 min
B A B A
* N.S.
* N.S.
** N.S.
*** N.S.
*** N.S.
** N.S.
* N.S.
** N.S.
** N.S.
*** N.S.
* N.S.
*** N.S.
Male
*** N.S.
N.S. N.S.
N.S. N.S.
N.S. N.S.
*** N.S.
N.S. N.S.
Mann - Whitney U Test

Figure 6.4. Correlation of feeding rates and chase rates of 12 female *C. multicinctus* during each 1 hr observation interval after male removal. Feeding rates are expressed as a percentage of the initial feeding rate to compensate for differences in absolute feeding rates among different females.


C. multicinctus
Female After Mate Removal
r = −0.47
p < 0.001
% Original Feeding Rate
120
100
80
60
40
20
0
0
20
40
60
80
140
Chases per Hour

Female Removal:

Agonistic encounters with neighbors also increased for males after their female pair-mate was removed (increase from 2.2 SD=2.4 chases per hour, to 19.2 SD=13.6 chases per hour; Combined Wilcoxon's signed-ranks test of mean chase rates for all males, $p<0.01$). These males without mates had higher chase rates than the concurrently monitored controls (Independent Wilcoxon's signed-ranks tests for each male, $p < 0.05$ to 0.001). Most chases were of neighboring males. Unlike females, solitary males were able to exclude these intruders unassisted. In all six cases, territories shrank less than 3% (Fig. 6.2a). In no case did feeding rates decrease, and for two of the six males, feeding rates increased significantly after the female was removed (Fig. 6.3). There were no changes in feeding or chase rates for the males of the concurrent control pairs.

Mate Replacement:

Mate replacement occurred quickly. Both males and females engaged in a behavior associated almost exclusively with pair-bond formation. The resident fish would approach within two to four body lengths of an individual of the opposite sex, then turn and rapidly swim away, usually toward the center of the territory. If the new individual did not follow, this behavior or "leading display" was repeated. This display was performed almost exclusively by the resident whose mate had been removed (Table 6.3). Pair-bonding was defined as having occurred, when an individual of the opposite sex spent more than 75% of its time within the resident's territory, and

Table 6.3. Summary of the results of the single fish removal experiments for *C. multicinctus* and *C. quadrimaculatus*.

	Source[a] of new mate	Mean number of suitors	Mean days to reform pair	Visible injuries		Change in territory size	Loss of territory	Leading display[b] Mean frequency per 5 min	
				Male	Female	%		Male	Female
C. multicinctus									
Male Removed (N = 12)[c]	A=3 O=2 ?=5	1.8 (SD=0.6)	2.05 (SD=1.26)	1	1	-46.1 (SD=17.4)	3 1 regained	0.06 (SD=0.08)	3.50 (SD=1.66)
Female Removed (N = 6)	A=4 O=0 ?=2	1.2 (SD=0.4)	3.83 (SD=2.87)	1	0	-1.0 (SD=1.7)	0	5.01 (SD=2.17)	0.04 (SD=0.07)
C. quadrimaculatus									
Male Removed (N = 6)	A=1 O=1 ?=4	2.3 (SD=1.0)	1.71 (SD=1.10)	2	0	-35.5 (SD=24.0)	0	0.04 (SD=0.06)	1.52 (SD=1.96)
Female Removed (N = 5)	A=1 O=1 ?=3	1.0 (SD=0)	1.00 (SD=0.00)	2	0	0 (SD=0)	1	0.26 (SD=0.11)	0.0 (SD=0)

---

a. Source of new mate: A = Adjacent Neighbor leaves its territory and switches to the single fish's area; O = Other neighbor (i.e. from a known but non-adjacent pair), leaves its territory and switches to the single fish's area; ?= source of new pair-mate unknown, not a nearby neighbor.

b. Leading displays performed by the remaining experimental individual or its new mate.

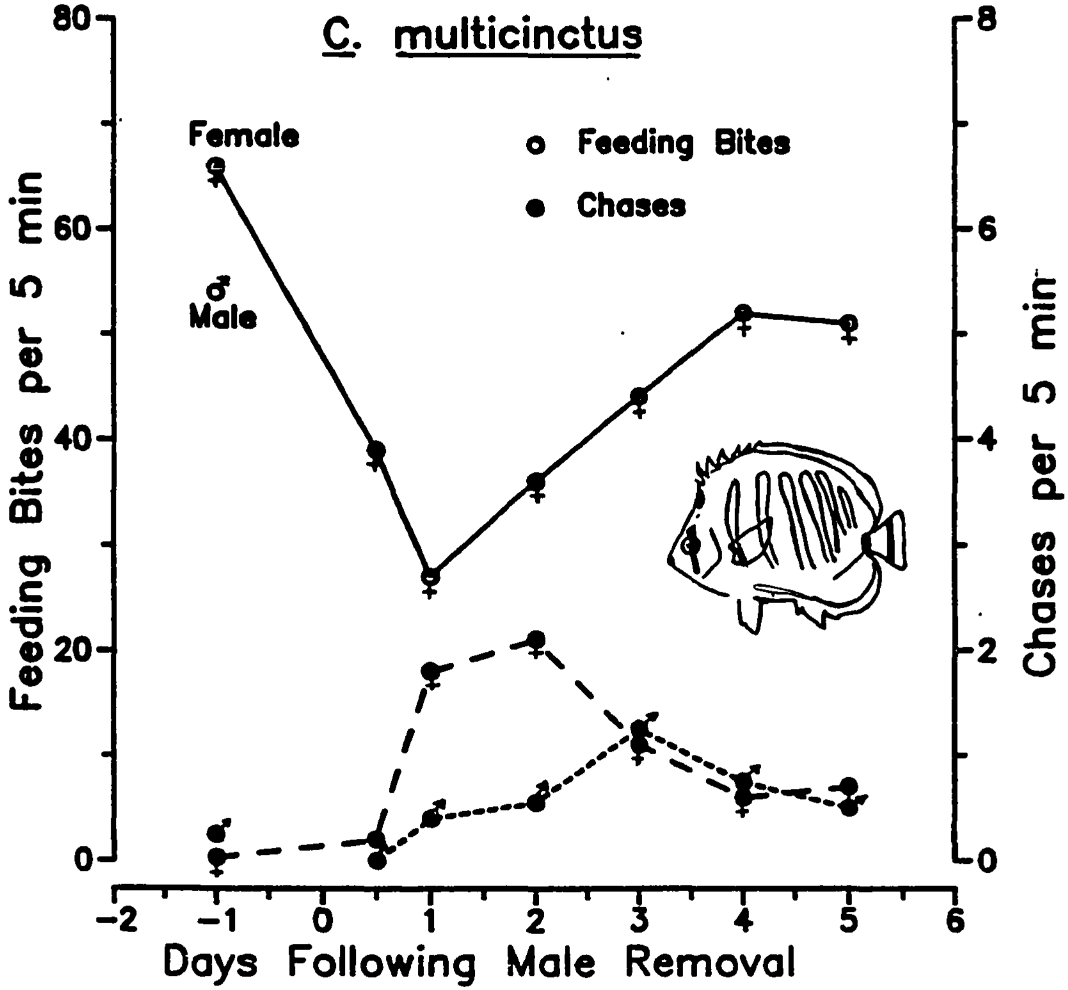
c. Two females did not regain their territories.

responded to the "leading display" by following. Mean time for pair-bond formation was 2 days after mate removal for females and 4 days for males (Table 6.3).

After pairing was complete, new males gradually assumed more of the defense activities. At this time, the female's chase rate decreased and her feeding rate increased (Fig. 6.5). Leading displays by the original territory holder were still observed after two months, though at a much reduced frequency and intensity. In 8 of 12 male removals, territories returned to their original size by two to three weeks after mate replacement. In two cases, there was a permanent loss of territory area of $3m^2$ (4%) and $5m^2$ (7%) respectively. The remaining two females lost their territories to neighboring pairs and did not regain them.

All mate replacements resulted in stable monogamous associations. After the original pair-mate was removed, a neighboring individual of the same sex as the removed mate often visited the solitary fish. In these cases, the neighboring male or female often attempted to swim with its old mate and defend its old territory part of the time and spent the rest of its time following the new mate within the experimental individual's territory. This resulted in a short term association between one male and two females (8 out of 12 cases), or between one female and two males (5 out of 6 cases). In most cases this shuttling relationship did not last more than one or two days, and the neighbor either returned to its old mate (N = 4), or switched territories and mates (N = 9), forming a new pair-bond with the

Figure 6.5. Time sequence of mate replacement, showing average feeding and chase rates for 12 female *C. multicinctus* before and after male removal. Male removal occurred at time 0. Chases by the new male which replaced the removed male are also shown.


C. multicinctus
Female
♀
♂
Male
○ Feeding Bites
● Chases
Feeding Bites per 5 min
Chases per 5 min
Days Following Male Removal
80
60
40
20
0
8
6
4
2
0
−2
−1
0
1
2
3
4
5
6

solitary fish. When neighboring males switched mates, the remaining solitary female in turn experienced intrusions by neighbors, with the associated territorial contraction, increased chases and decreased feeding rates. Thus the removal of one individual often resulted in a "domino effect", disrupting several pairs. One female successfully maintained a relationship for eight days with her old mate as well as a small widowed neighboring male. After this time a new female mated with the small male and the "polyandrous" female returned to her old mate. The longest association of one male with two females was four days. Thus a stable monogamous situation developed within two to eight days.

The identity of the new pair-mate was known in 9 out of 16 cases (see: Source of New Mate, Table 6.3). New mates had switched territories and partners from adjoining territories in seven cases, and in an additional two cases, males were known to have switched from territories farther away. In all four cases where females switched from adjoining territories, they moved from territories with lesser coral cover to territories with greater cover of the preferred food-coral, Porites lobata (Table 6.4; For feeding preferences see Hourigan et al. 1987). Coral cover was determined by measuring the planar area of coral in photographs of ten randomly selected $1m^2$ areas within the territories.

Table 6.4. Coral cover[a] in the original territories of females before they switched mates, compared to the coral cover in the new territories of these females after they switched.

	CORAL SPECIES					
	Porites lobata		*Porites compressa*		*Poc. meandrina*	
	Before	After	Before	After	Before	After
C. multicinctus						
Female 1	29%	46% *	37%	33%	0%	1%
Female 2	25%	58% **	53%	26% *	0%	0%
Female 3	27%	49% **	25%	29%	0%	0%
Female 4	14%	24% *	0%	0%	3%	6%
C. quadrimaculatus						
Female 1	9%	26% *	0%	0%	3%	13% *
Female 2	11%	15%	0%	0%	1%	7% *

a. Coral cover was determined by measuring the planar area of coral in photographs of ten randomly selected $1 m^2$ areas within the territories. Arcsine transformed percent cover for each coral species in the two territories was compared by t-test (N = 10; * = $p<0.05$; ** = $p<0.01$).

Chaetodon quadrimaculatus:

Male Removal:

The responses of individual *C. quadrimaculatus* to the removal of their mates were very similar to the responses of *C. multicinctus*. When a male was removed from a territory, neighboring pairs encroached on the territory of the remaining female. Territory sizes of solitary females decreased an average of 38% (Fig. 6.2b) with a concomitant increase in chase rates by the solitary female (frequency of chases increased from 0.36 $SD=0.84$ per hour to 8.52 $SD=6.48$ per hour; combined Wilcoxon's signed-ranks test of mean chase rates for all females, $p<0.001$). Females without mates had higher chase rates than the concurrently monitored controls (Independent Wilcoxon's signed-ranks tests for each female, $p < 0.05$ to 0.01).

Female feeding rates also decreased significantly after mate removal (Mean reduction: 61%; Mann-Whitney U test $p<0.05$; Fig. 6.6) and were negatively correlated with chase rates (Pearson coefficient $r = -0.76$, $N=21$; Fig. 6.7). After mate removal, experimental females fed significantly less than the concurrent control females in intact pairs (Independent Wilcoxon's signed-ranks tests for each female, $p < 0.01$ to 0.005), although there was no significant difference before male removal ($p>0.05$; Fig. 6.6).

Female Removal:

When the female pair-mate was removed, male territory size and feeding rate did not decrease (Fig. 6.2b and 6.5). This was

Figure 6.6. Mean feeding rates (± 95% confidence limits) of female (6 experimental and 6 control) and male *C. quadrimaculatus* (5 experimental and 5 control) before (B) and after (A) removal of the pair-mate. Shaded bars show feeding rates of each experimental individual whose mate was removed, while the unshaded bars show concurrent feeding rates of the individual of the same sex in the unmanipulated control pair. (Mann-Whitney U- test: * - $p < 0.05$; ** - $p < 0.01$; *** $p < 0.001$; N.S. - not significant, i.e. $p > 0.05$).

