

LIFE HISTORY, FORAGING ECOLOGY, AND TERRITORIAL BEHAVIOR
OF THE HAWAIIAN BUTTERFLYFISH, CHAETODON MULTICINCTUS

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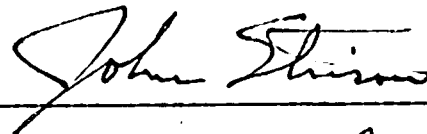
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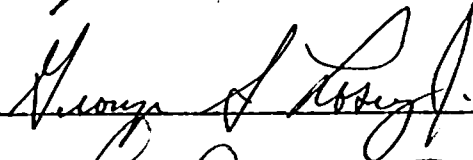
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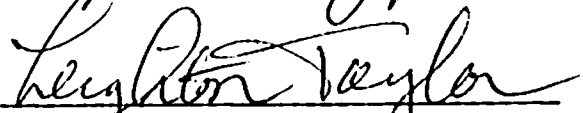
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PREFACE TO THE ELECTRONIC VERSION

The hard copy of my dissertation was deposited in 1986 at the Hamilton Library on the University of Hawaii at Manoa campus. Since that time three publications have appeared from Chapters I, III & IV which are cited below and available on my website at www.hawaii.edu/fishlab. This document contains some additional figures and data, and Chapter II on *C. multinctus* life history which is still on the 'to do' list for publication. Please excuse smudges on some of the Tables, and skewing of some figures during scanning. Hopefully, access to this searchable pdf will be of use to butterflyfish aficionados.

Chapter I:

Tricas, T.C. and J.T. Hiramoto. 1989. Sexual differentiation, oocyte development, and spawning seasonality of the butterflyfish, *Chaetodon multinctus*. Environmental Biology of Fishes 25:111-124.

Chapter III:

Tricas, T.C. 1989. Prey selection by coral-feeding butterfly-fishes: strategies to maximize the profit. Environmental Biology of Fishes 25:171-185.

Chapter IV:

Tricas, T.C. 1989. Food and competitors as determinants of territory size in the Hawaii butterflyfish, *Chaetodon multinctus*. Animal Behaviour 37:830-841.

Aloha,

Tim Tricas

June 21, 2006
Honolulu, Hawaii

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This work is dedicated to those who, in unselfish ways, devote their lives to understand and preserve the earth's ecosystems.

ABSTRACT

This dissertation examines behavioral and ecological adaptations of the butterflyfish, Chaetodon multicinctus (family: Chaetodontidae), in relation its life history and reproductive biology. This species is an obligate coral feeder endemic to the Hawaiian Islands and Johnston Atoll. Adults form long-term monogamous pairs that together defend a single feeding territory from intrusion by other corallivorous fishes, especially neighboring pairs.

Reproductive output and growth are two important aspects of individual fitness for this species. Large males defend the largest feeding-territories, and have the largest female mates. For females, fecundity increases rapidly with body length. Adults spawn across a protracted season from about September through May. Females are highly fecund, and spawn multiple egg batches on a semi-lunar period during the weeks prior to the new and full moon phases. Both sexes deposit large visceral fat stores during the short non-reproductive summer season, which coincides with the period of maximum growth of their food corals. It is suggested that spawning in this and other coral-feeding fishes may be limited by food availability.

Living tissues of food corals for C. multicinctus are high in water content and low in net energy content. As a result, fish invest over 90% of their time budget feeding, and selectively forage on corals that are the most energetically profitable. The strong preference for rose coral, Pocillopora meandrina, is explained by its relatively high energy content. In contrast, the preference for the massive coral, Porites lobata, over finger coral, Porites compressa, is explained by handling

costs associated with their different gross morphologies. Searching for coral polyps on finger coral returns energy at the lowest rate.

Both food abundance and competitor density are important determinants of feeding-territory size. Field experiments show that territory area changes as an inverse function of food competitor abundance. When coral food supply is decreased, fish increase territory size. In contrast, fish maintain or expand their territories when food abundance is increased and levels of attracted food competitors remain low. When high densities of competitors are attracted to increased food resources, territory holders contract their borders so that exclusive use of food resources is maintained. This energy-maximizing species defends the largest amount of food possible, and adjusts territory size according to costs associated with border defense.

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PREFACE

"A óhe pau ka 'ike i ka hālau ho ókāhi"

'All knowledge is not taught in the same school'

-Hawaiian Proverb

Fish communities on coral reefs exhibit a remarkably diverse species composition in habitats often limited in area (Ehrlich, 1975; Goldman and Talbot, 1976; Sale, 1980). Within the past decade, this group has been the focus of an increasing number of studies on ecological, behavioral, and social theory (e. g. Reese and Lighter, 1978). Perhaps the best example is found in tests of classical competition theory which was first rigorously challenged by Sale (1977), and even today remains a topic of strong debate. The diversity of habits found in assemblages of reef fishes make them unique among vertebrate communities, and they will continue to be the subject of intense behavioral and ecological study.

In spite of the increased interest in reef fishes, much remains to be learned about the proximate factors that structure the size and social organization of their populations. Of particular significance is the lack of information on the selective pressures in their life history that influence fitness. Because almost all coral reef fishes have a pelagic larval phase, it is difficult to directly assess individual reproductive success by tracking survival of offspring. As a result life history data on adult populations are especially crucial to this problem, but remain unknown for most species that inhabit coral reefs.

Butterflyfishes of the family Chaetodontidae are conspicuous members of almost all coral reefs, with well over 100 species known worldwide (Burgess, 1978). This family exhibits a diverse array of food habits (e.g. Hiatt and Strasburg, 1960; Hobson, 1974) and social behaviors (e. g. Zumpe, 1965; Reese, 1975; Gore, 1984). They have been the specific focus of studies on community ecology (e. g. Anderson et al., 1981; Findley and Findley, 1985), and are well-suited to direct observation in the field. Coral-feeding butterflyfishes may also be of applied value as indicator species for the condition of coral reefs (Reese, 1981; Hourigan et al., in press).

This dissertation examines behavioral and ecological adaptations of the Hawaiian butterflyfish, Chaetodon multicinctus Garret, in relation to specific features of its life history. This species is endemic to the shallow coral reefs of the Hawaiian Islands and Johnston Atoll. Adults are generally less than 10 cm in length and have a laterally compressed body with a series of five or six conspicuous brown vertical bands on a white background. It has a small protrusible jaw and feeds upon polyps and surface tissues of hard corals (Hobson 1974; Reese 1975). Adults occur almost exclusively in male-female pairs (Reese 1975) that vigorously defend permanent contiguous feeding territories against intrusion by other conspecifics and to a lesser extent other corallivores (Tricas 1985). This species was chosen for study because it is an obligate coral feeder, is ubiquitous on almost all shallow Hawaiian coral reefs, and has sibling species on reefs throughout the Indo-Pacific. The life history traits of C. multicinctus should be

similar to those for many other corallivorous fishes, and thus this system should present a good model for future comparative studies.

The first two chapters address sexual differentiation, gonad and gamete development, size, growth, reproduction, and recruitment of C. multinctus. Histological analyses and extensive fishery techniques are used to quantify parameters of their life history. The remaining chapters examine aspects of their foraging ecology and territorial behavior. Preferences for specific corals exist for a number of butterflyfishes, but the proximate factors of coral quality that structure the patterns have not been addressed in detail. Chapter III examines the relative profitability of corals in terms of their energetic benefits and time costs during foraging. The final chapter experimentally tests the influence of food supply and competitor abundance on the use of space by this species in the context of recent theoretical models.

Although the primary purpose of this dissertation is to address specific questions about behavioral adaptations of coral-feeding butterflyfishes to their ecology and life history, it will hopefully stimulate other workers to examine these remarkable systems in more depth, and with a variety of other species.

CHAPTER I

SEXUAL DIFFERENTIATION, GONAD DEVELOPMENT, AND SPAWNING ACTIVITY: AN HISTOLOGICAL ANALYSIS

INTRODUCTION

Sexual maturation and spawning are important aspects of the life history of coral reef fishes, yet our understanding of the reproductive biology of this group is remarkably limited (recently reviewed by Thresher, 1984). The vast majority of studies used direct observation of spawning (e. g. Bauer and Bauer, 1981; Neudecker and Lobel, 1982; Marraro and Nursall, 1983; Robertson, 1983; Moyer, 1984), gonadosomatic indices (e. g. Ralston, 1981), or macroscopic classification of gonad ripeness (e. g. Munro et al., 1973; Nzioka, 1979) to obtain information on spawning activity. With the exception of studies on sex change (e. g. Reinboth, 1962; Fishelson, 1975; Moyer and Nakazono, 1978; Ross, 1984a) only a few provide detailed histological analyses of gonad development (e. g. Kuo and Nash, 1979; Takita, et al., 1983; Bouain and Siau, 1983; Hourigan and Kelley, 1985). This latter method is emerging as a superior approach to the study of fish reproduction since other methodologies may involve biases when comparing gonadal activity between individuals (de Vlaming et al., 1982).

Butterflyfishes of the family Chaetodontidae are among the most abundant and conspicuous members of coral reefs, but information on their reproduction is generally anecdotal (e. g. Burgess, 1978; Lobel, 1978; Suzuki et al., 1980). Detailed reproductive data exist for only one species, Chaetodon miliaris, studied by Ralston (1976a; 1981), and

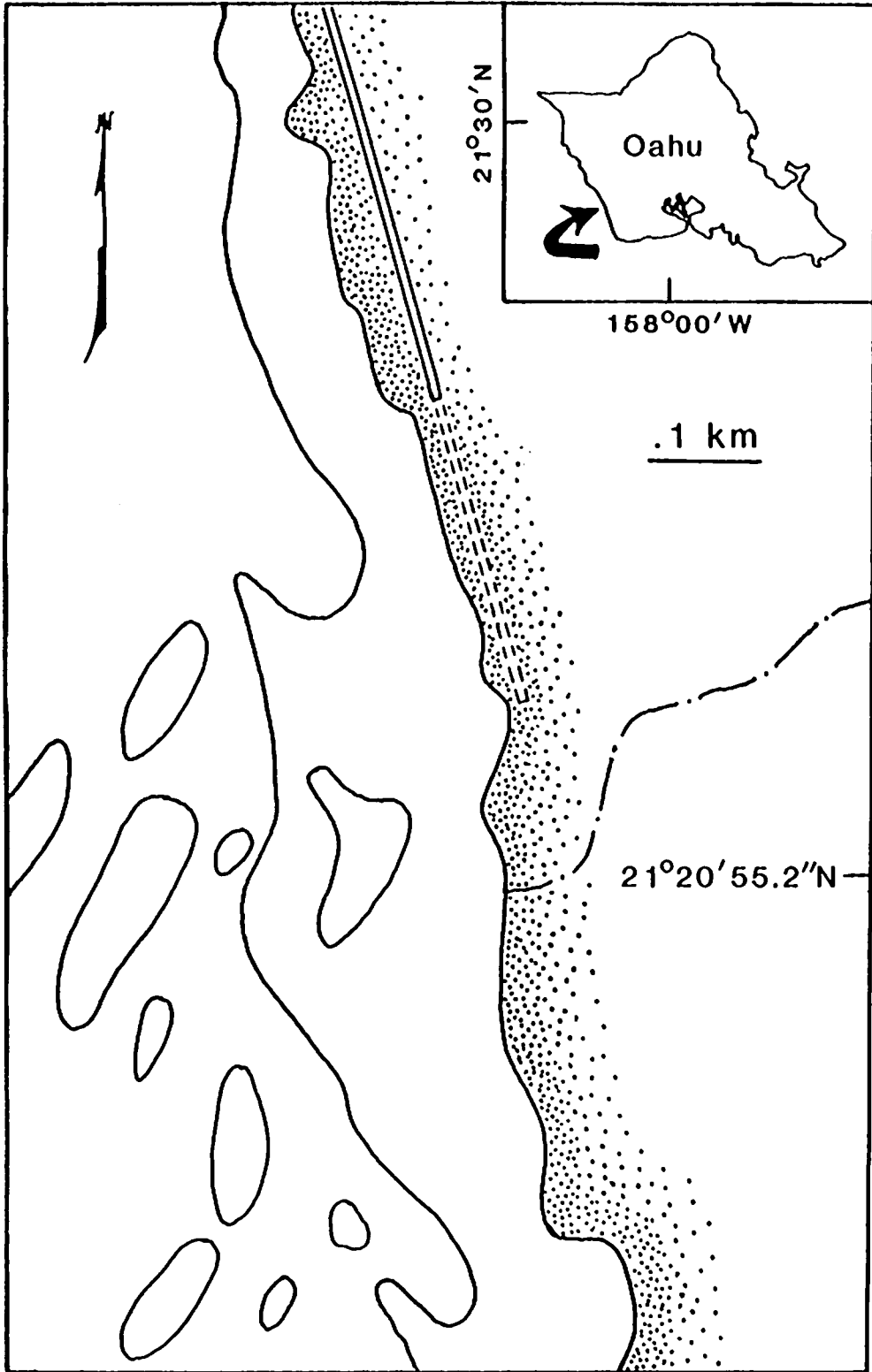
no published analyses of sexual differentiation, gonad maturation, or egg development are available for any chaetodontid. The banded butterflyfish, Chaetodon multicinctus Garrett, is endemic to the Hawaiian Islands and Johnston Atoll (Burgess, 1978) where it occurs on most coral reefs. It is a small obligate coral feeder and forms monogamous pairs that defend permanent feeding territories (Tricas, 1985). It is closely allied with the congeners Chaetodon punctatofasciatus, Chaetodon guttatissimus, and Chaetodon pelewensis that occur regionally in the Indo-Pacific (Burgess, 1978) and thus represents a good species for comparative study.

This chapter presents the first detailed histological analysis of the reproductive biology of a member of the family Chaetodontidae. The patterns of sexual differentiation and gonad maturation are described for both sexes, including evidence of sex inversion among some pre-reproductive females. Histological analyses of oocyte development, egg atresia, and postovulatory follicles in mature females show that this species spawns over a protracted annual period that begins in the fall and peaks during late spring.

STUDY SITE AND METHODS

C. multicinctus were collected over an 18-month period in 1981-1982 on shallow coral reefs (3-10 m deep) near Kahe Point on the west shore of Oahu, Hawaii (Figure 1). All but one of the 1981 collections were taken semi-monthly from July through December, while those in 1982 were made every week. Fifty-eight separate samples were taken.

Figure 1. Study site at Kahe Point on the leeward coast of Oahu, Hawaii. Primary collection area is located at south end of dirt access road (dashed icon). Limits of collection areas include patch reefs and shoreline that extend approximately .5 km to the north of area shown. Stream bed indicated by dot-dash line. Submarine relief shows approximate 4 meter contour. Figure adapted from U.S. Geological Survey Map: Ewa, Hawaii (7.5 minute) 1983.



Fish were speared between 0900 and 1200 h by divers using scuba, placed in plastic bags, and transported on ice to the laboratory for preparation. All individuals were measured for standard length (SL) and their gonads removed. In fish less than approximately 60 mm SL, gonad tissue was not macroscopically visible, thus the thin fold of the dorsal mesentery between the hindgut and dorsal wall of the coelomic cavity was dissected. All tissues were fixed in 10% buffered formalin for at least 5 days and then preserved in 70% isopropyl alcohol. Gonad tissue preparations were dehydrated and cleared in ethanol and xylene, respectively, or by a single series of ethanol-butanol (ENBA) washes. Tissues were embedded in Paraplast, and longitudinal or transverse serial sections (approximately 7 μ m-thick) cut on a microtome.

Various staining methods (Humason, 1979) were employed to maximize tissue contrast and cellular detail. Standard hematoxylin/eosin or hematoxylin/triosin stains were used to study general tissue morphology. Additional preparations of testicular tissue were stained with Mallory's and hematoxylin/triosin/Mallory's. An aqueous PAS treatment was used to identify carbohydrate inclusions characteristic of cortical alveoli in oocytes (Aketa, 1954). Feulgen's stain was used to confirm the presence of DNA-rich material in aggregates of small cells found in ovaries suspected of sex inversion.

Two techniques were used to confirm the lipid nature of suspected oil droplets in oocyte cytoplasm. Fresh tissue was preserved in Formalin for 24 h and then washed in water for 8 h. Samples were then refixed in a 1% solution of osmium tetroxide (Humason, 1979), dehydrated in an ethanol series, and embedded. Sections were counterstained with

hematoxylin/eosin. In the second method, fresh tissue was frozen on a cryostat, sectioned at 40-45 μ m, and stained with Sudan Black B.

The structure and presence of postovulatory follicles in spawned ovaries were examined by inducing ovulation in captive C. multinctus. During February, March, and May 1982; and March, 1983, sixteen adult female fish (71-94 mm SL) were collected with handnets by divers and transported to the Waikiki Aquarium. Each fish was given a single intramuscular injection of human chorionic gonadotropin (Sigma) (approximately 10 IU/gbw) and placed in large holding tanks. Water temperatures ranged between 23.5 and 25.0 °C. After 32-36 hours, fish were stripped of ovulated eggs by applying gentle finger pressure along the abdomen. Gonads were prepared as above and stained with hematoxylin/eosin.

The term oocyte is defined to include all stages of female germ cell development and atresia. The term ova refers to oocytes that have entered or completed the yolk stage of development. Eggs are defined as fully yolked and spawnable female gametes.

RESULTS

Gonads were examined from 416 fish between 29 and 95 mm SL. Sexual differentiation first occurred among females, with the smallest at 44 mm SL (Table I). Sections from the dorsal mesentery of smaller fish revealed only beds of connective tissue, although attempts were not made to identify oogonia and spermatogonia in those undifferentiated

Table I. -- Sex ratios by size class during sexual differentiation for *C. multicinctus* as determined from gonad histology. Transitional gonads that contained both oocytes and spermatogenic tissue were classified as male.

| Size Class (mm SL) | n | Percent | | |
|-----------------------|-----|---------|-------|-----------------------|
| | | Females | Males | Undiffer- entiated |
| <30 | 2 | 0 | 0 | 100 |
| 31-35 | 5 | 0 | 0 | 100 |
| 36-40 | 2 | 0 | 0 | 100 |
| 41-45 | 6 | 17 | 0 | 83 |
| 46-50 | 5 | 100 | 0 | 0 |
| 51-55 | 12 | 67 | 0 | 33 |
| 56-60 | 9 | 56 | 0 | 44 |
| 61-65 | 25 | 72 | 20 | 8 |
| 66-70 | 22 | 64 | 36 | 0 |
| 71-75 | 70 | 52 | 47 | 1 |
| 76-80 | 125 | 66 | 34 | 0 |
| 81-85 | 225 | 56 | 44 | 0 |
| 86-90 | 100 | 35 | 65 | 0 |
| 91-95 | 20 | 25 | 75 | 0 |

individuals. The first evidence of testicular tissue was found in tissue sections from a 62 mm individual. All fish smaller than this size were either undifferentiated or showed ovarian development.

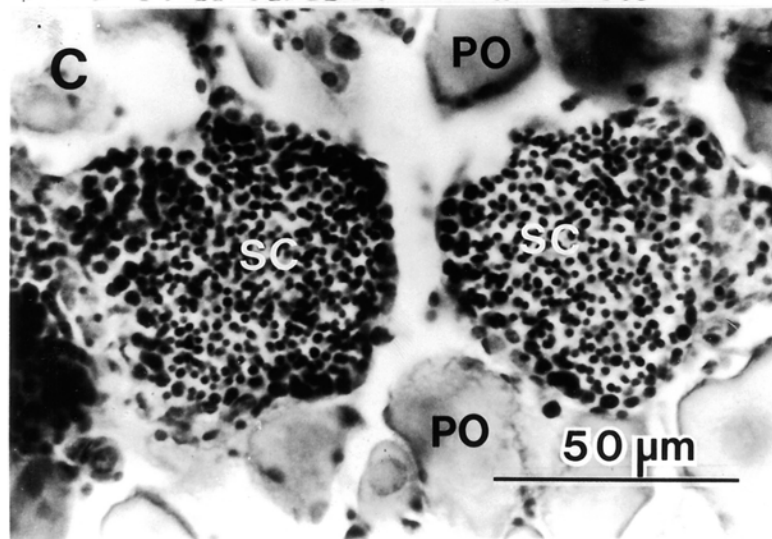
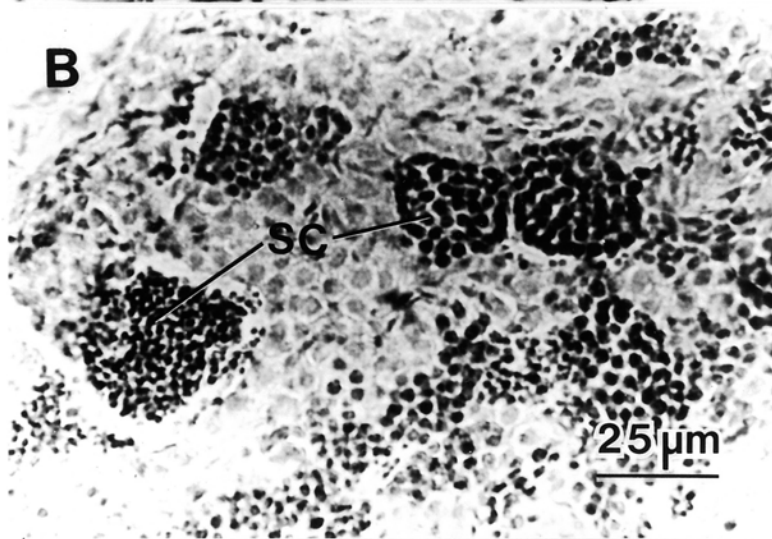
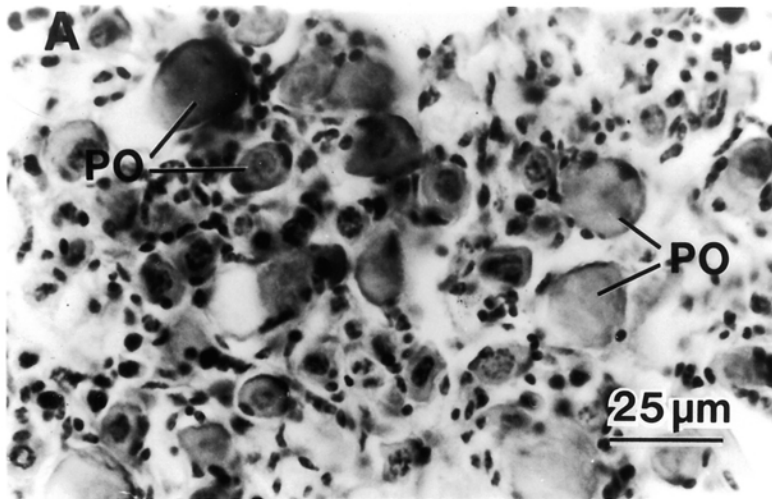
Ovaries

The onset of ovarian morphogenesis in C. multicinctus is marked by the proliferation of the stroma and oogonia in the dorsal mesentery fold. Germ cells could be distinguished from connective tissue by their round shape, clear cytoplasm, and relatively large nuclei. This sheath of cells thickened and eventually gave rise to small secondary villiform extensions that formed the rudiments of the ovarian lamellae.

Concurrent with the structural development of the ovary is the appearance of primary oocytes (Figure 2A). These cells formed in the lamellar folds and basal tissue layers, and were characterized by enlarged basophilic cells with large nuclei. Within the developing lamellae, primary oocytes generally arose from peripheral oogonia, grew inward, and formed interstitial lamellar lacunae. Growth of primary oocytes occurred throughout ovarian differentiation. Proliferation of the stromal layer became less pronounced as the ovary differentiated to form well-developed lamellae with primary oocytes.

Mature ovaries were fused medially to form a single large organ separated by a thick band of fibrous connective tissue. Ovaries distended with eggs were anteriorly bilobed. The lamellae were attached medially and pervade the interior towards the outer ovarian wall. An ovary lumen was present in each lobe but varied positively in size with the stage of egg development. The entire organ was encapsulated by a

Figure 2. Differentiation of gonad tissue in C. multicinctus. (A) Newly forming female (44 mm SL). (B) Newly forming male (73 mm SL). (C) Spermatogenic crypt formation within lamellae of immature female (67 mm SL). All tissues stained with hemotoxylin/eosin. PO: primary oocytes; SC: spermatogenic crypts.



tunic of connective tissue, with a common external oviduct attached to the ventral posterior surface.

Testes

The initial stages of testicular morphogenesis were similar to ovarian development in that stroma and germ cells (spermatogonia) first formed a thick cell layer over the dorsal mesentery. Spermatogonia were associated with loose aggregations of small basophilic cells that organized into discrete nests of spermatocytes. In early testicular development, the spermatogenic crypts were dispersed throughout a bed of connective tissue and spermatogonia (Fig 2B). These crypts eventually fused to form tubules that extended towards the medial axis of the testis. Fully developed sperm ducts that contained spermatozoa were observed in males as small as 65 mm SL.

The testes of mature C. multicinctus were elongate paired organs fused along the medial axis. Their structure was of the unrestricted spermatogonial testis-type common to most teleosts (Grier, 1981). Each testis was packed with tubules separated by a thin basement membrane and showed a radial branching pattern about the medial axis. Spermatogenesis occurred in small discrete crypts that lined the inner surface of the tubules. Spermatogonia near the basement membrane of the lobules showed evidence of mitotic divisions and formed discrete aggregations of spermatocytes. These cells groups divide meiotically to form spermatids that develop into spermatozoa which are released into the central tubule lumen. These ductules (vas efferentia) join medially and ultimately

collect into a large single vas deferens that exits the testes on the ventral posterior surface.

In addition to the development of primary testicular tissue, evidence for secondary development of spermatogenic tissue within previously differentiated ovaries was found (Figure 2C). In these fish, gonads were small but had well developed ovarian lamellae. Most ovaries contained only small primary oocytes of the central nucleoli stage, but one individual had oocytes of the more advanced perinucleolar stage (see below). A distinct proliferation of epithelial, stroma, and germ cells (presumably spermatogonia) occurred along the surface of the ovarian lamellae. In more advanced stages, the lamella were packed with groups of germ cells. These cells showed mitotic activity, and presumably gave rise to the adjacent crypts that stained strongly with hematoxylin and Feulgens.

Crypts in transitional gonads often contained two cell types. Small, new developing sites contained aggregations of basophilic spermatocytes (Figure 2C). Larger crypts showed a central concentration of smaller cells (presumably spermatids) surrounded by a layer of spermatocytes. Although presumed spermatogonia were associated with the developing crypts, they were not prolific. A comparison was made of the sizes of presumed spermatocytes and spermatids with those from normal mature males. No difference was found in mean cell diameter of primary spermatocytes or spermatids between adult testes and transitional gonads (Two-way analysis of variance, $F = .054$, $P < .90$). No sperm tubules had formed in transitional gonads, and no flagellated cells (an indication of spermatozoa) were identified within the crypts. A similar

predominance of spermatids and lack of spermatozoa was found in primary testes prior to tubule formation. It appears that spermatozoa are not formed in the early stages of testicular differentiation.

Atretic oocytes sometimes were associated with ovo-testes. Early degeneration of oocytes usually occurred throughout hermaphroditic ovaries and was not restricted to sites juxtaposed to spermatogenic crypts. Nucleoli from ova in primary growth were less distinct than those of normal females of comparable size collected at the same time. Numerous immature and vitellogenic females showed signs of epithelial cell proliferation at the surface of the lamellae, but only five virgin non-vitellogenic females showed evidence of organized spermatogenic tissue. No remnant of an ovarian lumen or secondary development of vasa deferentia on the gonad surface, as occurs in many protogynous hermaphroditic fishes (e. g. Reinboth, 1962; Dipper and Pullin, 1979; Ross, 1984) was observed in any mature testes.

Oocyte Development

Oogenesis marked the beginning of female reproductive activity and was characterized by distinct nuclear and cytoplasmic events, and rapid cell growth. While oocytes in all developmental stages were present in some fish, most were periodic in their occurrence. Ovarian tissue was examined from fish in all size classes collected during all months of the study, and oocyte stages classified below. Most transverse histological sections were taken from the midregion of ovaries to maximize cross sectional area. Comparison of primary growth and

vitellogenesis among anterior, mid, and posterior regions of mature females showed that oocyte development was homogeneous throughout the ovary ($P < .025$; 3-sample Smirnov test; Conover, 1971). Dimensions of various stages and associated structures are given in Table II.

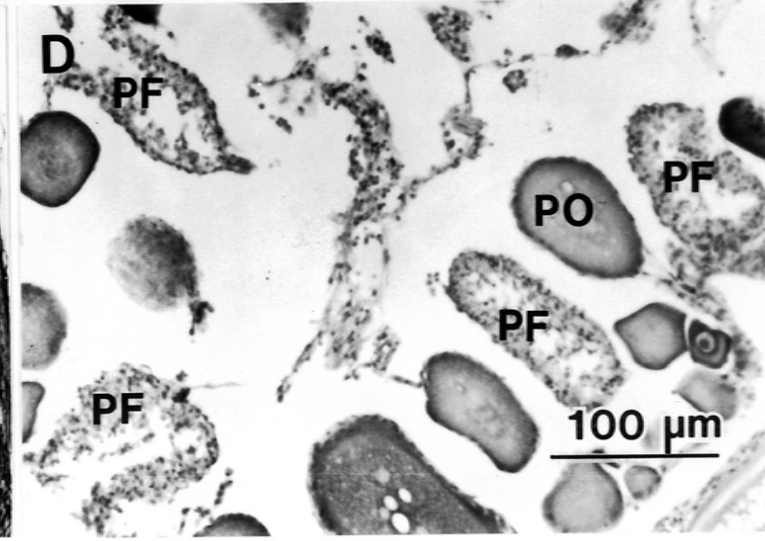
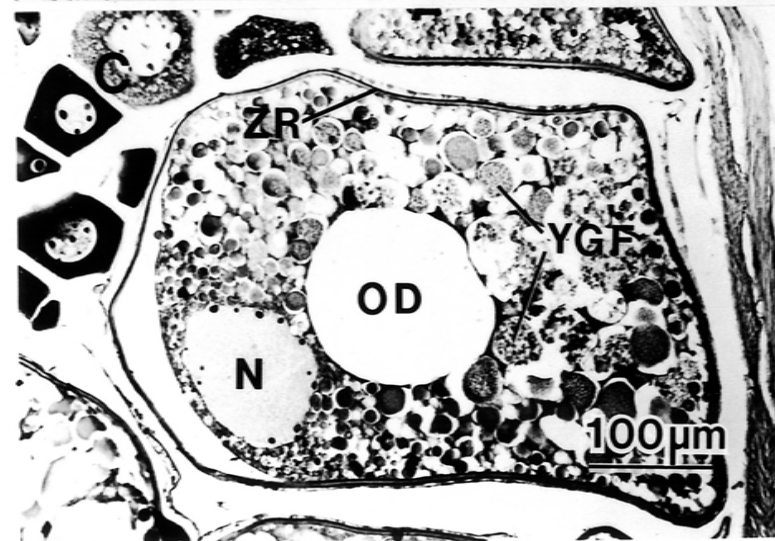
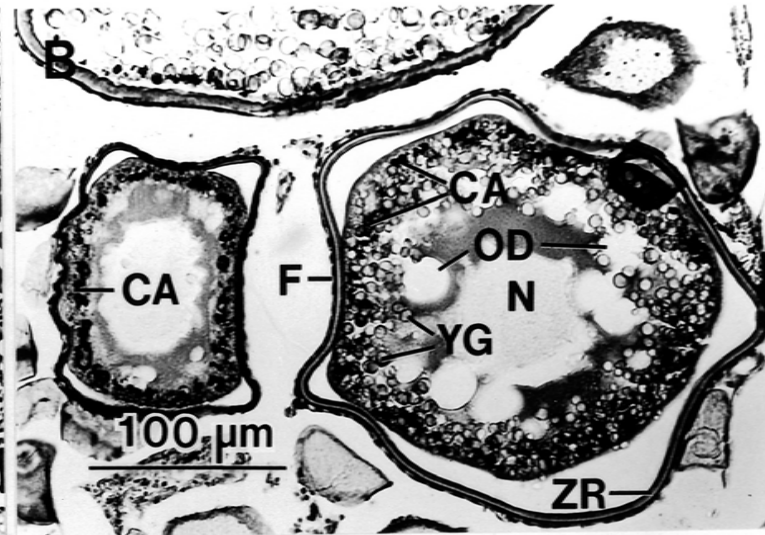
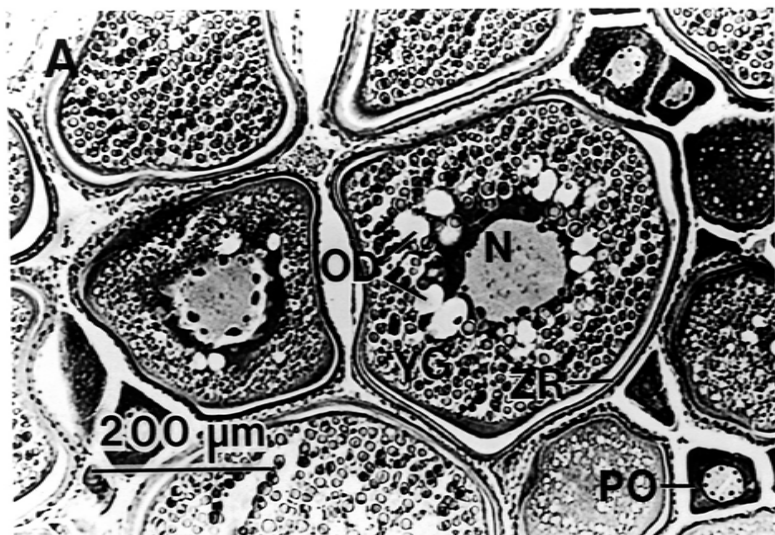
Primary growth (Figures 2A, 3A)- Primary growth was characterized by enlargement of primary oocytes and the appearance of basophilic nucleoli in a centrally located nucleus. The layer of cytoplasm adjacent to the nucleus often stains basophilic, and may contain ribonucleoproteins (Wallace and Selman, 1981). As oocyte size increased, the cytoplasm appeared more heterogeneous, less basophilic, and contained other distinct organelles or Balbiani bodies. Lampbrush chromosomes became visible within the germinal vesicle. Oil inclusions appeared as small transparent droplets under hematoxylin/eosin stain and black when fixed with osmium tetroxide. A perinucleolar stage (c. f. Kuo et al., 1974) occurred after nucleoli migrated near to the nuclear membrane. Nucleoli in this arrangement persisted in oocytes throughout vitellogenesis. Oocytes in primary growth were present in gonads during all months of the year.

Cortical Alveoli formation (Figure 3B)- Prior to vitellogenesis, small yolk vesicles formed within the ooplasm. The positive PAS reaction of the vesicles indicated a high saccharide content and precursory formation of cortical alveoli. Unyolked oocytes with yolk vesicles were relatively large and had a mottled basophilic cytoplasm. Vitellogenic oocytes contained peripheral cortical alveoli that also exhibited the positive PAS reaction. Yolk vesicles appeared as clear areas when stained with hematoxylin/eosin (Ng and Idler, 1983), but

Table II. -- Cell diameters and structural dimensions for stages of egg development in C. muticinctus. n = number of cells or structures measured. Measurements in microns.

| Stage / Structure | n | Range | Mean \pm SD |
|-------------------------|-----|---------|---------------|
| Primary Growth | | | |
| Central nucleoli stage | 201 | 31-92 | 58 \pm 12 |
| Perinucleolar stage | 220 | 51-154 | 92 \pm 20 |
| Cortical alveoli | 23 | 123-179 | 142 \pm 14 |
| Early vitellogenesis | 180 | 113-299 | 207 \pm 34 |
| Zona radiata (width) | 32 | | 3 \pm 6 |
| Yolk spherule (diam) | 42 | | 5 \pm 1 |
| Late vitellogenesis | 331 | 227-453 | 338 \pm 39 |
| Zona radiata (width) | 46 | | 8 \pm 2 |
| Yolk globule (diam) | 56 | | 13 \pm 2 |
| Maturation | 36 | 350-453 | 399 \pm 25 |
| Hydration | 61 | 391-618 | 498 \pm 56 |
| Postovulatory follicles | 84 | 52-206 | 101 \pm 28 |
| Ovulated eggs | 4 | 464-639 | 525 \pm 78 |
| Atretic eggs | | | |
| Alpha | 21 | 258-381 | 316 \pm 41 |
| Beta | 53 | 206-412 | 298 \pm 50 |
| Gamma | 83 | 103-381 | 213 \pm 75 |
| Delta | 162 | 21-484 | 104 \pm 63 |

Figure 3. Stages of oocyte development in mature C. multicinctus. (A) Primary growth and vitellogenesis. Note lampbrush chromosomes and nucleoli in nuclei of oocytes. (B) Cortical alveoli stage (PAS stain). (C) Maturation. (D) Postovulatory follicles from ovary of female (79 mm SL) collected in April 1982. All tissues except (B) stained with hemotoxylin eosin. CA: cortical alveoli; F: follicle; OD: oil droplet; N: nucleus; PF: postovulatory follicles; PO: primary oocyte; YG: yolk granules; YGF: yolk granule fusion; ZR: zona radiata.



could not be reliably distinguished in C. multincinctus ova due to obscurant cytoplasmic mottling, cell shrinkage, and scattered small lipid droplets.