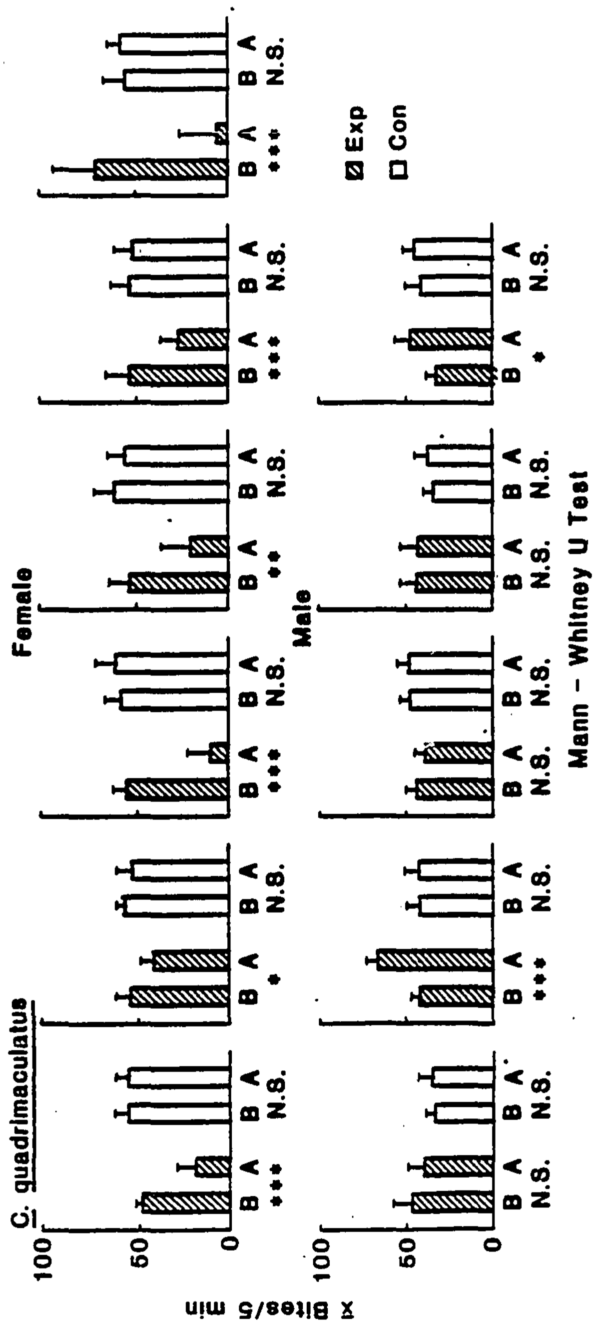
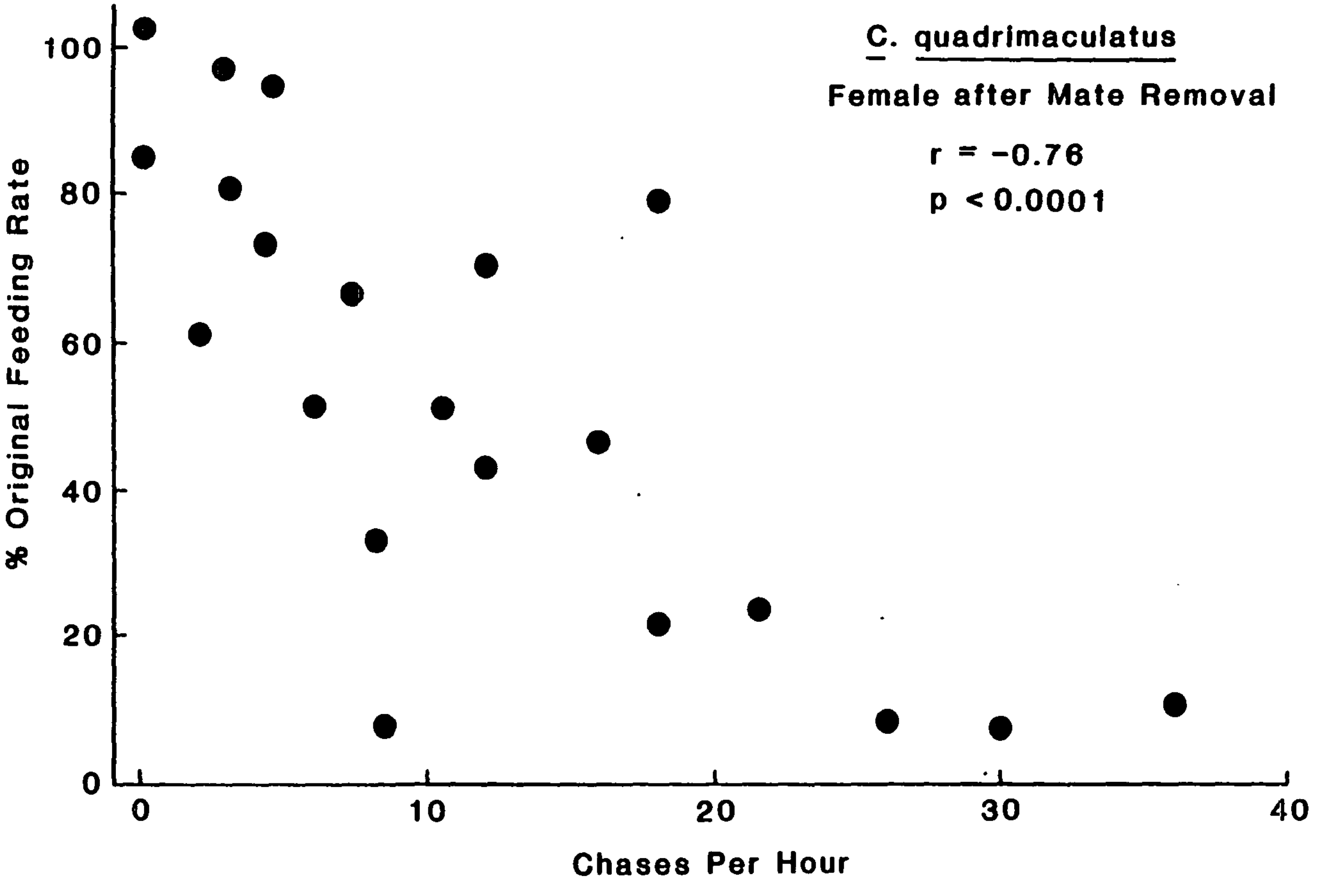

C. quadrimaculatus
Female
Male
x̄ Bites/5 min
100
50
0
B A B A
*** N.S.
* N.S.
*** N.S.
** N.S.
*** N.S.
*** N.S.
N.S. N.S.
*** N.S.
N.S. N.S.
N.S. N.S.
* N.S.
▨ Exp
☐ Con
Mann - Whitney U Test

Figure 6.7. Correlation of feeding rates and chase rates of female _C. quadrimaculatus_ during each 1 hr observation interval after male removal. Feeding rates are expressed as a percentage of the initial feeding rate to compensate for differences in absolute feeding rates among different females.


C. quadrimaculatus
Female after Mate Removal
r = −0.76
p < 0.0001
% Original Feeding Rate
0
20
40
60
80
100
0
10
20
30
40
Chases Per Hour

comparable to results of female removal experiments conducted on C. multicinctus. In two cases, feeding rates of solitary males increased. Frequency of chases with neighboring pairs increased from a mean of 1.2 (SD=1.68) per hour to 9.45 (SD=6.48) per hour (Combined Wilcoxon's signed-ranks test of mean chase rates for all males, $p<0.05$). Males without mates had higher chase rates than the concurrently monitored, paired control males (Independent Wilcoxon's signed-ranks tests for each male, $p<0.05$ to 0.001). There were no significant changes in territory sizes, chase rates or feeding rates for either males or females in the concurrent control pairs.

Mate Replacement:

The greatest differences between the two species occurred during new pair formation. Solitary individual C. quadrimaculatus exhibited "leading displays" similar to those of C. multicinctus. Whereas solitary female C. multicinctus were approached by one or two males which responded singly to her leading displays, female C. quadrimaculatus were followed by one to four males, often at the same time. These males were usually not neighbors, and some appeared to be non-territorial floaters (Table 6.3). There were violent chases among these "suitors", and in two cases, males had fresh scars on the sides of their bodies, evidently as a result of these encounters. In a third case, a male which had been newly paired with a female for four days, was forcefully supplanted by a larger male. This was the only example of disruption of a pair-bond after pairing had occurred. Once pair formation was completed, females fed more, territory sizes expanded to nearly pre-manipulation levels, and chase rates decreased.

Male-male competition and resulting injuries also occurred in cases where a female was removed, and the remaining male attempted to court a neighboring female. In one of these cases, the female swam and fed with the solitary male, and then returned to her own territory. When the solitary male attempted to follow, he was repeatedly attacked by the resident male, and on two occasions, the female he was following turned and joined her mate in attacking the intruder. By the third day, the solitary male was badly battered, with scars on his side and broken first dorsal spines. On the following day this individual had disappeared from its territory, the only loss of a territory by a male of either species. With the exception of the above case, pair formation by solitary male *C. quadrimaculatus* occurred very quickly, in all cases beginning the day after the female was removed (Table 6.3). One of the new females was a neighbor, while another was from a pair three territories removed. These females switched from territories of low abundance of the preferred food-coral *Pocillopora meandrina* to territories where this coral was more abundant (Table 6.4). The remaining three females were not close neighbors, and they could have been non-territorial floaters.

Experiment 2. Male mate replacement while mate is still present.

Methods:

Females whose mate was removed decreased their feeding rates and territory sizes. This decrease could result from either the loss of male assistance in territorial defense (since males contributed most to the territorial defense), or from increased time spent courting new males, or from some combination of both. To attempt to separate these two alternatives, male _C. multicinctus_ from three experimental territories in the coral-rich habitat were captured using hand nets, and replaced in the center of the territory inside a 25cm diameter clear plastic dome. The dome was placed so that the male inside was easily visible to his resident female pair-mate, but obscured from most of the surrounding neighbors. Thus, the male pair-mate was still visibly present to the female, but could not participate in territorial defense.

Results:

In each case, when a male _C. multicinctus_ was placed in the clear dome within his territory, his female pair-mate was still unable to defend the original territory. Chase rates increased for all three experimental females, while feeding rates decreased (Independent Mann-Whitney U-Tests, $p < 0.05$ to 0.01). During the first 24 hours females spent 19% of all minute intervals in the vicinity (< 0.5m) of the container. "Leading displays" directed toward other intruding males were not observed until the third or fourth day, and pairing with a new male occurred on the fourth, fifth, or sixth day. This time for mate replacement was longer than that for mate replacement in all but one of the original 12 experiments (Mann-Whitney U test, $p<0.025$). Thus the decrease in feeding rate observed during the first days was not a result of increased courting of new males. The confounding factor of increased time spent by the female around the male's container could not be eliminated.

After new pair formation, the new male made repeated rushes toward the container as well as lateral and frontal displays with extended soft dorsal and anal fins. The original resident male was released from its container on the seventh day. In all three cases, it was chased out of the territory by both the female and her new mate. The former resident male attempted to return to his territory several times during the following two days, and each time was successfully chased away by the pair. In all cases the old male fled, and by the third day after release he was no longer seen in the area.

Experiment 3. Removal of both male and female members of a pair.

Methods:

In order to observe the results when neither male nor female was left to defend an area, three pairs of _C. multicinctus_ and three pairs of _C. quadrimaculatus_ were removed by spearing. As no changes were noted in controls in the previous experiment, only one concurrent, unmanipulated control pair was observed for each species.

Results:

In all pair removals, neighboring pairs expanded their territories to include the vacated area. This expansion began within hours of the removal. During the next four days, chases among these neighboring pairs increased in the newly vacant areas. In only one case was there a change in territory size along other borders. This occurred when one pair of C. quadrimaculatus expanded into the new area while apparently giving up some coral-poor area in the opposite end of their territory. The control pairs showed no changes in territory size. In no case was the newly vacant area occupied by previously non-territorial individuals or by non-adjacent pairs. The new territorial boundaries remained stable, and were unchanged eight months after the manipulation.

Experiment 4. Removals of one male from a pair and the simultaneous removal of a female from the adjacent pair.

Methods:

A major difference between males and females in the mate removal experiments was that males continued to defend their whole feeding territory despite the fact that one less fish was feeding in the area. This, along with the observation that females switched to areas of higher food-coral abundance, suggested that defense of a larger area by a male might serve to attract a female. The purpose of Experiment

4 was to create a situation where neighbors known to the observer would be likely to pair with each other on one of their two territories. Observations could be made on whether pairing occurred by the female moving into the male's area or visa-versa. Two neighboring pairs with contiguous territorial boundaries were observed as above. After four days, the male of one pair was removed, as was the female of the adjacent pair. Both remaining individuals were observed for a week following the removal. Three replicate experiments were conducted for each species.

Results:

In all three experiments involving C. multicinctus pairs, the female whose mate was removed paired with the neighboring male whose mate had also been removed. In each case, contraction of the female territory occurred first, and pairing occurred when the female entered the male's territory. Both individuals performed leading displays, directed towards each other. Even after one week, the female still only chased other intruding pairs in the area of her old territory. About 60% of the female's territory was regained by the newly formed pair, after the male began moving into the female's old area. In one case, a portion of the male's original area was lost when the male, after pairing, expanded his movements into the females old area.

In contrast, in all three experiments involving C. quadrimaculatus, both the male and female paired with new individuals of the opposite sex, rather than with their solitary neighbor.

Pairing occurred in much the same way as described in the first experiment.

Experiment 5. Food reduction and mate removal experiments.

Methods:

As noted above, switching of mates occurred in several cases when a mate was removed. In all of these cases, females switched from areas of lower coral cover to areas of higher coral cover (i.e. higher food availability). Coral manipulation experiments were conducted to determine more directly the effect of food availability on mate switching and pair-mate choice by female *C. multicinctus*.

In this experiment, six pairs of *C. multicinctus* in the deep coral-rich habitat were observed for four days as described above. For three of these pairs, $12m^2$ to $24m^2$ of the preferred coral, *Porites lobata* was covered with cloth material (a total of 25% - 35% of the total territory area). Changes in territory size, agonistic encounters and time which pair-mates spent together were recorded and compared to the concurrently monitored controls. After two weeks, territory sizes were measured again to determine any long-term changes. Following these measurements, the female of a pair adjacent to the food reduction area was removed. If food abundance within a territory was an important criterion of mate choice, the female from the territory with the reduced coral abundance would be predicted to switch mates and pair with the widowed male with the richer territory.