Vitellogenesis (Figures 3A, 3B)- Oocyte growth accelerated during vitellogenesis due to the rapid incorporation of yolk into the oocyte. Yolk spherules were first deposited near the ooplasm periphery and then migrated towards the cell interior. In early vitellogenesis, the vitelline membrane (zona pellucida) appeared as a thin eosinophilic band that surrounded the oocyte. As cells enlarged, the zona pellucida thickened, developed clear radial striations, and formed a thick and distinct zona radiata. In later stages of vitellogenesis, yolk spherules appeared as large globules that filled the oocyte interior, and numerous small lipid droplets aggregated near the nucleus.

Maturation and Hydration (Figure 3C)- The first sign of maturation in C. multincinctus involved the coalescence of lipid droplets into a single drop followed by migration of the nucleus to the cell periphery. The nuclear membrane then degenerated and its contents were released into the cytoplasm. Hydration involved the uptake of large amounts of water into the cell, yolk fusion, and cytoplasmic clearing. Early phases of yolk fusion were observed during nuclear migration and after breakdown of the nuclear membrane. Early hydration was characterized by fusion of yolk globules into large plates, while the zona radiata remained distinct. In late hydration, cells typically contained a heterogeneous mixture of liberated basophilic nucleoplasm, eosinophilic yolk, and basophilic cytoplasm at the cell periphery. At this stage, the striations of the zona radiata became less distinct presumably due

to the retraction of the macro- and microvilli prior to ovulation.

Ovulation and Postovulatory Follicles (Figures 3D, 4A, 4B)- At ovulation, hydrated eggs discharged from their follicular envelope into the ovary lumen. The egg follicle was retained within the lamella and appeared as a small hollow mass of cells attached to the lamellar surface (Table II, Figure 3D). These structures were routinely observed in ovaries from field collections during the spawning season.

Vitellogenic C. multicinctus females injected with HCG produced clear, buoyant, and fertilizable eggs, and showed histological evidence of postovulatory follicles within the ovarian lamellae (Figures 4A, 4B). Follicle cells were identified in all sections up to 36 h after injection of HCG.

Oocyte Atresia

Not all yolked ova were spawned. After the peak of spawning activity had passed, some vitellogenic ova arrested development and showed distinct degenerative stages. Atresia of yolked oocytes in C. multicinctus was similar to that described for other fishes (Bretschneider and de Wit, 1947; Lambert, 1970; Khoo, 1975; Saidapur, 1978; Hunter and Macewicz, 1985) and their general terminology was followed.

Alpha atresia (Figure 5A)- In alpha atresia, vitellogenic eggs began to deform and their contents degenerated. Oocytes sometimes decreased in size and convolutions of the zona radiata appeared. Early stages were generally characterized by breakdown of the cell nucleus,

Figure 4. Postovulatory follicles in ovary after induced ovulation. Gonad from female C. multicinctus (94 mm SL). (A) Photomicrograph showing two postovulatory follicles attached to wall of lamella. (B) Close up of follicle in 4A. F: follicle; FL: follicle lumen; GC: granulosa cell layer; OL: ovarian lumen; TC: theca cell layer; YO: yolked oocyte.

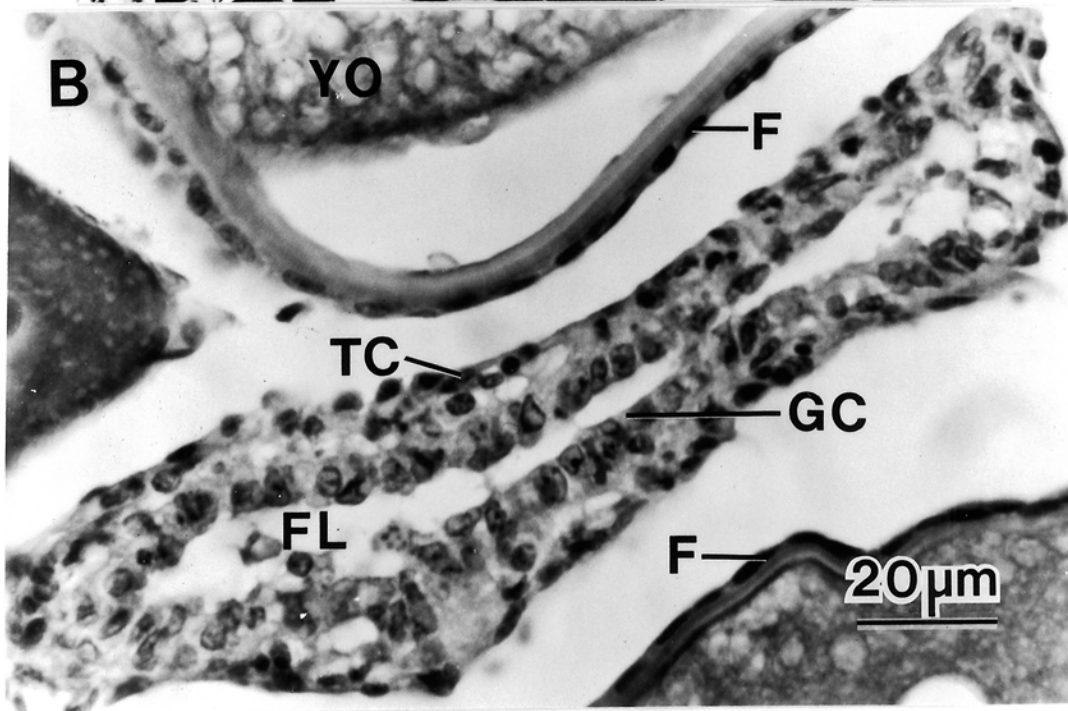
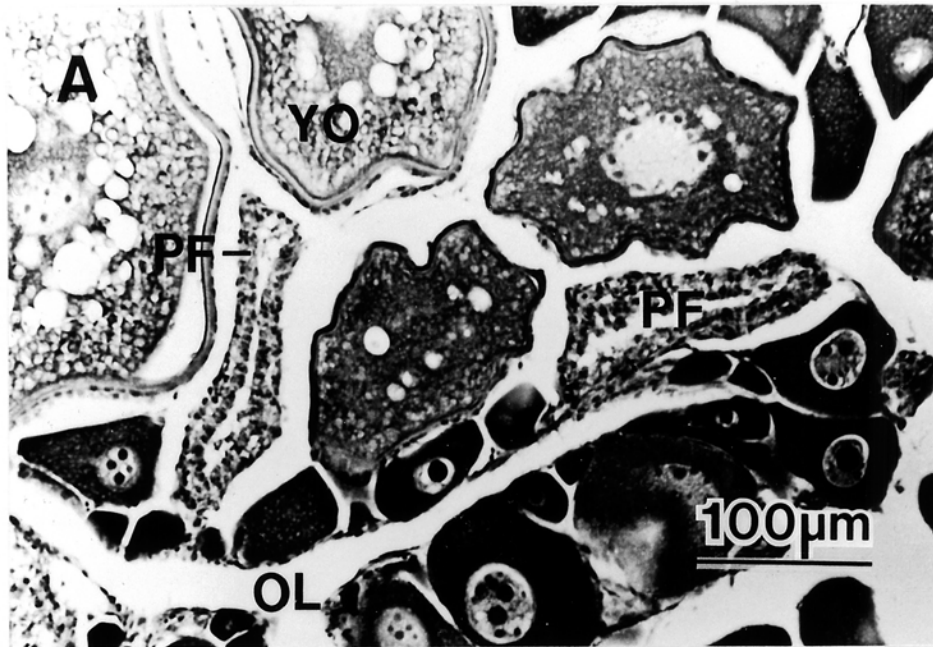
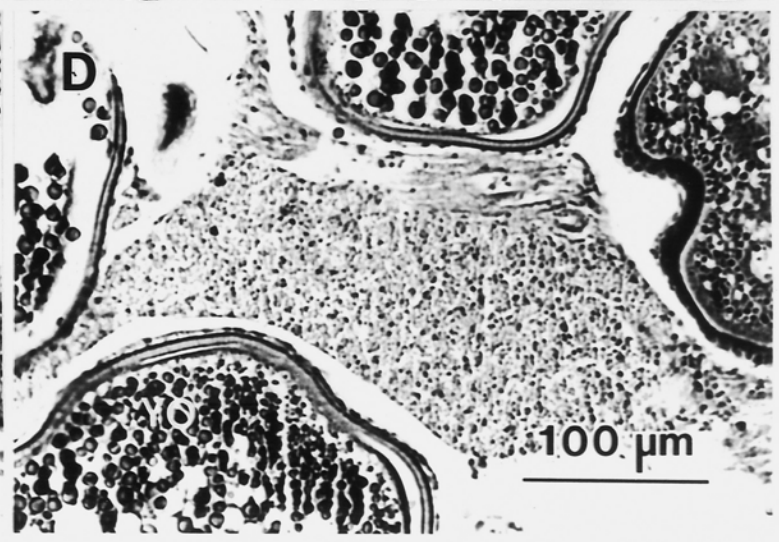
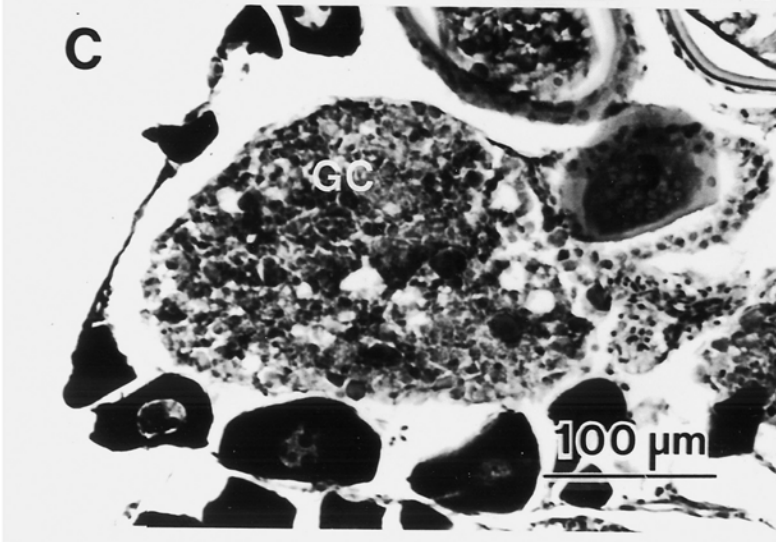
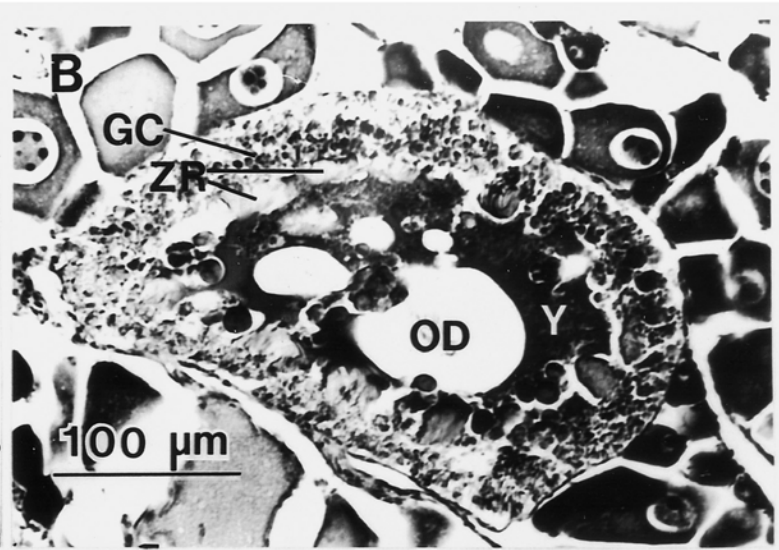
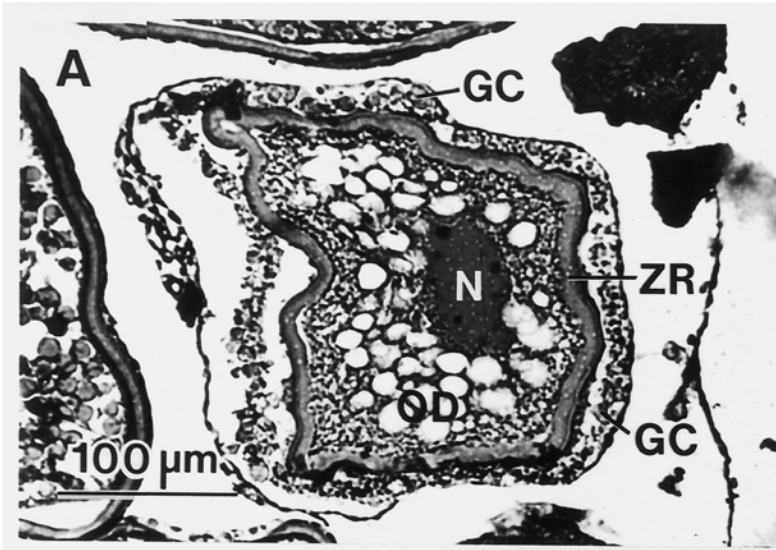


Figure 5. Stages of atresia in yolked oocytes of female C. multinctus. (A) Alpha stage showing hypertrophy of follicle granulosa cells and coalescence of oil droplets. (B) Beta atresia indicated by disruption of the zona radiata (C) Gamma stage in advanced resorption of yolk and cytoplasm by granulosa cells. (D) Delta atresia characterized by large brown-body after full resorption of cytoplasm and yolk. GC: granulosa cells; N: nucleus; OD: oil droplets; Y: yolk; YO: yolked oocyte; ZR: zona radiata.



partial fusion of yolk globules, the centralization of lipid droplets, and the hypertrophy of granulosa cells exterior to the zona radiata. Thecal cells were not observed to invade the egg interior. Similar to that described for the goldfish, Carassius auratus, by Khoo (1975), the end of alpha atresia was defined by the disruption of the zona radiata.

Beta atresia (Figure 5B)- During beta atresia, granulosa cells phagocytosed yolk and enlarged. Amorphous masses of granulosa cells and yolk globules formed within the oocyte. Following Khoo (1975), the end of beta atresia was characterized by the full disintegration of the zona radiata. The presence of blood vessels associated with the oocyte cavity reported for many species (e.g. Bretschneider and de Wit, 1947; Lambert, 1970; Hunter and Macewicz, 1985; Saidapur, 1978) was not observed in atretic ovaries of C. multincinctus.

Gamma atresia (Figure 5C)- Resorption of oocyte contents continued during gamma atresia until completed. Small irregular shaped follicles (lutein cells?) were formed that stained orange-yellow in hematoxylin/eosin (Bretschneider and de Wit, 1947; Hunter and Macewicz, 1985; and Saidapur, 1978). Theca cells of the follicle still surrounded the remnant oocyte.

Delta atresia (Figure 5D)- The delta stage of atresia was identified by the residual cell components after resorption of yolk and cytoplasm. Hunter and Macewicz (1985) and Lambert (1970) reported a dark yellow-brown pigment in the granulosa cells at this stage while Bretschneider and de Wit (1947) described a light yellow material. In C. multincinctus, oocytes contain light brown material under

hemotoxylin/eosin stain and were observed in ovaries examined throughout the year.

Khoo (1975) reported a fifth stage (epsilon atresia) in his study of the preovulatory corpus luteum of the gold fish, C. auratus. He suggested cells of the corpus luteum differentiate into new oogonia cells. The evidence for the epsilon stage was "partially differentiated cysts" that consisted of both oogonia and corpus luteum with yellow pigments. This was not apparent in histological preparations of C. multicolor.

Seasonality of Oocyte Development

The monthly distribution of egg stages from mature females indicates that C. multicolor has a protracted annual spawning season. Histological evidence for impending or recent spawning activity (maturation, hydration, or postovulatory follicles) occurred throughout much of the year, but showed peak activity during March and declined during summer months (Figure 6A). Fish with primary and yolked oocytes were present in all months of the year (Figures 6A, 6B) thus no distinct period of gonad inactivity was found within the sample population. The end of the spring spawning peak in 1982, however, was followed by increases during June and July in the proportion of females that showed no vitellogenic activity (Figure 6C) indicating subsidence of vitellogenic and spawning activity among individuals within the population. Further evidence for a decline in spawning activity was seen in the cycle of alpha and beta atresia in ovaries collected from April through July 1982 (Figure 7A). The occurrence of alpha and beta

Figure 6. Monthly summary of oocyte development in C. multicinctus from field population at Kahe Point. (A) Ovaries that showed histological evidence of impending (oocyte maturation or hydration) or recent (postovulatory follicles) spawning activity. All ovaries in this class also contained yolked oocytes and those undergoing primary growth (PG). (B) Ovaries with oocytes in primary growth and vitellogenesis but no evidence of spawning. (C) Ovaries with only primary growth oocytes. No yolked ova present. Sample size indicated above each month.

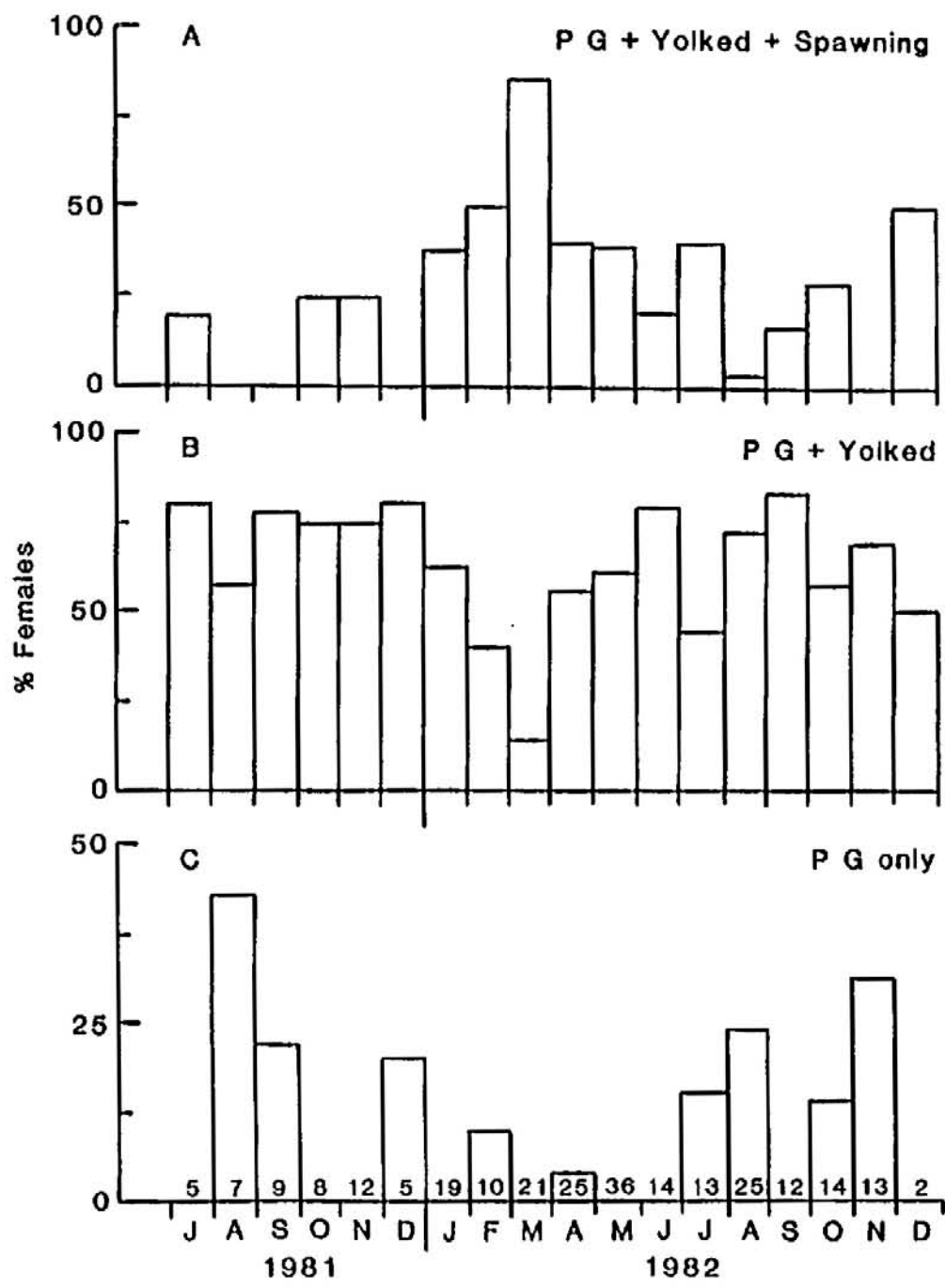
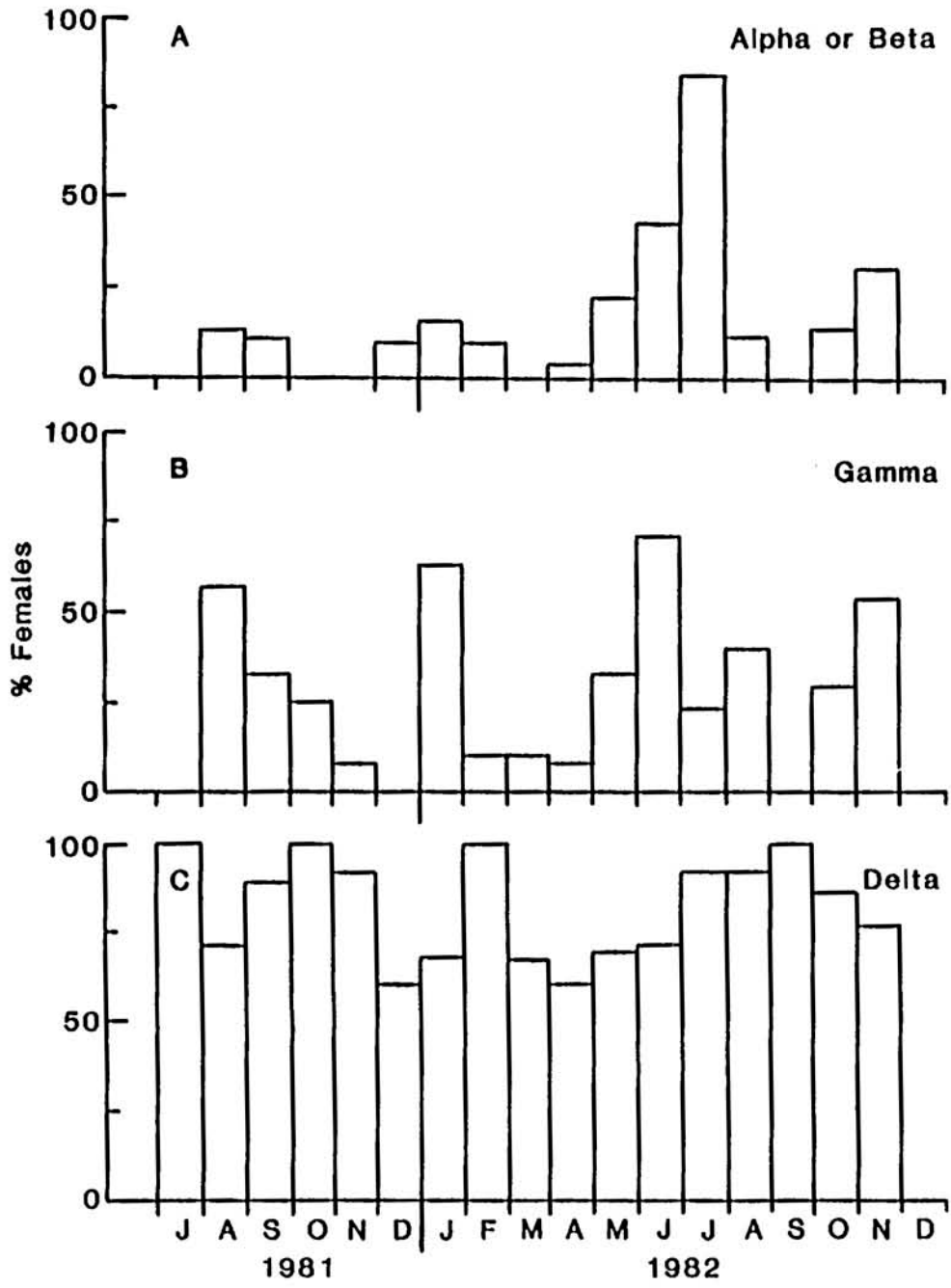


Figure 7. Monthly summary of oocyte atresia in C. multicinctus from field population at Kahe Point. (A) Females with oocytes in alpha or beta atresia. (B) Females containing oocytes in gamma stage. (C) Females with delta stage characterized by brown pigmented cells. Monthly sample sizes as for Figure 6. This classification involves the non-exclusive presence of each atretic stage, thus monthly totals may exceed 100%.



stages of atresia generally coincided with the gamma stage (Figure 7B), but not with delta atresia (Figure 7C), which persisted for much longer periods.

A relatively weak spawning peak was indicated during October through November 1981, and September through October 1982 (Figure 6A). Fall spawning differed markedly from the spring cycle by its relatively short duration and low proportion of spawning females. Both bimonthly periods were followed by one month of spawning inactivity. These apparent fall surges in spawning activity were followed by brief periods of egg atresia from December 1981 through February 1982, and from October through November 1982 (Figure 7A).

Although atresia of yolked oocytes occurred seasonally, the proportion of atretic ova per female was always low even during peak months of atresia for members of the population. Advanced atresia among females, in which greater than 50% of yolked oocytes were degenerate, was highest during August through October 1981 and peaked at 22% (2 of 9 females) in September. Only 8% or less of females undergoing egg atresia in monthly samples during 1982 were in the advanced state. In addition, the presence of atretic oocytes in ovaries of recently spawned females shows that spawning and oocyte regression overlapped. Thus, although spawning may be reduced in intensity during periods of egg degeneration, it is not fully terminated within members of the population.

DISCUSSION

Oocyte Development and Atresia

Oocyte development in C. multicoloratus followed general patterns described for other marine and freshwater teleosts (reviewed by Wallace and Selman, 1981; Nagahama, 1983). In early growth of primary oocytes, nucleoli were centrally arranged within the nucleus as cytoplasm began to increase in volume. As both the cell and nucleus enlarged, nucleoli became peripherally distributed similar to that described for the grey mullet, Mugil cephalus (Kuo et al., 1974). Unlike grey mullet, however, nucleoli in C. multicoloratus persisted in that arrangement throughout vitellogenesis until nuclear degeneration during final oocyte maturation (Figure 3C). Lampbrush chromosomes which first appeared in the nucleus during primary growth also were conspicuous throughout vitellogenesis.

The cortical alveoli stage in C. multicoloratus marked the formation of endogenous "yolk vesicles" and the acceleration of oocyte growth. PAS-positive vesicles formed within the cytoplasm of previtellogenic eggs and contained polysaccharide/glycoprotein compounds (Aketa, 1954; Wallace and Selman, 1981). The redistribution of the vesicles to sites just beneath the cell membrane and the retention of the positive PAS reaction support their precursorial role in the formation of cortical alveoli (Wallace and Selman, 1981). Recently, Selman and Wallace (1986) suggested that the term "yolk vesicles" of earlier literature not be applied to the cortical alveoli precursors since they do not contain exogenous yolk. Cortical alveoli release their contents into the perivitelline space during the cortical reaction at fertilization

(Masuda et al., 1986). This reaction strengthens the egg membrane to protect the embryo and may prevent polyspermy (reviewed by Laale, 1980).

Yolk uptake is an important aspect of egg development for oviparous broadcast spawners because embryos as well as newly hatched larvae depend upon yolk for nourishment. The striations of the zona radiata, which were present throughout vitellogenesis, result from the interdigitation and penetration between follicle/egg cell microvilli (Laale, 1980). Protein yolk precursors transported to the ovary in the bloodstream are incorporated into the oocyte by micropinocytosis (reviewed by Ng and Idler, 1983). Early and late vitellogenic phases could be identified by the width of the zona radiata and diameter of yolk spheres (Table II). Quantitative classification of vitellogenesis by measurement of these subcellular structures eliminated the need to measure egg diameters to determine whether an egg was fully yolked and reduced difficulties in identifying vitellogenesis by egg section diameters.

The cellular events associated with egg maturation overlapped those of egg hydration in C. multicinctus. For example, maturation involved both the migration of the germinal vesicle to the periphery of the cytoplasm, and the fusion of yolk granules into large globules and irregular plates. This broad overlap of cellular changes was also shown for ranges in egg diameters between the two stages (Table II). The onset of egg maturation in morning hours (when all fish were collected) indicates that final maturation begins at least 6-8 hours before dusk, when this species spawns (Lobel, 1978). Final maturation also began in the morning for the related Caribbean pomacanthid angelfish, Holacanthus

tricolor, and was completed in the afternoon for dusk spawning (Hourigan and Kelley, 1985). The total fusion of yolk observed in hydrated eggs increased egg transparency and buoyancy, characteristics that respectively may reduce egg predation by planktivores and enhance egg dispersal for a pelagic spawner like C. multicolor.

Atresia of yolked oocytes occurred at various stages in all months of the year (Figure 7). Alpha atresia was not frequently observed due in large part to the breakdown of the zona radiata relatively early in the atretic process, and it is very likely the most ephemeral of the four stages of atresia. In contrast, alpha atresia in some species was described to include resorption of cytoplasm and yolk (e. g. Bretschneider and deWit, 1947; Hunter and Macewicz, 1985). The complete resorption of egg contents by female C. multicolor was of relatively long duration when compared to other cellular events, and no formation of blood vessels was found as described for other species (Bretschneider and deWit, 1947; Lambert, 1970; Hunter and Macewicz, 1985). Beta and gamma atresia in C. multicolor were more commonly observed, and were probably longer-lived than the alpha stage because the former include yolk and cytoplasm resorption. In this regard, egg atresia in C. multicolor was most similar to that reported for the goldfish, Carassius auratus by Khoo (1975) who also described termination of egg resorption at the end of gamma atresia. Delta atresia was present in many ovaries throughout the year which indicates that this stage persists for very long periods of time. Although not verified for the

present species, these structures may be involved in the formation of new oogonia (Khoo, 1975).

Deteriorated postovulatory follicles are often difficult to distinguish from later stages of atresia (Khoo, 1975; Hunter and Macewicz, 1985). Fresh postovulatory follicles could be readily identified by a distinct cavity within a multilayered band of follicle cells that showed clear cellular detail (Figure 4B). In contrast, older postovulatory follicles usually formed small solid masses of degenerate follicle cells. The smaller size of postovulatory follicles compared to alpha, beta, and gamma atretic structures (Table II) was also a useful means to eliminate confusion between the two structures (sensu Khoo, 1975). To avoid problems related to age of postovulatory follicles, only fresh follicle masses were used in analyses of spawning activity.

Unfortunately, quantitative estimates of degenerative rates for each stage of atresia could not be made from this study. These could be determined, however, by experiments in which ripe females are placed under starvation conditions, sacrificed at regular intervals, and oocyte resorption histologically determined. Hunter and Macewicz (1985) observed that ovarian atresia was a more sensitive indicator of female anchovy reproductive seasonality in different size classes than the occurrence (or lack) of postovulatory follicles. In tropical marine species, where atresia occurs relatively rapidly, data on rates of ovarian atresia in conjunction with the presence of postovulatory follicles would greatly increase the accuracy of characterizing reproductive patterns.

Spawning Seasonality

The broad pattern of oocyte development across sample months shows that C. multincinctus has a protracted annual spawning period. The occurrence of oocytes undergoing primary growth during all months of the year indicates a constant recruitment of new eggs and a lack of complete ovarian inactivity for the population. This is further supported by the presence of yolked ova in all monthly samples and direct histological evidence of spawning activity throughout most of the year (Figure 6).

Although C. multincinctus clearly exhibited a protracted spawning period, two seasonal peaks may exist. Reproductive activity was highest during March in 1982 when 86% of females showed signs of spawning (Figure 6A). This was preceded by a decline in the monthly proportion of adult females without yolked eggs (Figure 6C) and indicates new reproductive activity of some females. High levels of spawning activity continued through the spring and subsided during the summer (Figure 6A). This decline was accompanied by an increased proportion of females that lacked vitellogenic eggs in July and August 1982 (Figure 6C), and an increase in females with alpha- and beta-stage atretic oocytes (Figure 7A). Advanced atresia (greater than 50% of yolked oocytes in atresia) occurred in 8% or less of females during that period, and thus does not appear to mark a clear postspawning period for the population as in temperate fishes with more distinct egg atresia that follows the spawning season (e. g. Crossland, 1977). Furthermore, alpha or beta atresia often co-occurred with maturing eggs or fresh postovulatory follicles. Thus, atresia in tropical species with protracted spawning periods may better indicate a decline in reproductive output by

individuals or termination of spawning among a portion of females rather than the end of the spawning for the entire population.

A second spawning peak may exist during the fall. Ovaries with histological evidence of recent or impending spawning were collected during October through November 1981, and September through October 1982 (Figure 6A). These periods were preceded by increased proportions of females that showed no vitellogenic activity (Figure 6C), thus indicating new periods of ovary recrudescence. Periods of fall spawning activity were followed by increased levels of egg atresia from December 1981 through February 1982, and October–November 1982 (Figures 7A, 7B).

Temperate species often have relatively short spawning seasons followed by long periods of gonad inactivity and prolific oocyte atresia (e.g. Crossland, 1977; Hunter and Macewicz, 1985). In contrast, oocyte atresia in C. multicinctus occurred among a comparatively low number of oocytes within an ovary, among only a portion of females, and peaked for only a few months during the year. The numerical paucity of atretic oocytes reflects a protracted spawning season of this tropical species and relatively short periods of arrested oogenesis. The overall reproductive activity of C. multicinctus may be limited by the amount of food available to fishes as demonstrated for other marine species (Tyler and Dunn, 1976; Wooten, 1979; Hunter and Macewicz, 1985).

The histological staging of eggs provided important indications of spawning activities. Egg maturation and hydration, for example, occur several hours prior to ovulation and spawning (Wallace and Selman, 1981; Hourigan and Kelley, 1985) and was used extensively to determine

spawning for C. multicoloratus. The best histological evidence of recent spawning activity, however, was the presence of postovulatory follicles. These structures are formed within the ovary after the egg is ovulated from its surrounding follicle cell layer just prior to spawning. Postovulatory follicles degenerate rapidly and become difficult to distinguish from the latter stages of normal follicle atresia (Khoo, 1975; Hunter and Macewicz, 1985). Furthermore, degeneration rates are probably an increasing function of water temperature and their value as indicators of recent spawning is limited to collections made immediately following spawning. For example, in the temperate northern anchovy, Engraulis mordax, identifiable postovulatory follicles persist up to 48 h after spawning (Hunter and Goldberg, 1980). Takita et al. (1983) reported the presence of postovulatory follicles in ovaries of aquarium held Callionymus enneactis (a tropical species) up to only 15 h after spawning. Assuming that C. multicoloratus of the present study ovulated the day following HCG-treatment, 24 h would be a conservative estimate of the persistence of postovulatory follicles in this species since ovaries were fixed about 36 h after injection. The presence of identifiable postovulatory follicles in field collections (all collected before 1200 h) supports this minimum estimate since C. multicoloratus spawns at dusk (Lobel, 1978). These rates would be subject, however, to ambient water temperatures and may vary with season. Rates of postovulatory follicle resorption could be more precisely determined for C. multicoloratus or other tropical fishes by examining an experimental time series of ovarian tissue from females induced to ovulate by

hormonal injection as done for temperate species (Leong, 1971; Hunter and Goldberg, 1980).

The distribution of oocytes within ovaries indicated that females produce multiple egg batches over the course of the spawning season. The recruitment of an egg batch began with vitellogenesis of oocytes at the end of primary growth, and often occurred while the preceding batch was still in vitellogenesis. The most critical finding to support multiple spawning was the hydration of almost all eggs within a batch and their concurrent association with groups of smaller vitellogenic ova. This dynamic distribution of eggs has been termed "group synchronous" development (Marza, 1938; Wallace and Selman, 1981) and indicates the existence of multiple batches that are shed serially over time. A more detailed analysis of the size-frequency distribution of ova shows that C. multicinctus spawns, perhaps multiply, during weeks prior to new and full moon phases with discrete modes of vitellogenic oocytes consistently present after each spawning (Chapter II).

Sexual Differentiation

Histological analysis of juveniles shows that C. multicinctus recruit to the reef at a small size and in a sexually undifferentiated state (Table I). Females differentiated as early as 44 mm SL and at body sizes approximately 20 mm smaller than males. Testicular tissue most commonly arose from undifferentiated cell lines, but apparently can secondarily arise from previously differentiated female tissue.

An important aspect of the secondary testicular development in C. multicinctus is its occurrence prior to ovarian maturation. In many

fish families, the development of the indifferent gonad into ovarian tissue by all fish ("undifferentiated gonochorists") is considered an indeterminate state prior to the development of male tissue (e.g. Atz, 1964; Yamamoto, 1969). In "differentiated gonochorists" the indifferent gonad develops directly into either testis or ovary. The fact that most C. multinctus males developed directly from indifferent gonads would indicate this species is better classified as a differentiated gonochorist. Because of the limited sample of fish undergoing sexual differentiation, however, it is difficult to determine whether sex inversion in C. multinctus is a common, short-lived process of male differentiation rather than a rare and relatively unimportant aspect of sexual differentiation in a predominantly gonochoristic species.

Sex change is widespread among teleost fishes (recently reviewed by Charnov, 1982), and has arisen separately among at least 12 different phyletic lineages (Smith, 1975). Sex change in strictly monogamous fishes, however, is relatively uncommon. The best known examples are from the protandric anemonefishes, Amphiprion bicinctus (Fricke, 1973; Fricke and Fricke, 1977) and A. melanopus (Ross, 1978) that form monogamous pairs and defend the anemone territory. Sex change in those systems may function to maintain heterosexual pairing in a resource-limited environment.

The best developed model for the adaptive value of sex change is the size-advantage hypothesis that states sex change will be favored when reproductive success is differential between sexes with respect to age or size (Ghiselin, 1969; Warner, 1975). This model, however, is

inappropriate for C. multicinctus because sex change always occurred prior to reproductive maturation. One possible advantage unrelated to adjustments in relative measures of reproductive effort between the sexes is the assurance of obtaining a mate under severe ecological conditions (sensu Liem, 1968) or existing social constraints. Like many obligate coral-feeding butterflyfishes, C. multicinctus forms long-term monogamous pairs that cooperatively defend permanent feeding territories from other corallivorous fishes (Tricas, 1985). New recruits show very limited movements and spend their first few months at a restricted site in close association with the reef interstices to avoid fish predators and aggression from larger conspecifics. At approximately 50 mm SL, histologically identifiable females often form pairs and begin to establish small feeding areas in suboptimal habitats or between existing adult territories. Because a mate is essential for defense of a feeding area and suitable coral habitat is often limited (Tricas, 1985), homosexual "protopairing" of juvenile females may represent an adaptation to enhance the early establishment of successful feeding territories in a highly competitive environment. Subsequent differentiation of one individual into a functional male may occur after pair formation, and is perhaps determined by behavioral interactions among pair members. This phenomenon may function to ensure a heterosexual mate in a monogamous mating system where social contact between sexes is constrained by strong selection for early site attachment.

CHAPTER II
GROWTH AND REPRODUCTIVE STRATEGIES

INTRODUCTION

Butterflyfishes represent an ecologically diverse family that forms a major component of coral reef fish communities throughout the world (Burgess, 1978). Chaetodontids are common and conspicuous inhabitants of most coral reefs, and are often the focus of studies on reef fish community structure (Anderson et al., 1981; Findley and Findley, 1985), social organization and mating systems (Reese, 1975; Gore, 1982; Neudecker and Lobel, 1982), and feeding ecology and behavior (Birkeland and Neudecker, 1981; Harmelin-Vivien and Bouchon-Navaro, 1983; Gore, 1984). In spite of their utility in such studies, very little is known about their life history and population dynamics. Ralston (1976a; 1976b; 1981) examined growth, food habits, and reproduction for the Hawaiian planktivore, Chaetodon miliaris, which is the only species studied in detail to date.

Of special significance to studies on the behavioral ecology of chaetodontids is their life history characteristics which may be used to assess individual fitness. Butterflyfishes, like many other reef species, are broadcast spawners which shed their gametes directly into the water column. This mode of reproduction makes it extremely difficult to assess reproductive success of adults because offspring can not be tracked through their early life history. Because of this, information on reproductive output, spawning periodicity, and growth

which can be determined for adult populations is crucial to explaining behavioral adaptations to their environment and social systems.

This chapter examines in detail the life history of C. multicinctus with emphasis on the strategies of growth and reproduction to help interpret the foraging and territorial behaviors of this species that are presented in subsequent chapters. Do females increase reproductive output with increased body size? Are all fish pairs heterosexual, and what is the size relationships among mates? What strategies do fish use to maximize fitness and the survival of offspring? How do individuals allocate resources to growth and reproduction during their lifetime, and what type of variability exists between individuals?

METHODS

C. multicinctus were collected over an 18-month period on shallow coral reefs (3-10 m deep) near Kahe Point on the west shore of the island of Oahu, Hawaii (Figure 1). A total of 58 collections were made during this study. All but one of the 1981 samples were taken semi-monthly from July through December, while those in 1982 were made weekly.

Fish were collected between 0900 and 1200 h by divers using scuba. When possible both male and female pair members were speared, placed in plastic bags, and transported on ice to the laboratory for preparation. Standard length (SL) was measured to the nearest mm. Whole body and gonad weights were determined to the nearest .001g. Reproductive tissues were fixed in 10% buffered Formalin for at least 2 days, rinsed

in fresh water, and preserved in 70% isopropyl alcohol. Fish bodies were then frozen and stored for subsequent fat and otolith analyses.

Visual surveys were made during collection dives to record periods of juvenile recruitment to the reef. New recruits were identified by their small size (approximately 30-35 mm SL) and relatively deep body. Recruitment data were supplemented with those taken during surveys of artificial settling "habitats" by researchers from the Hawaiian Electric Company (Coles et al., 1982). Ambient water temperatures at Kahe Point were obtained from a thermal monitoring records of the Hawaiian Electric Company at sites within the sampling area.

Sexual Maturation

Sexual maturity in this study was defined as those individuals that could potentially spawn viable ova. For females, this was histologically determined by the presence of yolked oocytes in their ovary. Mature males were identified by either the microscopically determined presence of live sperm during gonad removal or the full development of testicular structures determined by histological examination (see Chapter I). Since reproductive activity in the study population varied over time, some females sampled during non-reproductive periods may not have appeared reproductively mature because of a lack of yolked ova. Thus, this is a conservative estimate of maturity, especially for females.

Gonad Analyses

Egg diameter frequency distributions were determined for ovaries collected during all months of the study by the general procedures of Clark (1934) and Hunter and Goldberg (1980). Preserved ovaries were blot dried and reweighed. Subsamples of approximately .01-.02 g were taken from the ovary midsection [oocyte development is homogeneous throughout ovaries (Chapter I)], teased apart with dissecting needles, and viewed under a compound microscope. All yolked and more advanced oocytes (approximately > .250 mm diam.) in each sample were measured with an ocular micrometer.

Total fecundity (F_t), defined here as the total number of yolked oocytes within an ovary, was estimated by the formula:

$$F_t = \frac{OW \times NO_t}{SW} ,$$

where OW = total ovary weight, NO_t = number of yolked ova in the subsample, and SW = subsample weight.

Batch fecundity (F_b), defined as the number of yolked eggs in the largest egg mode, was estimated by the formula:

$$F_b = \frac{OW \times NO_b}{SW} ,$$

where NO_b = the number of yolked ova in the largest egg mode (the batch) within the subsample.

Final egg maturation, hydration, and ovulation can be induced in many species by the administration of gonadotropin hormones (Donaldson and Hunter, 1983). This technique was used in the present study to

verify that all eggs in the largest mode were shed in a single spawning. During February, March, and May 1982; and March, 1983, a total of 16 adult female fish (standard length = 71-94 mm) were collected with handnets by divers and transported to the Waikiki Aquarium. Each fish was given a single intramuscular injection of human chorionic gonadotropin (Sigma) (approximately 10 IU/gbw) and placed in large holding tanks supplied with fresh running seawater at 23.5-25.0 °C. After 32-36 hours, ovulated eggs were stripped from fish by applying finger pressure along the abdomen and deposited into a known volume of seawater. Ovaries were removed and any free ovulated eggs collected from the body cavity and added to the sample. The egg suspension was stirred, a 1-cm volume pipetted, and the number of eggs in the sample counted. The mixture was subsampled in this way a total of six times. From the mean density of eggs per ml was calculated the total number of eggs in the seawater which represented the estimate of batch fecundity.

The presence of postovulatory follicles was used as an indicator of recent spawning for determination of reproductive synchrony among females within collection samples and subseasonal spawning periodicity. Details of tissue preparation and staining are described in Chapter I. Histological data from 138 females were used in this analysis.

Body Fat

Fat stores in C. multicinctus are deposited along the intestinal tract and peritoneal lining of the body cavity. To determine seasonal patterns of visceral fat deposition, gravimetric analyses of lipids was

performed on 297 individuals. Frozen fish were thawed, dissected, and all organs (except gonads) and fat bodies contained within the coelomic cavity removed. Visceral masses were placed individually in large test tubes containing 30 ml of pre-warmed chloroform-methanol solvent (2:1 ratio by volume), sealed, and incubated in a waterbath at 37 °C for 18-24 h. After extraction, visceral tissue was removed, rinsed with a chloroform-methanol stream collected back into the test tube, then discarded. Undissolved sediments in the solvent were removed by double filtration through a syringe filter fitted with a two-ply layer of paper and glass-fiber filter discs. The lipid-solvent mixture was reduced by evaporation, transferred to preweighed aluminum pans, and dried in a 50 °C oven. After solvent evaporation was complete, pans were reweighed and residual lipid weight calculated. Ten pans that contained only chloroform-methanol solvent were also processed as controls to determine the mass of solvent contaminants. This value (always negligible) was subtracted from each lipid sample weight.

Age Determination

Prior to estimation of age-length data from otolith analyses, experiments were conducted to verify the daily deposition of growth increments on otolith sagittae in fish collected from the field. At the Hawaii Institute of Marine Biology a total of five fish (33-52 mm SL) were given a single intramuscular injection of tetracycline hydrochloride at a dose of 100-225 mg / kg body weight. Fish were held individually in aquaria supplied with fresh running seawater at 22.0-26.0 °C and exposed to a 12:12-h photoperiod. Aquaria were supplied

each day with fresh colonies of the highly preferred food coral Pocillopora damicornis. Fish that recovered from handling and injection stress fed readily on the coral polyps within about three days. After termination of the post-treatment period, otolith sagittae were removed (see below), cleaned, dried, placed in non-florescent immersion oil, and examined under a reflected ultraviolet (350 nm) light through a compound microscope at 800 x. At filtered reflected wavelengths of 700-800 nanometers, the tetracycline mark appeared as a florescent blue-green band inside the outer edge of the otolith. An ocular pointer was used to mark the band location and rings beyond that point enumerated under a tungsten light source.

Otoliths of 27 C. multicinctus collected at Kahe Point were prepared to count lamellar curculi in order to establish a species growth curve. The sagittae, which is the largest otolith pair, were accessed by a horizontal section through the top of the head just above the orbits and the sulcus (a membranous sac that contains the sagittae) extracted. Membranes were removed under a dissecting scope and otoliths air dried. One sagitta was randomly chosen from each fish and embedded in casting resin. A frontal section was cut on a diamond saw, hand sanded on 400 grit carbide paper until the core and its concentric rings were visible under a compound microscope, and polished with fine aluminum oxide paper. Otolith sections were etched in a 1% HCl solution for approximately 1 min, rinsed in water, and air dried. Each finished preparation was mounted in Euparal clearing medium on a glass slide and covered with a glass cover slip. Most small otoliths could be read

immediately while some larger preparations required up to 2 months to clear. Otoliths were read from the core to the outer margin along the postrostral axis under a compound microscope at 600-800 x. Each sagitta was read at least 3 times and the mean number of rings calculated. Count repeatability within each otolith was good as coefficients of variation (ratio of variance to mean x 100) was low among samples ($\bar{X} = 2.9$, S.D. = 1.5, n = 27).

RESULTS

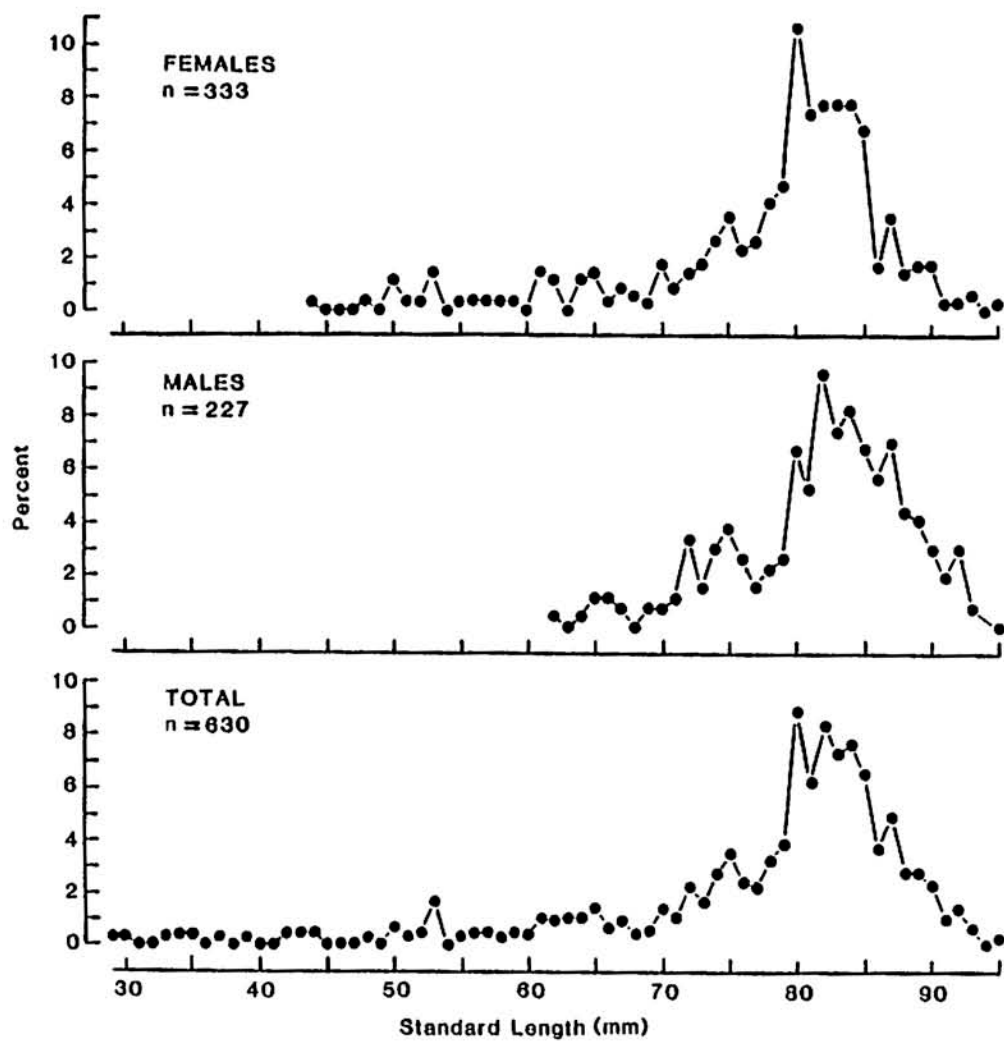
A total sample of 630 C. multicinctus between 29-95 mm SL was collected over the 18-month study period. Seventy individuals showed no evidence of sexual differentiation as determined by gonad histology. Females generally differentiated at smaller sizes (minimum = 44 mm SL) than did males (minimum = 62 mm SL). The largest undifferentiated individual examined was 64 mm SL (see Chapter I).

Length frequency data of fish from all collection dates are given in Figure 8. All size classes that occur on the reef were sampled. The smallest fish were new recruits and the largest a 95 mm-SL female. The highest proportion of reproductively mature fish fell within the 80-84 mm size class (females = 43%; males = 53%). Males generally reached larger sizes than females as reflected in their greater proportion in size classes above 85 mm SL.

Sexual Composition of Social Pairs

While attempts were made to collect both members of a fish pair, first priority was given to capture of females (often distinguished by a

Figure 8. Length frequency distribution of fish sampled at Kahe Point.
Data combined from all collections.



swollen abdomen or behavior) for reproductive analyses. As a result, males escaped capture more often than females. This sampling bias and the collection of unpaired immature fish resulted in females comprising 60% (333/560) of sexually differentiated individuals and thus does not reflect the natural sex ratio of the adult population. Of 229 pairs that included reproductively mature individuals, 97% were heterosexual associations with the remainder homosexual female pairs. Complete breakdown for pair combinations in the entire sample is given in Figure 9. Of these, 90% were heterosexual associations and males averaged 1.5 mm longer than their female mates ($P < .0001$; paired t-test, $n = 250$ pairs). The remaining associations consisted of homosexual pairs or associations between adults, immature fish, and sexually undifferentiated individuals, and no homosexual adult male pairs were found.

Sexual Maturity

Size at sexual maturity can be identified as the size class in which greater than 50% of a given sex is mature. Over half of the females sampled between 71-75 mm SL were reproductively mature as determined by the presence of yolked oocytes in ovaries (Table III). Although the proportion of mature females was high in larger size classes, only ovaries from females greater than 86 mm SL always contained yolked ova. Of all females > 76 mm which failed to show evidence of yolked oocytes, only one was collected during months other than July through September (non-reproductive season). These large

Figure 9. Sex composition of all social pairs of C. multicinctus collected at Kahe Point. M = male, F = female, U = undifferentiated.

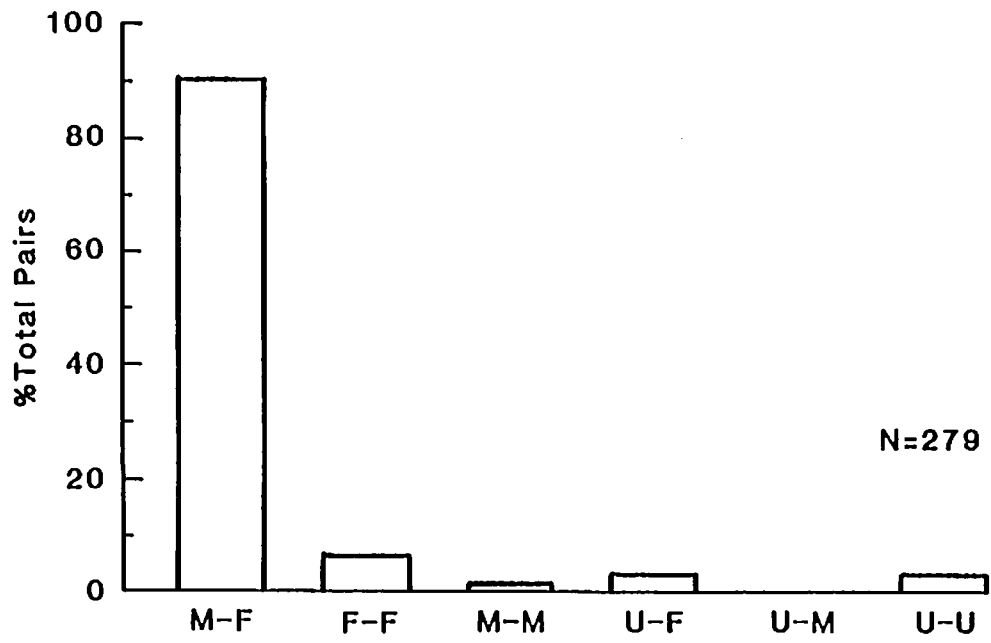


Table III. -- Size at sexual maturity for C. multicinctus. Maturity classified by presence of yolked oocytes (females) and live sperm or complete testicular development (males).

| Size Class (mm SL) | Females | | Males | |
|-----------------------|---------|----------|-------|----------|
| | n | % Mature | n | % Mature |
| 44 - 65 | 37 | 0 | 4 | 50 |
| 66 - 70 | 14 | 11 | 8 | 50 |
| 71 - 75 | 34 | 59 | 28 | 82 |
| 76 - 80 | 78 | 89 | 36 | 100 |
| 81 - 85 | 123 | 94 | 100 | 100 |
| 86 - 90 | 33 | 100 | 65 | 100 |
| 91 - 95 | 5 | 100 | 15 | 100 |

females may have been collected when sexually mature but reproductively inactive.

Fully developed testicular tissue was found in over half of the males between 71-75 mm SL. Although live sperm was often not detected during preparation of fresh gonads (especially during the non-reproductive season), all males > 75 mm showed full development of unrestricted spermatogonia, associated efferent ducts, and vas deferentia (see chapter I) as determined by histological examination. Thus, both sexes of C. multicinctus reach sexual maturity at about 75 mm SL even though females may differentiate at smaller sizes than males (Chapter I).

Length-Weight Relationships

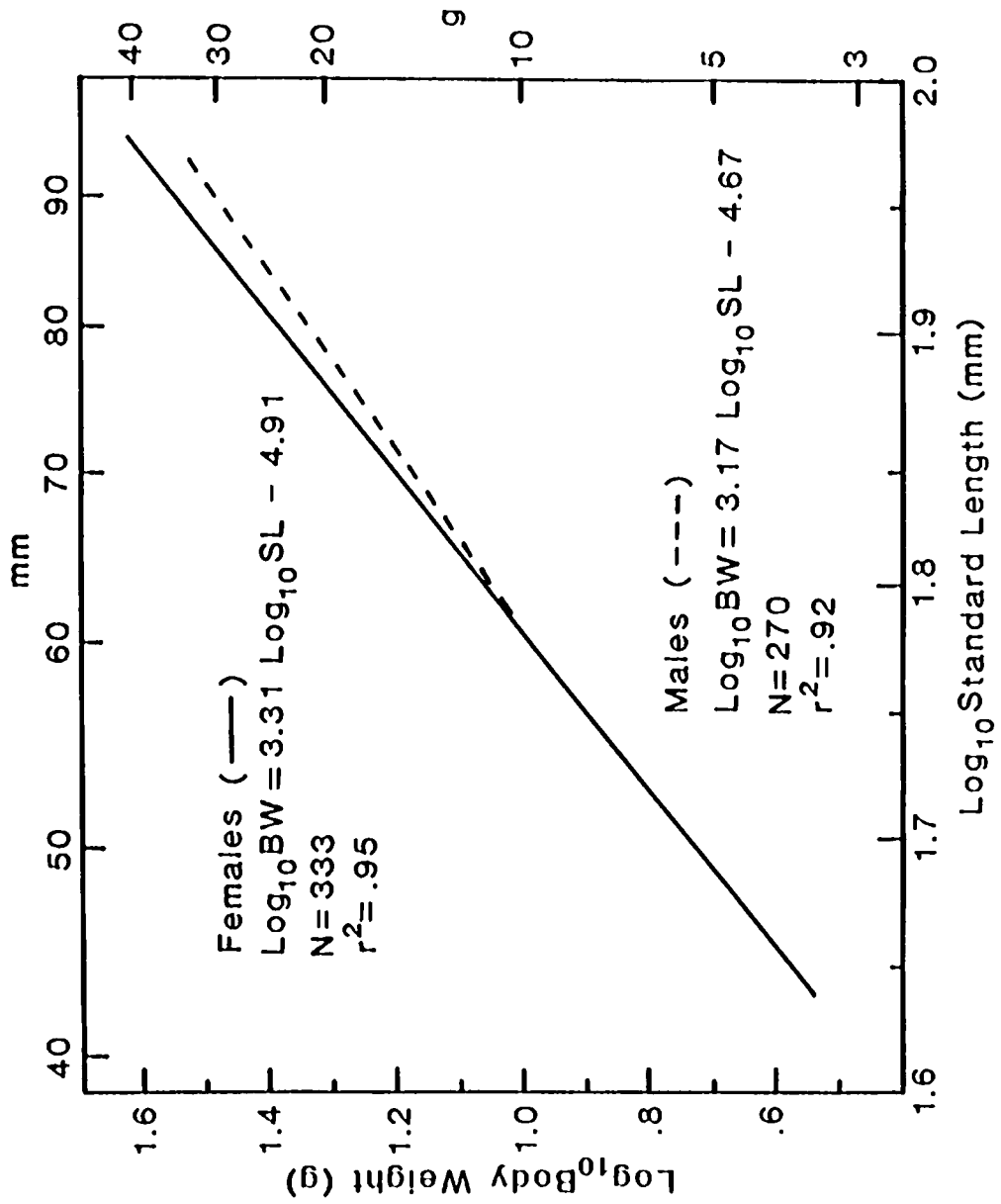
Length-weight relationships for sexually differentiated fish are given in Figure 10. Although both sexes attain sexual maturity at about 75 mm SL, females differentiated at smaller sizes than males (Chapter I) and therefore span a greater range of body sizes. An analysis of covariance shows that the slopes of length-weight relationships differ between sexes ($df = 1$, $F = 6.64$, $P < .01$), thus separate regression equations were calculated. The functional regression equation (sensu Ricker, 1973) for the total sample of C. multicinctus (including undifferentiated individuals) is:

$$\log_{10}BW = 3.26 (\log_{10}SL) - 4.82$$

$$(n = 603; r^2 = .95)$$

where BW = body weight in grams and SL = standard length in mm.

Figure 10. Length-weight relationships by sex in C. multinctus.
Regression equations expressed as functional regression (Ricker, 1973).



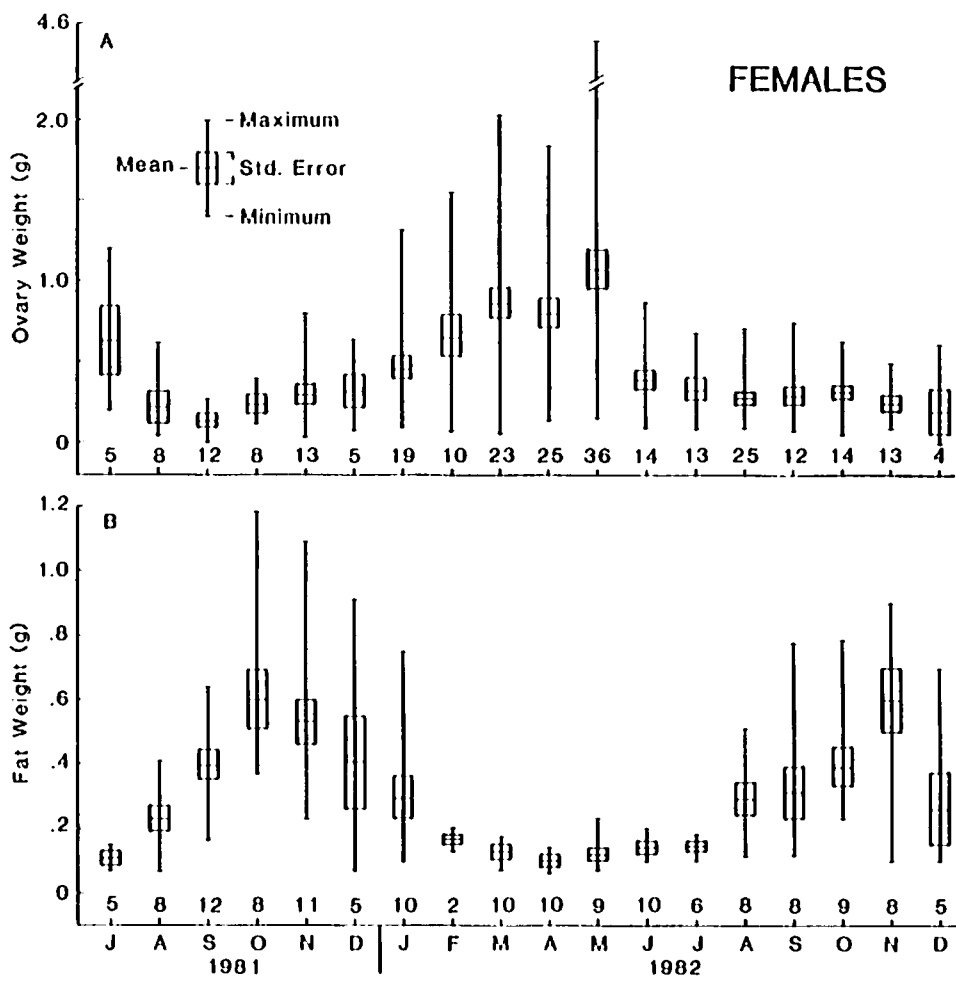
Although length-weight relationships are undoubtedly related to differential gonad development, the difference still holds true on a gonad-free weight basis (327 females, 266 males. Analysis of covariance: $df = 1$, $F = 4.15$, $P = .042$). Thus, females gain body mass faster than males independent of differential gonad development.

Seasonal Patterns of Gonad Development

Seasonal variation in gonad size was expressed as mean gonad weight for fish collected in each month. A gonadosomatic index (ratio of gonad weight to body weight) was not used because of problems in comparison between fish of different sizes, and associated gonad-body allometries (de Vlaming et al., 1982). An analysis of covariance of log gonad weight versus log body length showed slopes of each monthly sample were homogeneous (females: $df = 17$, $F = 1.30$, $P = .20$; males: $df = 17$, $F = 0.98$, $P = .49$), and adjusted means followed patterns very similar to the monthly means plotted for gonad weights. Differences in monthly means, therefore, were a result of true changes in gonad size and were not due to variability in lengths of fish sampled each month.

Sexually mature individuals of both sexes showed seasonal recrudescence and diminution in gonad size. For females, mean ovary weight decreased from July through September 1981, increased each month, and peaked in May 1982 (Figure 11A). Ovary size then abruptly declined and remained at low levels for the remainder of the year. Testicular size among males showed a similar seasonal pattern. Like females, male gonads declined in average weight from July through September 1981 but exhibited a less distinct pattern of increase through their peak in May

Figure 11. Monthly pattern of mean gonad and visceral fat weight for female C. multicoloratus. Numbers indicate monthly sample sizes.



1982 (Fig 12A). Testes size decreased during the remaining months of the year.

Reproductively active females exhibit a multimodal distribution of developing ova in their ovaries. Mean diameter of the largest mode of developing ova are shown for monthly samples of females in Figure 13. Mean egg size was lowest during August in 1981, increased through the fall months, and peaked from winter through spring 1982. Maximum diameter decreased from June through August 1982 and then showed a brief increase during the fall months. Ova diameters increased to near maximum size in November 1981 and indicated spawning activity even though mean gonad weight was relatively low (Figure 11A). Spawning activity, however, was not consistent among all members of the population as shown by the high variability in ova diameters among females in some monthly samples. For example, although mean ova size was relatively large among females in February and March 1982, these samples included large females without yolked eggs. Conversely, reproductive activity among some females was indicated in August of both years since some females had fully yolked eggs. Thus, on the basis of ova diameter C. multicinctus showed a period of spawning activity from October through May. This agrees with histological evidence presented in Chapter I for spawning during fall and spring months. While this protracted spawning season may be a valid description of the population, however, there is a high degree of individual variability in spawning activity. Furthermore, samples were taken at least six hours prior to spawning and large hydrated eggs were rarely found.

Figure 12. Monthly pattern of mean gonad and visceral fat weight for male C. multicoloratus. Numbers indicate monthly sample sizes.

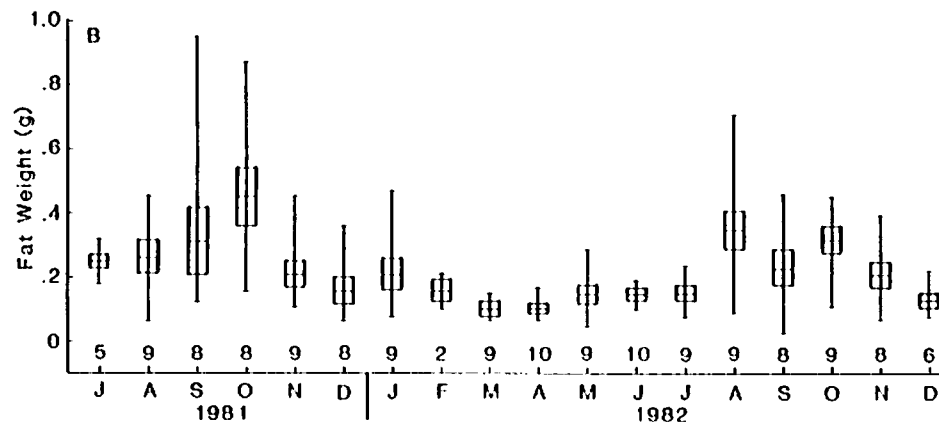
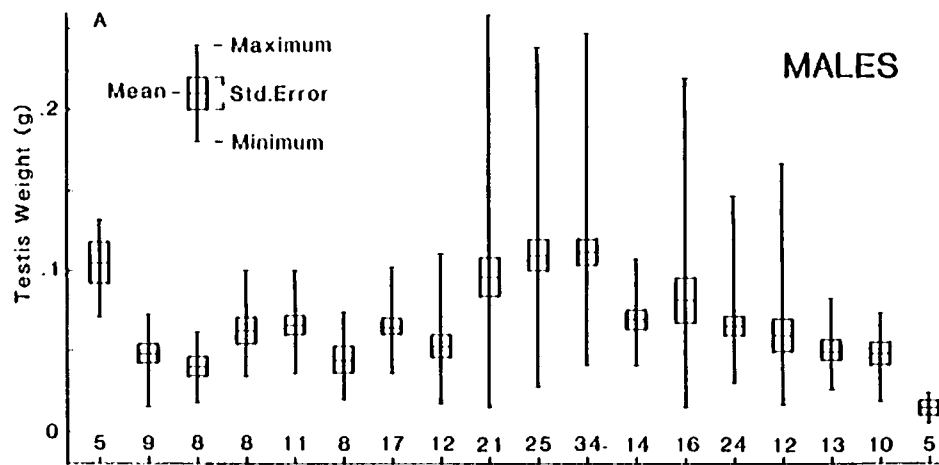
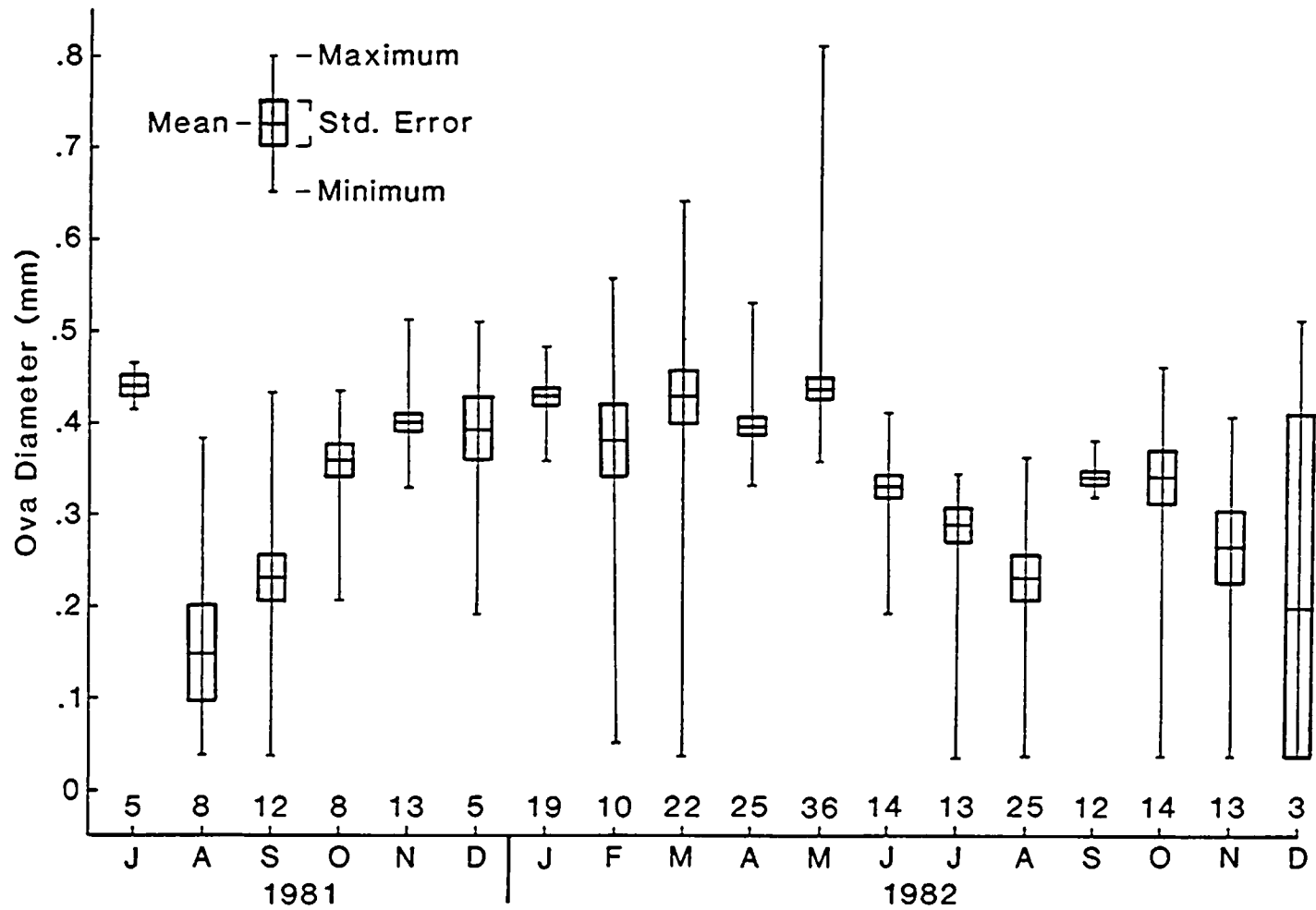


Figure 13. Mean monthly diameters of largest egg mode in female C. multicinctus. Numbers indicate monthly sample sizes.