Each territory from which a female was removed had four to five neighbors, including the neighbor whose coral cover was reduced. Thus, if only the fish in adjacent territories were considered, there was a 20% to 25% chance that the new female would come from the food reduction area, if the choice occurred randomly. The chance was even less if individuals from other areas were considered. These experiments were not conducted with C. quadrimaculatus due to the difficulty of manipulating the much larger territories of these fish.

Results:

Territorial expansion occurred in all cases after corals were covered. A total of 25% to 35% of the area within the territory was covered, but territories expanded only 7% to 14% during the two weeks following food reduction. Territorial expansion by the experimental pair was resisted by the neighboring pairs, and the number of agonistic encounters with these pairs increased from 0.44 encounters per hour to 4.37 per hour. Since chases were rare events, they were analyzed as a proportion of 5 min observation periods in which at least one chase occurred. Differences between the means were tested by generating 95% confidence limits for the binomial proportion (Tate and Clelland 1957), and found to be significant. Intra-pair relations also appeared to be affected. In all three cases, the time that the pair members spent together with their mates increased significantly during the four days after food reduction (Mean time together before: 62% of all 1 min intervals; Mean time together after: 95%; t-test, arcsine transformation, $p<0.05$).

After a neighboring female from an adjacent pair was removed, in two out of three of the cases, the female from the food reduction area abandoned her old mate and switched, as predicted, to the area with the richer coral cover and the male whose mate had been removed. In the third case, although the female visited the neighboring male, the male paired with a different female of unknown origin. The two males in the food reduction areas which were deserted when their females switched mates, formed new pairs after four and six days respectively. This was longer than the average time for mate replacement in the female removal experiments. One of these males formed a pair with another fish barely half the size of its former mate.

DISCUSSION

The formation of male-female pairs which jointly defend a territory is a common strategy among butterflyfishes (Reese 1975; Barlow 1984; Sutton 1985; Tricas 1985, 1986; Fricke 1986; Hourigan 1986a, Chapter II). It also occurs among other coral reef fishes where it is less well documented (Barlow 1984, 1986; Thresher 1984). The present study experimentally induced pair formation in the Hawaiian butterflyfish species, *C. multicinctus* and *C. quadrimaculatus*. When one individual of either sex was removed, mate replacement was rapid. Access to territorial food resources appeared to be the major advantage accrued by paired females, as well as a criterion of mate choice when females switched from one male to another. Although the two species are closely related and had a similar breeding social organization, they differed in the extent to which neighboring breeders and non-breeders responded to the disappearance of individuals.

Recruitment to the breeding population.

Observations and experiments indicated that entry to the breeding population occurred primarily when an adult member of a pair died. For each species, all areas with preferred food resources appeared to be occupied by reproductive pairs which defended contiguous territories (Hourigan Chapter II). Juveniles and sub-adults of both sexes were excluded from these areas and were non-reproductive.

Saturation of available habitat is known to restrict breeding opportunities of both sexes in numerous territorial birds (Brown 1974, 1978; Ricklefs 1975; Koenig and Pitelka 1981; Emlen 1982, 1984; Rabenold 1984; Wolfenden and Fitzpatrick 1984; Freed 1987), but similar results have not been convincingly demonstrated in reef fishes.

Resident territorial pairs were able to resist territory takeovers by non-territorial individuals or pairs. This differs from the situation in several pair-bonded, territorial birds where such takeovers have been observed (Rowley 1983, Freed 1986, 1987). When both members of a pair were removed, the area was not colonized by new individuals, but was taken over by neighboring territorial pairs. When a male was kept in a clear container until after his female had remated, the male was unable to regain his territory or to oust another territorial male in the vicinity. Similarly, blennies which lose their territories are unable to regain them (Nursall 1977). Under situations of natural pair disappearance during four years of observations, territories of pairs which disappeared were always filled by neighbors (N = 2 cases for each species). This occurred despite the presence of non-territorial sub-adults in the vicinity. Natural disappearance of a pair may occur when a male dies and the remaining single female is unable to retain its territory alone. This occurred in two of the C. multicinctus male removal experiments. If pairs disappear, one might expect an ever decreasing number of territorial pairs. This was not observed, suggesting that some areas may be taken over by new pairs, perhaps when territories become too large for one pair to defend alone. Tricas (1986) removed pairs of C. multicinctus adjacent to an experimental pair. The experimental pair expanded its feeding range up to 360% and attempted to defend this new area, but territory sizes eventually decreased as new individuals intruded (T. Tricas pers. comm.). All these factors indicate that territorial pairs can constrain conspecifics from establishing territories and mating.

Recent studies of the recruitment of coral reef fishes have emphasized the stochastic nature of larval recruitment (Sale and Dybdahl 1975, 1978; Sale 1977, 1978, 1980; Doherty 1981, 1982, 1983; Williams and Sale 1981; Victor 1983, 1986; Sale and Douglas 1984; Eckert 1984). Differences in larval recruitment between years have also been reported for paired butterflyfishes (Walsh 1987; Hourigan Chapter II). The long life of adult butterflyfishes, and their ability to exclude smaller individuals of the same species, however, suggest that populations of breeding adults may be limited by intraspecific territoriality, and that within certain limits, they are independent of larval recruitment patterns. Most territories returned to nearly the same size after a new individual replaced the pair-mate which had disappeared. As long as larval recruitment is sufficient to support a pool of non-territorial floaters, the number of breeding pairs occupying a reef habitat would remain relatively constant over time despite variable larval recruitment and mortality. Population constancy will be increased by high adult survival (Snow and Lill 1974; Schoener 1985). The same pairs of C. multicinctus and C.

quadrimaculatus inhabited the same territories during four years of observation, and visual censuses of larger areas of the reef during these years indicated relatively constant numbers of adults (Hourigan Chapter II). Recognizable individuals in pairs of other butterflyfish species have been observed together in the same territories for periods of three years (Fricke 1986), six years (Fricke 1986), seven years (Reese 1981) and ten years (L. Fishelson, pers. comm.).

The function of pair-bonds and territorial defense.

The formation of new pair-bonds by both sexes occurred quickly, indicating that there was an advantage to being paired. The details of pair-bond formation provided evidence of advantages of pair-bonds and territoriality for individuals of both sexes in these fishes. Territories of butterflyfishes serve both reproductive and feeding functions. A C. multicinctus pair spawns in the water column above its territory, and the male successfully defends his female from intruding males which attempt to spawn with her (Hourigan Chapter VII). Lifetime reproductive success of a male is probably limited by access to a female pair-mate for spawning. Spawning of C. quadrimaculatus was not observed, but is likely similar. Spawning of pair-mates within their territory has been reported for other species of butterflyfishes (Neudecker and Lobel 1982; Thresher 1984; Fricke 1986).

Territories also serve a feeding function in both species. All feeding occurs within the territory, and feeding range boundaries are the same as the boundaries of territorial defense (Tricas 1985, 1986; Hourigan Chapter III). The feeding function of territories was supported by the observation that territory size expanded when food resources within a territory were reduced. Tricas (1986) conducted food reduction experiments on C. multicinctus in the same area and also observed territorial expansion when food-corals within the territory were covered. No territorial expansion occurred when areas not containing corals were covered, providing a more suitable control for the manipulation.

The results of the mate removal experiments indicated that pair-mated females had access to larger feeding areas, and spent more time feeding than would be possible for solitary females. This evidently occurred because the male pair-mate assumed the majority of the defense activities. Feeding and chase rates were inversely related. Females fed more than the males with whom they were paired, while males spent more time and energy in territorial defense activities. Unlike female feeding, male feeding did not appear to be time limited, since male feeding rates did not decrease after female removal, even though territorial chases increased.

Defense of a territory by a pair provided the female with exclusive access to increased food resources and the male exclusive access to a female. Female reproductive success in these species is probably food limited (Tricas 1986, Hourigan Chapter I, V), while male reproductive success is limited by the number of eggs he can inseminate, and thus also depends indirectly on female food intake. Intrasexual competition for different resources - males for females, and females for food - would explain why males primarily chased males, and females chased females. Similar sex specific defense of feeding territories has been reported for other monogamous fishes (Barlow 1984, 1986; Fricke 1986). The benefits of assured reproduction for males and increased food for females would also explain why both males and females attempted to attract new mates to their territories by the "leading display". Robertson et al. (1979) postulated a similar advantage to pairing in the surgeonfish Acanthurus leucosternon. In this species also, males defend feeding territories, and paired females feed more than males. Paired females also feed more and have larger ovaries than females without mates. Monogamy in other coral reef fishes is also associated with the defense of feeding territories (Barlow 1984, 1986).

Male butterflyfishes of these two species were unable to monopolize more than one female. In several cases, a male attempted to control two mates when his male neighbor was removed. In no case was the bigamous male successful, and male-male aggression resulted in visible injuries. Females were also unsuccessful at consorting with more than one male and feeding in both territories. Territorial aggression directed toward members of the same sex may constrain possibilities for polygamous mating. The adaptive significance of pair-bonding and monogamy in these fishes is dealt with in greater detail elsewhere (Hourigan Chapter VII).

If the primary benefit of pairing and territoriality for females is access to food resources, then female mate choice may be based to some degree on the food resources within the male's territory. This would explain why females switched to territories which were richer in coral (Table 6.4). A male which lost his mate would be more likely to attract a new female if he continued to defend his original territory, even though it contained more resources than were needed by the male alone.

Variation in mate quality, especially in terms of body size may also affect mate choice. In C. multicinctus, territory size in the deep coral-rich habitat at Puako was positively correlated to male length (Tricas 1986). If larger males can defend larger feeding territories, they should be more attractive to females. Males may also choose larger females, since female fecundity increases with female size (Tricas 1986; Hourigan Chapter V). Assortative mating by size may have contributed to the observed patterns of mate switching. Unfortunately, pair-mates and their neighbors were not collected following the experiments, so differences in size could not be determined.

Due to habitat saturation by breeding pairs, opportunities for mate choice and switching may be limited to cases where one pair member dies. The costs of deserting a mate and territory and evicting another individual may be more than the cost of remaining on a less favorable territory. There were no observations of natural mate switching between intact pairs in either species during the four years of observations. Reese (pers. comm.) observed one incident of mate switching among six pairs of Chaetodon trifasciatus over a seven year period. This occurred between two pairs in adjacent territories.

Fricke (1986) conducted a series of mate removal experiments with another butterflyfish, Chaetodon chrysurus. This species forms heterosexual pairs, and each pair defends a feeding territory from conspecifics. When one individual was removed from each of ten pairs (all ten individuals were apparently removed simultaneously), extensive mate switching as well as an influx of of new individuals from outside the area was observed. In all cases, heterosexual pairs were re-established, and territory boundaries were similar to those before the manipulation. In several cases, individuals switched from areas of low topographic complexity to areas of high topographic complexity which may have been associated with greater food resources. Fricke concluded that pairing increased the efficiency of territorial defense. When a male was removed (N = 1), the remaining female's foraging area decreased by 75%, and later expanded when she formed a new pir-bond. In a second experiment (data shown for one fish of each sex), when a mate was removed, conspecific intrusions and chases increased, foraging areas decreased, but feeding rates did not decrease. The responses of C. chrysurus appeared similar to those of the two species in the present study in most respects.

Population structure and mate replacement.

Mate replacement differed between C. multicinctus and C. quadrimaculatus in the number and identity of suitors and in the time required for new pair-bonds to form. When male C. quadrimaculatus were removed, females were approached by up to four males, which competed with each other. In contrast, *C. multicinctus* females had only one or two suitors. Formation of new pair-bonds by both males and females which had lost their mates also occurred more quickly in *C. quadrimaculatus*. Finally, while most pair-mates of *C. multicinctus* switched from adjoining or nearby territories (64% of new mates in Experiment 1 and 4 combined), most *C. quadrimaculatus* came from elsewhere (only 24% of new mates in Experiment 1 and 4 combined came from adjoining or nearby territories), even when the neighboring individual of the opposite sex was also single. This suggests that that there was more competition for mates in *C. quadrimaculatus*, perhaps as a result of a larger pool of non-territorial individuals.

The differences in mate replacement reflect differences in the population structures of these closely related species. *Chaetodon multicinctus* is a coral-feeding generalist (Hourigan et al. 1987; Hourigan Chapter II), and pairs held contiguous territories over most areas of the reef. Non-territorial individuals were constrained to skirt the boundaries of adult territories, or shelter in the "no-man's land" corners where territories met. The size of sub-adult groups (one to three individuals) and the number of adjacent adult pairs which they contacted were restricted. In contrast, adult *C. quadrimaculatus* are specialists on the food-coral, *Pocillopora meandrina*, and territories of pairs were restricted to the shallows where this coral occurred, ending abruptly at an underwater cliff (Hourigan 1986a, Chapter II; Hourigan et al. 1987). This habitat discontinuity created a boundary zone where sub-adults formed groups of up to 20 individuals which swam over large areas at the edge of the adult territories (Hourigan Chapter III). Thus, the number of non-territorial individuals which could effectively respond to the disappearance of an adult was greater for _C. quadrimaculatus_ than for _C. multicinctus_. This was true, despite the fact that the absolute abundance of _C. multicinctus_ was greater than that of _C. quadrimaculatus_ (Hourigan Chapter II).

The speed with which mate replacement occurred on territories after the loss of one pair member indicated that pair-bonding is of great importance to the fitness of individuals of both sexes. In addition, the formation of pair-bonds and the joint defense of feeding territories acts to limit the entrance of new individuals into the breeding population, and thereby affects the opportunities for mate choice and the structure of the population.

CHAPTER VII

THE ADAPTIVE SIGNIFICANCE OF PAIR-BONDING AND MONOGAMY IN FISHES WITHOUT PARENTAL CARE

INTRODUCTION

Social systems result from the adaptive responses by animals to their physical, biotic and social environment. Each individual competes among members of its own sex to produce the greatest number of successful offspring. The observed mating system is a compromise between hypothetical optimal male and female strategies given the constraining factors of the environment and the reproductive biology of the species (Wrangham and Rubenstein 1986).

The individual strategies which are followed by males or females will depend on the benefits provided by theses strategies balanced against their costs. Reproductive success of females is usually limited by the number of offspring which they can produce and for which they can care. The production of successful offspring by females is often limited by the availability of resources (Wilson 1975). In contrast, males can increase their genetic representation in the next generation by increasing the number of females with which they mate (Bateman 1948; Trivers 1972). This leads to competition among males for mates, which favors polygyny (Emlen and Oring 1977).

The formation of monogamous pair-bonds is rare among animals. In vertebrates, monogamy is most often studied among birds and mammals (Rubenstein and Wrangham 1986), where it generally occurs when the survival of offspring is maximized by both parents providing parental care (Tinbergen 1936; Eisenberg 1966; Williams 1966; Lack 1968; Emlen and Oring 1977; Wittenberger 1979; Wittenberger and Tilson 1980). Recent reviews of monogamy have shown, however, that it can occur for reasons other than the care of offspring in mammals (Kleiman 1977), birds (Wittenberger and Tilson 1980; Oring 1982), fishes (Barlow 1984, 1986), and in invertebrates (Johnson 1966, 1977; Wickler and Seibt 1981).

Fishes which produce pelagic eggs have often been assumed to be promiscuous or polygynous, since no parental care is possible (Perrone and Zaret 1979). Spawning occurs in the water column, and the fertilized eggs are scattered widely by tides and currents. However, many such fishes form long term, apparently monogamous pair-bonds. Unlike reproduction in birds and mammals, the production of pelagic eggs precludes parental care and probably kin selection. These characteristics should make the ecological constraints on social behavior clearer and easier to study in reef fishes than in tetrapods (Thresher 1977).

Pair-bonds are best documented among the butterflyfishes (Chaetodontidae; Table 7.1). Heterosexual pair-bonds among butterflyfishes can last more than seven years (Reese 1981), with the male and female sharing the same feeding territory (Reese 1973, 1975, 1981; Sutton 1985; Hourigan 1986a, Chapter II, Chapter III; Tricas

Table 7.1 Social grouping of butterflyfishes with reference to size and feeding guild. Social grouping may differ with age or locality. S = Solitary, P = Pairs, G = groups.

SPECIES	ADULT SIZE (TL in mm)	FEEDING GUILD		
		Corallivore	Omnivore	Planktivore
Chaetodon aculeatus	100		S	
C. capistratus	100	P		
C. octofasciatus	100	P		
C. punctatofasciatus	110	P		
C. guttatissimus	120	S,P,G ---------	S,P,G	
C. larvatus	120	P		
C. melapterus	120	P		
C. multicinctus	120	P		
C. zanzibariensis	120	S,P,G		
C. citrinellus	125	P -------------	P	
C. assarius	130			School
C. aureofasciatus	130	P		
C. austriacus	130	P		
C. fremblii	130		S (Harems)	
C. mertensii	130		S	
C. nigropunctatus	130	S,P		
C. pelewensis	130	P		
C. plebius	130	S,P		
C. rainfordii	130	S,P		
C. kleinii	140			S,P
C. miliaris	140			School
C. mitratus	140		S,P,G	
C. paucifasciatus	140		P	
C. xanthurus	140		S,P	
C. baronessa	150	P		
C. melannotus	150		S,G	
C. meyeri	150	P		
C. reticulatus	150	P		
C. sanctaehelenae	150		P	G
C. speculum	150	S		
C. triangulum	150	P		
C. tricinctus	150	S,P,G		
C. trifasciatus	150	P		
Forcipiger flavissimus	150		S,P,G	
Heniochus diphreutes	150			School

Table 7.1 (cont.) Social grouping of butterflyfishes with reference to size and feeding guild. S = Solitary, P = Pairs, G = groups.

SPECIES	ADULT SIZE (TL in mm)	FEEDING GUILD		
		Corallivore	Omnivore	Planktivore
C. collare	160	P		
C. dichrous	160		P	
C. quadrimaculatus	160	P -------------	P	
C. striatus	160	P --------------	P	
Hemitaurichthys zoster	160			School
C. smithii	170			School
C. humeralis	180		P,G	
C. ornatissimus	180	P		
C. trifascialis	180	S		
C. ulietensis	180		S,P,G	
C. weibeli	180		S,P	
Hemitaurichthys polylepis	180			School
Hemitaurichthys thompsoni	180			School
Heniochus intermedius	180		P,G	
F. longirostris	190		P	
C. argentatus	200		P,G	
C. ephippium	200		P	
C. falcula	200		P	
C. flavirostris	200		P	
C. unimaculatus	200	G		
C. xanthocephalus	200		S,P	
Chelmon rostratus	200		S	
C. auriga	230		P	
C. vagabundus	230		S,P,G	
C. fasciatus	250	S,P ------------	S,P	
C. lunula	250		S,P,G	
C. lineolatus	260		P,G	

Data from Reese 1975; Burgess 1978; Allen 1979; Neudecker and Lobel 1982; Hourigan Ch II; and pers. obs.

1985, 1986; Fricke 1986; Hourigan et al. 1987). Spawning occurs between pair-mates (Neudecker and Lobel 1982; Fricke 1986), indicating that these bonds represent truly monogamous social and mating systems (Wickler and Seibt 1983). Although poorly studied, pair-bonds are also found among other families of coral reef fishes without parental care, including Acanthuridae (Barlow 1974a, 1984; Robertson et al. 1979), Branchiostegidae (Thresher 1984), Labridae (Potts 1973), Pomacanthidae (Neudecker and Lobel 1982; Moyer et al. 1983; Hourigan et al. in press), and Serranidae (Pressley 1980). In addition, such bonds also occur where only one parent provides direct parental care, e.g. Canthigasteridae (Barlow 1984), Gobiidae (Lassig 1976, 1977), Monacanthidae (Barlow 1984), Pomacentridae (Fricke 1974; Fricke and Fricke 1977; Moyer and Nakazono 1978a), Sygnathidae (Gronell 1984), and others. Pair-bonds may be relatively widespread among fishes and are reviewed by Thresher (1984) and Barlow (1984, 1986).

Long-term fidelity in pair-bonds, as occurs among butterflyfishes, must entail certain costs. Among butterflyfishes in which pairs share a feeding territory (Fricke 1986; Tricas 1986; Hourigan Chapter III) these costs include sharing food resources with another individual. Monogamy also limits mate choice, and may limit the number of possible spawnings. This is especially important to males, which are generally assumed not to be sperm limited (Baylis 1981). Given these constraints, there may be counterbalancing selection favoring pair-bonding which is of selective advantage to both males and females. Alternately, monogamy might still be a stable strategy if it is advantageous to one sex, and that sex is able to manipulate members of the opposite sex (Barlow 1984). Finally, monogamy may result from social or ecological constraints on the number of mating partners. This appears to be the case for many birds, where apparently monogamous males become polygynous when neighboring males are removed (Freed 1987).

Hypotheses Explaining Pair-Bonds for Fishes Without Parental Care:

Several hypotheses have been presented to explain pair-bonding and monogamy in fishes without parental care. These hypotheses are generally not mutually exclusive. To date they have not been experimentally tested.

1. Low density hypothesis.

Among species with low population densities, pairing may be advantageous, since the chance of finding a mate in reproductive readiness would be small (Ghiselin 1969; Wickler 1972; Fricke 1973). Paired chaetodontids, however, are often very abundant in the tropics. They are also highly mobile, and are probably able to travel long distances to find mates. Chaetodon multicinctus adults are almost always found paired (Reese 1975; Hourigan 1984, Chapter III, V; Tricas 1985, 1986), yet this species is among the ten most abundant species of fishes in many coral reef habitats in Hawaii (Hobson 1974; Hayes et al. 1981; Hourigan and Reese 1987; Hourigan Chapter II). Likewise in the Red sea, Chaetodon chrysurus is the most abundant chaetodontid in all habitats, yet adults are always found in pairs (Fricke 1986). Low density cannot be a general explanation for pair-bonding in chaetodontids.

2. Anti-hybridization hypothesis:

Many closely related species of butterflyfishes occur together on tropical reefs. In such situations, pairing may reduce the chances of hybridization, preventing the waste of reproductive effort that would occur from producing potentially sterile offspring (Fricke 1973). Hybrids occur among both paired and unpaired species of butterflyfishes (Burgess 1978), and there is no evidence that hybrids are proportionately more common among the latter. There is also no reason to assume that monogamous pair-bonds would be more likely to reduce hybridization than long term polygynous bonds. Thresher (1984) noted that there is no correlation between the number of sympatric chaetodontids in a region, and the proportion of those which form pair-bonds, as might be predicted from the anti-hybridization hypothesis.

3. Breeding synchronization hypothesis:

Elaborate courtship has not been recorded among butterflyfishes (Reese 1975; Lobel 1978; Thresher 1984; Fricke 1986). Reese (1975) proposed that pairing "obviates the need for courtship behavior ... since the behavior associated with pair-bond maintenance could serve to keep both sexes of a pair in sexual readiness." Gronell (1984) suggested that monogamy in the pipefish, Corythoichthys intestinalis resulted from a maximization of spawning efficiency by minimizing the time spent by individuals searching for a mate. Breeding synchronization may indeed be important for butterflyfishes (see below), but its importance does not explain why courtship activity also appears to be lacking in butterflyfishes which do not form pairs. As in the case of the previous hypotheses, this hypothesis does not explain why monogamy should occur in preference to a haremic social system.

4. Site attachment hypothesis:

Several authors have suggested that site attachment and territoriality may be prerequisites to pair-bonding (Fricke 1975, Barlow 1984). This may be especially true if a fish's movements are limited to a small patch which is unable to support more than two breeding individuals. Pairing in anemonefishes of the genus Amphiprion allows fish access to a mate without leaving the shelter of the anemone (Fricke 1974; Moyer and Nakazono 1978a; Ross 1978). Monogamy is apparently enforced by the small size of the anemones, precluding the occurrence of more than one mature pair (Fricke and Fricke 1977; Moyer and Nakazono 1978a). Gobies which are restricted to small coral heads also form pairs, evidently due to similar constraints (Lassig 1976, 1977). It is probable that most or all paired chaetodontids are site attached, although home ranges may be very large (Reese 1975; Sutton 1985; Fricke 1986; Hourigan Chapter II). Butterflyfishes generally exploit relatively evenly distributed resources, rather than being limited to small resource patches. In addition, adults are very mobile and do not appear to be subject to high levels of predation (Reese 1981; Norris 1985; Hourigan Chapter II), which might restrict their movements.

5. Feeding advantage hypothesis:

Pair-bonds may be advantageous if they increase the effectiveness of foraging or of defense of a feeding territory (Robertson et al. 1979; Pressley 1981; Fricke 1986). Two fish in a pair can patrol a larger shared area than the total area that could be patrolled by two single fish defending separate territories. Territory borders, and therefore patrolling effort, increase in linear proportion to the radius of the territory, while territory area, and therefore access to food resources, increases as the square of the radius (Robertson et al. 1979). Two fish together may also provide a more effective territorial advertisement than two fish separately (Fricke 1986). These feeding advantages should accrue equally to the male and female. It is not clear, however, why there should be only two fish or why pairs should be heterosexual.

Feeding advantages may also be asymmetrical between the sexes. Paired females may accrue an advantage if they can feed more than single or polygynously mated females. This can result from a differentiation of behavior between males and females which form a pair-bond (Barlow 1974). Robertson et al. (1979) described the feeding and social behavior of a pair-bonded surgeonfish _Acanthurus leucosternon_ in the Indian Ocean. Heterosexual pairs defend non-contiguous territories. Females outnumber males, and paired females have more fat and larger ovaries than unmated females. When a female pair-mate is removed, excess females fight over the male and mate replacement occurs quickly. The authors suggested that females benefit by the presence of the male who assists in territorial defense, allowing the female to feed more and thus produce more eggs. They did not suggest an advantage to the male. This situation appears similar to the case of the butterflyfishes.

Any social system is maintained by a variety of selective forces. Several factors may contribute to pair-bonding as a stable strategy for fishes such as butterflyfishes. Each of the hypotheses listed above, however, leaves major questions unanswered. Individual behaviors which combine to comprise social systems have evolved as adaptations to the environment given the breeding biology of the species. In the following sections, I briefly review relevant evidence concerning the breeding biology and ecology of butterflyfishes (Family Chaetodontidae) and then present an *a priori* hypothesis to explain pair-bonding and monogamy in butterflyfishes. Predictions from this hypothesis are compared to the results of observations and field experiments on three species of butterflyfishes.

The Breeding Biology and Feeding Ecology of Chaetodontids:

1. Breeding biology.

Evidence from the reproductive biology of butterflyfishes indicates that there may be selection for spawning synchronization.

Unlike many fishes which spawn daily, butterflyfishes appear to spawn only once or twice a month during their extended breeding season (Lobel 1978; Ralston 1981; Fricke 1986; Tricas 1986). Examination of the ovaries of four species of butterflyfishes in the genus *Chaetodon* indicate that most vitellogenic oocytes (yolked eggs) mature synchronously and all (>10,000) are spawned at the same time (*C. miliaris*: Ralston 1981; *C. multicinctus*: Tricas 1986; *C. multicinctus*, *C. quadrimaculatus* and *C. fremblii*: Hourigan Chapter IV). Cursory examination of the ovaries of four additional species (*C. ornatissimus*, *C. trifasciatus*, *C. unimaculatus*, *Forcipiger flavissimus*) showed similar trends (Hourigan unpubl. data). In contrast, fish which spawn on a daily basis, such as the closely related pomacanthids, produce many fewer eggs per spawn (e.g. Bauer and Bauer 1981; Hourigan and Kelley 1985). This may explain why so few observations of spawning by butterflyfishes have been reported (Thresher 1984). All observations of spawning in Hawaii have been during the week before the new or full moon (Lobel 1978; Hourigan Chapter V).