Lunar Spawning Periodicity and Population Synchrony

Spawning activity within the Kahe population was synchronized with a semi-lunar cycle. For the peak spawning period from January through June 1982, histological evidence of recently formed postovulatory follicles appeared in ovaries over a span of nine days prior to and one day beyond the new moon phase, and nine days prior to the full moon (Figure 14). No histological evidence of spawning was found other than those days for any female.

Spawning activity of females within the population, however, was not highly synchronized on a daily schedule. Individuals from the same collection showed high variability in the size of the largest egg mode (Figures 15, 16, 17). Furthermore, females collected on the same days in March showed histological evidence of either recent spawning (probably on the previous day), final stages of egg maturation, or no evidence of spawning. Of 40 females in which fresh postovulatory follicles were identified, only two showed coincident final egg maturation or hydration. This provides good evidence that fish do not spawn on successive nights. The mean diameter of the next developing egg batch in recently-spawned females was .321 mm compared to .375 mm for fully yolked ova just prior to maturation. These data indicate that females spawn all eggs in the largest mode at each spawning, and that egg batches differ in mean diameter by approximately .05 mm.

Seasonal Patterns of Fat Storage

Seasonal variation in fat storage was expressed as mean fat weight for fish collected in each month rather than a ratio of body weight for

Figure 14. Lunar spawning periodicity of C. multicolor as determined by the presence of postovulatory follicles in ovaries from females collected at Kahe Point from January through June 1982. Moon phases indicated by open (full), closed (new), and half-filled (quarters) circles. Numbers above lunar day indicate number of females examined.

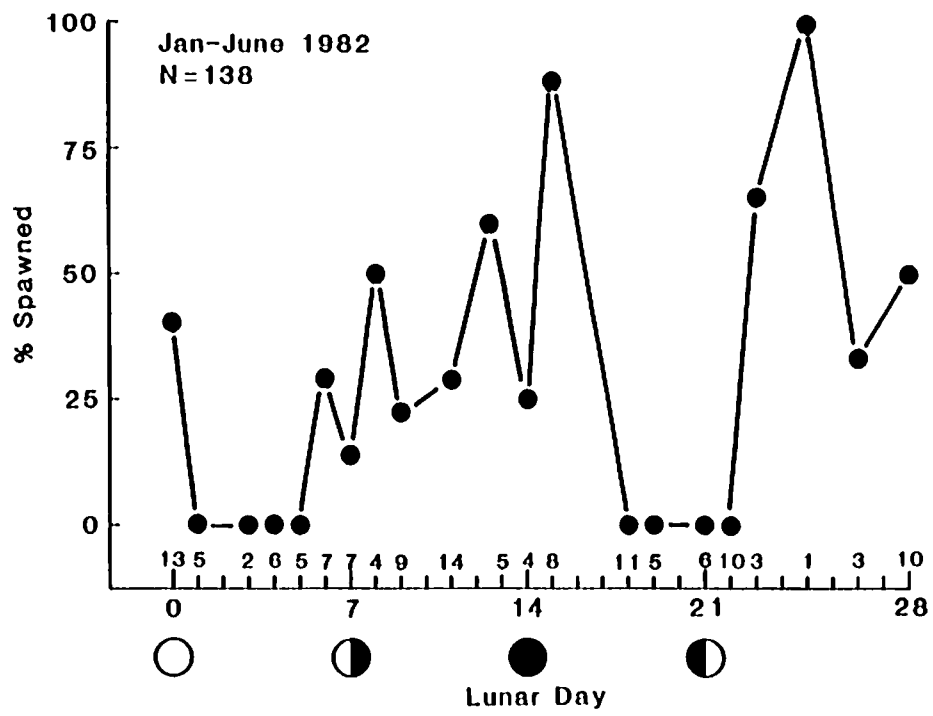


Figure 15. Size frequency distribution of yolked ova in ovaries collected during March 1982. Numbers in parentheses indicate lunar day as in Figure 14. Each distribution is for one female.

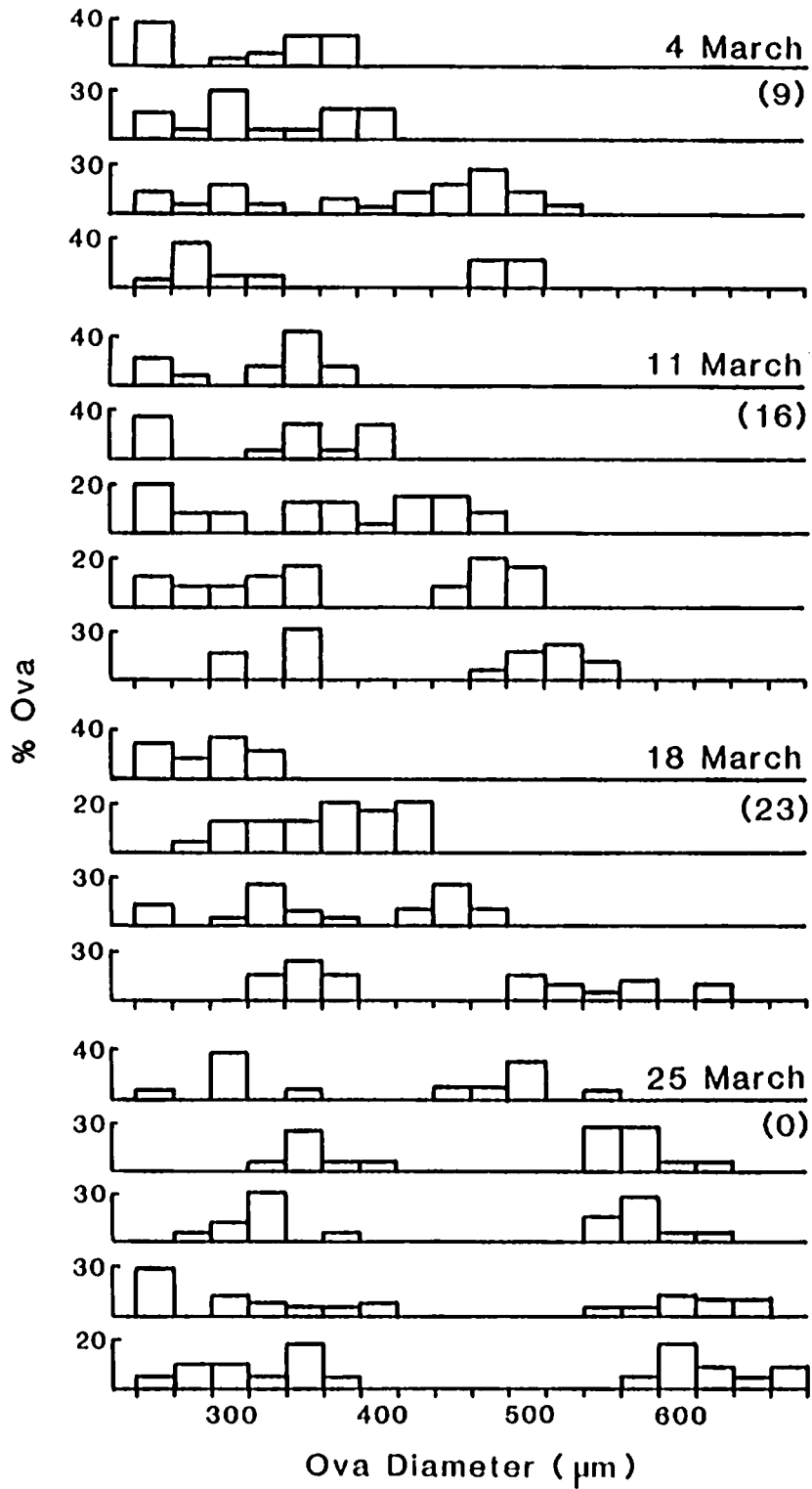


Figure 16. Size frequency distribution of yolked ova in ovaries collected during April 1982. Numbers in parentheses indicate lunar day as in Figure 14. Each distribution is for one female.

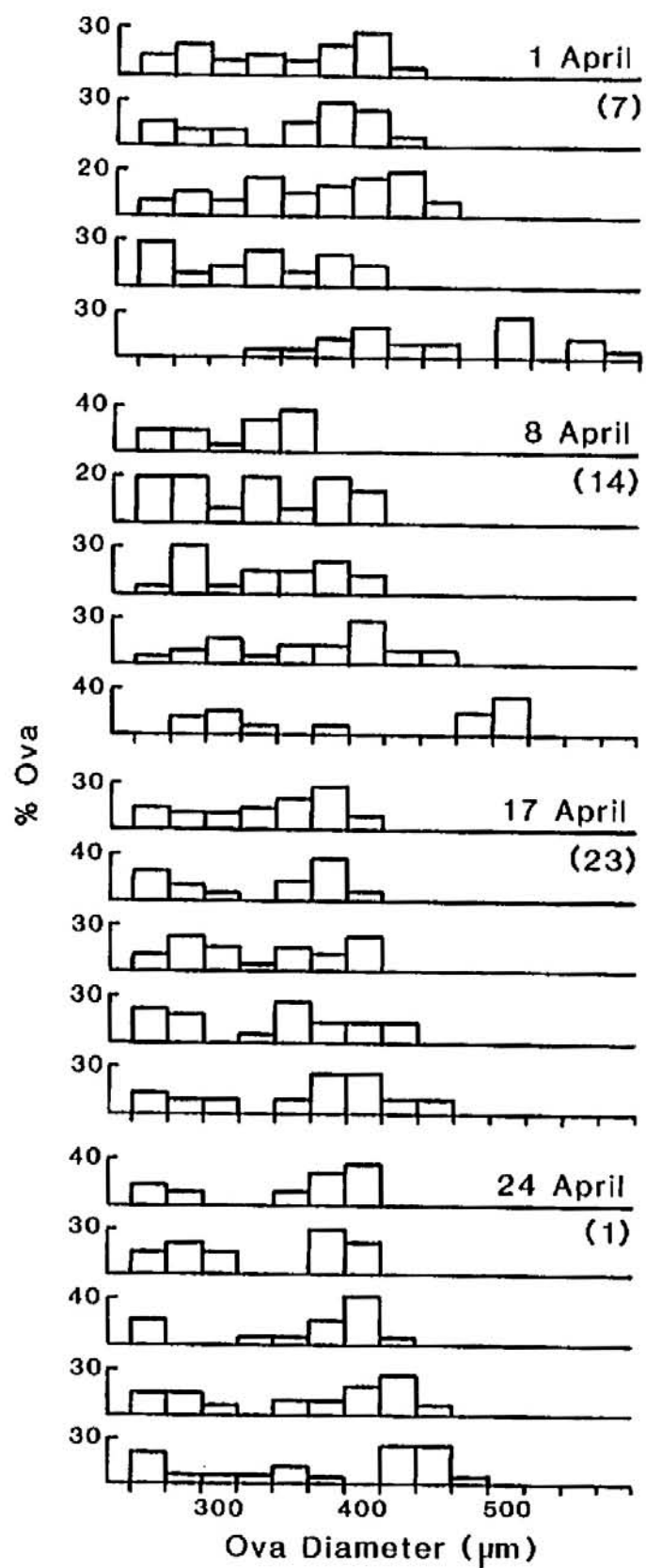
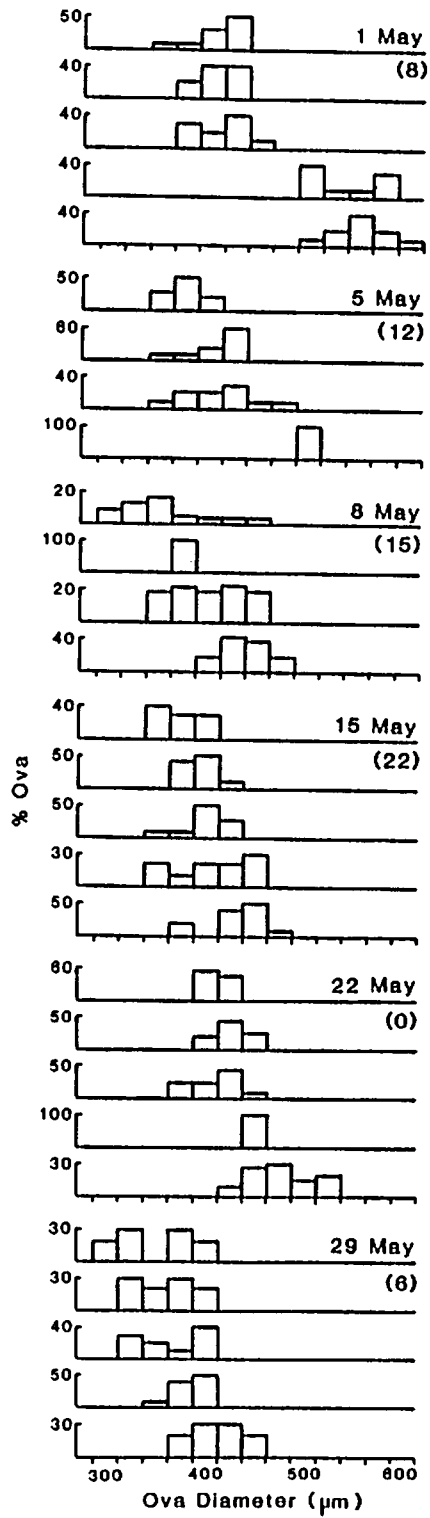


Figure 17. Size frequency distribution of yolked ova in the largest egg mode within ovaries collected during May 1982. Numbers in parentheses indicate lunar day as in Figure 14. Each distribution is for one female.



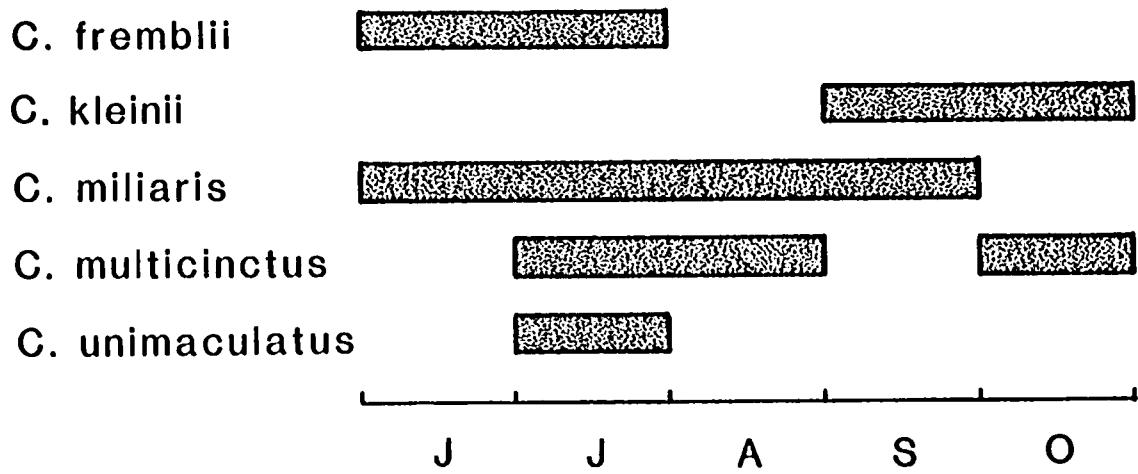
the same reasons given above in the gonad weight analysis. Analysis of covariance of log-fat weight and log-body length showed slopes among monthly samples were homogeneous (females: $F = 1.22$, $df = 17$, $P = .264$; males: $F = .67$, $df = 17$, $P = .82$), and adjusted means followed a pattern very similar to simple monthly fat weight means. Differences in mean monthly fat weight, therefore, were due to true changes in fat deposits, and were not a result of differences in the size of fish sampled each month.

Seasonal patterns of fat deposition were out of phase with gonad recrudescence for both sexes. Females showed peaks in mean visceral lipid deposits during October 1981 and November 1982, and minimum deposits during July 1981 and Feb through July 1982 (Figure 11B). Males showed peaks in October 1981 and August 1982 (Figure 12B).

Recruitment

C. multicinctus and other chaetodontid larvae recruit to the reef near Kahe Point from early summer through the fall months (Figure 18). Very recent recruits could be distinguished from other juveniles by their semi-translucent body. Newly settled fish and juveniles sequestered in the reef interstices most often within the finger coral, Porites compressa. While juveniles were most frequently encountered as solitary individuals, small ephemeral social groups up to 8 fish were also observed shortly after settlement. However, more permanent social aggregations of small juveniles generally consisted of pairs.

Figure 18. Recruitment of chaetodontids at Kahe Point during 1981 and 1982. All recruitment was observed between the months of June and October. Bars are a qualitative indication that new recruits were observed sometime during that month.



Water Temperature

The seasonal ranges of ambient water temperatures in the Kahe study area are given in Figure 19. In both 1981 and 1982 temperatures peaked during August through October. Maximum temperature during the sampling period (27.76 °C) was recorded on 23 September 1981. Seasonal lows were recorded in February, March, and April of both years, with the lowest reading (23.54 °C) taken on 11 March 1982. Although differences did occur between yearly maximum and minimum temperature, this seasonal thermal cycle at Kahe shows little temporal variability as indicated by temperatures taken in 1983 and years previous to this study (Coles et al., 1983).

Fecundity

Total fecundity, considered here as the total number of yolked ova per ovary, ranged from 82 to 17,327 ($n = 46$) for the total sample period. Batch fecundity, or number of yolked ova in the largest egg mode, ranged from 8 to 14,509. These broad ranges of female fecundity are due in part to the seasonal patterns of reproduction and differences in body size among females.

Fecundity data during the January through May 1982 peak spawning season were examined in relation to fish length and body weight for both linear and power function equations. Total fecundity expressed as a power function of length yielded the best fit, although only 34% of the variation in fecundity was explained by fish length (Table IV). The estimate of 9.51 for the fitted exponent was very large and significantly greater than 3. Similarly, when total fecundity was

Figure 19. Ambient water temperatures at Kahe Point during the study.
Data given as monthly means taken at approximately weekly intervals.

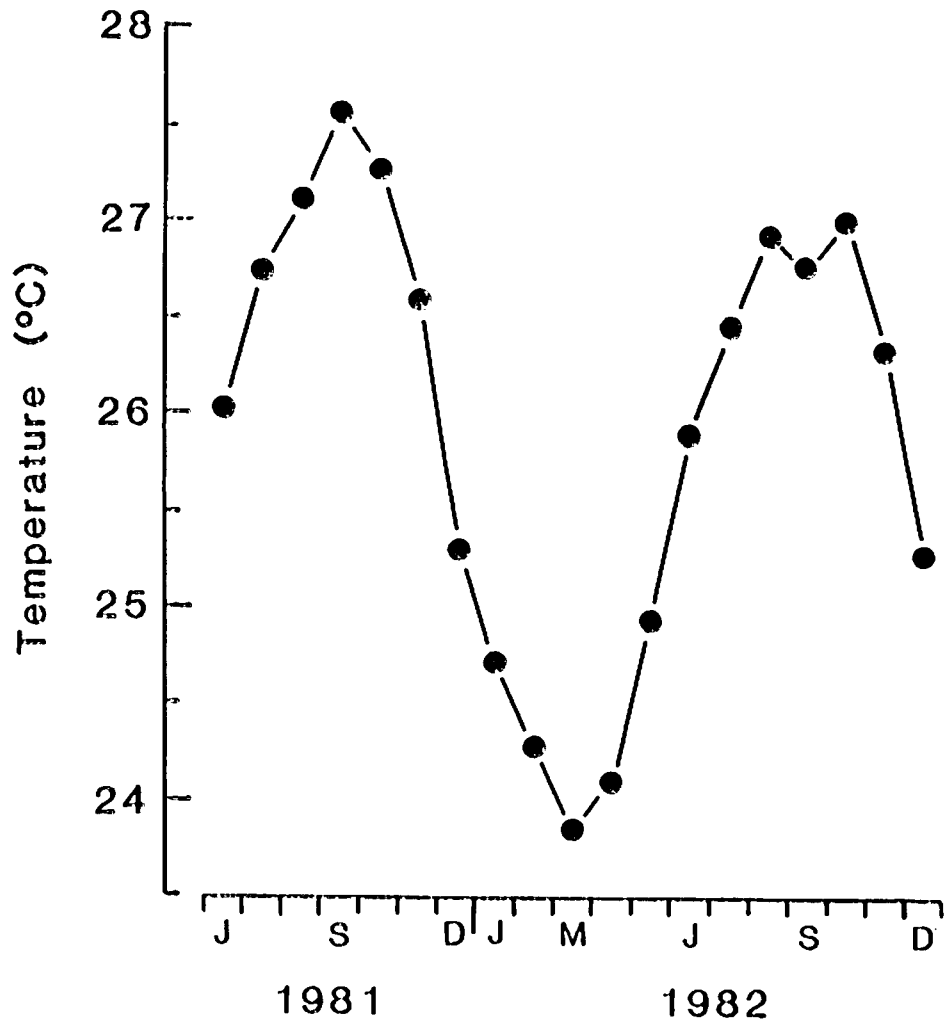


Table IV. -- Regression analyses of total fecundity (F_t) as a function of standard length (SL) and net body weight (BW) for 37 female *C. multicinctus* collected during the spawning period of January through May 1982 at Kahe Point. Weight in grams and length in millimeters. Regression equations given for both linear and power function equations. Test for correlation coefficient (r^2) is $H_0: B = 0$.

| Model (variable) | Equation | r^2 | \underline{P} < | 95% Confidence Limits for Parameter | |
|---------------------|--|-------|-------------------|-------------------------------------|--|
| | | | | B | a |
| $F_t = BX+a$ | | | | | |
| (length) | $F_t = 611SL - 43,295$ | .26 | .0013 | 256 < B < 966 | -72,712 < a < -13,878 |
| (weight) | $F_t = 568BW - 7,602$ | .16 | .0129 | 461 < B < 675 | -19,153 < a < 3,949 |
| $F_t = aX^B$ | | | | | |
| (length) | $F_t = 3.34 \times 10^{-15} SL^{9.51}$ | .34 | .0001 | 4.98 < B < 14.04 | 7.31×10^{-24} < a < 1.53×10^{-6} |
| (weight) | $F_t = 5.65 \times 10^{-1} BW^{2.83}$ | .22 | .0037 | .99 < B < 4.68 | 1.40×10^{-3} < a < 2.28×10^2 |

analyzed in relation to body weight, the fitted exponent is 2.25 and significantly greater than one. These relationships indicate that the total number of eggs within an ovary increases in far greater proportions than predicted by normal isometric relationships.

Although the number of eggs in an ovary can provide a valid estimate of egg production for species that shed their entire egg stock during the reproductive period, this method can result in serious underestimates of seasonal fecundity if a multiple spawning species is sampled after the spawning season begins, or additional yolked eggs are produced during the spawning season. The data clearly show that individual females spawn over a protracted spawning season (Figures 11 and 13) and have new batches of yolked eggs developing immediately after spawning (Figures 14 and 15). It is evident that counts of all yolked eggs within an ovary underestimate annual reproductive output.

The relationships between fish length and batch fecundity followed a pattern similar to that for estimates of total fecundity (Figure 20, Table V). The length-power function again provided the best fit although correlation coefficients were still of low magnitude. Batch fecundity increased extremely fast with length ($B = 10.37$) and weight ($B = 3.27$). The equation estimated from least-squares regression is shown in Figure 20 for comparative purposes. The functional (or geometric) regression (sensu Ricker, 1973) is:

$$F_b = 9.86 \times 10^{-31} SL^{17.55}$$

The estimated exponent, 17.55, indicates that batch fecundity increases extremely fast with increased body length.

The number of eggs shed per spawning was estimated from 8 females

Figure 20. Batch fecundity as a function of fish length in C. multicinctus. Dark circles represent the number of eggs in largest egg mode estimated from ovaries collected at Kahe Point. Open circles show fecundity as determined by induced ovulation in captive fish. Equation determined from least-squares regression analysis. See text for functional regression equation.

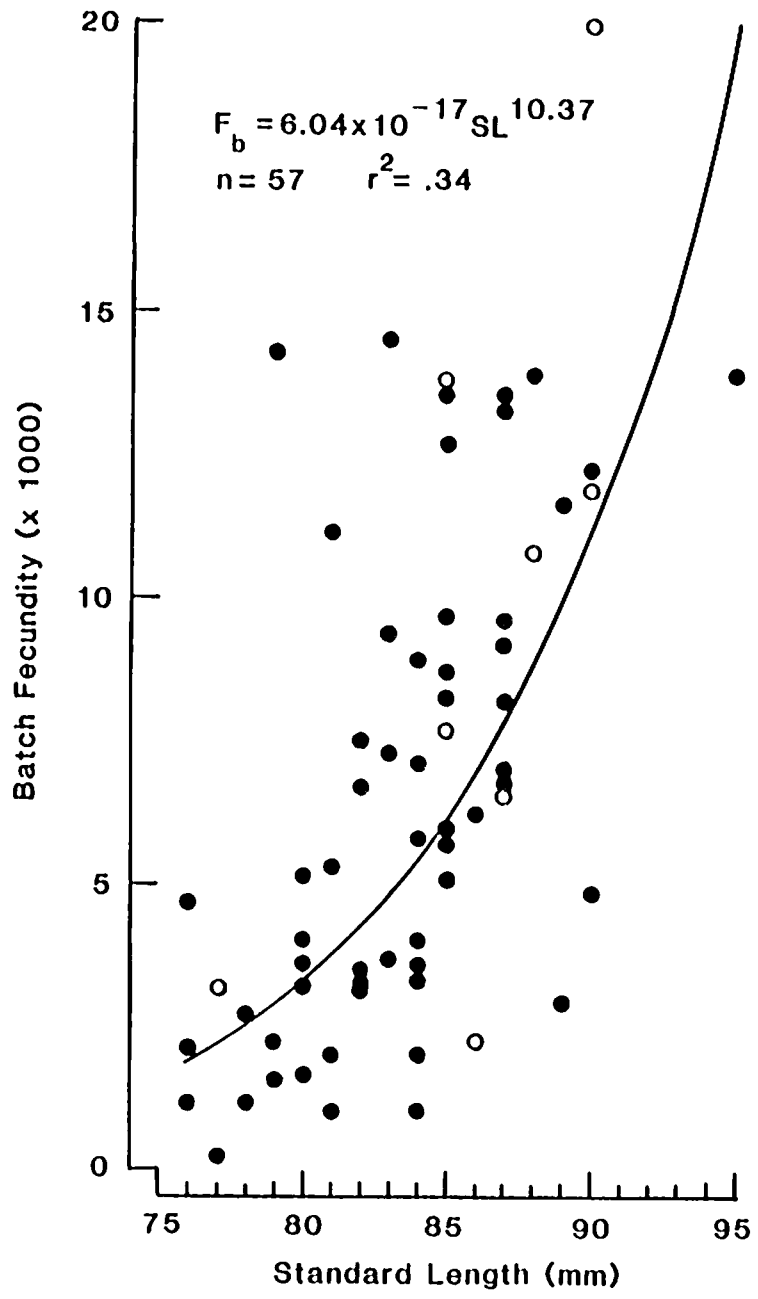


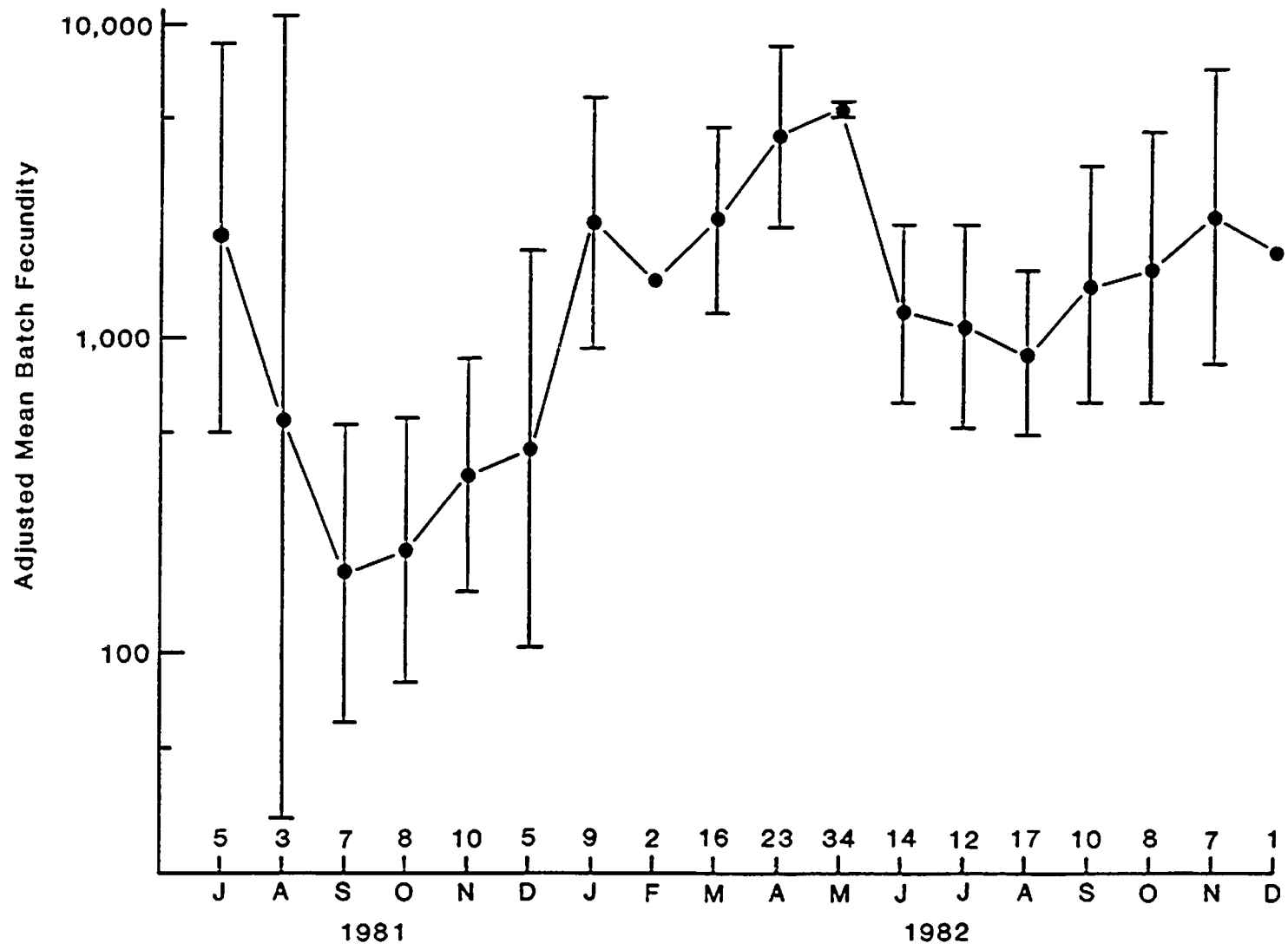
Table V. — Regression analyses of batch fecundity (F_b) as a function of standard length (SL) and net body weight (BW) for 57 female C. multicinctus collected during the spawning period of January through May 1982 at Kahe Point. Weight in grams and length in millimeters. Regression given for both linear and power function equations. Test for correlation coefficient (r^2) is $H_0: B = 0$.

| Model | | 95% Confidence Limits for Parameter | | | |
|--------------|---|-------------------------------------|-------|--------------------|--|
| (variable) | Equation | r^2 | $P <$ | B | a |
| $F_b = BX+a$ | | | | | |
| (length) | $F_b = 584SL - 42,308$ | .29 | .0001 | $340 < B < 829$ | $-62,687 < a < -21,929$ |
| (weight) | $F_b = 606BW - 9,782$ | .25 | .0001 | $319 < B < 893$ | $-17,473 < a < -2,091$ |
| $F_b = aX^B$ | | | | | |
| (length) | $F_b = 6.04 \times 10^{-17} SL^{10.37}$ | .35 | .0001 | $6.54 < B < 14.20$ | $2.67 \times 10^{-24} < a < 1.37 \times 10^{-9}$ |
| (weight) | $F_b = 1.09 \times 10^{-1} BW^{3.27}$ | .26 | .0001 | $1.78 < B < 4.76$ | $8.15 \times 10^{-4} < a < 1.44 \times 10^1$ |

which were induced to ovulate by hormonal injection (Figure 20). These fish produced clear hydrated eggs that were neutrally bouyant when placed in seawater. Other fish which ovulated partially hydrated or uncleared eggs were not included in the analysis. Length-fecundity data overlapped considerably with that estimated from gonads of the field collections, although one notable 90-mm female from the hormone-treated group released 19,909 eggs. Covariance analysis of log batch fecundity regressed on log fish length indicated that the slopes and intercepts did not differ between the induced spawning and largest-egg-mode methods (wild fish = 57; hormone treatment = 8 fish; $df = 1$; $F = .03$; $\underline{P} = .86$). This indicates that batch fecundity, as determined by number of ova in the largest egg mode, is a valid estimate of the number of eggs shed in a single spawn, and that all ova in the largest mode are shed at a single spawning.

Mean batch fecundity for monthly samples is shown in Figure 21. Mean egg mode size used in the analysis ranged from .189 to .637 mm. Because fecundity is a function of body length, an analysis of covariance was performed to control for variation due to fish length among monthly samples. The log-log transformation of batch fecundity (dependent variable) and standard length (the covariable) showed homogeneous slopes among all 18 month samples ($\underline{P} < .06$), and were therefore analysed for intercepts and adjusted monthly (treatment) means. Data are presented for adjusted mean batch fecundity (and 95% confidence limits) for the averaged size female (82.4 mm SL) among all samples. The number of eggs produced per spawn steadily increased from low summer 1981 levels throughout the 1982 spawning season and peaked in

Figure 21. Monthly batch fecundity of female C. multicolor collected at Kahe Point. Adjusted means (and 95% confidence limits) indicate predicted number of eggs shed in a single spawning for an 82.4 mm SL female. Numbers above months indicate sample sizes.



May. This was followed by a precipitous decline in batch size during the summer of 1982, although these levels were higher than the previous summer. A second increase in batch fecundity is seen during the fall and may indicate the onset of the 1983 spawning season. This shows that the number of eggs shed per spawning increased during the peak spawning period, and that seasonal fecundity may vary significantly between years for fish that spawn during the summer as shown in comparison of fecundity in summer months.

Validation of Daily Growth Increments

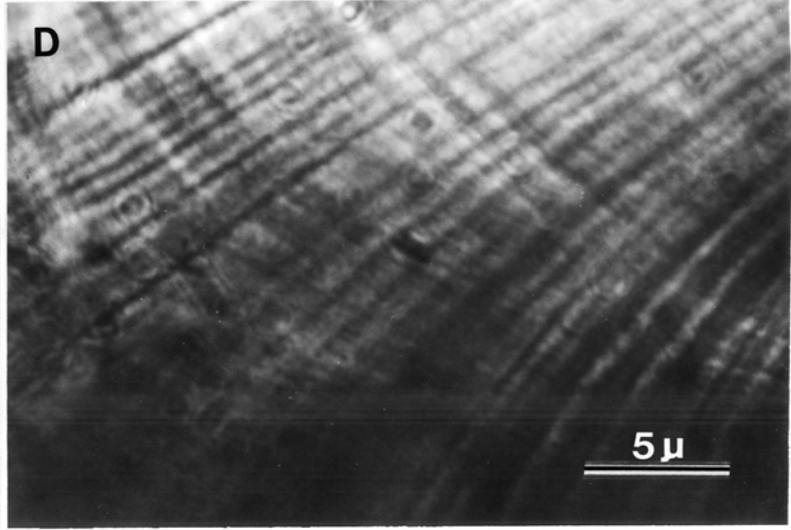
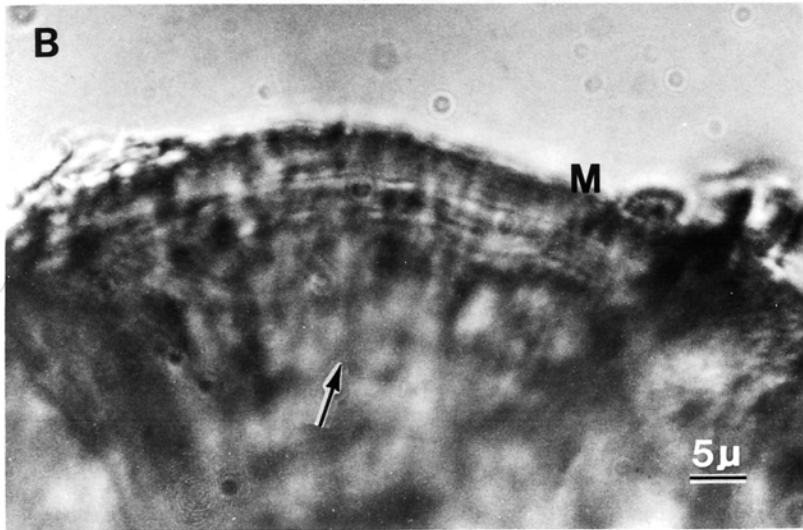
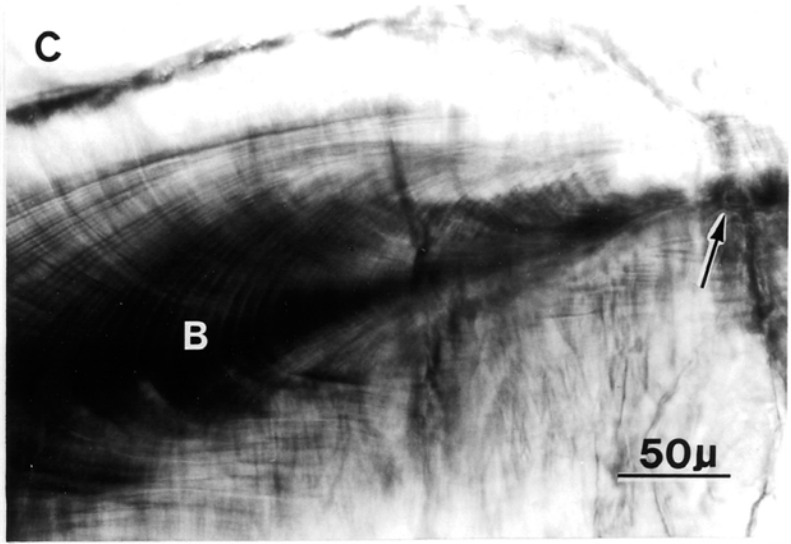
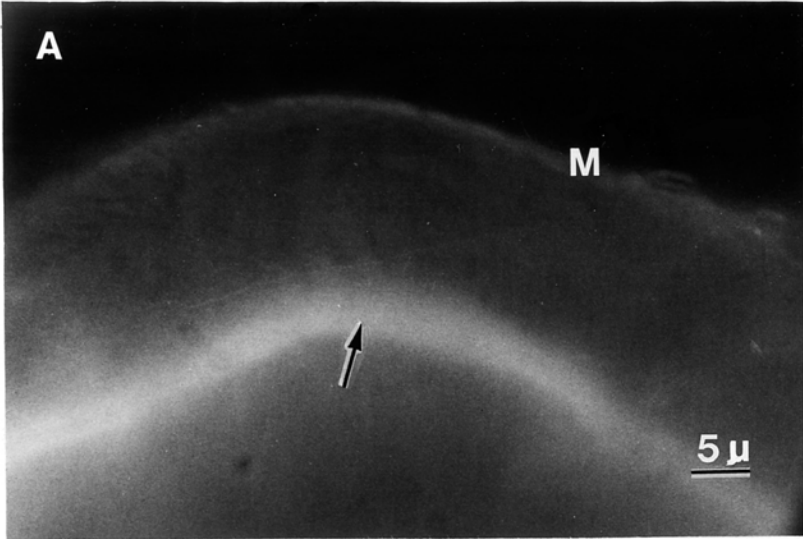
The handling of juvenile fish and the intramuscular injection treatment induced short-term stress characterized by cessation of feeding and general inactivity for approximately 3 days. After that period, surviving fish resumed normal feeding behavior. Three of five fish survived injection treatment and were used in experiments to verify daily growth increments. Fish number 3 (Table VI) was sacrificed but fish numbers 4 and 5 died by asphyxiation due to failure of the sea water system at HIMB.

Deposition of increments continued beyond the tetracycline band in otoliths from treated fish. A narrow florescent blue-green band was visible inside a non-florescent peripheral margin in which increments could be enumerated (Figures 22A and 22B). There was high variability in both the width and lucidity of the post-treatment margin between sites on the otolith, thus the entire margin of each otolith pair was carefully inspected for regions with a clear series of bands. The clearest zones were found on the rostral and post-rostral margins of the

Table VI. -- Summary of daily increment deposition following tetracycline injection in 5 C. multincinctus.

| Fish | Length (mm) | Weight (g) | Dosage (ug/gbw) | Post-treatment Life (days) | Number Post-treatment Increments | |
|------|----------------|---------------|--------------------|-------------------------------|-------------------------------------|------------------|
| | | | | | Range | $\bar{X} \pm SD$ |
| 1 | 46 | 4.2 | 100 | 1 | - | - |
| 2 | 49 | 4.9 | 100 | 3 | - | - |
| 3 | 52 | 5.8 | 225 | 47 | 41-47 | 44.3 \pm 2.3 |
| 4 | 46 | 4.4 | 225 | 19 | 14-17 | 15.3 \pm 1.2 |
| 5 | 33 | 2.0 | 225 | 19 | 15-16 | 15.7 \pm 0.5 |

Figure 22. Photomicrographs of otolith sagittae from C. multincinctus.
A) Florescent tetracycline band (arrow) under ultraviolet light in sagitta (whole mount) of 52 mm SL fish. M = outer margin of sagitta.
B) Region of growth beyond tetracycline marker of same otolith shown in Figure 22A when illuminated by tungsten light source. Arrow indicates location of tetracycline band. C) Photograph of sagitta from 78 mm SL female. B = region of broad dark bands probably formed during larval development. Arrow indicates otolith core. D) Close up of Figure 22C that shows daily growth increments.



sagittae. Counts of post-treatment increments for treated fish are shown in Table VI. Although the experimental sample size of three fish is small, there was a good correspondence between the number of increments deposited and number of days following tetracycline injection. The difference between post-treatment life and number of post-treatment rings is consistent with the duration of treatment stress and the failure of fish to feed observed in the lab. These results provide reasonable verification of the daily deposition of otolith circuli.

Daily increments from otoliths of 27 C. multicinctus between 30 and 95 mm SL were counted. The sagitta core exists as a distinct centralized point near the lateral otolith surface with concentric increments extending radially in the anterior, posterior, and medial directions (Figure 22C). Frontal sections of the sagittae of this species could be easily read along the post-rostral axis. Increments deposited in early life are very broad and exist within a dark brown central portion of the otolith. In most sagittae examined, the last few dark central increments were extremely broad and were often followed by a clear zone in which no increments could be identified. This clear zone on the post-rostral axis was then followed by alternating continuous and discontinuous zones typical of daily increments reported for other tropical marine fishes. This abrupt change in otolith increment structure may represent the period of larval metamorphosis when post larvae settle from the plankton back onto the reef. To obtain estimates of larval life, the broad increments in the dark zone were enumerated in addition to total increments per sagitta.

Growth

Data for fish age in relation to body length were fitted to the von Bertalanffy growth equation (Figure 23) and estimates of the model's three parameters determined (Table VII). The estimate of 95 mm for the largest attainable size, L_{inf} , agrees in magnitude with the largest individual sampled in collections made at Kahe Point. Note, however, that the upper 95% confidence limits for this parameter is 116.66 mm, thus larger individuals may exist in the population. The parameter, K , which describes the rate at which the growth curve approaches L_{inf} is relatively large and is reflected in the rapid growth during the first year of life. For example, the predicted length at one year of age is 72 mm (76% of L_{inf}), and at 2 years is 89 mm (94% of L_{inf}). It has been previously shown that C. multicinctus females reach reproductive maturity at about 75 mm length which translates to about 405 days or just over 13 months of age.

Increments within the dark central region of 28 otoliths were enumerated to obtain estimates of larval life. Counts ranged from 52 to 83 days and averaged 66.6 days (S.D. = 7.0, $n = 28$) or about two months. This estimate, however, makes the assumption that the broad dark rings are formed on a daily period and only during pre-settlement life. This is likely for this species since natural settlement marks have been reported for other tropical species (Victor, 1982; 1983).

Figure 23. Age-length data from 27 C. multicinctus fitted to the von Bertalanffy growth equation. Equation parameters given in daily time units.

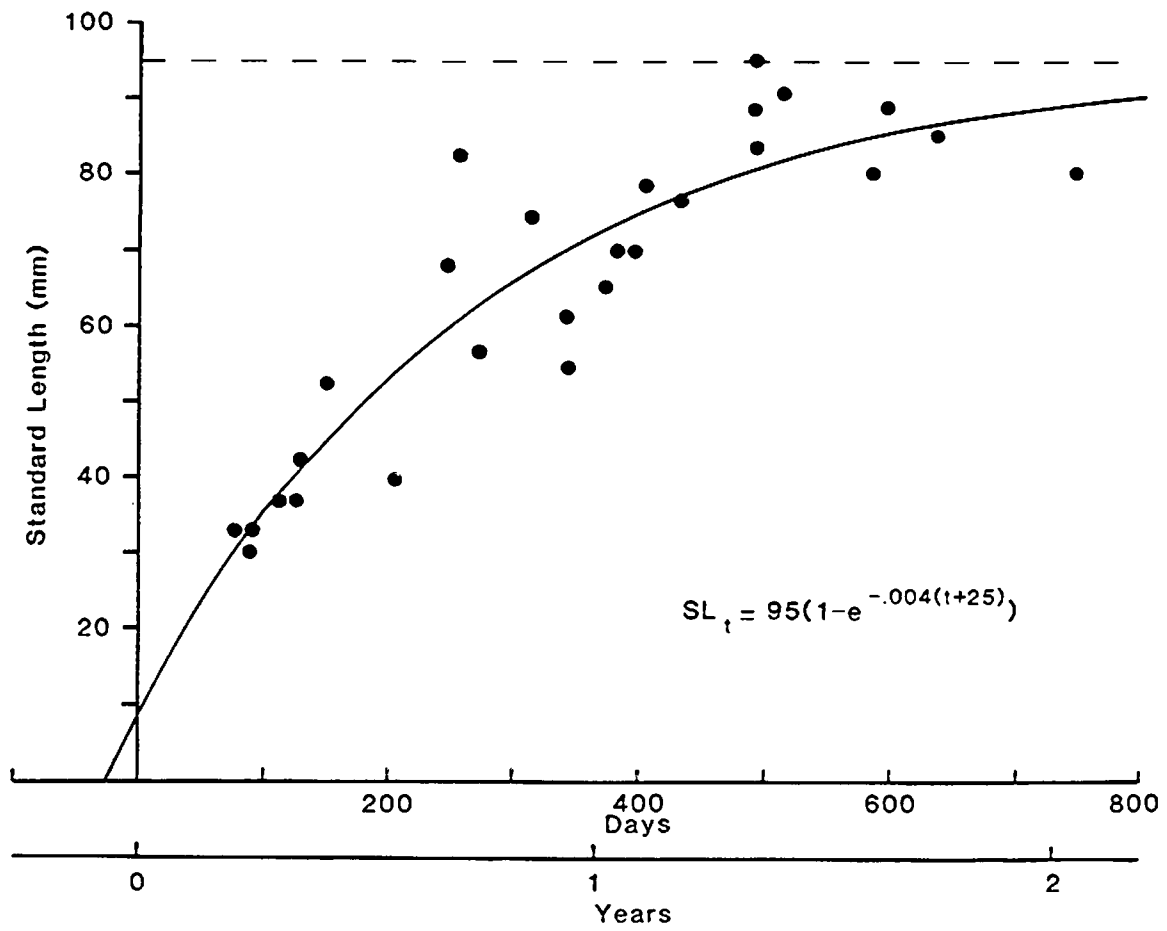


Table VII. -- Parameters of the von Bertalanffy growth equation fitted to age determinations of 27 C. multicinctus from analyses of otolith growth increments. Time-based parameters (K and t_0) provided for both daily and yearly periods.

| Parameter | Estimate | Std. Error | 95% Confidence Limits |
|---------------|-----------------------|-----------------------|---|
| L_{inf} | 95.02 | 10.50 | $73.38 < L_{inf} < 116.66$ |
| <u>Daily</u> | | | |
| K | 1.33 | .49 | $.03 < K < 2.33$ |
| t_0 | -.07 | .11 | $-.29 < t_0 < .15$ |
| <u>Yearly</u> | | | |
| K | 3.63×10^{-3} | 1.33×10^{-3} | $8.89 \times 10^{-4} < K < 6.37 \times 10^{-3}$ |
| t_0 | -25.34 | 39.12 | $-107.59 < t_0 < 55.40$ |

DISCUSSION

Population Structure and Social Pairing

The adult population of C. multicinctus at Kahe Point is composed of individuals that span a narrow range of body sizes. After reproductive maturity (at approximately 75 mm SL) fish grow less than an additional 20 mm in length since the largest fish collected was 95 mm SL. Almost half of all adults fell into the 80-84 mm size class, which indicates growth after reproductive maturity for most fish is on the order of about 10 mm or less.

Adults form monogamous social pairs. Of reproductively mature pairs, 97% were heterosexual associations. The small differences in body length between mates accounts in large part for the similarity in adult size distribution. Although sexually immature fish formed pairs that consisted of other sexual associations (Figure 9), adult male homosexual pairs were never found.

In spite of the similarity in length of pair members, males were larger by an average of 1.5 mm. This difference may reflect a balance between the ability of males to control food resources and intrasexual competition for mates. Male size is an important factor that determines territory size and the availability of food resources (see Chapter IV). By defending the largest possible territory, males may attract larger females (or enhance the fitness of his current mate through increased growth or reproductive output). With a large female mate, however, males would be subject to increased competition from large males for the female (and large feeding territory). Given that larger males can dominate smaller individuals, males must adopt a strategy where they can

control both food and reproductive resources against competitors. Thus, this slight size dimorphism between pair mates may reflect a stable strategy in which males can maintain both the feeding territory against conspecifics and the largest defensible mate.

Length-Weight Relationships

Power coefficients generated for length-weight relationships indicate that C. multicinctus gains weight in an allometric fashion since parameters were significantly larger than 3. Furthermore, females had a larger coefficient than males and thus gain weight faster. Although many of these sex differences can be explained by differential development of gonads, slopes also differed between sexes in length and gonad-free body weights with females being heavier for a given length. Power coefficients greater than 3 indicate that larger individuals are more rotund. Many advantages for accelerated weight gain with length for this species may exist. For males, body size is an important correlate of territory size. Because males (and females) vigorously defend their feeding territories (see Chapter IV) larger body depth or mass might be advantageous during agonistic encounters that involve visual displays such as lateral presentations. In addition, a more massive fish should be at an advantage over a fish of lesser weight (but of the same length) when physical contact occurs during fighting. In addition to advantages of increased weight with agonistic interactions, females may accrue reproductive benefits from increased body weight by

an increased maximum gonad weight that can be contained within the body cavity.

Sexual Maturity

Although females undergo sexual differentiation at smaller sizes than males (Chapter I), both sexes reach reproductive maturity at about the same size. Over half of the members of the 71-75 mm size class for each sex were reproductively mature (Table III). It is especially difficult to identify sexually mature females during the non-reproductive periods because of the lack of yolked ova in some large individuals. Most females larger than 75 mm and classified as immature were from collections made between months of July and September. It is likely that these fish were reproductively inactive rather than immature.

Growth and Size

The analysis of age in relation to fish length shows that C. multicinctus exhibits rapid growth during its early life. Fish at one year of age reach an average length of 72 mm or about 76% of their average maximum length. Sexual maturity is reached at about 75 mm for both sexes and translates to an average age of about 13 months. Growth during the second year of life slows considerably with the average fish reaching 89 mm or about 94% of average maximum length.

Comparison of size among individuals of approximately the same age reveals a high degree of variability in individual growth rates. For example, one 54 mm female was estimated to be almost 1 yr of age (345

days), whereas an 82 mm female was aged at only 8 months (257 days) (Figure 23). This disparity in growth can have major implications for reproductive output since fecundity rises steeply with fish length.

Estimates of growth rates are available for only one other chaetodontid. Ralston (1976a) aged juvenile C. miliaris (a planktivore) and reported rapid growth similar to C. multincinctus when his age-length data were fitted to the von Bertalanffy growth model. He found that C. miliaris reached 70% of its asymptotic length after one year, and became reproductively mature at that time. The two species differ primarily in their food habits and that C. miliaris reaches and L_{inf} of 127 mm or approximately 34% larger than that of C. multincinctus. Ralston's estimate of 1.13 for the parameter, K , which describes the rate at which fish length approaches L_{inf} , was extremely high when compared to other species (Beverton and Holt, 1959), and the estimate of 1.33 for C. multincinctus exceeds that of C. miliaris. Growth rates for the two chaetodontids studied to date are very rapid during the first year of life but quickly decelerate in subsequent years.

Seasonal Patterns of Spawning and Fat Deposition

Monthly variation in gonad weight shows a seasonal cycle for C. multincinctus. This is best seen in the increase in mean ovary weight of females during the fall of 1981 and peak in spring of 1982 (Figure 11A). There was little change in the low average ovary weight among monthly samples taken during the remainder of 1982. Males showed a similar seasonal pattern of testes development as females although the monthly

changes exhibited more erratic transitions that probably reflect high variability among males (Figure 12A). From the data on female gonad development alone spawning appears to occur continuously from fall through spring. This is supported by mean ova diameter in the largest egg mode of females (Figure 13). Note, however, that ova larger than approximately .375 mm diameter have reached the final stages of vitellogenesis and are potentially spawnable. By this interpretation, spawning could occur among some females during all months of the study except July and August 1982. In comparison, histological analysis of ovaries showed no evidence of spawning activity during August, September, December 1981, or November 1982 (Chapter I). In addition, spawning activity during October through November 1982 was followed by increased alpha and beta atresia during December through February 1982 (Chapter I). Thus, although it is possible that some individuals spawned continuously beginning in October 1981, it is likely that many fish spawned briefly in October and November 1981 and resumed again in January 1982.

Little is known of the spawning seasonality of C. multicinctus on other Hawaiian reefs. Lobel (1978) observed pair spawning during February and March 1975 but was not specific as to the geographic location. Walsh (in press) reported regular periods of juvenile recruitment between May and July for this species on the south Kona coast. Assuming an average larval life of two months, back-calculation from his recruitment data places spawning from March through May which coincides with peak spawning period found in the present study. A fine scale analysis of recruitment over four years (from his Figure 2)

indicates additional spawning activity during months other than spring. Although major spawning clearly occurred during spring in three of four years, it also occurred during September or October in all years and is consistent with the fall spawning observed for the Kahe population. Of particular interest is the high number of recruits observed in 1977 that reflects spawning activity across all summer months. This indicates that spawning activity may vary between years or different populations since spawning was low during two summers at the Kahe site.

Information on the spawning of other chaetodontids is also limited. The only other Hawaiian species studied in detail is the millet seed butterflyfish, C. miliaris. It is endemic to Hawaii and differs from C. multicinctus primarily by its zooplanktivorous food habits and formation of large social aggregations (Hobson, 1974; Ralston, 1976b, 1981). Burgess (1978) suggested that members of the Kaneohe Bay population on Oahu spawned from early February to early March, and provided some macroscopic evidence of gonad ripeness in January. Based largely on his C. miliaris data and observations of juvenile settlement patterns to inshore reefs, Burgess (1978) concluded that most butterflyfishes in Hawaii spawn during winter months. Ralston (1981) analysed gonad development from individuals collected at numerous sites in Hawaii and concluded that this species spawns from January through May. Lobel (1978) observed spawning in February or March for both Chaetodon fremblii and Chaetodon unimaculatus. Walsh (in press) reported recruitment for Chaetodon ornatissimus in spring, summer and fall months which probably translates to spawning activity from winter through

summer. In general, Hawaiian chaetodonids follow the seasonal peak spring spawning patterns found in many other Hawaiian coral reef fishes (reviewed by Walsh, in press).

Fecundity and Batch Spawning

Fecundity data show that the number of eggs produced increased very rapidly with female size. Power function models showed very high estimates of the power coefficient for both total (9.51) and batch (10.37) fecundities which were both significantly larger than 3 (Tables IV and V). This indicated that the relative allocation of energy to reproduction is far greater than that predicted by normal isometric growth relationships. The generally poor correlations between fecundity data to both linear and curvilinear functions are due most likely to the small range of body sizes represented by mature females, the pooling of collections over the protracted spawning season, and failure to account for the semi-lunar spawning activity.

All evidence indicates that C. multicinctus spawns multiply over a protracted spawning season. Histological analyses and size-frequency distributions of yolked ova from individual ovaries show that recently spawned females almost always possessed at least two groups of vitellogenic oocytes. Further, patterns of egg atresia within the population were seasonal and followed periods of decreased spawning activity (Chapter I). If females spawned but once per season, certain trends should be apparent. As the spawning season progressed there should be a decrease in average ovary weight, an increase in the proportion of females that show degeneration of unspawned ova, or a

decrease in the proportion of females that spawned. The data do not support these predictions since throughout most of the spring gonad weight was high (Figure 11), mean ova diameters of spawnable size (Figure 13), atresia low (Figure 7), and spawning activity high (Figures 6, 15, 16, and 17) among females.

Because C. multicinctus spawns multiply, there is little value in estimates of total gonad fecundity since additional yolked oocytes must be produced over the spawning season. The large proportion of total ova in the gonad that are in the largest mode is indicated by the similarity in parameter estimates for both measures of fecundity (Tables IV and V). For example, estimates from the power function estimate of total fecundity (5,945 eggs) for an 83 mm female exceeds the estimate of batch fecundity by only 24%. This indicates that only a small proportion of yolked ova in the ovary are not spawned since mean batch fecundity was consistent among monthly samples from January through May 1982 (Figure 21).

Results of the induced spawning experiments provide further evidence that all eggs within the largest egg mode are released at each spawning. The relationship between fish length and batch size was not different from that calculated for number of eggs in the largest mode (Figure 20). This is supported by the observation that females with ova undergoing final maturation or hydration also contained a smaller batch of yolked oocytes (Figures 15 and 16). It is likely that injection of gonadotropin emulates natural ovulation since administered dosages were based on fish weights, only fully yolked ova will undergo final

maturation (Masui and Clarke, 1979), and the number of eggs shed is apparently not dose-dependent (Stevens, 1966).

Reproductive output, as measured by adjusted mean batch fecundity, may vary seasonally between years. Females had higher fecundities during September through November 1982 than the same period in 1981 (Figure 21), and some females spawn during those months (Figure 6).

Spawning Periodicity

The protracted spawning season of C. multicinctus and constant recruitment of oocytes into a spawning batch make it impossible to estimate the number of eggs shed spawned over an entire spawning season from fecundity data alone. To estimate annual or lifetime fecundities, information must be obtained on the spawning frequencies of individuals.

Data from recently spawned females collected from January through May 1982 show that all spawning occurs during the weeks prior to the new and full moon phases (Figure 14). It is difficult to conclude from these data, however, the periodicity of spawning by individual females. Only 5% (2/40) of females showed evidence of possible spawning on successive nights by the coincident presence of postovulatory follicles and oocytes in final maturation. Since postovulatory follicles may persist for at least 24 h after spawning (Chapter I) it is possible these fish had spawned two days earlier. The possibility that females spawn two or three times during a weekly period can not be excluded.

Eggs are fully yolked and ready for final maturation at a diameter of approximately .375 mm. The average diameter of yolked ova in the second largest egg mode in females undergoing final egg maturation or

hydration was .321 mm. This .054 mm difference is very small and recruitment to the larger mode should be possible within a few days. In the norther anchovy, Engraulis mordax, vitellogenic eggs in the largest mode advance at a rate of approximately .04 mm/day (Hunter and Goldberg, 1980). Thus, while evidence indicates that C. multicinctus does not spawn on sequential nights, it is possible that individual females spawn more than once within a semilunar period. This could be verified relatively easily by monitoring individual females in the field for swollen abdomens or spawning activity on consecutive evenings during weeks prior to the full and new moon phases. Alternatively, the rate of ova development could be monitored by serial cannulation and measurement of yolked eggs taken from females during a semilunar cycle.

Estimates of fecundity have been made for only one other chaetodontid. Ralston (1981) reported a unimodal distribution of eggs in C. miliaris and simultaneous egg maturation from which he suggested that only one batch of eggs were produced per season. Unlike that discovered for C. multicinctus, Ralston found relatively low variability among his length-fecundity data when fitted to the power model ($r^2 = .83$) which supports the probability of less frequent or more synchronized spawning. Like that found for C. multicinctus, his fitted exponent (6.26) was significantly higher than 3. He concluded that an increasing proportion of resources are channeled into reproduction with increased fish length. The same appears to be true for C. multicinctus.

Adaptiveness of Seasonal Spawning

Numerous hypotheses have been proposed to explain seasonal spawning patterns among tropical reef fishes with much of the literature extended from that developed for temperate stocks. Most invoke arguments for adaptations to a single dominant environmental constraint. These explanations should not, however, be viewed as mutually exclusive in their action or assumed to exert equivalent selective pressures upon different species. Below is a discussion on the major ideas relevant to the spawning seasonality and life history of C. multicolor and other Hawaiian butterflyfishes.

The majority of Hawaiian fishes studied to date show peak spawning during the spring. Spawning activity that is closely tied to water temperatures below seasonal maxima may enhance planktonic survival. Larvae, for example, are generally thought to be more stenothermal than adults (Orton, 1920; Qasim, 1956), thus their exposure to extreme temperatures are reduced during spring spawning in cool waters. In addition, maximum survival of larvae through the yolk stage may occur at intermediate temperatures of their thermal tolerance range (Alderdice and Forrester, 1971). The spring spawning observed in C. multicolor occurs during months of lowest water temperature. Assuming that planktonic larval life is approximately 2 months, the majority of larvae will grow, develop, and metamorphose during months of increasing but submaximal temperatures. Unfortunately, almost nothing is known about the temperature tolerance or the depth distribution of tropical fish larvae (including chaetodontids) so hypotheses that advocate avoidance

of maximal temperatures to explain spawning seasonality must at present remain tentative.

Advantages may also be realized by broadcasting larvae during periods of increasing water temperature. By placing offspring at sea under warming thermal conditions larvae can experience more rapid growth and perhaps a reduced time in the plankton. This may minimize the period of exposure to pelagic predators such as tunas that feed on chaetodontid larvae (Reintjes and King, 1953; King and Ikehara, 1956; Brock, 1985). In addition, accelerated growth of larvae in warm temperatures may achieve more rapid metamorphic competency, and reduce the probability of being carried away from inshore areas in large seaward-moving gyres. Recruitment in warming waters was found for C. mutlicinctus in Kona, Hawaii between July and September (Walsh, in press) and during the summer months at Kahe Point and Puako, Hawaii (Figure 18; unpublished data). While the increasing-temperature hypothesis seems to be congruous with the observed peak spawning and recruitment seasons, it does not account for the second spawning pulse (and subsequent cold water recruitment) of C. mutlicinctus and other species in late summer and early winter.

Many workers have suggested that spawning patterns of Hawaiian reef fishes are timed to reduce loss of larvae due to seasonally strong current patterns that move past the Islands (Watson and Leis, 1974; Johannes, 1978; Lobel, 1978; MacDonald, 1981; Ross, 1983). This is an important aspect of spawning strategies considering that over 30% of Hawaiian fishes are endemic (including 5 of 22 chaetodontid species (Allen, 1980)) and therefore do not receive recruits from other Pacific

locations. Because of the large scale of the geographic and hydrographic features of this model, however, it is virtually untestable in a natural experimental framework where environmental variables or fish populations can be manipulated, and not much beyond correlative support can be provided.

Leis (1982) studied the distribution of larval fishes near Kahe Point and found that reef species with pelagic eggs were not abundant inshore (no chaetodontids were found) and concluded they were more than 3 km out to sea. This offshore distribution of chaetodontid larvae is in agreement with findings in other areas of Hawaii (Leis and Miller, 1976). The neritic patterns of butterflyfish larvae and other broadcast spawning reef species at Kahe are probably partially maintained by the localized tidal eddy and nearshore upwelling (Leis, 1982). It appears that the larval-retention hypothesis can not be rejected by the spring spawning of C. multicinctus and C. miliaris given that water flow from the North Equatorial Current in Hawaii is at lowest velocities during the first half of the year (Wyrтки, 1974). Local current patterns around the Hawaiian Islands, however, are extremely complex and often differ greatly between areas (Levastu, et al., 1964; Patzert, 1969). The optimal spawning strategies to cope with a diversity of coastal current patterns would likewise differ between areas. It is unlikely that fish could adopt any single locale-specific spawning strategy since larvae are unlikely to recruit back to their reefs of origin.

Lobel and Robinson (1986) studied a cyclonic current eddy off the Kona coast that formed in mid-July 1982. No eddies were detected for

two months prior by the investigators which includes the peak spawning season for many reef fishes. The residence of the gyre near shore was about 60 days, and is similar to that reported for other Hawaiian eddies (Patzert, 1969). If spawning peaked in May then relatively few larvae would have been affected by that gyre if previously swept out to sea. Unfortunately, the authors did not provide details of current patterns prior to the eddy formation which could provide insight into the fate of larvae spawned during months immediately following peak spawning. They did, however, find fish larvae entrained within the summer gyre. More developmentally advanced larvae occurred closer to the edge of the eddy, which may facilitate their return to inshore reefs. Zooplankton abundance was greatest at stations monitored nearest the center of the gyre.

Food availability for larvae is an important determinant of spawning activity for temperate species (Cushing, 1972; Jones, 1980; Sherman et al., 1984) and is also suggested for coral reef fishes (Russell et al., 1977; Kock, 1982). In central oligotrophic seas, however, plankton productivity is relatively low (Steemann Nielsen and Jensen, 1957). Although phytoplankton production varies considerably over time (Bienfang and Szyper, 1981) and shows increased production between January and May (Bienfang et al., 1984) little evidence exists for seasonal peaks in zooplankton abundance (e. g. Noda et al., 1980). This is due primarily to the lack of offshore upwelling of nutrient-rich waters (Dungdale and Guering, 1967). Based upon what is currently known about plankton productivity in Hawaiian waters, it is unlikely that the spawning seasonality observed in C. multincinctus is an adaptation to

take advantage of pronounced seasonal peaks in zooplankton production. Entrapment in current gyres, however, may be advantageous when productivity is low since zooplankton may concentrate near their center (Lobel and Robinson, 1986). Current shear from eddies that impinge upon an island landmass may provide an important source of nutrient upwelling that increase plankton productivity (Bienfang et al., 1984).

At the Waikiki Aquarium, S. Kraul (personal communication) reared chaetodontids partially through their larval stages. Both C. multicinctus and Forcipiger flavissimus larvae hatched approximately 24 h after fertilization at approximately 24 °C, the former species expiring shortly thereafter. Forcipiger larvae were successfully raised by Kraul through the yolk-sac stage and began to feed on copepods approximately 2-3 d after hatching. These times to hatching and first feeding are similar to that reported for C. nippon by Suzuki et al. (1980). Although much remains to be done on butterflyfish larvae, their planktotrophic nature indicates they are susceptible to food-limited growth and survival as demonstrated for other fishes (e.g. Arthur, 1977; Houde, 1978).

Although rates of primary productivity are depressed in tropical seas, it is widely known that plankton exhibits patchy horizontal and vertical distributions over wide areas (e.g. Steele, 1978; Mackas and Boyd, 1979). Since most reef fish larvae (including chaetodontids) are planktotrophic, survival is highly dependent upon finding adequate food resources in a temporally and spatially unpredictable environment. The spawning of multiple egg batches over a protracted spawning season seen

in C. multicinctus and many other tropical species could reflect a strategy to spread offspring over space and time to maximize the probability of a cohort successfully completing their larval life. Although this hypothesis is attractive and has been theoretically addressed for reef fishes (Doherty et al., 1985), much work is needed to determine the feeding ecology of tropical larvae in relation to local productivity levels before it can be better addressed.

The availability of food resources has an important influence on reproductive output of adult fishes. Egg production, for example, is dependent upon food supply in many species (Bagenal, 1966; Tyler and Dunn, 1976; Wooton, 1977; Hirschfield, 1980) and shortages may induce oocyte resorption (Scott, 1962; Hunter and Macewicz, 1985). Although food supply may very likely regulate reproductive output in tropical reef species, it would be difficult to demonstrate its effect in species with protracted spawning seasons and that shed multiple batches of pelagic eggs.

For many fishes, patterns of lipid deposition are out of phase with the cycle of reproductive activity which suggests fat reserves are mobilized for reproductive energy (Shul'man, 1974; Wooton and Evans, 1976; Diana and MacKay, 1979; Delahunty and de Vlaming, 1980; Hunter and Leong, 1981). For those species in which lipid stores are mobilized to enhance reproduction, food levels can effect reproductive output indirectly by mediating fat reserve levels. For example, Hunter and Leong (1981) suggested that plankton production levels in one year regulate northern anchovy lipid reserves which would be used for reproduction in the subsequent spawning season. It is also significant,

however, that lipids are a major source of metabolic energy for fishes (reviewed by Cowey and Sargent, 1979), thus fat reserves may provide energy for metabolism while food resources and perhaps protein reserves are channeled into egg production.

For the few corallivorous fishes for which patterns of reproduction and fat deposition were studied, a distinct trend is seen that indicates reproductive output may be limited by energy stores. C. multinctus meets its total energy requirements from coral food resources within its territory. The Porites corals that dominate Hawaiian reefs (and territories of C. multinctus) are of high water content (>95%), low energy density, and relatively poor overall quality (Chapter III; Tricas, 1985). As a result, both male and female C. multinctus spend over 90% of their time budget in feeding-related activities (Chapter IV). Fish feed at high rates throughout the year on corals but fats are accumulated by both sexes only during the summer.

The rate of acquisition of body fat by corallivores may be maximized during the summer. Coral skeletal growth is a highly influenced by the photosynthetic activity of symbiotic zoxanthellae algae (Young et al., 1971; Schmitz and Kremer, 1977), and is greatest during summer months of high solar irradiance (Maragos, 1972; Gladfelter, 1984). Increased skeletal growth also infers increased production of the living tissues which cover their surface. Annual secondary production of reef corals was estimated at approximately 1,000 Kcal /m²/y (Lewis, 1981) in reefs of about 40% live coral cover. Presumably tissue growth is accelerated during increased photosynthetic

activity of zooxanthellae since about 1% of the photosynthetically derived energy is channeled into growth of animal tissue (Davies, 1984).