If these fishes spawn only once or twice a month, selection should favor strategies which insure male access to females ready to spawn, and synchronization of spawning behavior (Hourigan 1984). Pair-bonding might be such a strategy, as suggested by the breeding synchronization hypothesis of Reese (1975). This does not explain why some of these fishes are paired (*C. multicinctus*, *C. ornatissimus*, *C. quadrimaculatus*, *C. trifasciatus*), while others are schooling (*C.*

miliaris), or haremic (C. fremblii), or occur in small groups (C. unimaculatus, F. flavissimus; Table 7.1).

Spawning by butterflyfishes occurs during a brief period at dusk Lobel 1978; Neudecker and Lobel 1982; Thresher 1984; Fricke 1986; Hourigan Chapter IV; W. Walsh pers. comm.). Combined with a strong lunar periodicity to spawning (Lobel 1978; Tricas 1986), this may result in high spawning synchrony within the population, and a resultant short period during which spawning is possible. This situation may limit the number of mates with which one male can spawn (Emlen and Oring 1977; Knowlton 1979; Barlow 1984). Since most observations of spawning have been of paired species, it is not known to what extent temporal synchrony may be a constraint resulting in pair-bonding in butterflyfishes. It does not seem likely, however, that such synchrony would be sufficient to preclude the formation of harems. Dusk spawning and lunar periodicity occur among haremic angelfishes (Lobel 1978; Neudecker and Lobel 1982) and apparently in the haremic butterflyfish C. fremblii (Lobel 1978). All these factors fail to explain why pairs should remain together beyond the breeding season (Fricke 1986).

2. Feeding ecology and social behavior.

Food resources are often important determinants of the distribution of females, and thereby of mating systems (Orians 1969; Jarman 1974; Wilson 1975; Bradbury and Vehrencamp 1977; Emlen and Oring 1977; Emlen 1980; Wrangham and Rubenstein 1986). The distribution of many corallivorous butterflyfishes on a reef is correlated to the distribution of preferred food resources (Hourigan et al. 1987; Hourigan Chapter II). There is also evidence that breeding populations of at least two species with heterosexual pairs (C. multicinctus and C. quadrimaculatus) are limited by food resources (Hourigan Chapter II, VI). Thus food may be an important resource affecting butterflyfish social systems.

Reese (1975) found that most coral-feeding butterflyfishes occurred in pairs. Corals are a temporally stable and relatively evenly distributed resource on most coral reefs. Even spacing of food resources favors an even spacing of females feeding on those resources. Temporal stability allows year-round residence and territorial defense of the area where the resource occurs (Brown 1964). This even spacing and territorial defense by females may make it difficult for any single male to monopolize more than one female, thus favoring monogamy (Emlen and Oring 1977). This situation corresponds to a high polygyny threshold. It does not preclude separate male and female territories as appears to occur in some coral feeding fishes, e.g. C. trifascialis (Reese 1975, 1981; Irons in press).

A survey of the literature and personal observations indicates a further correlation between diet and social structure (Table 7.1). Pairing appears to be correlated with both diet and size. Both small and large coral-feeding butterflyfishes occur in pairs. Also, most planktivores, which exploit a temporally and spatially unpredictable food source, occur in schools (Reese 1978; Ralston 1981; Fricke 1986;

Hourigan Chapter II). Large omnivores are also commonly found in pairs, while smaller omnivores are often not paired. Corallivores depend on a food source which is relatively low in caloric value (Tricas 1986) and assimilate less energy per bite than do omnivorous species (Hourigan Chapter V). Larger animals will also have higher total energetic needs than smaller animals. Thus the ratio of energy requirement to energy intake per bite may be large in both corallivores and large omnivores. This suggests a possible correlation between energetic intake and pairing.

Monogamy in Butterflyfishes: An Hypothesis:

I propose an hypothesis to explain pair-bonding and monogamy in butterflyfishes and other coral reef fishes without parental care:

> **Pair-bonding and monogamy are of selective advantage to both sexes, because fecundity is food limited, and pairing:**
>
> **a) increases time available to females for feeding, and**
>
> **b) enables the male pair-mate to share in the increased fecundity.**

This may occur by a division of labor between the sexes, whereby the male assumes an increased proportion of territorial defense activities, allowing the female to spend more time feeding. Part a) of this hypothesis is similar to the explanation of Robertson et al. (1979) for pair formation in an acanthurid. The present hypothesis is based on the following assumptions:

1. Reproductive success of females is limited by feeding time.

2. A male is capable of excluding other males from spawning with his pair-mate. This assures that the gains in reproduction made by the female as a result of the male pair-mate's behavior will also be shared by that male.

The hypothesis leads to a set of testable predictions concerning pair-bonded fishes:

1. Males spend more time in defense related activities than do their female pair-mates. Females spend more time feeding than their male pair-mates.

2. When pair-mates are removed experimentally, solitary females feed less and defend smaller areas than paired females or than solitary males.

3. Manipulation of food resources alters the cost-benefit ratio of being paired. Food reduction should encourage a female to abandon her pair-mate in favor of a different male with a territory richer in food resources.

4. Males are unable to defend territories containing more than one female. This final prediction is the constraint resulting in monogamy.

Appropriateness of the assumptions and tests of the predictions of the hypothesis:

1. Species studied:

The assumptions and predictions of this hypothesis have been investigated in the course of a six year field study on three species of butterflyfishes (Hourigan Chapter II - VI). The banded butterflyfish, Chaetodon multicinctus, and the fourspot butterflyfish, C. quadrimaculatus, were chosen to test these predictions because male and female conspecifics form heterosexual pairs. The species differed in food resources utilized, but both appeared to meet the assumptions of the hypothesis. A third species, C. fremblii, was chosen for comparison because it did not form pairs. All three species are site attached, similar in size, and closely related, belonging to the same sub-genus, Chaetodon (Burgess 1978; Blum in prep.). Closely related species have undergone differentiation in response to different ecological pressures. Comparisons among such species may provide information on these pressures which would not be possible to assess from single species studies.

These three species are among the most abundant Hawaiian chaetodontids. The sizes, diets and social systems of these species are compared in Table 7.2. Chaetodon multicinctus is the smallest species. It feeds on live coral polyps. Male-female pairs defend contiguous feeding territories against conspecifics as well as some other coral-feeding chaetodontids. Pair-mates remain together throughout the year, and four pairs have been observed in the same

Table 7.2 Adult size, diet, energy intake and absorbtion efficiency, and social systems of the three butterflyfish species investigated in the present study.

SPECIES	ADULT SIZE (SL in mm)	DIET	ENERGY INTAKE PER DAY	EFFICIENCY OF ENERGY ABSORPTION	SOCIAL SYSTEM
<u>C. multicinctus</u>	70 - 100	Coral	1.6 - 2.0 kcal	22.4%	Intersexual Pairs
<u>C. quadrimaculatus</u>	80 - 120	Coral, Non-coralline Invertebrates, Algae	4.2 - 7.6 kcal	14.5%	Intersexual Pairs
<u>C. fremblii</u>	80 - 125	Non-coralline Invertebrates, Algae	2.6 - 4.5 kcal	42.1%	Harems

Data summarized from Hourigan Chapter III, IV, and V.

territories for four years. *Chaetodon quadrimaculatus* is larger and has a higher energy diet, supplementing coral as food with algae and non-coralline invertebrates, especially polychaetes. Its social behavior is similar to that of *C. multicinctus*. *Chaetodon fremblii* is similar in size to *C. quadrimaculatus*, and its diet consists of non-coralline invertebrates and algae. Its social system is haremic polygyny. Females defend feeding territories from other females. Males defend larger territories which contain the territories of one to four females.

In this study I observed individual butterflyfishes of each species to determine differences in feeding rates and territorial behavior of males and females with overlapping areas. Individuals were removed to test their contribution to factors affecting the fitness of their mates. Food reduction experiments were conducted to determine the effects of food abundance on the maintenance of the pair-bond.

METHODS

Field observations and experiments on the behavior of Chaetodon multicinctus and C. quadrimaculatus were conducted on the coral reefs of the island of Hawaii. Chaetodon fremblii was studied on reefs of the island of Oahu. Individual butterflyfish, identified by natural markings, were followed and their foraging areas mapped. The number of feeding bites and agonistic encounters during each 5 min observation interval was counted. Fishes were observed at all times of day, and during all seasons of the year. After a minimum of twenty 5 min observations on each member of 20 pairs of C. multicinctus and 18 pairs of C. quadrimaculatus, both members of the pair were removed in order to determine the sexes of the paired fishes. To prevent unnecessary killing of fishes, in an additional ten cases only one individual was removed (in conjunction with mate-removal experiments), and the pair-mate was assumed to be of the opposite sex. Members of twelve harems of C. fremblii were also observed as described above, and a sample of 12 fish were speared to determine the sexes. Speared fishes of all three species were utilized for gut content analysis, fecundity estimates and calorimetric studies (Hourigan Chapter III, IV, V).

In order to determine the contribution of a mate to the social system, one member of a pair or harem was removed. In the mate removal experiments, two non-adjacent pairs of C. multicinctus or C. quadrimaculatus were observed as described above, for four consecutive days. The male or female of one pair (the experimental pair) was then removed, while the second pair (the control pair) was left intact. Observations were then repeated and territory sizes re-mapped for a minimum of six subsequent days for both experimental and control pairs. Twelve male and six female C. multicinctus, and six male and five female C. quadrimaculatus were removed from their respective mates. Removals of male or female C. fremblii were conducted in a similar manner. An experimental and control harem, each containing at least three females, were observed and data on each individual were collected. One male or female from the experimental harem was then removed, and changes in territory sizes, feeding rates, and behavior of harem members and neighbors were observed and compared to unmanipulated control harems. Three males and three females were removed from six separate experimental harems.

Food manipulation experiments were conducted on two species. Six pairs of C. multicinctus and six harems of C. fremblii were observed for four to eight days as described above. For three of the pairs of C. multicinctus, 12 to 24m^2 of the preferred food coral, Porites lobata was covered with cloth material. Changes in territory size, agonistic encounters and time that the pair spent together were recorded and compared to the controls. After two weeks, territory sizes were measured again to determine any longer term changes. After these measurements, the female of a neighboring pair was removed to see if the female from the territory with the reduced food density would switch to a new mate in the richer territory. Twenty, 1 m^2 covers were placed over the areas where most feeding occurred within the territory of one female C. fremblii in each of three separate harems. Changes in feeding rates, agonistic encounters and territory size were measured as above, and compared to the behavior of three control females. Methods are explained in greater detail in (Hourigan Chapter II, III, IV, V, VI).

RESULTS

Relevance of the assumptions to the species studied.

Assumption 1. Reproductive success of females is limited by feeding time.

Paired Species:

Support for this assumption comes from five lines of evidence discussed below: 1) Energetic return per bite of food was very low for these species; 2) Foraging occupied nearly all the time that the fish were active; 3) Reproductive pairs defended feeding territories, and non-territorial females did not reproduce; 4) Gamete production constituted a significant energy investment by females; and 5) Females from food-poor areas had smaller gonads than females from food-rich areas.

The energy return per feeding bite was very low (Hourigan Chapter IV). Coral tissue has a high water content, leading to a low caloric intake per feeding bite. Even more surprising, both C. multicinctus and C. quadrimaculatus had very low absorption efficiencies: less than 25% of energy intake was absorbed (Table 7.2). These values are low compared to average values from the literature of 80% - 85% absorption efficiency for carnivorous fishes and 58% - 60% absorption efficiency for herbivorous fishes (Brett and Groves 1979; Pandian and Vivekanadan 1985).

Foraging was the primary activity for females of both paired species (Table 7.3; Hourigan Chapter III). Activity periods of fish

Table 7.3 Activity budgets and feeding rates of the three species of butterflyfishes studied.[1] All observations were conducted between sunrise and sunset. Values are means for all individuals observed. * denotes a significantly higher mean for that sex at the 95% confidence level or higher (Wilcoxon's signed-ranks tests between conspecific pair-mates sharing a territory, or in the case of *C. fremblii*, between males and their harems.

ACTIVITY BUDGETS[2]

	C. multicinctus		*C. quadrimaculatus*[3]		*C. fremblii*	
	Males	Females	Males	Females	Males	Females
Number of fish observed	30	30	28	28	12	30
Hours of observation	58	58	50	50	18	24
Time spent foraging	96.2%	98.4% *	92.5%	98.1% *	91.3%	96.5% *
Time spent sheltered	0.03%	0.03%	8.9%	3.8%	0.8%	0.4%
Time with mate(s)	74%	74%	50%	50%	28.4%	13.9%
Time spent posing for cleaning	1.4%	0.8%	1.4%	0.7%	0.4%	1.1%
Chases/hr. of						
Adults	2.84 *	0.66	1.89 *	0.33	1.16	2.83 *
Juveniles	2.53 *	1.79	1.26 *	0.19	0.75	0.40
Other species	1.40 *	0.00	0.36 *	0.00	0.00	0.00
Agonistic displays/hr.	1.45 *	0.71	0.99 *	0.28	0.25	0.53
FEEDING RATES in bites/hr	685	835 *	502	667 *	568	647 *

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1. Data are summarized from (Hourigan Chapter III and IV).
2. Activity budgets are expressed as the percent of all minute observation intervals in which a particular behavior occurred.
3. Since *C. quadrimaculatus* feeds on a lunar day, the occurrence of feeding and sheltering represents only those daylight observations after moonrise (Hourigan 1986a).

lasted 12 to 13 hrs, during which time females foraged almost continuously. The amount of time spent feeding by both species was much higher than the 12% to 20% of total time spent feeding by other fish species reviewed by Nursall (1981). Continuous foraging is compatible with the low amount of energy ingested per bite and absorbed by these fishes.