Photosynthetic zooxanthellae, which are symbionts in all hermatypic corals, are a major source of energy and nutrients present in their host's tissue. The algae fix carbon into lipids which are translocated back to the host (Patton et al., 1977; Blanquet et al., 1979; Crossland et al., 1980; Patton et al., 1983; Battey and Patton, 1984) or into glycerol which is synthesized by the host into lipids, peptide/proteins, polysaccharides, and skeleton (Muscatine and Cernidairi, 1969; Trench, 1971; Young et al., 1971; Schmitz and Kremer, 1977). The production rates of lipid droplets by zooxanthellae appear to be correlated with ambient light levels (Blanquet et al., 1979; Crossland et al., 1980; Battey and Patton, 1984; Patton and Burris, 1983). Although it remains to be demonstrated, seasonal variation in light levels and total daily irradiation may result in highest lipid production during summer months. If this is the case, summer would be the best time for coral-feeding fishes to maximize the rate of fat intake.

Porites corals in Hawaii spawn during summer months (Stimson, 1978; C. Hunter, personal communication). Given the low energy content of Porites tissues, this may represent a short period where energy-rich gametes stored in coral polyps are available. Lasker (1985) reported that the Caribbean butterflyfish Chaetodon capistratus showed lunar periodicity in feeding on gorgonian polyps which coincided with the production of ripe eggs. Such opportunism on a seasonal basis for C. multicinctus may represent a significant strategy to maximize energy intake.

MacDonald (1981) studied the reproductive strategies of the Hawaiian corallivorous pomacentrid, Plectroglyphidodon johnstonianus, in relation to its feeding. He found that visceral fats were deposited when food acquisition was highest during the non-spawning summer season and were mobilized during winter spawning. MacDonald argued that reproductive output could be maximized in that species only if food was acquired at the highest possible rate. During the spawning season, males invested over 15% of their time budget in parental care of eggs that represented a significant loss of time for the acquisition of food. Females also experienced similar increased foraging costs.

The patterns of fat deposition and gonad development in P. johnstonianus are remarkably similar to those found in C. multicoloratus. Both species show increased gonad weight from January through May followed by a decline in summer months. Fat deposition patterns were out of phase with gonad development and lowest during spring. These similarities suggest that seasonal patterns of food quality in corallivores may be fundamental determinants of spawning seasonality for both species.

Although coral food resources may be more productive during summer months, it may be that morphological and physiological constraints determine patterns of fat storage prior to reproduction. For example, the small coelomic cavity of C. multicoloratus and P. johnstonianus may limit the space available to digestion, gonad development, and fat deposit systems. Diurnal feeding activities are high in C. multicoloratus and the long gut full during most of the day (Hobson, 1974; personal observations). That the remainder of the coelomic space is limited is

indicated in the complementary adjustment of ovary and fat weights to a monthly total of just under 1 g in females (Figure 11B).

If females depended solely upon their short term food intake between lunar spawning periods to produce each batch of eggs, their reproductive output during the spring season most favorable to larval survival would be much less than that if supplemented by mobilized energy reserves. Although the energetic pathways remain to be worked out, it is clear that fish are able to accrue large energy stores over a very short period (August and September). It follows that female reproductive success is directly related to rates of energy intake and fat deposition during the non-spawning season. The food-limitation hypothesis for coral-feeding fishes is attractive especially since it presents experimentally testable predictions from food resource manipulations in contrast to other oceanographic explanations of spawning seasonality.

During the summer months, conditions are favorable for growth of adults. Water temperature is warm, solar irradiance (and hence coral productivity) is high, and energy partitioned for reproduction is low. By spawning prior to summer peaks in food productivity, adults may increase their future reproductive success by channeling energy towards growth. The allocation of energy to growth during the first year may be especially important to future reproduction since size is an important aspect of fitness for both sexes. Growth of juveniles may be enhanced by recruiting to the reef during the summer months when food corals are most rich in energy content. Rates of growth during the first year of life would correlate with increased reproductive output since fecundity

is related to body length. For example, it was found that reproductively mature fish that differed in age by approximately four months were about the same length. Assuming equivalent growth to sexual maturity, this can mean a potentially large difference in reproductive output during the first spawning season, especially if seasonal maturation is achieved by late summer which is just prior to beginning of the spawning season. Jones (1980) suggested similar benefits of increased adult growth during the non-reproductive summer season for the wrasse, Pseudolabrus celidotus, when more time was available for feeding, and also presented a similar argument for new recruits.

In summary, the peak spring spawning of C. multincinctus and other corallivorous chaetodontids is most likely an adaptive strategy to 1) maximize reproductive output, 2) enhance larval survival in the offshore environment, and 3) maximize growth of juveniles in the first year of life. Larvae are dispersed during favorable periods of warming water temperatures and generally avoid seasonal maxima. This season also coincides with the period of lowest flow of oceanic currents past the Islands and may enhance retention of larvae in local waters. Although more work is needed, planktonic food resources for larvae apparently do not exhibit pronounced seasonal peaks in Hawaiian waters and therefore do not seem particularly relevant to the timing of spawning. The protracted spawning season, however, may be a response to the spatial and temporal patchiness of planktonic food for larvae. The rapid storage of energy as body fat by adults during summer peaks of coral growth is viewed as a strategy to maximize reproductive output over a subsequent protracted spawning period. Inter-year differences in batch

fecundity support the hypothesis that reproductive output of C.
multicinctus may be limited by the seasonal productivity of food
resources that are inherently low in energy content.

CHAPTER III

FORAGING STRATEGIES OF CORAL-FEEDING BUTTERFLYFISHES: A BALANCE BETWEEN ENERGY MAXIMIZATION AND PREY PROFITABILITY

INTRODUCTION

The acquisition of food is an important aspect of individual fitness since it directly supplies resources allocated to maintenance, growth, and reproduction. When in short supply, food can limit one or more of these physiological processes. Under more favorable conditions, the selection of specific items from a diet set may be advantageous when quality or accessibility vary among prey types.

The differential selection of food items by animals has been extensively modelled and tested through optimality theory (reviewed by Pyke et al., 1977; Krebs, 1978; Krebs et al., 1983; Krebs and McCleery, 1984). The fundamental assumption of this approach to explanations of prey choice is that animals should choose selectively those food items that maximize their fitness under a given set of operative constraints. Although measurable features of food quality such as prey size (Werner and Hall, 1974) or protein content (Milton, 1979; Owen-Smith and Novellie, 1982) can (or are assumed to) influence fitness, energy content is most commonly modelled. The use of energy content as the benefit currency is limited because it may not be used alone to discriminate between the nutritional content of different prey types. However, it can be quantified relatively easily and often covaries with more precise measures of the organic content of food. The criterion of choice among a set of food items is relative profitability, defined as

the rate of return of the selected benefit. For animals with energy maximization strategies, the optimal diet set consists of those items that maximize the net rate of energy gain. Less profitable items are excluded from the diet that would decrease the rate of energy intake (Pyke et al., 1977; Krebs, 1978).

One-factor approaches to foraging behavior, however, may be too simplistic, and may not adequately account for observed food choices. For example, inorganic nutrient constraints (Belovsky, 1978), risk sensitivity (Caracao et al., 1980), predation risk (Heller and Milinski, 1979), or motivational factors related to hunger (Heller and Milinski, 1979; Pastorok, 1980) may alter energy maximization strategies. It is crucial to identify the major constraints within a given system so they may be appropriately included in foraging models.

There are good indications that the fitness of Chaetodon multicinctus (and probably most other coral-feeding butterflyfishes) is enhanced by maximizing the rate of food intake. Growth is extremely rapid during the first year of life, and reproductive output for females increases rapidly with body length (Chapter I). Male body length is related to feeding-territory area and the size of his female mate (Chapter IV). The storage of body fat during the summer may influence reproductive output during the following spawning season (Chapter II). Over 90% of this species' time is spent foraging for food (Chapter IV; Tricas, 1985). It appears that an energy maximization strategy would adequately characterize this species because it would also reflect increased nutrient intake, such as protein or fat, that are used for growth and reproduction.

Most coral-feeding butterflyfishes show distinct preferences for specific food corals (Reese, 1977; Birkeland and Neudecker, 1981; Motta, 1980; Cox, 1983; Gore, 1984) yet the proximate factors that structure these foraging patterns are not understood. C. multicinctus feeds selectively on the polyps of three primary coral species, Porites lobata, Porites compressa, and Pocillopora meandrina that occur naturally within feeding territories (Tricas, 1985). This chapter tests the simple prediction that preferred food corals have a higher profitability (defined here as energy intake per unit time) than less preferred species, and elucidates the constraints that structure the food preferences. Patterns of prey choice are first shown for fish in the field, and are reproduced under laboratory conditions. Each food type is examined for its energy content, relative polyp accessibility, and potential noxious qualities through the coral's nematocyst defense. It is shown that food preferences observed in the field and lab follow those predicted by relative profitability of food corals, although defensive nematocyst strategies of food corals may also operate. High energetic value may best explain the strong preference for the coral, Pocillopora meandrina, but experimental manipulation of gross coral morphology shows that handling-time constraints structure food preference patterns on corals of the genus Porites.

METHODS

Field Measurements and Observations

Field data on food abundance and fish foraging patterns were collected at Puako reef on the island of Hawaii (see Chapter IV). The

study area includes the shallow reef flat and adjacent coral rich area that extends seaward along a gently sloping shelf to depths of about 12 m. The coral community is composed of extensive fields of Porites lobata and Porites compressa corals. A third species, Pocillopora meandrina also is found within the Porites stands but is much less common.

Abundance of each coral within fish territories was estimated by quadrat subsampling methods described in Chapter IV. Percent coral cover for each species was calculated from its proportion of the total counts for all species. Coral abundance within 18 fish territories was estimated by random sampling of 20 quadrats per territory.

Feeding data for both pair members from the 18 study territories were recorded. Divers followed fish and scored the coral species taken in each bite during alternate 5-minute observation periods. Each fish was observed for at least 50 total minutes. All data were collected between 1000 and 1400 h. Food choice patterns were expressed as the percent total bites taken on a particular food item in relation to its relative abundance expressed as percent cover.

Energetic Analyses

The caloric content of the three primary food corals was determined by Phillipson microbomb calorimetry (Phillipson, 1964). Corals were collected from reef habitats on the island of Oahu and transported to the lab. Tissue was removed from the surface of corals with a stream of recirculating distilled water shot from a dental water jet. Samples were then frozen, lyophilized, pelletized, and bombed. The calorimeter

was calibrated using a benzoic acid standard. Endothermic processes due to combustion of carbonate were adjusted for according to Paine (1966). Non-organic content was determined by ashing pellets for 3 hours at 500 °C in a muffle furnace.

Water Content

The water content of both Porites corals was determined by dry weight analysis. Individual coral colonies were drip dried and placed inside a large dry plastic bag. Live coral tissue was removed by a high-pressure stream of air directed across the colony's surface. The viscous goo was removed from the bag, weighed, dried in an oven at 40°C, and then reweighed. Percent water content was calculated as the ratio of dry to wet weights x 100.

Polyp Densities

The average number of coral polyps per unit area was estimated for both Porites corals. A circular template (2 cm diameter) was placed haphazardly at 10 locations on the surface of the coral colony and the number of polyp calices enumerated.

Nematocyst Densities

The density and size of nematocysts in polyp tentacles was determined for Porites compressa, Porites lobata, and Pocillopora meandrina. Various nematocyst types were classified according to Mariscal (1971; 1974). Corals collected from the field were fixed in

formalin for at least two days, rinsed, and individual polyps removed from the coral surface with small dissecting needles and forceps. The distal 1-mm of the polyp was then removed, opened by an incision along the oral-aboral axis, and placed on a glass microscope slide. A squash of the preparation was made with a glass cover slip and examined under a compound microscope at 400 x. The number of polyps in five ocular fields (approximately 4.17 mm²) was counted for ten polyps of each coral species.

The dimensions of the nematocysts were determined for each species. The length (L) and diameter (D) of ten nematocysts of each species was measured with an ocular micrometer. From these data mean nematocyst volumes were estimated by the formula for volume of an elipse,

$$\frac{4}{3}(\pi)D^2L.$$

Laboratory Experiments

Fish used in laboratory tests were obtained from shallow coral reefs on the leeward coast of Oahu by divers using handnets. Individuals were acclimatized for approximately 3 days in large aquaria supplied with sea water from a flow through system at Hawaii Institute of Marine Biology. Fish were supplied with colonies of Pocillopora damicornis for food prior to and between experiments.

Handling time

Foraging time can be defined as the total time spent in search, capture, and handling of prey. For the present study, I consider time spent foraging as that time required to locate, remove, and ingest a suitable polyp on an individual coral head. This definition is

synonymous with the handling component of the broader definition given above. In an ethological context, foraging was defined by the approach of a fish to within one head length of a coral colony to inspect the surface for polyps. While foraging upon corals, fish maneuvered their body about the colony in order to position the mouth for feeding. The other foraging component, search time, relates to the abundance of food items and is not considered in the laboratory experiments. The effects of coral density upon foraging preferences, however, are addressed in the discussion.

Relative handling costs were determined for Porites lobata and Porites compressa. C. multinctus is a highly visual feeder and closely inspects the coral surface before feeding on individual coral polyps. Motion of the eye during inspection of polyps can be readily observed at close range by movement of the black vertical band which passes through the center of the eye. It is relatively easy to enumerate the number of eye movements a fish makes while foraging.

Five fish were presented a single colony of each coral species and observed from behind a black plastic blind placed against the front of the aquarium which allowed for very close observations. For each 10-minute run the following data were recorded: 1) the total time spent feeding on the coral head (total foraging time), 2) the number of bites taken, and 3) the number of eye movements during foraging. Test fish were presented each of the two Porites spp. corals three times. From these data were calculated the mean number of eye movements per minute foraging time, and mean number of eye movements per bite.

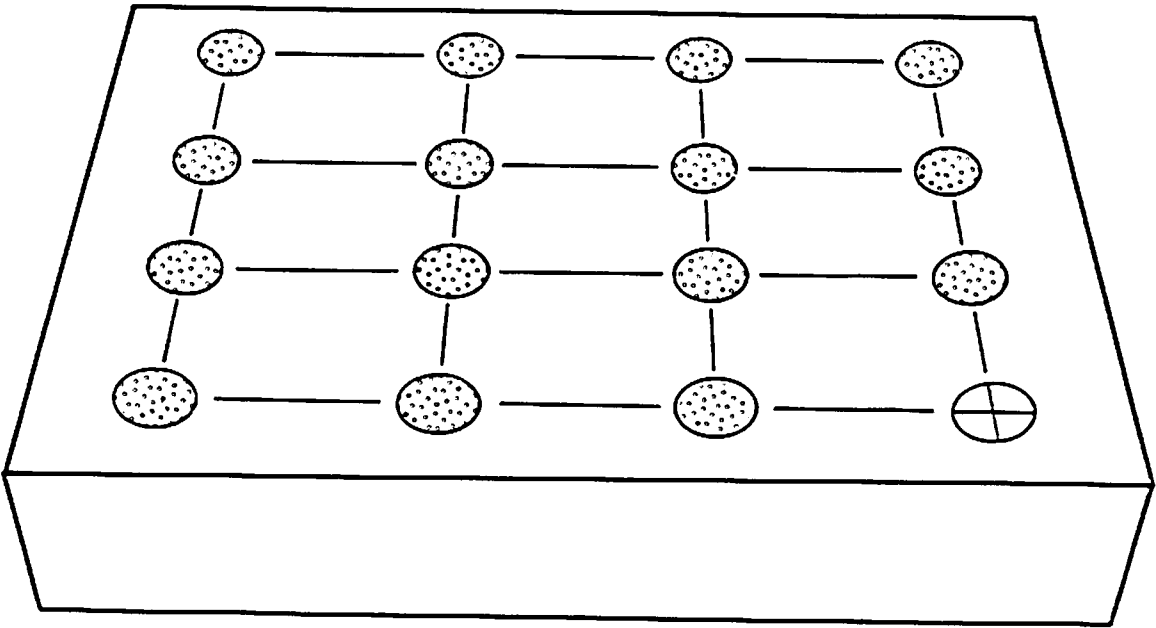
Coral morphology

The effect of colony morphology on handling time was experimentally examined for both Porites lobata and Porites compressa. The prediction was made that preference for one species when presented as whole colonies should not be present if gross coral morphologies were masked and handling times equalized.

Two identical feeders were constructed for paired presentation of live corals (Figure 24). Sides were made from 1/4-inch plexiglass covered with white tape and the surface from 1/16-inch white PVC sheet vinyl. Overall dimensions were 8 x 8 x 2 inches. A square matrix of sixteen 5/8-inch (2 cm²) holes was drilled on the surface and rows of elastic bands strung so that they crossed under each hole. Small pieces of coral were positioned on the underside of the feeder and held flush with surface by the bands so that fish were presented a flat surface of coral polyps.

In the experimental procedure fish were simultaneously presented both coral species under treatments 1) normal whole colonies, and 2) corals in separate feeders. Considerable effort was made to minimize differences between corals to reduce visual or gustatory bias. Coral heads of approximately the same size were used for whole colony presentations. Color differences and polyp condition between species were controlled by visually matching species for color and polyp length, respectively. Coral pieces placed in feeders were taken from the same colonies used in whole colony presentations. The position of coral heads and feeders in the aquarium during each run was randomized to

Figure 24. Coral feeder. Dimensions are 8 x 8 x 2 inches. Holes are 5/8 inch in diameter (2.0 cm²). Elastic bands (indicated by black lines) are woven across surface of feeder, cross under holes, and support coral pieces flush with feeder surface. Empty hole with support bands shown in right front corner.



eliminate any position effects. The order of presentation for whole colonies and feeders was also randomized for each test sequence.

Prior to each experimental run subjects were given a minimum of 5 minutes to sample each colony or feeder for at least 5 feeding bouts. A few pre-trial periods required a few minutes longer to meet that criterion. The first presentation (either colonies or feeders) was immediately followed by the second. Experiment durations were 15 minutes for whole colony, and 30 minutes for feeder presentations. Eight individual fish were used in three experimental runs each.

Data were analysed as the mean proportion of bites taken on each coral species. Data were compared between whole colony and feeder presentations by analysing pooled data from all fish for each treatment. A paired-comparison test was used to detect trends of directional changes common to all fish.

RESULTS

Food Preferences in the Field

Eighteen fish territories were examined on the shallow reef flat and in the deeper coral rich zone. Total coral cover within territories ranged from 8 to 48%, and averaged 33%. Porites lobata was the most abundant species (Table VIII). Other corals such as Montipora verrucosa, Leptastrea purpurea, and Leptastrea bottae also occurred but in patches usually less than a few centimeters in diameter and were not picked up in quadrat counts. Non-coral substrata that consisted primarily of small patches of exposed basalt, dead coral, rubble, and sand covered 67% of the bottom.

Table VIII. -- Abundance of food items and feeding patterns (means and standard deviations) of residents in territories of 18 C. multicinctus pairs. Total observation time = 3490 min. Total number of bites = 39,785. B/C = ratio of proportion of bites to proportion of bottom cover. P determined from Wilcoxon 2-sample test.

| Food Item | Percent | | | |
|------------------------------|-------------|-------------|-------|----------|
| | Total Cover | Total Bites | B / C | <u>P</u> |
| <u>Porites lobata</u> | 25.8 ± 10.9 | 65.1 ± 15.2 | 2.52 | <.0001 |
| <u>Porites compressa</u> | 6.9 ± 6.2 | 7.8 ± 9.7 | 1.13 | .76 |
| <u>Pocillopora meandrina</u> | .6 ± .5 | 2.1 ± 4.0 | 3.50 | .90 |
| Hard Substrate | 66.7 ± 11.5 | 25.0 ± 13.4 | .38 | <.0001 |

Seventy-five percent of all bites were taken on living corals. The proportion taken on each species is listed in Table VIII. Porites lobata was the most frequent food item with 87% of all coral bites taken on this species. In addition to coral tissues, fish consumed small quantities of benthic filamentous algae that grew on dead corals and basalt, and occasionally invertebrates such as amphipod crustaceans and pieces of polychaete worms. These food items, however, were rare and estimated to comprise less than 1% of the total stomach content volume.

The relationship between coral abundance (measured as percent substrate cover) and feeding preferences for Porites corals and hard substrate is illustrated in Figure 25. A test of independence between food abundance and diet composition show that no pair foraged on the substrates in proportion to their abundance (Independent G-test for 18 pairs: $df = 3$, $P < .001$) or when data for all pairs were pooled (G-test: $df = 3$, $P < .001$). Fish preferred Porites lobata and fed on it in excess of its abundance (Table VIII). In contrast fish fed upon Porites compressa in proportions not different from its abundance within territories. Hard substrates (filamentous algae and invertebrates) were grazed less frequently than expected by its proportion of cover.

Examination of bites taken on corals (excluding bites on non-coral substrates) in relation to their relative abundance are shown in Figure 26. Porites lobata is taken in excess proportion to its abundance (Wilcoxon 2-sample test: $n = 18$; $P < .05$), while Porites compressa is taken less than expected (Wilcoxon 2-sample test: $n = 18$; $P < .05$). The relatively rare coral, Pocillopora meandrina, was taken in greater

Figure 25. Proportions of coral and hard cover substrate in territories and among feeding bites of C. multicolor. Open (% cover) and closed (% bites) circles indicate mean values for a foraging pair. Vertical scale for each food type is found to the right of its abscissa.

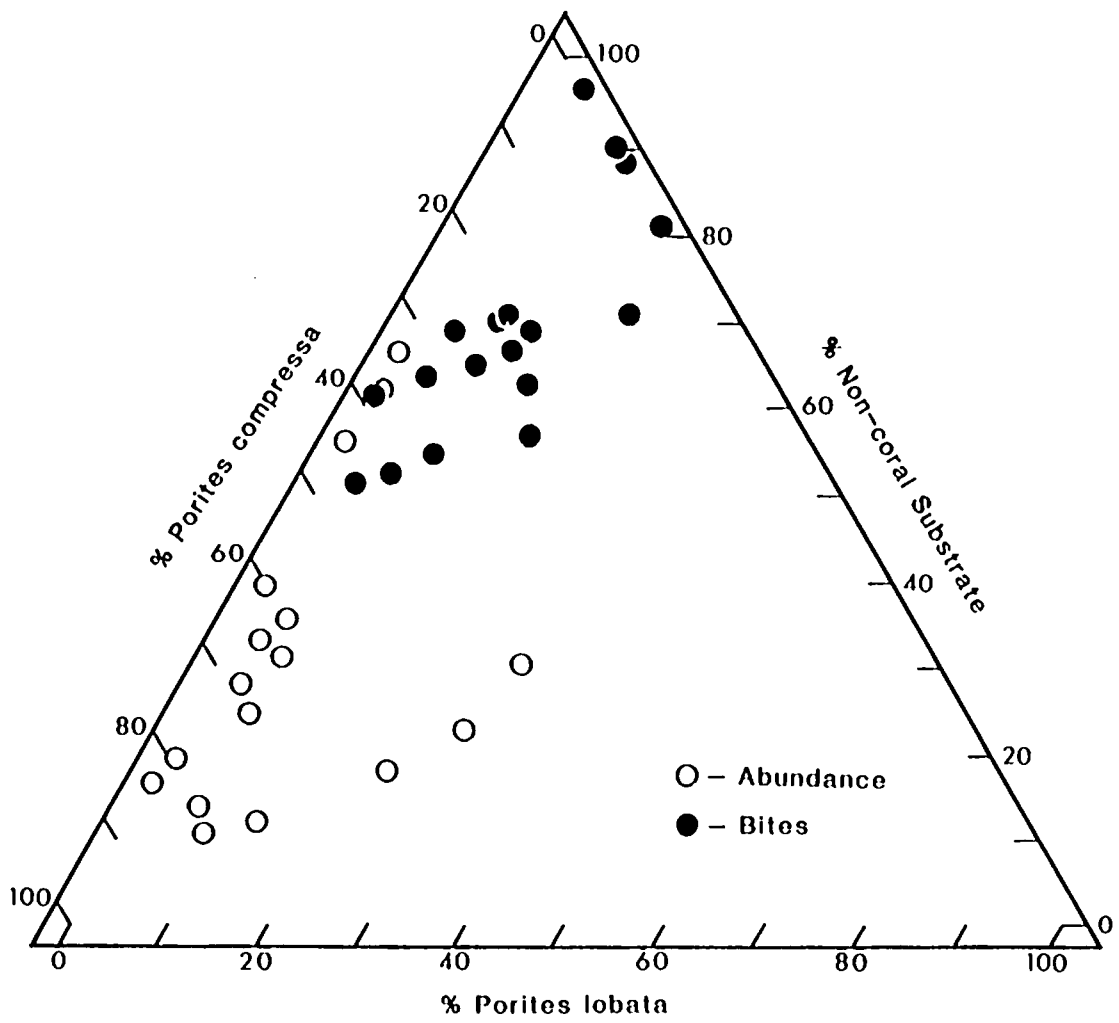
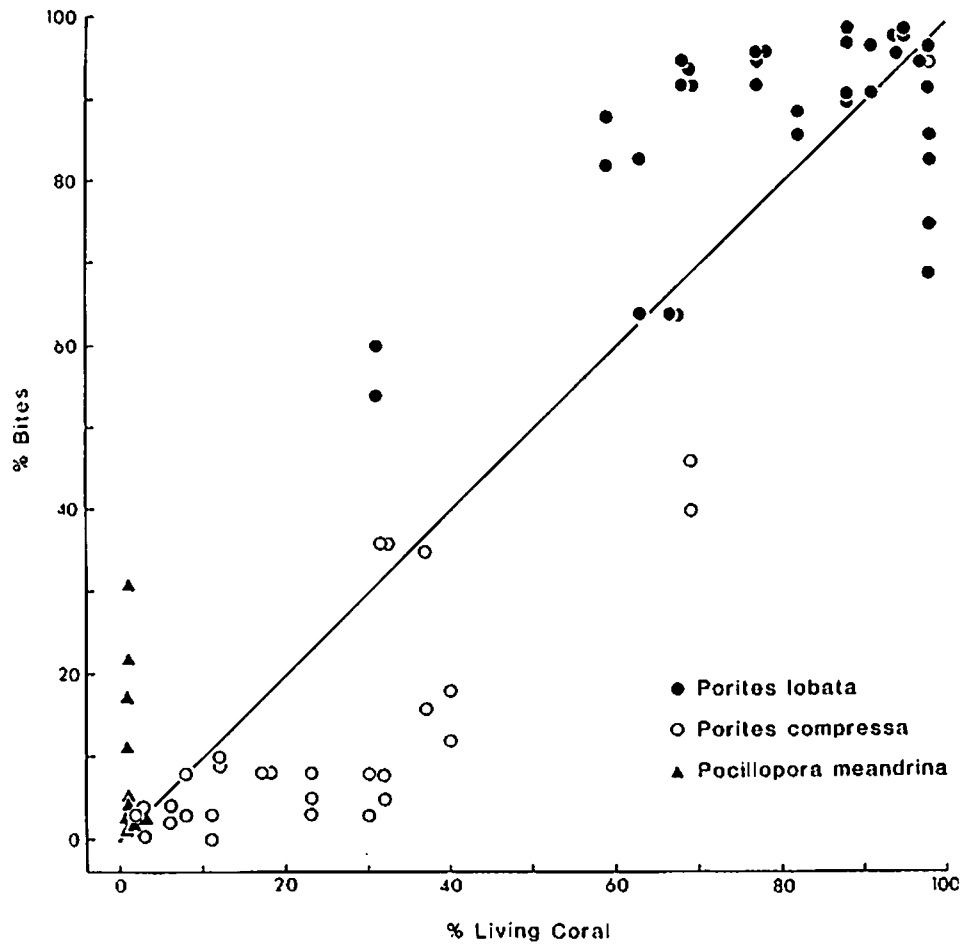


Figure 26. Proportions of living coral cover and bites in feeding-territories of C. multicolor. Each symbol represents mean value of foraging pair.



proportion than expected by its distribution (Wilcoxon 2-sample test: $n = 18$; $\underline{P} < .05$).

Energy and Water Content of Food Corals

Caloric densities of coral tissues are shown in Table IX. Mean values for Porites lobata and Porites compressa were very low on an ash-free dry weight basis and were not different (t-test, $P > .05$). In contrast, Pocillopora meandrina had a mean caloric density approximately 15% higher than the pooled Porites data ($p < .002$, Wilcoxon 2-sample test). This analysis shows that energy contents of the Porites corals do not differ but are both lower than Pocillopora meandrina.

The tissues of both Porites lobata and Porites compressa have a water content of about 95% (Table IX). This equality indicates that energy content on a wet weight basis is approximately equivalent between species of Porites.

Nematocyst Size, Distribution, and Abundance

Nematocysts differ qualitatively between the two genera of corals examined. Pocillopora meandrina has two types of small nematocysts (Table X). The larger is a relatively translucent capsule with the base of the undischarged shaft prominently visible in the interior. This is probably the stinging mastigophore described for this species by Mariscal (1971). The smaller nematocyst resembles that of the spirocyst. Although numbers of nematocysts were not enumerated in detail for this species, they were the most abundant of the 3 corals and often exceeded 40 per field.

Table IX. -- Caloric values and water content (means and standard deviations) for soft tissues of Hawaiian corals. AFDW = ash free dry weight. n = number colonies analysed.

| Species | Energy | | Water | |
|------------------------------|--------|--------------------|-------|-----------|
| | n | calories / mg AFDW | n | Percent |
| <u>Pocillopora meandrina</u> | 7 | 5.29 ± .08 | - | - |
| <u>Porites lobata</u> | 8 | 4.65 ± .32 | 4 | 96.1 ± .4 |
| <u>Porites compressa</u> | 3 | 4.53 ± .10 | 3 | 94.4 ± .3 |

Table X. — Nematocyst dimensions, volume, and density (means and standard deviations) for three Hawaiian corals. Ten polyps measured for each species. Nematocyst volumes estimated from length and diameter data fitted to equation for volume of an ellipse. Density expressed as mean number of nematocysts per 400 x field of magnification on compound microscope (area = 4.17 mm²). Two nematocyst types measured for P. meandrina.

| Species | Length (mm) | Diameter (mm) | Volume (x10 ⁻⁵ mm ³) | Density (No./Field) |
|------------------------------|----------------|------------------|--|------------------------|
| <u>Porites lobata</u> | .063 ± .003 | .017 ± .001 | 7.36 ± .92 | 4.30 ± 2.1 |
| <u>Porites compressa</u> | .076 ± .001 | .018 ± 0.0 | 10.21 ± .20 | 6.40 ± 3.2 |
| <u>Pocillopora meandrina</u> | 1) .022 ± .003 | .003 ± 0.0 | .06 ± .01 | - |
| | 2) .040 ± .003 | .005 ± 0.0 | .39 ± .04 | > 40 |

Nematocysts were qualitatively similar for both species of Porites examined. They appear to be of the macrobasic nature since some everted threads were almost 50 times their capsule length. Undischarged nematocysts of both Porites corals were much larger than those found in Pocillopora. A between-species comparison shows that nematocysts of Porites compressa are larger than those of the preferred Porites lobata although of less magnitude than the inter-generic size differences (t-test, $t = 9.55$, $P < .001$).

Nematocyst density in polyp squashes was higher in Porites compressa than in Porites lobata (F-test (square root transformation of raw data), $F = 2.20$, $df = 8$, $P < .05$). The distribution of nematocysts in Porites compressa appeared to be more clumped than in Porites lobata. This is reflected by a higher coefficient of dispersion (ratio of variance to mean) of 1.60 for Porites compressa than 1.03 calculated for Porites lobata.

Polyp Densities

Corals of the genus Porites have very similar calyx morphologies but some fine-scale differences exist. Calices are on average smaller in Porites lobata than Porites compressa, thus their overall density is higher in the former species (Table XI, t-test, $t = 4.16$, $P < .005$). In addition, calices (and presumably polyps) were more variable in size for Porites compressa due primarily to its more complex surface structure and greater 3-dimensional relief. Although the majority of feeding activity is directed at the tips of Porites compressa by C.

Table XI. -- Polyp densities on surfaces of three corals. Density expressed as number of polyps per cm². CD = coefficient of dispersion (ratio of variance to mean).

| Species | n | Mean \pm SD | CD |
|------------------------------|----|-----------------|-----|
| <u>Pocillopora meandrina</u> | 5 | 66.4 \pm 15.3 | 3.5 |
| <u>Porites lobata</u> | 10 | 76.7 \pm 5.7 | .4 |
| <u>Porites compressa</u> | 10 | 61.0 \pm 10.5 | 1.8 |

multicinctus, fish were routinely observed in the field feeding along the length of the accessible branches.

Pocillopora meandrina is very different in its surface morphology from Porites corals. It is covered with small verrucae on which the polyps are located. The size of the verrucae and numbers of associated polyps vary greatly between sites and thus this species shows considerable variability in number per unit area (Table XI). Since polyps are clustered in a three-dimensional space but were enumerated over a two-dimensional area the density estimate is in reality much lower over the true coral surface. The present estimate is a realistic approximation, however, since fish inspect the fine scale surface relief from a distance. Polyp density in this species was not different from either Porites coral (Tukey's multiple comparisons test, $P > .05$).

Laboratory Experiments

Handling costs

Lab feeding experiments show that fish take on average approximately 50% more bites per unit foraging time on Porites lobata than on Porites compressa (Table XII, paired t-test, $t = 2.97$, $P < .05$). The fewer bites taken during foraging on Porites compressa also indicates a longer duration between bites. This foraging cost is reflected in the eye movement data. Fish searched more, as indicated by number of eye movements per minute, to find polyps on Porites compressa than on Porites lobata (Table XII, paired t-test, $t = 5.05$, $P < .01$). Over twice as many eye movements per bite were made while foraging on Porites compressa (Table XII, paired t-test, $t = 3.44$, $P < .05$). Eye

Table XII. -- Frequency of eye movements (means and standard deviations) of C. multincinctus during foraging on corals of the genus Porites.

| Species | Bites | Eye Movements | |
|--------------------------|----------------------|----------------------|--------------------|
| | minute ⁻¹ | minute ⁻¹ | bite ⁻¹ |
| <u>Porites lobata</u> | 19.3 ± 7.8 | 33.3 ± 8.0 | 2.1 ± 0.9 |
| <u>Porites compressa</u> | 13.1 ± 8.1 | 42.1 ± 11.4 | 4.6 ± 2.4 |

movement data support the view that foraging on Porites compressa is more costly in handling time, which is associated with a low profitability (bites per unit foraging time) than on Porites lobata.

The constraint of coral morphology

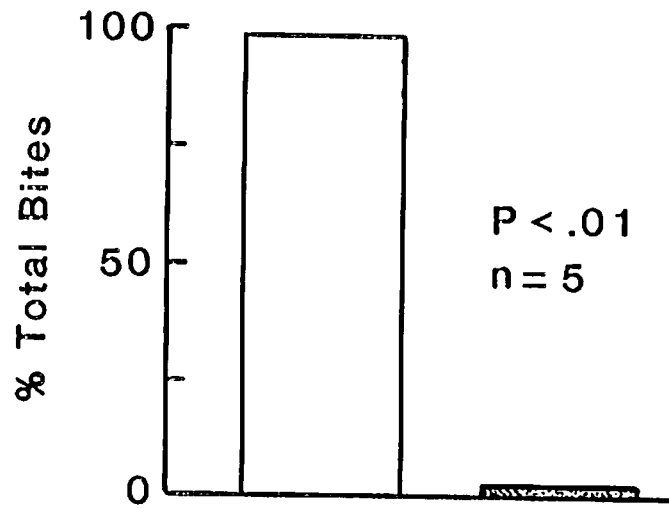
C. multicinctus shows distinct preferences for corals in the lab. Whole colonies of Pocillopora meandrina were highly preferred over those of Porites lobata (Figure 27) which were preferred over Porites compressa (Figure 28). This preference hierarchy is the same as that observed for fish feeding in the field based on the ratios of bites to coral abundance (Table VIII).

Fish were also able to discriminate between Pocillopora meandrina and Porites lobata when their gross morphologies were masked by the feeders (Figure 27). The proportion of bites on Pocillopora meandrina in whole colony presentations (98%) remained very high when the two corals were presented in the feeders (88%). This indicates that fish can discriminate between the two corals when their gross morphologies are masked and associate the preference with the position of the feeder in the tank.

The preference for whole colonies of Porites lobata over Porites compressa, however, was not replicated when corals were presented in feeders (Figure 28). For pooled feeding data, fish did not show preferences for either coral when morphology was masked (Wilcoxon 2-sample test, $P > .05$). Fish showed a significant trend for a decreased proportion of bites on Porites lobata in feeder experiments compared with associated presentations of whole colonies (Wilcoxon paired-sample sign test, $n = 8$, $P < .05$, one-tailed test). These results indicate

Figure 27. Feeding preferences of 5 C. multicinctus for the corals, Pocillopora meandrina and Porites lobata. Corals presented together in whole colony and feeder treatments (see Fig. 1). P determined by Wilcoxon 2-sample tests of proportions of bites within each treatment.

Whole Colonies



Feeders

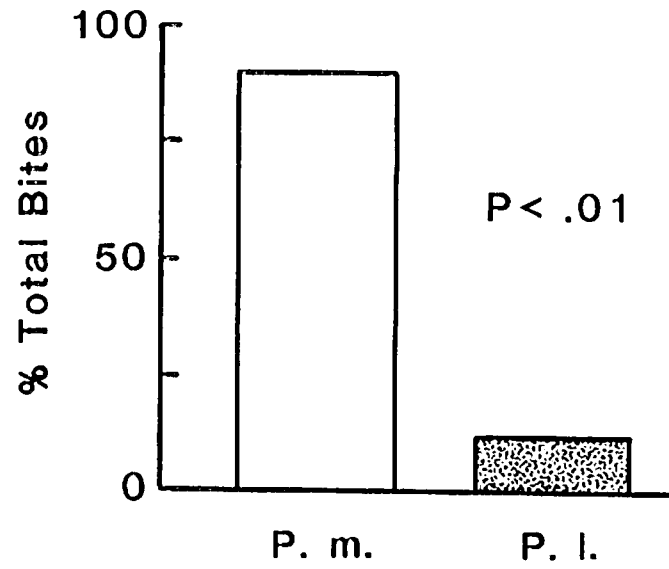
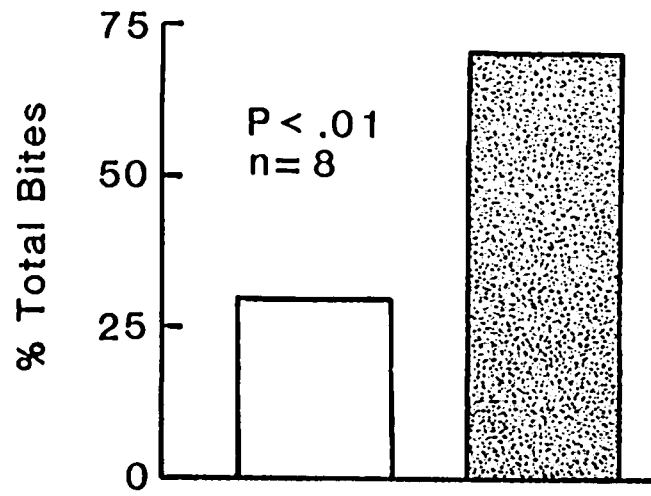
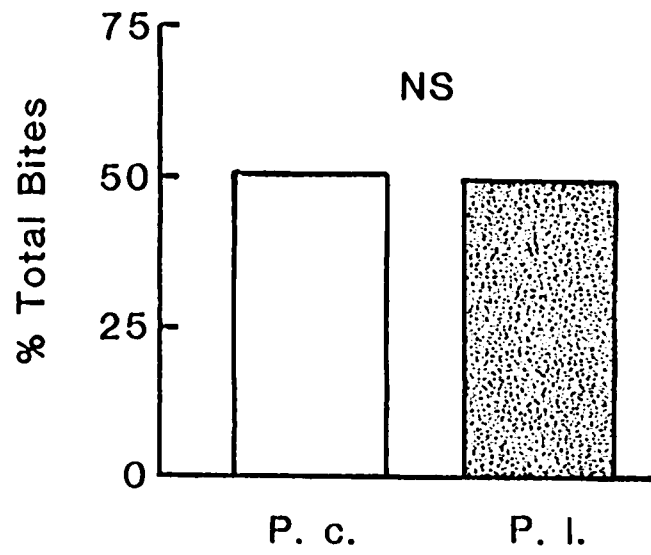


Figure 28. Feeding preferences of 8 C. multicinctus for the corals, Porites compressa and Porites lobata. Corals presented together in whole colony and feeder treatments (see Fig. 1). \bar{P} determined by Wilcoxon 2-sample tests of proportions of bites within each treatment.

Whole Colonies



Feeders



that fish do not distinguish between the two species of Porites when the factor of gross morphology is equated.

DISCUSSION

Specific coral food preferences exist for C. multicoloratus. Porites lobata is taken in higher proportion than its abundance both in terms of its composition of total bottom cover (Figure 25, Table VIII) and living coral cover (Figure 26). In contrast, Porites compressa is taken in equal proportion to its percent bottom cover but much lower than its proportion of living corals. Although relatively rare, Pocillopora meandrina was highly preferred when it occurred within fish territories. This apparent preference for Pocillopora corals is reported for corallivores in Guam (Neudecker, 1979) and other tropical reefs (Randall, 1974).

Feeding preferences observed in the field also occurred under laboratory conditions. Pocillopora meandrina is highly preferred over Porites lobata, while Porites lobata is highly preferred over Porites compressa. Similar preference hierarchies for corals of the genus Pocillopora over Porites exist for other Hawaiian chaetodontids. Reese (1977) and Cox (1983) found Pocillopora damicornis was preferred over Porites compressa and Montipora verrucosa by Chaetodon ornatissimus and Chaetodon trifasciatus.

The observed preferences for Pocillopora by butterflyfishes is consistent with its relatively high energy content. Pocillopora meandrina has a mean caloric density of 5.29 calories/gAFDW. This elevated energy content is at least partially due to relatively high

lipid, since this species often has small fat bodies within the soft tissue that compose about 35% of the tissue weight (J. Stimson, personal communication). The congener, Pocillopora damicornis, shows about the same caloric content of adult tissue, and even higher caloric and lipid content when brooding planula larvae (Richmond, 1982). Pocillopora meandrina, however, apparently does not undergo the regular lunar planulation as does Pocillopora damicornis (Stimson, 1978) and probably does not show the frequent fluctuations in its caloric value. In comparison, corals of the genus Porites showed a caloric density only slightly above that of carbohydrates (4.10 cal/mg AFDW), and well below that of either pure protein or lipid (5.65 and 9.45 cal/mg AFDW, respectively). Approximately 25% more calories per bite are taken by C. multincinctus on Pocillopora than on Porites corals (Hourigan et al., in press).

Structural differences between these two coral genera may also be important to their relative attractiveness to foragers. Corals of the genus Porites have a perforate skeleton where much of the living tissue extends beneath the surface. This subsurface tissue is inaccessible to coral-feeding chaetodontids like C. multincinctus that remove surface tissues without damaging the underlying corallite. In contrast, Pocillopora corals have imperforate skeletons with all living tissue at the colony surface and available for feeding. This relative availability probably further enhances the profitability of Pocillopora.

Polyp density was correlated with feeding preferences among Porites corals. Porites lobata averaged about 25% more polyps per unit surface

area than Porites compressa. The higher polyp density may increase the rate at which fish can harvest polyps, and thus influence their foraging patterns.

There is also correlative evidence that nematocyst size, abundance, and distribution within polyp tentacles may affect food preferences.

Nematocysts in the highly preferred Pocillopora meandrina were 19 to 26 times smaller in volume than those in Porites corals (Table X).

Nematocysts in the least preferred species, Porites compressa, were larger and more numerous than in Porites lobata. In addition, nematocysts were relatively more clumped in their distribution in tissues of the former species. Fish may experience relatively infrequent but more intense stings while foraging on Porites compressa.

Although higher energy content may explain preferences for Pocillopora corals, the clear preference for Porites lobata over Porites compressa is not energetically based since their caloric densities (and water content) did not differ. In this case, the preference is correlated with differences in handling costs. The branching morphology of Porites compressa effectively reduces the numbers of polyps available per unit area. The higher number of eye movements per unit foraging time on Porites compressa indicates that more time is required to locate suitable polyps on this species. This results in a lower rate of return as measured in bites per unit foraging time (Table XII). Although I was unable to make quantitative determinations in the field, fish routinely made many eye movements while searching for polyps on coral colonies, and appeared to spend more time searching per bite taken on Porites compressa than on Porites lobata. Furthermore, there were no

qualitative differences in the number of eye movements made by fish foraging on either species of Porites during the coral feeder experiments even though polyp densities differed. Increased eye movements appear to be a result of the structural complexity of the coral colony.

The preference for Porites lobata over Porites compressa seen in whole colony presentations was not found when coral morphology was masked in the feeder experiments (Figure 28). Fish did not distinguish between the two species, as measured by number of bites, and individuals showed a decreased proportion of bites taken on Porites lobata when paired presentation of colonies and feeders are compared. This indicates that fish did not use gustatory or olfactory cues to make food choices over the 30-minute duration of these experiments. It is unlikely that feeding choices between the two species are based on differential noxiousness related to nematocyst densities. It can not be ruled out, however, that over longer periods fish may detect cumulative effects of nematocyst toxins. Unfortunately, feeders could not support experiments of longer durations because of polyp depletion.

The food preferences shown by C. multicinctus follow general patterns of energy profitability as predicted by optimal diet theory but the prediction that low ranking prey should always be ignored fails in this system. Although Porites compressa was the least preferred of the food corals, it was taken regularly in both field and in the lab. It is difficult to identify why partial preferences for this species exist. Explanations as simple as profitability reinforcement or sampling errors during foraging are possible, and numerous others are discussed by Krebs

and McCleary (1984). Foraging on Porites compressa may be profitable if fish selectively feed on exposed portions of branches that require less handling time. In this case, the effective abundance of Porites compressa would be considerably lower than that estimated from quadrat sampling methods. Motta (1980) described selective feeding on the tips of branching corals for a variety of coral-feeding butterflyfishes. Partial preferences might also be explained by cumulative effects of nematocyst toxins which might set an upper limit on the amount of tissue that can be ingested per unit time. Unfortunately, nothing is known about the effects of coral toxins on coral-feeding fishes.

In summary, C. multinctus shows distinct coral preferences consistent with those observed for other corallivorous fishes. The strong preference for Pocillopora meandrina is consistent with the high caloric content of its tissues. In contrast, energetic differences among living tissues can not explain the strong preference for Porites lobata over Porites compressa. This preference is at least a partial function of handling constraints imposed by differences in gross structural morphology. Species differences in nematocyst quality and abundance indicate the defensive biology of corals could also influence preferences patterns among coral-feeding fishes.

CHAPTER IV
FOOD AND COMPETITORS AS
DETERMINANTS OF TERRITORY SIZE

INTRODUCTION

Territorial behavior usually involves the defense of space and food, shelter, or reproductive resources that can enhance inclusive fitness (reviewed by Hinde, 1956; Wilson, 1975; Davies, 1978; Wittenberger, 1981). Because territoriality results in spatial adjustments among groups of individuals, it can have major influences on both the size, structure, and social organization of populations (e.g. Orians, 1961; Horn, 1968; Fretwell and Lucas, 1969; Brown and Orians, 1970; Maynard Smith, 1974).

Although territories often include multiple resources, food supply is of particular importance because it is used to meet energetic and nutritional requirements for maintenance, growth, and reproduction. The proximate factors that determine feeding territory size in natural populations, however, are not clearly understood. Two general hypotheses have been proposed to explain the intraspecific variability of feeding territory size in relation to food supply (reviewed by Meyers et al., 1979). The food maintenance hypothesis (sometimes referred to as the sufficient food hypothesis) states that animals defend areas that contain a food supply adequate to satisfy their short-term energy requirements. Any food defended beyond that level would accrue no additional value at an increased defense cost. The major prediction of this hypothesis is that territory size is adjusted by residents as an

inverse function of local food abundance. Support comes primarily from studies in which feeding territory area was negatively correlated with food supply (Stimson, 1973; Slaney and Northcote, 1974; Gill and Wolf 1975; Simon, 1975; Gass et al., 1976; Kodric-Brown and Brown, 1978). In contrast, the competitor constraint hypothesis points to increased defense costs that may accompany increases in food abundance. By this hypothesis, food competitors act to constrain territory area below some maximum through competitive interference with residents (Krebs, 1971; Schoener, 1971, 1983; Crook, 1972; Myers et al., 1979; Franzblau and Collins, 1980; Hixon, 1980; Schoener and Schoener, 1980; Norton et al., 1982). This hypothesis predicts that territory size is adjusted by residents as an inverse function of competitor abundance rather than direct assessment of food supply.

The two hypotheses, which generate conflicting predictions of spatial changes to varying food supplies, have usually been examined independently. It should be recognized, of course, that in natural systems they would not always be mutually exclusive. For example, in populations where food is potentially limited, areas of higher than average food abundance often attract additional competitors (reviewed by Myers et al., 1981). Thus, although animals may defend smaller territories in resource-rich habitats, it can be difficult to establish whether territories are adjusted to accommodate a higher level of food, higher concomitant costs of resource defense, or some synergistic effect. In most territorial systems where food is potentially limited, both food and competitor abundances should influence the use of space.

Many of these problems may be addressed by integrating the costs and benefits of territorial defense in terms of specific foraging goals of the individual. The distinction between time minimizers and energy maximizers (Schoener, 1971) has provided insight into how different biological, energetic, and time constraints can influence predicted territorial and foraging behaviors. For example, the idealized time minimizer requires a fixed daily food ration and would receive no increased benefit by feeding in excess of that amount. Its strategy is to minimize time spent feeding so as to increase available time for territory defense, reproductive activities, predator avoidance, etc. In contrast, the fitness of an energy maximizer is directly related to energy intake and therefore it behaves in ways to maximize foraging time and net food consumption. Clearly, the optimal behavior of these two feeding strategists may differ, and separate models would be required to predict their activity budgets and territorial behavior.

Recently, several theoretical papers have examined how energy maximizers should adjust feeding territories in response to environmental fluctuations in food abundance and competitor density (reviewed by Schoener, 1983). Hixon (1980) modelled the effects of various environmental factors on optimal territory size for an energy maximizer constrained by its daily time budget. Time available for feeding was a function of the time spent in territory defense, and both food production and competitor density varied independently. This model predicted that territory size should be inversely related to both food supply and competitor density, and also provided predictions of how foraging and defense time should covary.

Ebersole (1980) modelled the effects of food supply on optimal territory size for an energy maximizer. His basic model assumed that defense costs were unaffected by changes in food density, and in contrast to Hixon (1980), predicted that territory size should vary directly with food supply. In a modified treatment developed for insectivorous birds, Ebersole considered the increased costs of defense associated with increased food supply. Fitness was limited by the time available for foraging and was an inverse function of the time required to defend the territory. This model predicted territory size to be inversely related to food abundance when the costs of defense changed directly with food supply. If defense costs remained stable during increased food density, however, territory size was predicted to increase.

Territorial behavior among fishes usually includes the defense of food resources (e. g. Rasa, 1969; Clarke, 1970; Vine, 1974; Brawley and Adey, 1977; Nursall, 1977; Hixon, 1981; Mahoney, 1981). For different species, however, territory size was reported to be highly variable in relation to food supply: positively (Ebersole, 1980; McNicol and Noakes, 1984), independent (Symons, 1971; Norman and Jones, 1984), and inversely (Slaney and Northcote, 1974; Dill et al., 1981; Hixon, 1981). The apparent lack of agreement between these studies is at least partially due to differences between the multipurpose utility of the territory, the dispersion and density of food supply, and analytical paradigm used in each study.

After one reviews the plethora of theoretical models and their variants advanced to explain the determinants of territory size, it becomes clear that each is based upon different sets of assumptions that can bear greatly upon the predictions that they generate (see Schoener, 1983). Even more remarkable, is the lack of attempts to validate or reject these models. Clearly, there is a need for empirical tests before any broad application of theoretical models to real systems can be made.

This chapter presents an analysis of the principal determinants of feeding territory size in the coral-feeding butterflyfish, Chaetodon multicinctus. I first describe the spatial and temporal characteristics of the territorial system and then demonstrate that this species is an energy maximizer operating under a time constraint. I then present an analysis of territory size in relation to numerous environmental correlates. In the experimental section, I test the major predictions of the food maintenance and competitor constraint hypotheses outlined above by manipulations of food and competitor abundances within a field population. The results show that both food abundance and competitor density influence the use of space in this system. These findings are then used to show that more comprehensive theoretical models can adequately illustrate the interaction of food and competitors on feeding territory size if the assumptions and benefit-cost relationships are carefully evaluated in relation to the test system.

METHODS

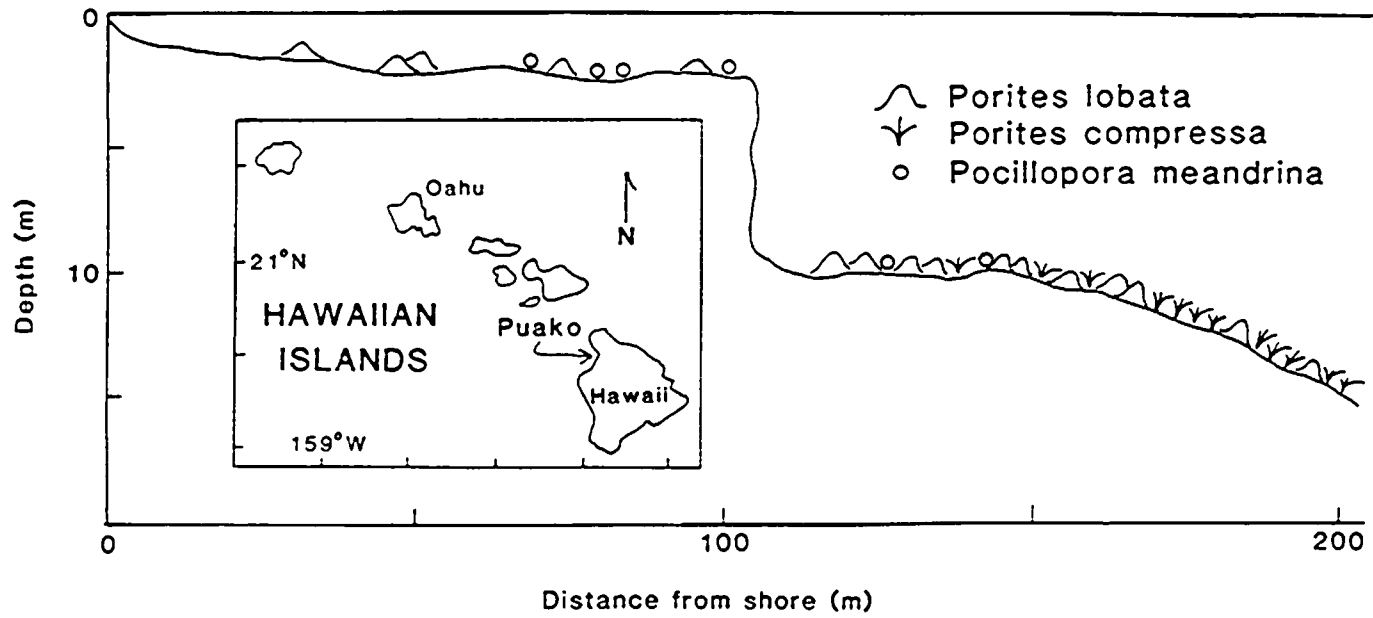
All field work was conducted on the reefs at Puako, Hawaii (Figure 29) between June and September, 1981-1984. The area is characterized by a shallow reef flat (2-5 m deep) that extends seaward approximately 100 m from shore to a precipitous drop to a deeper coral rich area (7-20 m deep). The reef flat habitat is subject to heavy winter surf activity and is composed largely of exposed lava with interspersed patches of living coral, rubble, and sand. Two stony corals dominate this area. Rose coral, Pocillopora meandrina, is a small erect species with heavy branches and is most common near the seaward edge of the reef flat in sediment-free locations. Porites lobata occurs in either encrusting or massive morphologies and forms large mounds in less exposed areas of the flat.

Extensive fields of P. lobata and Porites compressa extend seaward beyond the base of the cliff. The latter coral is a fragile branching species that dominates deeper areas protected from wave surge. The coral community is typical of other shallow reefs of Hawaii, and a more detailed description of Puako reef habitats is provided by Hayes et al. (1982).

Observations

Divers using scuba recorded the movements and activities of fish pairs on the reef that totaled over 3,000 man-hours of data collection. Individual fish were identified by distinctive variations in their patterns of body spots and bars. Strips of 10 cm-long plastic surveyor's tape attached to nails were used to mark feeding sites within

Figure 29. Bathymetric profile of the study site at Puako, Hawaii.



territories. Observers remained at sufficient distances (usually > 2 m) to minimize influence on the foraging path or behavior of fish. Each member of the pair was observed for alternate 5-min intervals during which feeding, agonistic, and other activities were recorded. Activity budgets were determined for 5 pairs by recording the time each sex spent feeding, in agonistic encounters, sheltering in holes and reef crevices, and at cleaning stations of the cleaner wrasse, Labroides phthriopagus. Generally, two dives were made each day during an experiment to provide samples of ten 5-min observations per fish per day. Feeding rates were recorded as the number of bites on each food item per 5-min period.

Tests for statistical differences between pre- and post-manipulation daily feeding rates were made using the Mann-Whitney U test. Rates of agonistic encounters were recorded as the number of aggressive events (primarily chases) per 5-min observation period. Because aggressive interactions in undisturbed territories were of short duration (usually < 15 s) and infrequent, data on agonistic behavior were analysed as the proportion of observation periods in which at least one agonistic event occurred. Differences between mean chase rates were tested by generating 95% confidence limits for a binomial proportion (Tate and Clelland, 1957). All statistical tests used a probability level > .05 for rejection of a null hypothesis.

The statistical treatments outlined above test for differences in the distribution of activity budgets of single fish pairs. Because replicate sample sizes were limited by logistic and time constraints, inferences about the behavior of the population must be made from observations on a relatively small sample of individuals. This caveat,

which is a problem with most extensive field studies, should not be ignored when data are interpreted.

After termination of each experiment, fish were collected underwater with hand nets, measured to the nearest mm (SL), sexed in situ by gonad cannulation (a modified procedure of Ross, 1984b), and returned to their home territory.

Measurement of Territory Size and Food Abundance

Planar and total surface area were measured for each territory. After termination of an experiment, a line was used to bisect the territory along its major axis. A second line and brass chain (each marked in .25-m increments) were then used to measure lateral linear and rugose (relief) distances, respectively, from the bisect line to the marked outer territory boundary. These measurements were taken at 1-m intervals on both sides of the bisect line and perpendicular to it. From these data, maps of each territory were drawn and 2-dimensional (planar) area (A_p) determined using a digitizer pad. Total surface area, A_t , was calculated as:

$$A_t = \frac{A_p \times R}{L} ,$$

where R is total relief distance for all lateral measurements, and L is the total linear distance for all lateral measurements. The ratio, R/L, provides a conversion factor to express surface area for the 3-dimensional relief.

The abundance of living corals within fish territories was measured by subsampling the proportion of bottom cover for each coral species. A 1-m² quadrat (.1-m grid) was placed at randomly determined locations within a territory and the coral species underlying each grid intersection point counted. The number of replicate quadrat counts per territory always exceeded asymptotic limits determined by species abundance-area curves.

Field Manipulations

Three major classes of experimental manipulations were performed in replicate to test the effects of food and competitor abundance on territory size and the time budgets of residents: 1) Food abundance including effects of food distribution, 2) Competitor abundance, and 3) combined effects of increased food and competitor abundance. Experiments were designed to test the null hypothesis that manipulation treatments had no effect on territory size or activities when compared to pre-manipulation data. At least one of 10 control sites was established concurrently with each of 16 experimentals to monitor natural fluctuation in territory sizes or activity budgets. Data from control territories were compared for the pre- and post-manipulation period of the associated experimental territory. For three experimental sites (decreased food 1 and 2, and increased competitors 1), controls consisted solely of territories within an undisturbed fish colony at which only territory area was regularly monitored. The recording of activity budget data from these three controls was omitted so that data could be taken from additional experimental sites and sample sizes

increased. This was justified in view of the extreme stability of territories observed in the previous controls. A detailed spatial design of experimental manipulations are provided in the Results figures.

I. Food distribution and abundance

In order to test for the effects of varying food abundance on territory size, activity budgets, and the attraction of competitors, food was manipulated in sets of separate supplementation and reduction experiments. In addition, the effects of food distribution were examined by adding corals to territories in four different spatial patterns.

Increased food (n = 4)- Preliminary experiments were performed to test for distributional effects of increased coral abundance upon foraging and territorial behavior. Supplemental colonies of rose coral, P. meandrina (approximately 15-20 cm dia.), were placed at predetermined points inside fish territories in random, clumped, and peripheral distributions. Random and clumped distribution points inside territory boundaries were determined with a random number generator. In the clumped food site, corals were centrally placed within the territory, spaced between .5 to 2.0 m from the nearest neighbor, and at least 2 m from territory borders. In the peripheral enhancement site, colonies were placed no greater than 0.5 m beyond the original borders and spaced approximately 2-m apart around the perimeter.

The above experiments showed a strong influence of food distribution on the behavioral response of residents (see Results).

Consequently, uniform distributions were chosen as the experimental food enhancement pattern for comparison with food reduction manipulations. Two low density (LD) sites were established by spacing coral colonies evenly 1.5 m apart. Two high density (HD) sites had corals spaced at 1.0 and .5 m intervals. To simulate a homogeneous increase in coral abundance within the habitat, all food supplementations extended at least 1 m beyond pre-manipulation borders. All control territories for food enhancement experiments consisted of unmanipulated territories.

Decreased food (n = 3)- Food abundance was reduced by covering portions of the substrate with 1-m² plastic or cloth sheets at randomly determined locations within 3 territories. In the first experiment, a two-step food reduction was performed that involved an initial decrease of 7 m² (11% of food and non-food substrates within the original territory) and a second 5 m² (8%; total = 19%) two weeks later. In the other two experiments 10 m² (19%) and 11 m² (24%) of P. lobata colonies within the original territory were covered in single reductions. In addition to unmanipulated controls, a single site was established to test for effects of the coral covers by placement of ten 1-m² plastic sheets over sand patches and within bare crevices (non-food substrates) within the territory.

II. Competitor abundance

The effects of competitor abundance on territory size and resident activity budgets was tested by sets of manipulations in which conspecific adults were either removed or introduced within boundaries of existing territories.

Decreased competitors (n = 4)- The maintenance of territorial boundaries in the presence of neighboring pairs primarily involved displays and overt chases against their neighbors. To test the importance of these conspecifics, adjacent contiguous pairs were removed around three experimental territories. To further limit conspecific agonistic encounters, any immigrating pairs or floaters were removed from the area during the post-manipulation period.

Increased competitors (n = 3)- Increased conspecific intrusions were simulated by introduction of live fish into experimental territories. At three sites, eight adult C. multicolor collected by handnet from a distant area were placed in clear glass jars, and spaced evenly in either pairs (n = 2) or as individuals (n = 1) approximately 1-m inside territory borders. This technique was used successfully in field studies of damselfish territoriality (e.g. Myrberg and Thresher, 1974). The present manipulations differed from realistic encounters primarily by the inability of bottled fish to flee or return an attack made by a territory holder. Nevertheless, this elicited the strong aggression towards conspecific intruders normally shown by territory residents and in effect approximated high rates of intrusion and associated increased cost of defense. The fish at these experimental sites responded to bottled intruders within a day or two, and did not habituate to bottled fish for approximately one week. In addition to concurrent unmanipulated control sites, a single control territory contained 8 empty bottles evenly spaced about the territory to test for any effects of the glassware. This site was monitored for changes in territory area.

III. Increased food in association with competitors

To test whether competitors directly inhibit access to food resources territorial pairs were presented supplemental food associated with a conspecific. At two sites, eight P. meandrina colonies were added in conjunction with bottled adult C. multinctus. Corals were spaced evenly around and < 1 m beyond the territory perimeter with a bottled fish positioned between each coral head and the territory border. In this way, fish would be confronted by a conspecific when feeding on supplemental corals. Three additional sites were established to test for independent effects of the corals and bottled conspecifics. On these areas, eight coral heads (n = 2) and eight bottled fish (n = 1) alone were arranged in the same configuration as the combined presentation experiments.

RESULTS

Territory Size and Temporal Stability

Undisturbed territories of C. multinctus show extreme stability in their spatial configuration. At a colony of 8 contiguous territories, no major change in size or shape was observed over a 1-yr period. Typically, an inter-territory buffer zone less than 1-m wide was the primary site of agonistic encounters between adjacent territory holders and minor spatial adjustments. Resident duration of many individual pairs has exceeded 4 years.

Mean surface area for undisturbed territories was 90.8 m² (SD = 56.8; n = 39). Smaller territories were held by fish in the deep

habitat ($\bar{X} = 75.2 \text{ m}^2$, $n = 34$) than on the reef flat ($\bar{X} = 205.7 \text{ m}^2$, $n = 5$, $P < .001$, t-test). Male residents ($\bar{X} = 78.1 \text{ mm SL}$) were larger than their female mates ($\bar{X} = 77.0 \text{ mm SL}$; $P < .01$, paired t-test).

Correlates of Territory Size

The total coral cover in fish territories at Puako ranged from 8% in the shallow habitat to 90% in the deeper coral-rich area. When data from 37 territories in both habitats were analyzed, territory area was inversely related to coral abundance (Table XIII). The highest correlation was found with the most abundant coral species, *P. lobata*, and to a lesser extent with *P. compressa*. The total supply of food within territories (calculated as the product of percent coral cover and territory area) also showed a significant relationship with territory size within the deep coral-rich site. Thus, fish holding larger territories in that habitat controlled more total food resources.

No variables other than coral abundance were significantly correlated with territory size in the pooled habitat sample. In contrast, when data from the coral-rich habitat were analysed separately, only male length was correlated with territory area. The five territories located in the shallow coral-poor habitat were not analyzed separately because of the small sample size. First order partial correlation analyses (cf. Myers et al., 1979) that controlled for coral abundance and chase rates (a measure of intrusion pressure), did not change the significance of associations between territory size and any variable analyzed.

Table XIII. -- Correlations between feeding territory size and associated variables for C. multinctus.

| | Percent Coral Cover | | | Total food | Male length | Female length | Male chases | Female chases | Total chases |
|-------------------------|-----------------------|--------------------------|------------|------------|-------------|---------------|-------------|---------------|--------------|
| | <u>Porites lobata</u> | <u>Porites compressa</u> | All corals | | | | | | |
| All Habitats (37) | -.592*** | -.356* | -.453** | .286 | .164 | -.027 | -.235 | -.128 | .052 |
| Coral Rich Habitat (32) | -.171 | .236 | .031 | .657*** | .324* | -.077 | .074 | .154 | .033 |

Territory area and total chase data normalized by log transformations, coral abundances by square root transformation. Sample sizes given in parentheses. Total food = total coral resources within a territory, calculated as (% coral cover x territory size). * = $P < .05$; ** = $P < .01$; *** = $P < .001$.

Activity Budgets

The time budget of C. multinctus is heavily biased towards activities related to feeding (Table XIV). Foraging behavior involved search, biting, and handling of coral tissue, and forms greater than 92% of the total daily time budget for both sexes. Fish foraged continuously from first light until dark with no significant intrasexual differences between morning and afternoon mean feeding rates (Wilcoxon paired sample test; $P < .05$, $n = 51$). Females, however, spent more time feeding than their mates ($P < .05$, Wilcoxon paired-sample test), while males spent more time chasing conspecifics ($P < .05$, sign test). The small amount of time spent sheltering by adults is consistent with the lack of any recorded predation in over 1000 h of observation. Fish also spent a small portion of their time at cleaning stations of the wrasse, Labroides phthirophagus, which occurred within most territories.

Field Experiments

Experimental manipulations of food resources and competitor abundances were performed after monitoring the pre-manipulation territory size and activity budgets of resident pairs. The baseline values presented for these experiments are consistent with those measured for both the experimental controls (Table XV) and other sites monitored during the study. Data from each manipulation are presented in two complementary forms. First, the design of each manipulation and the associated spatial responses of resident fish are presented in line drawings of territories. Second, changes in both total territory area

Table XIV. -- Activities (means and standard deviations) of 5 pairs of C. multicinctus given as proportion of total time budget.

| Activity | Males | Females |
|-------------|-----------------|-----------------|
| Forage | .928 \pm .044 | .962 \pm .036 |
| Chase | .034 \pm .027 | .014 \pm .009 |
| Shelter | .030 \pm .037 | .020 \pm .028 |
| Clean | .008 \pm .008 | .004 \pm .006 |
| Observation | | |
| time (min) | 1215 | 1200 |

Table XV. -- Pre-manipulation territory area, activity budgets, and control sites for experimental C. multicinctus pairs. Increased food manipulation data given for four distribution patterns. Data for control sites given at end of table.

| | Area | Feeding Rate | | Chase Rate | | Control Site No. |
|----------------|------|--------------|------|------------|-----|------------------|
| | | M | F | M | F | |
| I. FOOD | | | | | | |
| Increase | | | | | | |
| Random | 94 | 41.3 | 60.8 | .28 | .08 | 8 |
| Central | 83 | 50.0 | 48.3 | .03 | 0 | 8 |
| Periph | 103 | 52.6 | 53.9 | .32 | .12 | 5,7,10 |
| Uniform | | | | | | |
| LD1 | 81 | 73.7 | 67.4 | .14 | .43 | 5 |
| LD2 | 113 | 53.7 | 53.8 | 0 | .15 | 9 |
| HD1 | 40 | 37.2 | 36.9 | .20 | .10 | 5,7,10 |
| HD2 | 49 | 70.5 | 71.4 | .27 | .20 | 6 |
| Decrease | | | | | | |
| 1 | 82 | 59.9 | 74.8 | .50 | .45 | 2,3 |
| 2 | 67 | 41.0 | 54.7 | .10 | .05 | c |
| 3 | 58 | 55.1 | 48.8 | .05 | .05 | c |

(Table XV, continued)

| | Area | Feeding Rate | | Chase Rate | | Control Site No. | |
|--------------------------------|------|--------------|------|------------|-----|------------------|-----|
| | | M | F | M | F | | |
| II. COMPETITORS | | | | | | | |
| Increase | | | | | | | |
| | 1 | 117 | 62.2 | 60.4 | .27 | .07 | 4 |
| | 2 | 76 | 56.5 | 62.2 | .21 | .13 | c |
| | 3 | 83 | 73.5 | 71.8 | .16 | .16 | 9 |
| Decrease | | | | | | | |
| | 1 | 60 | 60.8 | 74.8 | .40 | .10 | 1 |
| | 2 | 63 | 61.6 | 69.5 | .14 | .05 | 2,3 |
| | 3 | 33 | 40.6 | 53.3 | 0 | 0 | 2,3 |
| | 4 | 38 | 71.0 | 65.9 | .10 | .10 | 1 |
| III. FOOD + COMPETITORS | | | | | | | |
| | 1 | 82 | 46.8 | 52.4 | .43 | .25 | 5 |
| | 2 | 81 | 66.7 | 64.8 | .45 | .38 | 5 |
| Food only | | | | | | | |
| | 1 | 85 | 32.2 | 49.8 | .22 | .12 | 5 |
| | 2 | 80 | 42.7 | 34.6 | .09 | .03 | 5 |
| Competitors only | | | | | | | |
| | 1 | 157 | 50.8 | 65.4 | .09 | 0 | 5 |

(Table XV, continued)

| | Area | Feeding Rate | | Chase Rate | | |
|----------|------|--------------|------|------------|-----|--|
| | | M | F | M | F | |
| CONTROLS | | | | | | |
| 1 | 38 | 51.6 | 67.5 | .40 | .30 | |
| 2 | 50 | 52.8 | 49.2 | .23 | .05 | |
| 3 | 56 | 34.1 | 43.7 | 0 | .20 | |
| 4 | 60 | 42.7 | 45.7 | .04 | 0 | |
| 5 | 116 | 69.0 | 67.1 | 0 | 0 | |
| 6 | 99 | 41.2 | 56.8 | .17 | 0 | |
| 7 | 114 | 39.7 | 35.5 | .12 | .08 | |
| 8 | 126 | 60.7 | 73.1 | .06 | 0 | |
| 9 | 61 | 34.8 | 35.4 | .10 | .05 | |
| 10 | 121 | 49.8 | 50.8 | .19 | .17 | |

Territory area in m^2 . Feeding rate = mean no. bites / 5 min; chase rate = mean no. agonistic interactions / 5 min. For three experimental sites, controls (c) consisted of eight territories at the long-term observation site; activity budgets of control sites were not quantitatively monitored for those experiments, see text. LD = low density, HD = high density food enhancement.

and activity budgets for pair members are summarized for each set of experiments.