The boundaries of the foraging areas of females coincided with the boundaries of the defended areas, indicating that these areas were feeding territories (Tricas 1985, 1986; Hourigan Chapter III). This was further supported by the observation that territory sizes of paired C. multicinctus expanded when food resources were reduced (Table 7.4; Hourigan Chapter VI). This expansion was resisted by neighboring males and females. Increased time spent chasing was accompanied by reduced feeding rates (Table 7.4). Tricas (1985, 1986) reduced the food abundance in territories of C. multicinctus with similar results.

Populations of both C. multicinctus and C. quadrimaculatus contained females which were excluded from the feeding territories of territorial pairs. These non-territorial females had lower feeding rates than territorial females and were not reproductive (Hourigan Chapter II, III, VI).

These data indicate that females maximize energy intake from feeding. The evidence linking reproductive success to feeding is strong but circumstantial. During the spawning season the gonads comprised a large proportion of the wet weight and organic content of

Table 7.4 Food reduction experiment conducted on three pairs of _Chaetodon multicinctus_ and three harems of _C. fremblii_. * denotes a significant difference at the 95% confidence level after food reduction compared to before (Hourigan Chapter V and VI).

	% Territory covered	% Change in territory size	Chases per hr Before	Chases per hr After	Feeding Rate (bites/hr) Before	Feeding Rate (bites/hr) After
C. multicinctus						
Male	25% - 35%	+7% - +14% *	0.31	3.00 *	657	476 *
Female	25% - 35%	+7% - +14% *	0.13	1.37 *	828	735 *
C. fremblii						
Male	2% - 3%	No Change	2.14	1.78	459	521
Female	7% - 11%	+1% - +4% *	3.12	6.79 *	647	422 *

the bodies of females compared to the gonads of males (Table 7.5; Hourigan Chapter V). Preliminary energy budgets indicate that the reproductive effort of females (estimated from the energy expended in the annual production of gametes) ranges from 3% to 7% of all energy assimilated (Table 7.5). Females accumulated visceral fat stores during the non-breeding season, but these were used up early in the breeding season. This suggests that fat stores accumulated during the non-breeding season are mobilized for reproduction.

The strongest evidence of food limitation comes from female C. multicinctus collected in coral-rich and coral-poor habitats (Hourigan Chapter IV). Females of pairs in the coral-poor habitat inhabited larger territories and had lower feeding rates than did the females in the coral-rich habitat. The former also had smaller gonadosomatic indices, fewer vitellogenic oocytes, and less stored fat than females from the coral-rich habitat.

Haremic Species:

Energy intake per bite did not differ between female C. fremblii and C. quadrimaculatus of a similar size, however the efficiency of energy absorption was much greater for C. fremblii (42.1%; Table 7.2) than for either paired species. Thus the net energy absorbed per feeding bite was much higher for C. fremblii than for the two paired species (Hourigan Chapter V).

Feeding was also the major activity of C. fremblii females (Table 7.3). Nevertheless, females were able to defend feeding territories without assistance from the male. As a result, chase rates of female

Table 7.5 Reproductive investment in gonadal tissues during the breeding season, for males and females of the three species of butterflyfishes studied. (Data from Hourigan Chapter V).

	C. multicinctus		*C. quadrimaculatus*		*C. fremblii*	
	Male	Female	Male	Female	Male	Female
GSI (%)[1]	0.268	2.365	0.215	3.319	0.198	3.756
Organic Material in Gonad[2]	0.2%	2.8%	0.1%	4.0%	0.2%	4.1%
Estimated Batch Fecundity[3]	-	8810	-	20150	-	21640
Energy per spawn[4] (calories)	78	920	73	1630	236	1900
Female Reproductive Effort[5]	4.2% - 7.3%		2.9% - 4.8%		2.1% - 3.5%	

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1) Gonadosomatic index (GSI) is expressed as the percent of wet body weight comprised by the gonad.

2) Organic material in the gonad is the percent of the total body organic content which is partitioned into the gonads.

3) Estimated batch fecundity of females is calculated as the mean number of eggs spawned.

4) Energy per spawn was estimated from the batch fecundity of females, and by assuming that the total contents of the testes are used in a single spawning effort.

5) Reproductive effort of females is calculated as 100 X (Annual energy expenditure in eggs / Annual energy injested and absorbed in the diet). Calculation is based on a minimum of two spawnings per month during a six month spawning season

C. fremblii were much higher than those of females of the paired species (Table 7.3).

Female C. fremblii were on average smaller than female C. quadrimaculatus, yet estimates of the numbers of eggs spawned were higher for the haremic females (Table 7.5). Nevertheless, the estimated reproductive effort expended by female C. fremblii was no higher than for the paired species (Table 7.5). These data suggest that energetic constraints on reproduction by female C. fremblii were not as intense as those on females of the paired species.

Taken together, these findings indicate that reproduction of females of the two paired species, and to a lesser extent, that of females of the haremic species, is limited by food intake, and probably by foraging time. Therefore, adaptations allowing increased foraging time by females should be selected.

Assumption 2. A pair-mated male is capable of excluding other males from spawning with his pair-mate. This assures that the gains in reproduction made by the female as a result of the male pair-mate's behavior will also be shared by that male.

Paired Species:

Evidence supporting this assumption is circumstantial. In both paired species, males contributed most to territorial defense, chased primarily other males (Table 7.6), and were very successful in excluding neighboring males from the territory.

Table 7.6. Intraspecific chases by adult male and female butterflyfishes of the three species, when both the sex of the defender and the intruder were known.

	C. multicinctus		*C. quadrimaculatus*		*C. fremblii*	
	Intruder		Intruder		Intruder	
Sex of Defender	Male	Female	Male	Female	Male	Female
Male	52	6	23	9	24	0
Female	2	11	1	6	0	31

There have been few observations of spawning of butterflyfishes. I observed two instances of spawning by known individuals of C. multicinctus and one instance by C. ornatissimus. In all three cases, spawning occurred between pair mates, in the water column within the boundaries of the pair's territory. In one spawning observation of C. multicinctus, three neighboring males intruded in the territory and attempted to follow the gravid female. These intruders were forcefully and repeatedly chased by the resident male, and successfully excluded from the territory before spawning occurred. The second pair of C. multicinctus spawned without interference. Similar observations were reported by Lobel (1978, pers. comm.). In the single observation of Chaetodon ornatissimus spawning, one neighbor attempted to intrude and was chased away before spawning. Pre-spawning behavior as described by Thresher (1984) was observed several times in both C. multicinctus and C. quadrimaculatus, and occurred exclusively between pair-mates within their territory. Neudcker and Lobel (1982) observed pair-mates of Chaetodon capistratus spawning together within their territory. They also noted unsuccessful attempts by a neighbor (probably a male) to interfere with a pair spawning. Fricke (1986) observed 18 spawning events of the paired butterflyfish Chaetodon chrysurus. All spawns were between pair-mates within their territory. Although neighboring males were often attracted to the gravid female, no successful spawning interference was observed.

Haremic Species:

I have not observed spawning of C. fremblii. As noted above, males inhabit much larger areas than those of the paired species and were less successful in excluding neighboring males which swam occasionally with their females. One observation was made of an apparently gravid female ready to spawn. The male which controlled that harem spent a much greater proportion of time with her than with the other females. Lobel (1978) observed spawning between one male and one female C. fremblii, suggesting that males may be able to prevent intruders from spawning with their mates. The small size of the testes of male C. fremblii is typical of pair spawning fishes, rather than group spawning fishes.

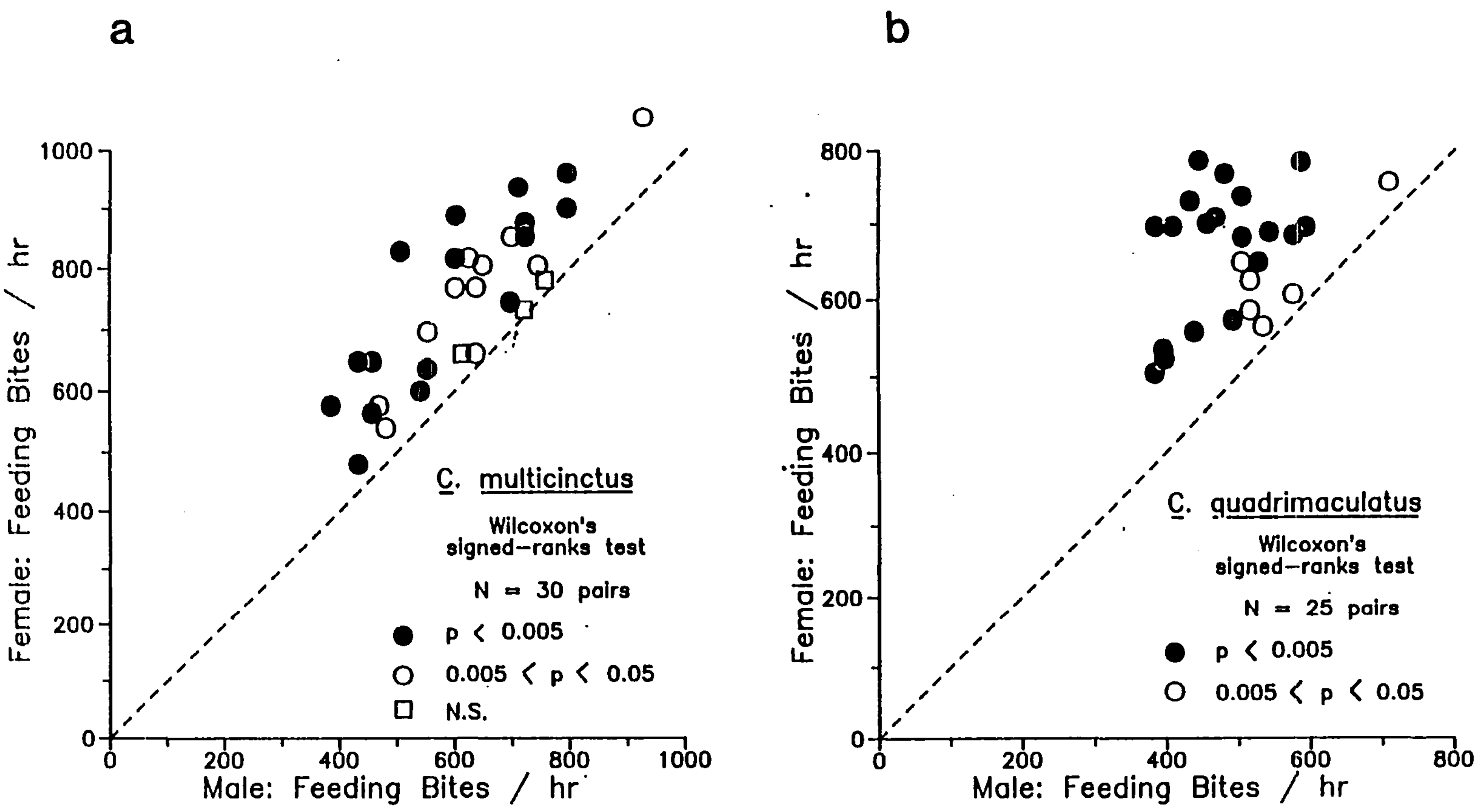
Tests of Predictions from the Hypothesis:

Prediction 1. Males spend more time in defense related activities than do their female pair-mates. Females spend more time feeding than their male pair-mates.

Paired Species:

Feeding and chase rates differed between males and females of the same pair for both paired species. Observations were conducted on thirty pairs of Chaetodon multicinctus. In 27 out of thirty cases, females fed significantly more than males (Wilcoxon's signed rank test, $P<0.05$ to $P<0.005$; Fig. 7.1a). Males spent more time hovering above the bottom, spent more time at the perimeter of the territory,

Figure 7.1. a. Mean feeding rates of male and female C. multicinctus from 30 pairs. b. Mean feeding rates of male and female C. quadrimaculatus from 25 pairs. Significance levels for the Wilcoxon's signed-ranks test were calculated on the basis of at least twenty 5 min feeding observations for each member of a pair. Points falling above the 45° line signify pairs in which the mean feeding rate of the female was greater than the mean feeding rate of the male.


a
b
Female: Feeding Bites / hr
Male: Feeding Bites / hr
0
200
400
600
800
1000
C. multicinctus
Wilcoxon's signed-ranks test
N = 30 pairs
● p < 0.005
○ 0.005 < p < 0.05
□ N.S.
C. quadrimaculatus
Wilcoxon's signed-ranks test
N = 25 pairs
● p < 0.005
○ 0.005 < p < 0.05

and were involved in more territorial chases directed toward neighboring pairs than were females (Table 7.3; Fig. 7.2a). Males also engaged in more territorial displays than females as well as more interspecific chases of other coral feeding fishes (Table 7.3). When conspecific pairs came together at a boundary, males usually chased males and females chased females, however, some chases of the opposite sex were observed (Table 7.6). Male chases were longer in duration, more vigorous, and covered greater areas than female chases (Hourigan Chapter VI).

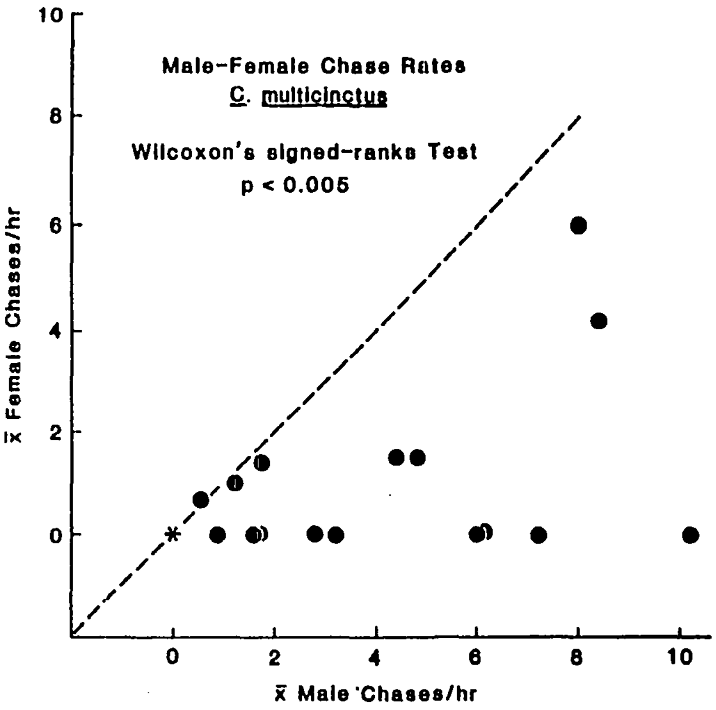
Feeding observations were conducted on 25 pairs of _Chaetodon quadrimaculatus_. Females fed significantly more than males in all cases (Wilcoxon's signed rank test, $P<0.05$ to $P<0.005$; Fig. 7.1b). Males spent more time in territorial defense related activities, and were involved in more territorial chases and territorial displays directed toward neighboring pairs than were females (Table 7.3, Fig. 7.2b). As was the case for _C. multicinctus_, males generally chased males and females chased females (Table 7.6). Male chases were longer in duration, more vigorous, and covered greater areas than female chases (Hourigan Chapter VI).

Haremic Species:

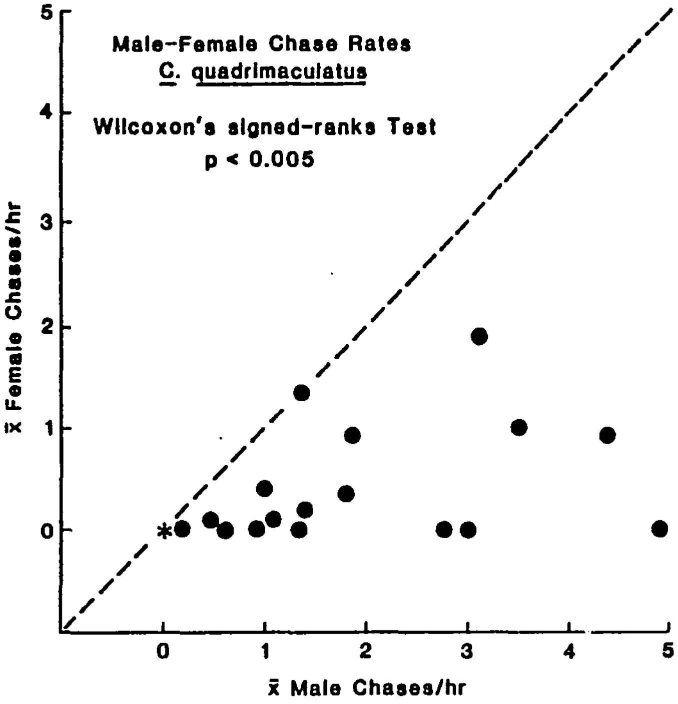
Observations were conducted on 12 male _C. fremblii_ and their associated females. Females fed more than the male in their harem (Table 7.3). In contrast to the paired species, females were involved in more chases than males (combined Wilcoxon's signed-ranks test; $p<0.05$; Table 7.3). No chases were observed between males and females

Figure 7.2. a. Mean chase rates of male and female _C. multicinctus_ from 30 pairs (* = 14 pairs for which no chases were observed). b. Mean chase rates of male and female _C. quadrimaculatus_ from 25 pairs (* = 8 pairs for which no chases were observed). Chases were rare events, and so significance levels were calculated for each species using a single, combined Wilcoxon's signed-ranks test of the mean chase rates of males and females of each pair.

a


Male-Female Chase Rates
C. multicinctus
Wilcoxon's signed-ranks Test
p < 0.005
x̄ Female Chases/hr
x̄ Male Chases/hr
10
8
6
4
2
0
0
2
4
6
8
10
*

b


Male-Female Chase Rates
C. quadrimaculatus
Wilcoxon's signed-ranks Test
p < 0.005
x̄ Female Chases/hr
x̄ Male Chases/hr
5
4
3
2
1
0
0
1
2
3
4
5
*

(Table 7.6). When a male encountered a female in his harem, the two fish would feed side by side with no aggression and few or no displays. Males and females, however, spent much less time together than was the case for pair-mates in the paired species (Table 7.3). Occasionally (less than 2% of all minutes observed), males would swim over to females in neighboring harems, while the resident male was occupied elsewhere. Females in these harems showed no differences in behavior toward these neighbor males compared to their own harem masters. Chases between males occurred most often when the resident male discovered these interlopers.

Prediction 2. When pair-mates are removed experimentally, solitary females feed less and defend smaller areas than paired females or than solitary males.

Paired Species:

In both paired species, each female showed a significant reduction in territory size and feeding rate following the removal of her male pair-mate from the territory. Within hours after male removal, neighboring conspecific pairs began to intrude successfully upon the area previously occupied by the pair. Chase rates for experimental females increased significantly after male removal (Table 7.7). Females appeared to be unable to exclude the neighboring pairs by themselves, and their feeding territories decreased by an average of 65% for <u>C. multicinctus</u> (Fig. 6.1, 6.2a) and 38% for <u>C. quadrimaculatus</u> (Fig. 6.2b). In three cases, solitary female <u>C.</u>

Table 7.7 Mean chase rates before mate removal, and after mate rmoval but before mate replacement occurred. Differences were determined using a combined Wilcoxon's signed-ranks test for all experiments: * = p<0.05, ** = p<0.05, NS = p>0.10.

	C. multicinctus		*C. quadrimaculatus*		*C. fremblii*	
	Chases/hr		Chases/hr		Chases/hr	
	Before	After	Before	After	Before	After
Female (Male Removed)	0.7	26.4 **	0.4	8.5 *	2.3	4.4 N
Male (Female Removed)	2.4	19.2 *	1.2	9.5 *	1.9	1.1 N

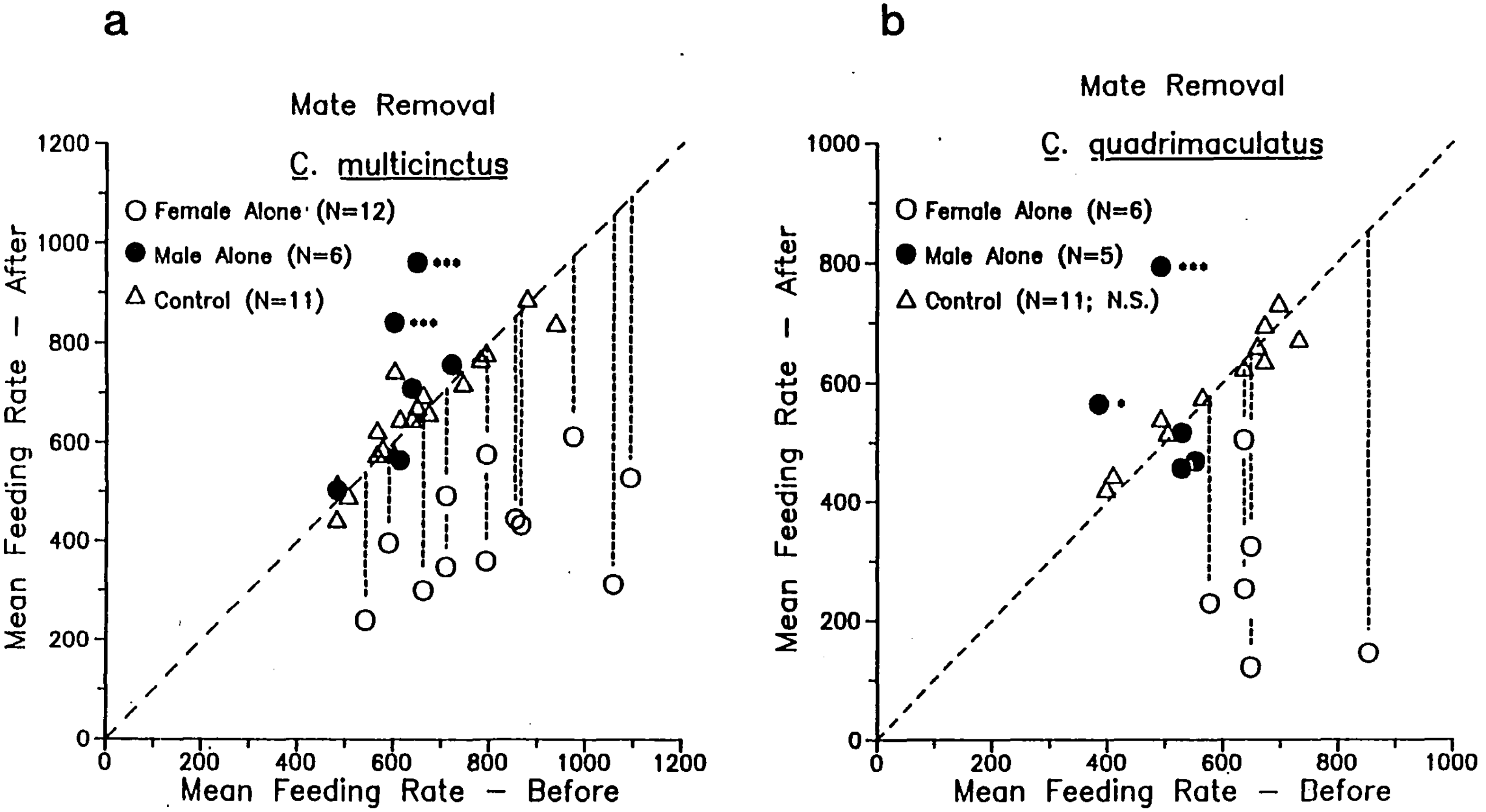
multicinctus were unable to defend an exclusive area at all. In only one of these three cases did the female regain her territory, and in that case, only several days after forming a new pair-bond.

Concomitant with the increased chase rates, all solitary females fed significantly less than before male removal (*C. multicinctus*: Mean reduction = 30%, Fig. 7.3a; *C. quadrimaculatus*: Mean reduction = 61%, Fig. 7.3b). There was an inverse relationship between chase rates and feeding rates (*C. multicinctus*: Pearson coefficient $r = -0.47$ $N=50$ observations, $p<0.001$, Fig. 6.4; *C. quadrimaculatus*: $r = -0.76$ $N=21$, $p<0.0001$, Fig. 6.7). There were no significant changes in territory sizes, chase rates or feeding rates for the females in the concurrent control pairs (Hourigan Chapter VI). Feeding rates of females whose mates had been removed were significantly lower than those of the concurrent controls (Wilcoxon's signed-ranks test, $p< 0.05$).

When a female pair-mate was removed, agonistic encounters between the remaining solitary male and its neighbors also increased (Table 7.7). Unlike females, however, solitary males of both species were able to exclude these intruders unassisted. In all cases, territories shrank less than 3% (Fig. 6.2a & b). In no case did feeding rates decrease, and for two of the six male *C. multicinctus*, and two of the five male *C. quadrimaculatus*, feeding rates increased significantly after the female was removed (Fig. 7.3a & b). There were no changes in feeding or chase rates for the males of the concurrent control pairs (Hourigan Chapter VI).

Mate replacement occurred quickly in both species. The individual whose mate was removed courted members of the opposite sex.

Figure 7.3. Changes in mean feeding rates of male and female butterflyfishes following pair-mate removal. All decreases in feeding rates for females were significant (Mann-Whitney U Test, $P<0.05$). *** denotes a significant increase in male feeding rate after pair-mate removal (Mann-Whitney U Test, $P<0.001$).
a. *C. multicinctus*. b. *C. quadrimaculatus*.


a
Mate Removal
C. multicinctus
○ Female Alone (N=12)
● Male Alone (N=6)
△ Control (N=11)
•••
•••
Mean Feeding Rate - After
1200
1000
800
600
400
200
0
Mean Feeding Rate - Before
0
200
400
600
800
1000
1200
b
Mate Removal
C. quadrimaculatus
○ Female Alone (N=6)
● Male Alone (N=5)
△ Control (N=11; N.S.)
•••
•
Mean Feeding Rate - After
1000
800
600
400
200
0
Mean Feeding Rate - Before
0
200
400
600
800
1000

Mean time for new pair-bond formation in C. multicinctus was 2 days after mate removal for females and 4 days for males. Pair-bond formation by solitary C. quadrimaculatus occurred more quickly, in all cases beginning the day after the mate was removed. After pairing was complete, new males gradually assumed more and more of the defense activities. At this time, the female's chase rate decreased and her feeding rate began to increase again (Fig. 6.5). In most cases territories had returned to their original size after two weeks (Hourigan Chapter VI). In six out of 11 cases when a female was removed, the vacancy was filled by another female which switched from another territory and mate. In all cases, the new territory was higher in coral cover (i.e. food resources) than her old territory.

Haremic Species:

In all three harems from which a male was removed, neighboring males quickly expanded their territories to include the ranges of the females from the experimental harem. Chases among neighboring males occurred in the area where the male was removed. These new males were immediately accepted by the females without noticeable courtship behaviors. There were no changes in female behavior, territory size, or feeding rates compared to controls. In the three cases where a female of a harem was removed, the area was quickly occupied by other females from the same harem. There were no changes in the behavior of the males associated with these harems. There were no changes in unmanipulated control harems (Hourigan 1986b; Chapter V).

Prediction 3. Manipulation of food resources alters the cost-benefit ratio of being paired. Food reduction should encourage a female to abandon her pair-mate in favor of a different male with a territory richer in food resources.

Paired Species (C. multicinctus):

In the food reduction experiment, territorial expansion occurred in all cases after corals were covered. A total of 25% to 35% of the area within the territory was covered, thereby effectively decreasing coral cover (i.e. food availability) by approximately 38% to 56%. Territories expanded only 7% to 14% during the two weeks following food reduction. Territorial expansion by the experimental pair was resisted by the neighboring pairs, and the number of agonistic encounters with these pairs increased (Table 7.4). Intra-pair relations also appeared to be affected, and in all three cases, the time that pair-mates spent together increased. There were no changes in control pairs whose territories were not covered.

As noted above, females switched to areas of higher food density when the opportunity arose. In two out of three cases, after a neighboring female was removed the female from the food reduction area switched to the area with the richer coral cover and the new male, as predicted. Since females could have switched from any of the four to six adjacent territories, as well as from further away, the chance that the experimental female would mate with the male whose female was removed was less than 17% to 25%. In the third case, the female visited the neighboring male, but he eventually remated with a different female (Hourigan Chapter VI).

Haremic Species:

When $20m^2$ of preferred feeding areas within the territories of three females in separate harems was covered, chase rates with neighboring females increased significantly, and territory sizes of the manipulated females increased 2 to $6m^2$ (Table 7.4). Territories of the associated males did not increase in size. Neither chase rates of males, nor the time they spent with mates increased (Table 7.4). No changes were observed in females or males of three concurrent controls whose territories were not covered.

Prediction 4. Males are unable to defend territories containing more than one female.

Paired Species:

Over a period of four years of observations in different habitats and on reefs of different Hawaiian islands, 44 pairs of C. multicinctus and 30 pairs of C. quadrimaculatus were observed. In no case were males observed defending areas with multiple females. Tricas (1985, 1986) observed an additional 39 pairs of C. multicinctus with similar results.

Further evidence supporting this prediction comes from the mate removal experiments. After the original pair-mate was removed, the remaining solitary fish was often visited by a neighboring conspecific of the opposite sex. This neighbor usually attempted to swim with its old mate and defend its old territory during part of the time, while spending the rest of its time following the new mate within the experimental individual's territory. This resulted in a short term association between one male and two females (C. multicinctus: 8 out of 12 cases; C. quadrimaculatus: 3 out of 6 cases), or between one female and two males (C. multicinctus: 5 out of 6 cases; C. quadrimaculatus: 2 out of 5 cases). This shuttling relationship seldom lasted longer than one or two days (Maximum, C. multicinctus: 4 days for one male and 8 days for one female; C. quadrimaculatus: 1 day for males and 2 days for one female). Following this time, the neighbor either returned to its old mate, or switched territories and mates, forming a new pair-bond with the solitary fish. In both species, interactions among males resulted in visible injuries.

Haremic Species:

In contrast to the previous two species, of the 12 males observed, 11 defended areas containing two to four females. Each male spent significantly less total time swimming together with all the females in his harem than a male C. multicinctus or a male C. quadrimaculatus spent swimming with their single female (ANOVA of arcsine transformed data, Duncan-Waller K-ratio t-test for multiple comparisons of means: $p<0.05$; Table 7.3). The territories of males were on average much larger than those of pairs of C. multicinctus and C. quadrimaculatus. One male C. fremblii had only one female in his area, but did not spend significantly more time with this female than other males did with any single female in their harem (Mann-Whitney U-test, $p>0.5$).

When a male was removed from his harem, neighboring males were able to successfully expand their territories to include the areas of the single females (Hourigan 1986b, Chapter VI). A year later, the same males were still observed defending these new areas and females. Food reduction within the territory of the male did not affect male territory size, suggesting that the primary significance of male territoriality was defense of females rather than food.

DISCUSSION

This study demonstrated the feeding advantages gained by female Chaetodon multicinctus and C. quadrimaculatus which form long-term pair-bonds with males. As predicted by the proposed hypothesis, a solitary female was unable to defend as large a feeding territory as a female which was paired with a male. The solitary female fed significantly less than paired females. Access to food resources was a determinant of mate choice by females which switched territories and mates. Females evidently had higher feeding rates and access to larger feeding areas because their male pair-mates assumed a greater portion of the territorial defense activities.

The adaptive significance of these feeding advantages was based on an increase in female reproductive success with increased food intake. Evidence from calorimetric studies on the paired species showed that females ingested more food and invested more energy into reproductive structures than did their mates. Females in coral-rich areas produced more eggs than females in coral poor areas, indicating that reproductive success of females may be food limited (Hourigan, Chapter V). Selection should therefore favor females with behavioral tendencies which lead to pairing, and thus maximize food intake. Monogamously mated males should have greater reproductive success than males mating with unpaired females. Males did not appear to be energy limited since, at least in the short run, solitary males defended territories alone without a decrease in feeding rate (in several cases there was even a significant increase in feeding rate). The behaviors which have resulted in pairing in these butterflyfishes are shown in Table 7.8.

The extent to which the fitness of female reef fishes may be limited by food intake is not known. Feeding territoriality is a common occurrence among such fishes (Reese 1964; Sale 1980). In general, fecundity of female fishes is positively correlated with food intake (Bagenal 1966; Tyler and Dunn 1976; Hirshfield 1980; Wootton 1977, 1985; Luquet and Watanabe 1986). Because of the high degree of random mortality suffered by the pelagic eggs and larvae of reef fishes (Sale 1980), there may be strong selection for iteroparity and high fecundity (Hourigan Chapter I). This will favor any adult strategies which increase food intake and survival. The long-lived butterflyfishes appear to exemplify this trend.

Robertson et al. (1979) postulated a similar advantage to pairing in the surgeonfish Acanthurus leucosternon. In that species also, males defend feeding territories in areas of intermediate food richness, and paired females feed more than males, and more than females without mates. The systems differ in several respects. Female A. leucosternon are larger than males, and territories are not contiguous and are defended primarily against herbivores of other species. The sex ratio appears skewed in favor of females, resulting in solitary females, occasional polyandry, and no replacement of lost males. Evidently, feeding advantages for females can lead to the evolution of similar pair-bond systems under varied environmental conditions. The generality of these system remains to be

Table 7.8 Behaviors which result in pair-bonding in _C. multicinctus_ and _C. quadrimaculatus_ and their putative adaptive significance.

BEHAVIOR	PROXIMATE OUTCOME	POSSIBLE ADAPTIVE SIGNIFICANCE
Male defense of territory from other males	1. Other males not associated with his female	1. Exclusive mating with female in territory
	2. Food resources available to female	2. Attraction of a female to territory, and more eggs to fertilize.
	3. Other males excluded from feeding	3. Exclusive access to food resources
Female defense of territory from other females	1. Other females excluded from feeding	1. Exclusive access to food resources
	2. Other females not associated with her male	2. Male assistance in territorial defense is not divided among two females.
Pair Swimming	1. Pair mates spend $\geq$ 50% of their time together, less time is available to spend with other fish.	1. Female recieves male assistance in territory defense. Male increases the probability that female will spawn with him.
	2. Joint territorial display.	2. Both fish expend less energy in territory defense.
	3. Information is available on reproductive state.	3. Reproductive synchronization.

investigated. There is however evidence that male assistance to females before mating may be common among pair-bonded animals whenever the male has some assurance of paternity in the resulting offspring (birds: Gowaty and Mock 1985; mammals: Kleiman 1977).

Male assistance to females may explain the occurrence of long-term heterosexual bonds, but it does not explain the occurrence of monogamy: i.e., it does not explain why there should be only one female per male. There are two possible alternatives. First, males may not be able to defend an area and provide assistance for two females. This could result from female-female competition, either for food resources or for the assistance of a male. Females which attempted to feed in the areas of two males were eventually excluded forcefully by a new female mating with one of the males. Second, males may not be able to defend much larger areas due to male-male competition for territories and females. The relatively even distribution of corals and low energy value of the food will tend to reduce the environmental potential for polygyny (Emlen and Oring 1977). One male will find it difficult to monopolize resources necessary for more than one female. Several males attempted to control two mates when neighboring male was removed, but in no case were they successful for more than four days. In several cases, male-male aggression resulted in visible injuries. Finally, males may be unable to defend more than one female from spawning with other males. It is not clear, however, why this last factor should constrain polygyny in C. multicinctus and C. quadrimaculatus, but not in C. fremblii. Most likely, some combination of these factors is involved.

The present study showed an advantage to pair-bonded females, and probably also to their mates, but it is not clear that this advantage is sufficient to explain the initial evolution of monogamy from another mating system, for example from harem polygyny as shown by C. fremblii. Such evolution would require that the monogamous male have the same or greater reproductive success by assisting a single female, as a haremic male with two or more females which receive no assistance. The alternative scenario is that males are constrained to one female by ecological factors and/or competition by other males. Given this initial starting point, any behavior by the male which increases the reproduction of the female will be selected. In this case monogamy is environmentally enforced, and the pair-bond behaviors are seen as a case of making the best of this "bad deal", rather than as a cause of monogamy.

Fricke (1986) investigated monogamous pair-bonds of the butterflyfish, C. chrysurus in the Red Sea. As in the present study, he found that pairs defend feeding territories, with males chasing males and females chasing females. He removed one mate each from different contiguous territories. Apparently seven males and three females were removed simultaneously. As in the present study, intrusions into the territories and chases increased after mate removal. Unlike the present study, the territories of both males and females decreased in size. Mate replacement occurred quickly from neighboring territories or from further away. Fricke concluded that the adaptive significance of pair-bonding was joint defense of a feeding territory which increased access of both males and females to food resources. This system appears to differ from that of C. multicinctus and C. quadrimaculatus in that no division of labor between males and females was observed. This raises the possibility that pair-bonding precedes the differentiation of male and female behavior, and that C. chrysurus represents an intermediate evolutionary step.

The haremic mating system of the closely related C. fremblii differed both in the number of females associated with each male, as well as in the nature of the bonds between members of the two sexes. Male home ranges conformed to the shapes of female territories, and males defended these areas from other males. Male territories expanded to include the areas of females which had lost their mates although there were no changes in food resources. Conversely, male territory size did not change when food resources were reduced. There was no evidence that males assisted females in territory defense or in any other way. Males and females rarely showed coordinated swimming and spent much less time together than did males and females of the paired, monogamous species. Neighboring males were immediately accepted by haremic females after mate removal with none of the courting behavior observed in single individuals of the paired species. Female feeding rates and territory sizes were independent of the presence or assistance of a mate. Harem sizes appeared to be limited by the number of site-attached females which a male was able to defend. This suggests that pair-bonded monogamy in C. multicinctus and C. quadrimaculatus is qualitatively different from the haremic system of *C. fremblii*, rather than implying that these systems represent two ends of the same continuum, as predicted by the polygyny threshold theory (Orians 1969; Emlen and Oring 1977).

A critical difference between the paired and haremic species appeared to be the lower absorption efficiencies of the former related to their corallivorous diets. The higher net energy assimilated by *C. fremblii* may allow defense of individual territories by females without male assistance, and perhaps also permit male defense of larger areas containing several females. The gain in reproductive success accruing to a male by assisting a solitary female is evidently less than the gain realized by acquiring a second (or third, or fourth) female. The more restricted energy budgets of female *C. multicinctus* and *C. quadrimaculatus* evidently require male assistance for any significant reproduction, since unpaired females were not reproductive. Energetic constraints may also apply to males, restricting the territory size and thereby the number of females that one male could defend.

The stable nature of food resources for these and many other coral reef fishes allows permanent territoriality, and has an important effect on competition for mates. For both the paired and haremic species, territoriality provided females with exclusive access to food resources and males exclusive access to females. This explains why males primarily chased males, and females chased females. One result is that territoriality by females may prevent some young females from breeding. This will reduce the environmental potential for polygyny. Barlow (1984, 1986) suggested that feeding territoriality may be a prerequisite for monogamous pair-bonds among coral reef fishes. Males and females are permanent residents of the area beyond the breeding season which decreases the action of, and opportunity for, mate choice. Except for cases where a neighbor of the same sex dies or disappears, a female may be constrained to remain in a particular territory and with the same mate. The structure of these systems differs from the structure of the better studied monogamous and polygynous temperate birds (Emlen and Oring 1977; Oring 1982) on which much of present theory is based. Evidence from tropical birds suggests that extended breeding seasons and permanent territoriality may be the norm, leading to different constraints on mating systems (Freed 1987). The concept presented here, of mating systems shaped by the stability and energetic value of food resources, and by male contributions to a female's fitness, including contributions other than care for the young, may apply to other fishes as well as other vertebrates.

CONCLUSIONS

This study presented tests of an hypothesis of the adaptive significance of pair-bonding in the butterflyfishes *Chaetodon multicinctus* and *C. quadrimaculatus*: Pair-bonding and monogamy are of selective advantage to both sexes, because fecundity is food limited, and pairing allows females to feed more, increasing their fecundity, and enables the male pair-mate to share in the increased fecundity. This hypothesis may provide a general explanation for monogamous pair-bonding in many reef fishes. In comparison, a third, closely related haremic species, *C. fremblii*, shows no evidence that females of the harem recieve feeding advantages in the presence of the male. These differences may be due in part to the greater amount of energy that female *C. fremblii* absorb from their diets.

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