Control sites

Only two of ten experimental control territories showed any changes in area over the duration of associated experimentals (Figure 30). These represented nominal increases that may have resulted from underestimates of pre-manipulation area due to the high vertical relief at these sites. Although activity budgets varied naturally over time, no statistically significant changes were detected among feeding or agonistic activities for control fish between the pre- and post-manipulation periods. The large percent change in chase rates for some control sites are actually of small magnitude when compared with pre-manipulation activity levels (Table XV). The high temporal stability of both control and long term monitoring sites indicates that changes in territory size among experimentals were responses to manipulation treatments.

Increased food

Initial experiments on the enhancement of food resources showed that territorial behavior was highly dependent upon the distribution pattern of supplemental food. Responses of experimental fish to each distribution treatment are summarized below:

Random- When Pocillopora coral heads were placed randomly within the territory, the resident pair concentrated its foraging activity within the perimeter circumscribed by the introduced corals (Figure 31). This resulted in a reduction in time spent feeding at areas beyond supplemental heads. Both fish increased their overall feeding rates on

Figure 30. Summary of changes in butterflyfish feeding-territory area and activity budgets for ten experimental control sites. Feeding and chase rates given for each pair member. Percent change calculated as $[(\text{post} - \text{pre}) / \text{pre}] \times 100$. nc = no change compared to pre-manipulation rates. Percent changes given qualitatively by arrows when pre- or post-manipulation rates = 0. No changes were statistically significant. Pre-manipulation data given in Table III.

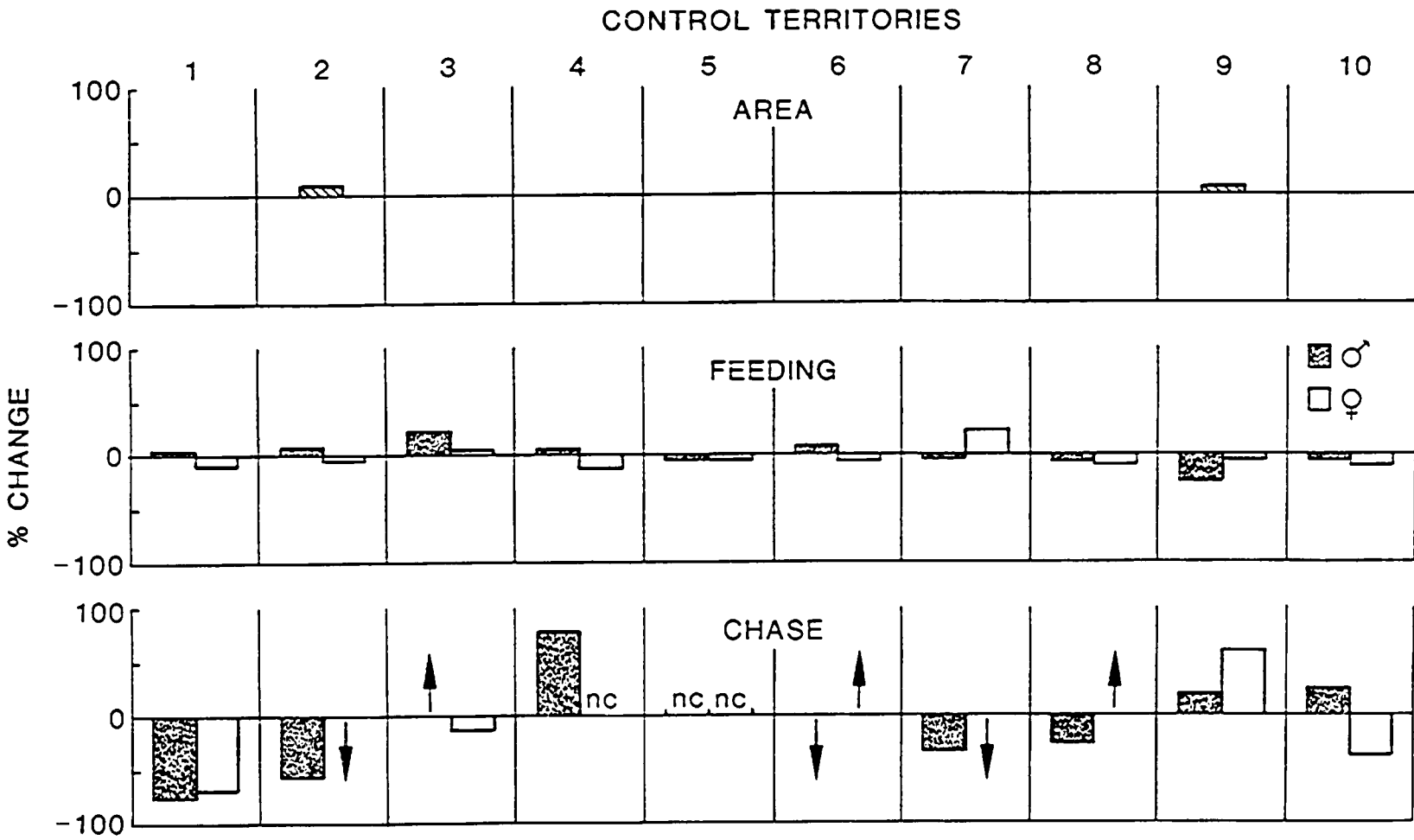
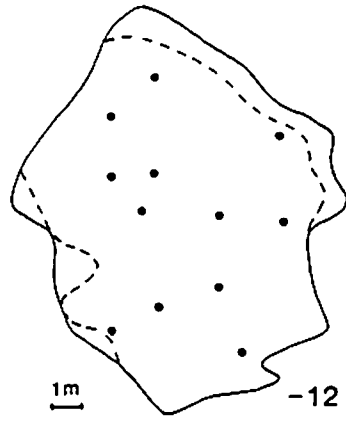


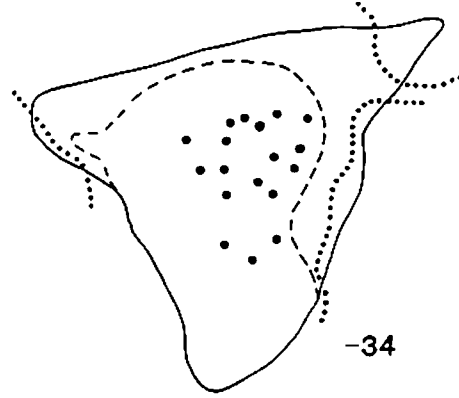
Figure 31. Changes in territory shape and area for food distribution experiments. Large dots indicate placement of supplemental coral heads. Lines of small dots show expansion of neighboring pair into territory. Lines indicate pre-manipulation borders (solid) and post-manipulation extension or contraction (dashed). Numbers at lower right of each territory show percent area change.

FOOD DISTRIBUTION

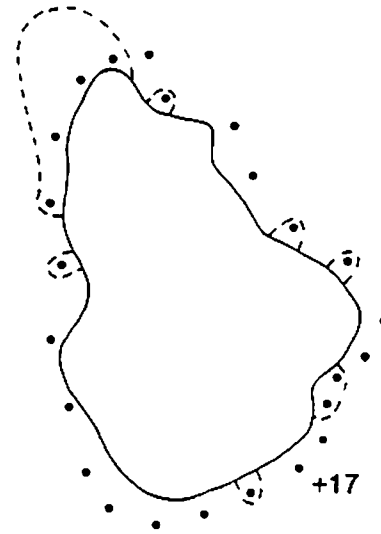
Random



Central



Peripheral



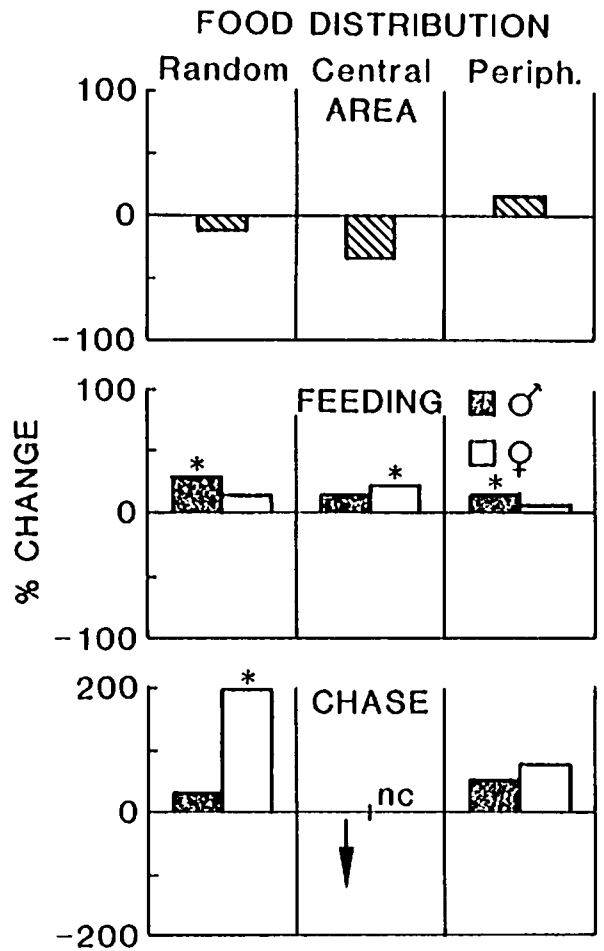
original and new corals (significantly for the male) and attempted to defend the original territory boundaries (a significant increase for the female; Figure 32). Their reduced foraging activities beyond the new heads, however, resulted in a 12% loss to encroaching neighboring pairs, and a net reduction in territory size.

Central- Resident fish responded in a similar manner to food placed in a centrally clumped distribution. Residents foraged along new paths that largely followed the location of supplemented corals on one side of their territory. Although feeding rates increased for both fish (significantly for the female), activities were much reduced beyond that area. Chase rates remained low due to less frequent visits to their original feeding borders (Figure 32), and as a result neighboring pairs expanded their territories into the undefended area (Figure 31).

Peripheral- When corals were placed just beyond the original border, resident fish expanded their defended area to include 11 of the 24 (46%) Pocillopora colonies (Figure 31). This represented a 17% increase in total territory area, some of which extended well beyond added corals. New corals not claimed by the experimental pair were eventually controlled by neighbors. New territory borders stabilized within about 3 weeks. Mean feeding rates increased for both fish (significantly for the male), as did chase rates due to contests with neighbors for the new food resources (Figure 32).

Uniform- The previous experiments showed that the distribution patterns of supplemental food have a major influence on the spatial and behavioral responses of test fish. To best approximate an homogeneous increase in food abundance within the habitat and minimize the

Figure 32. Summary of changes in butterflyfish feeding-territory area and activity budgets for food distribution experiments. Legend as in Figure 30. * = $\underline{P} < .05$.



localization effects seen above, corals were added in a uniform distribution pattern within pre-manipulation territory boundaries. The placement of corals beyond original borders served to buffer the attraction of neighboring pairs and provided the opportunity for experimental fish to expand territories.

Results of uniform food enhancement varied with supplemental food density (Figure 33A). In the two low-density enhancement experiments ($.44 \text{ heads/m}^2$), overall territory area increased slightly by the inclusion of a few new heads of Pocillopora. During expansion of one territory (LD1) fish also relinquished a small part of their original territory area to intruding neighbors. In these experiments, all fish increased their chase rates (3 of 4 significantly) in defense of the original and newly obtained areas. Although mean feeding rates also increased for all fish, none were of significant magnitude (Figure 34).

In contrast, territories contracted radically in the two food enhancements at higher densities (Figure 33A). Residents successfully repelled all attracted conspecific intruders from their territory for at least 3 days, after which they abandoned large portions of their original area. Daily changes in activity budgets, territory size, and number of intruders is shown for site HD2 in Figure 35. Note that although chase rates increased in the early post-manipulation period, territory size decreased only after conspecific intruders (7 adult pairs and one trio) successfully invaded and began to defend small, highly contested areas within the original territory. As a result of the large increase in time spent chasing intruders, feeding rates decreased (significantly for two of four fish) in these experiments (Figures 34

Figure 33. Changes in territory shape and area for food manipulation experiments. A) Increased food supply in low (LD 1 and 2) and high density (HD 1 and 2) uniform distributions. Hatched area in HD 1 and 2 indicates post-manipulation territory. B) Decreased food supply. Large squares indicate placement of substrate covers. Hatched squares at site 1 show location of second coral reductions; hatched areas indicate increases following second reduction. Remaining legend as in Figure 31.

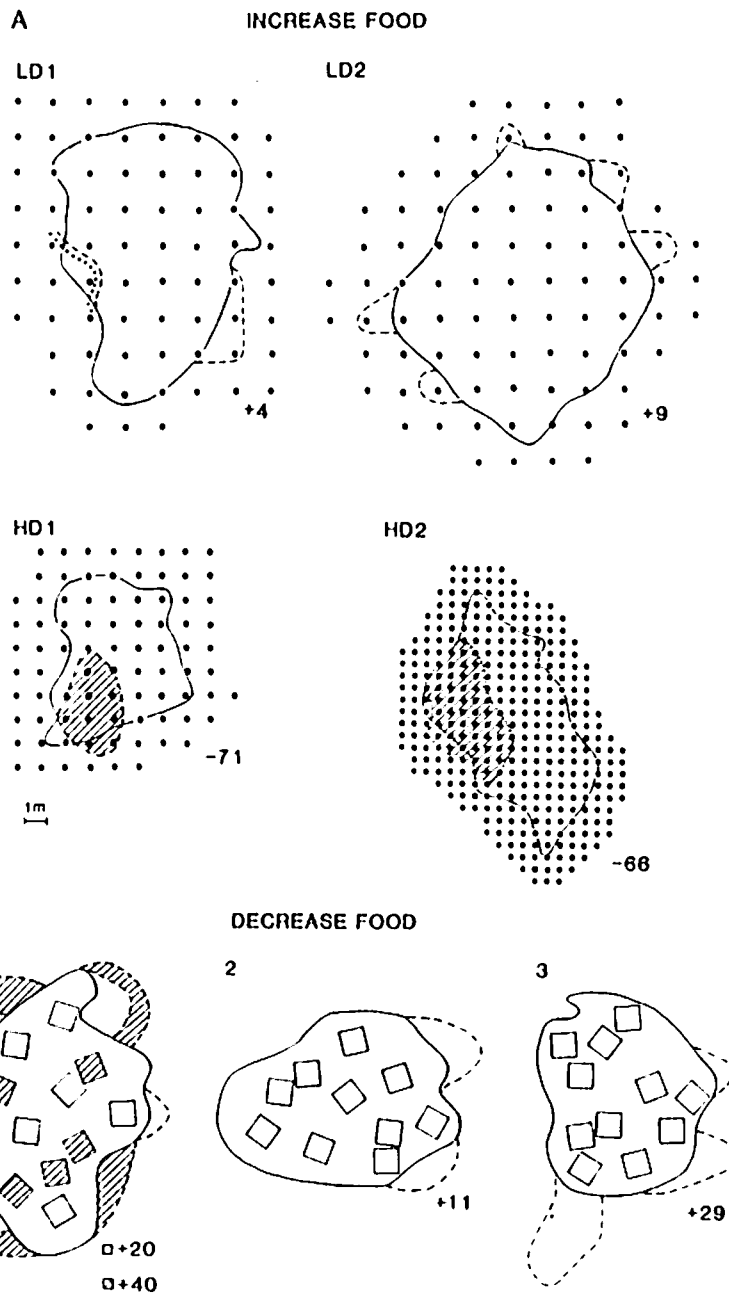


Figure 34. Summary of changes in butterflyfish feeding-territory area and activity budgets for uniform low density (LD) and high density (HD) food enhancement experiments. Legend as in Figures 30 and 32.

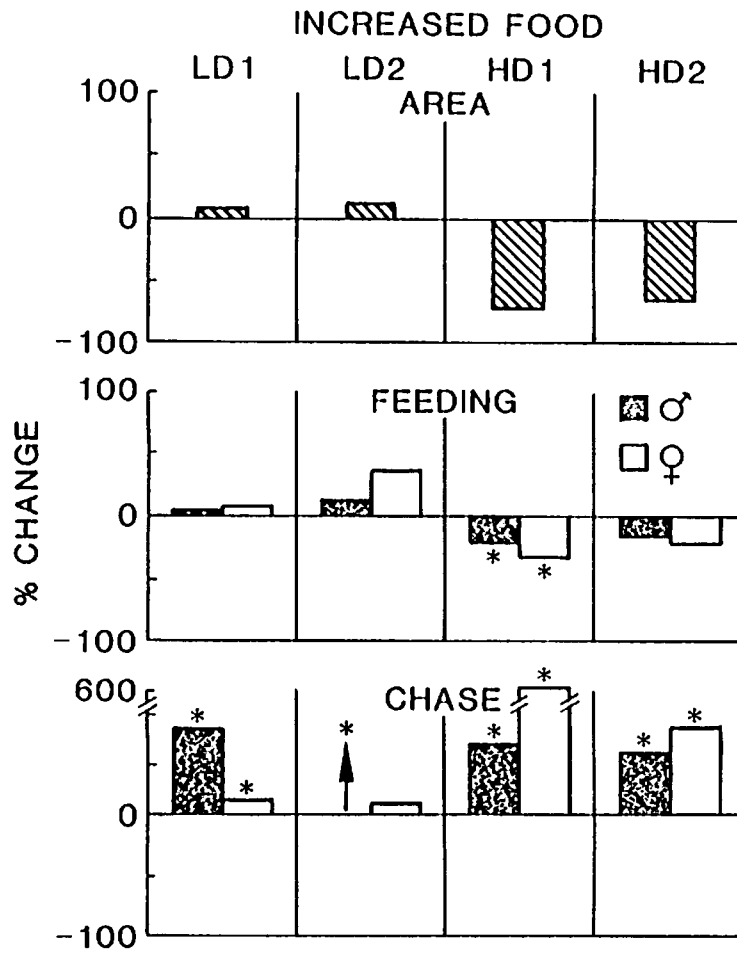
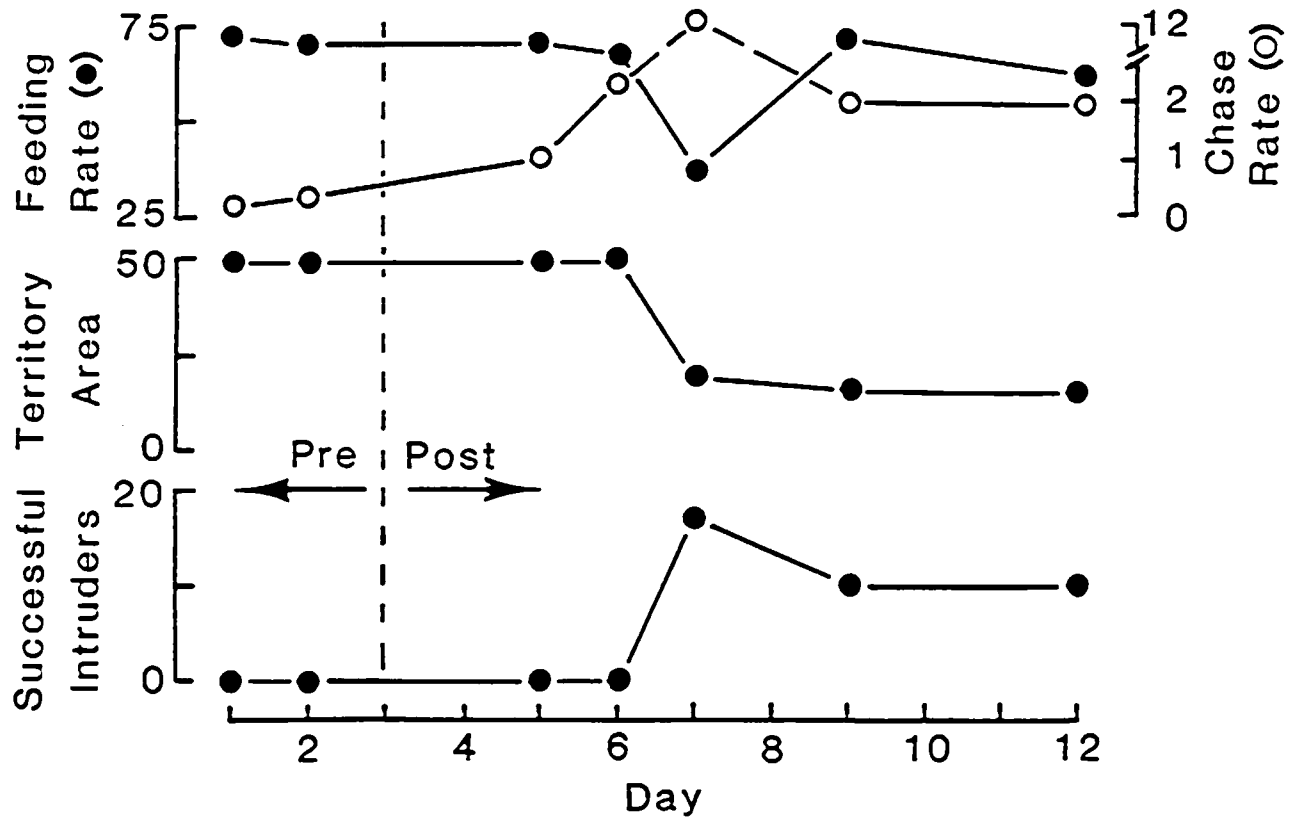


Figure 35. Changes in activity budgets, territory area, and number of intruders for food enhancement experiment HD 2. Feeding (bites / 5 min) and chase (chases / 5 min) rates are averaged for the experimental pair. Territory area in m^2 . Successful intruders = number of intruding C. multinctus that successfully invaded and defended areas within original territory boundaries. Dashed vertical line indicates addition of supplemental coral and start of post-manipulation period.



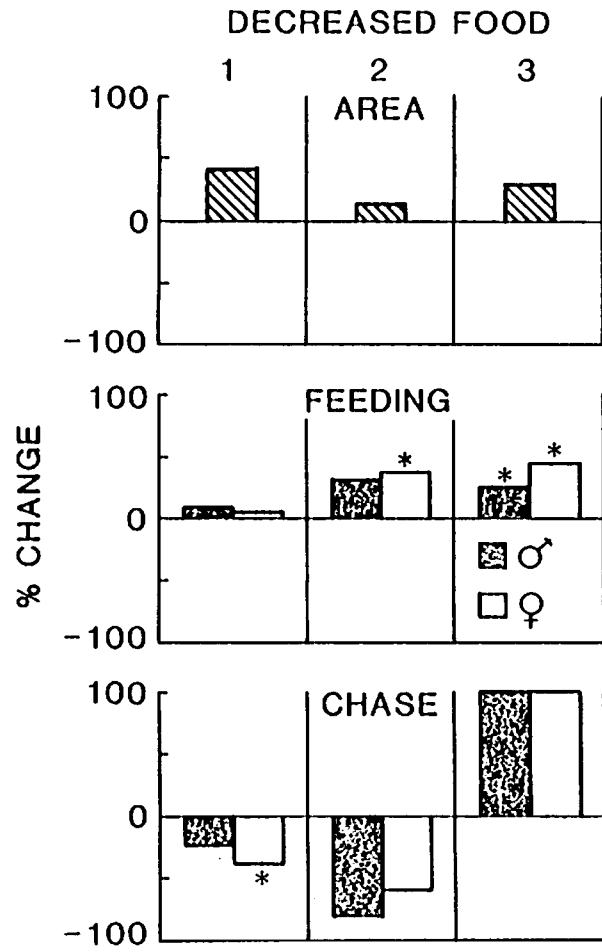
and 35). Although there were also many heterospecific corallivores attracted into the territory (Chaetodon ornatissimus, Chaetodon quadrimaculatus, Chaetodon trifasciatus, Chaetodon unimaculatus, Cantherhines dumerilli, and Plectroglyphidodon johnstonianus), almost all aggression by the resident pair was directed towards conspecifics.

Decreased food

Territory area expanded in all food reduction experiments (Figure 33B) and stabilized after a period of approximately 4 weeks. Each phase of the two-step food reduction resulted in an associated stepwise expansion into adjacent territories. Feeding rates increased for all 3 experimental fish pairs (significantly for 3 of 6 fish) primarily by more feeding bouts within their own territory (Figure 36). The drop in chase rates among fish in experiments 1 and 2 were due to increased feeding activity and a decreased number of advances by neighboring pairs. The apparent doubling in magnitude of chase rate for both fish in experiment #3 actually represents an increase to only .1 chases / 5 minute period, and is low when compared to the average for undisturbed territories (Table XV). The low levels of overt aggression associated with territory expansion were due to the gradual encroachment of test fish into territories of smaller, less aggressive pairs.

The control site in which only sand and substrate were covered showed no change in territory size. Although activity budget data were not taken for these fish, their foraging and agonistic behaviors also appeared to remain unchanged. This site provided evidence that the increased territory size in the food reduction experiments was due to the manipulation of food resources and not a response to the covers.

Figure 36. Summary of changes in butterflyfish feeding-territory area and activity budgets for three food reduction experiments. Legend as in Figures 30 and 32.



Decreased competitors

Within a few hours after removal of adjacent pairs, experimental fish began to forage beyond their original territorial boundaries (Figure 37A). In less than two days, foraging area had increased between 81 and 364% at all 4 sites. Although rigorous efforts were made to remove all conspecifics that entered the experimental area, some minor confrontations occurred and are reflected as increases in post-manipulation chase rates (Figure 38). These increases, however, were of small magnitude and had little effect on the overall activity budget. No general pattern for changes in either direction or magnitude of feeding rates are apparent for these manipulations, although one female showed a significant 13% reduction.

Increased competitors

Model-bottle simulations of intruding conspecifics caused territory shifts in less than one day in all experimental territories. (Figure 37B). At two sites (Figures 37B.1 and 37B.3), borders receded to near the locations of bottled intruders. In the third (Figure 37B.2), residents contracted one border, but expanded another into the territory of a smaller neighboring pair (\bar{x} TL < 70 mm). Chase rates, most frequently expressed as displays and attacks at bottled fish, increased significantly for all individuals (Figure 39). As a result of the large amount of time spent in attempts to displace bottled intruders, feeding rates decreased for five (three significantly) of six fish. Experiments were terminated after 7-10 days post-manipulation when residents began to habituate to bottled fish which were in good health throughout the experiments.

Figure 37. Changes in territory shape and area for competitor manipulation experiments. A) Decreased competitors. Three of four experiments shown, see Table III and Figure 38 for data on fourth. All adjacent neighboring pairs removed. B) Increased competitors. Small squares indicate placement of bottled individual fish. Remaining legend as in Figure 31.

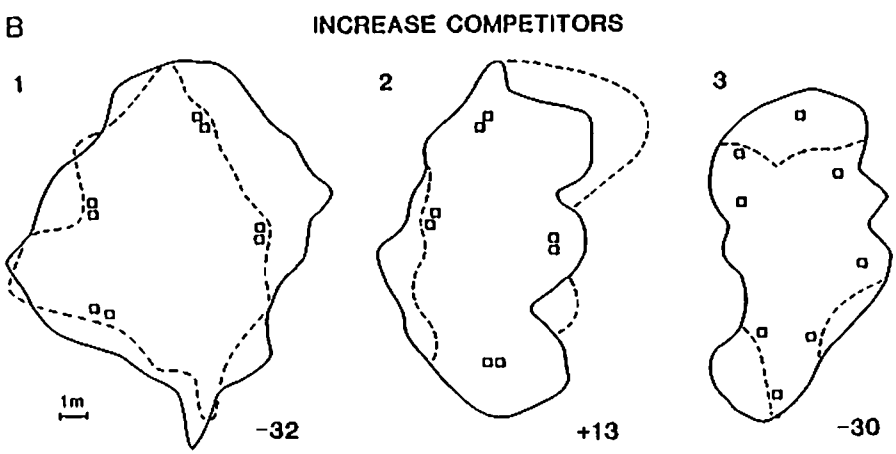
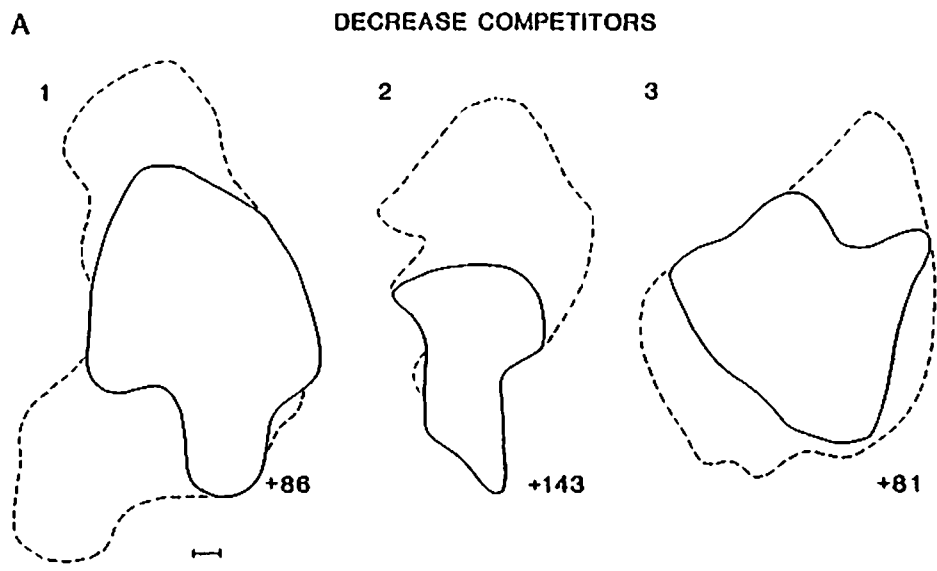


Figure 38. Summary of changes in butterflyfish feeding-territory area and activity budgets for four competitor reduction experiments. Legend as in Figures 30 and 32.

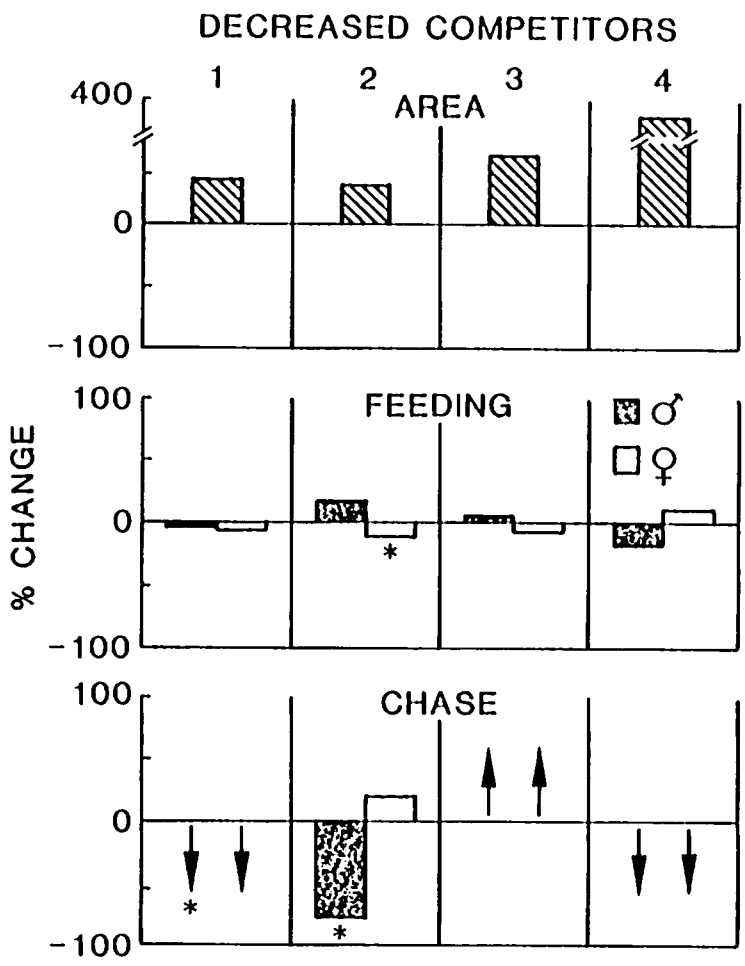
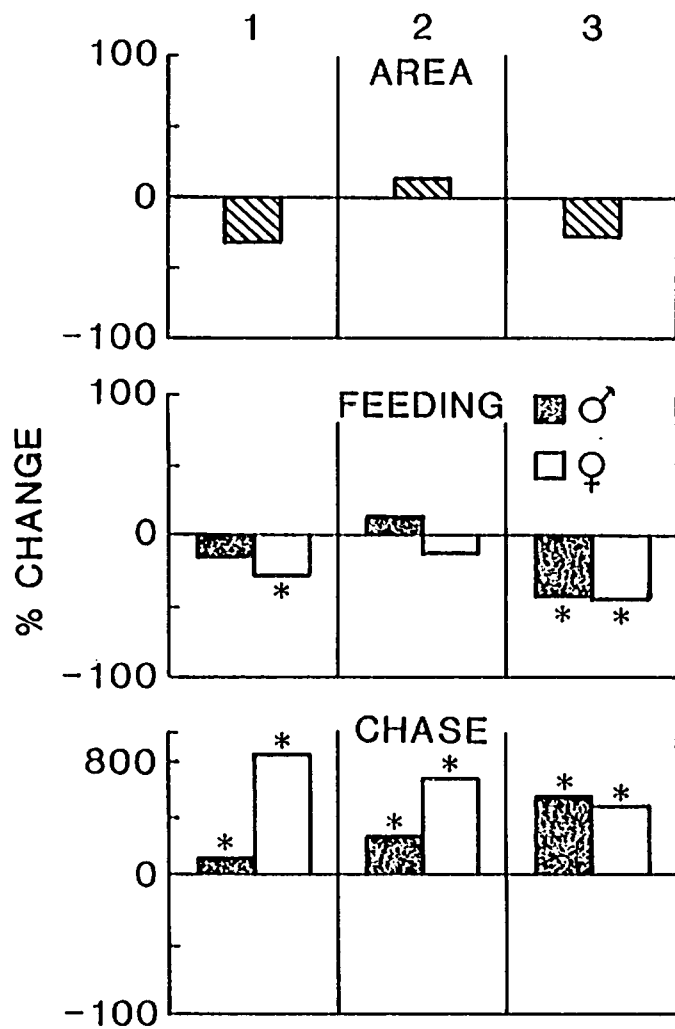


Figure 39. Summary of changes in butterflyfish feeding-territory area and activity budgets for three increased competitor experiments. Legend as in Figures 30 and 32.

INCREASED COMPETITORS



No change in area occurred for the control territory in which empty bottles were placed. Although activity data were not taken for these fish, changes in feeding or agonistic behaviors were not detected during qualitative observation. This site provided evidence that the decrease in area was not a response to the holding bottles.

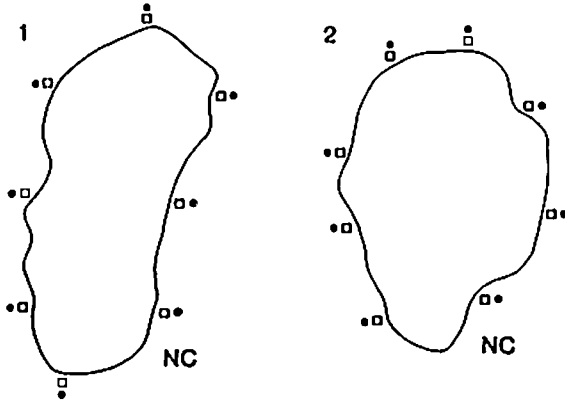
Increased food and competitors

When only Pocillopora corals were added beyond territory boundaries resident pairs expanded their territories to include new food colonies (Figure 40). The close proximity of feeding among experimental and neighboring pairs resulted in agonistic encounters at both sites but not at significantly higher levels (Figure 41). At site F1 agonistic encounters were much more frequent than at site F2 (Table XV) and caused a significant decrease in time spent feeding for both fish. After approximately 3-4 days, added corals were defended and exclusively used by a single pair. These experiments were similar to the peripheral food enhancement design described above and showed that fish will increase their defended area to include more food resources.

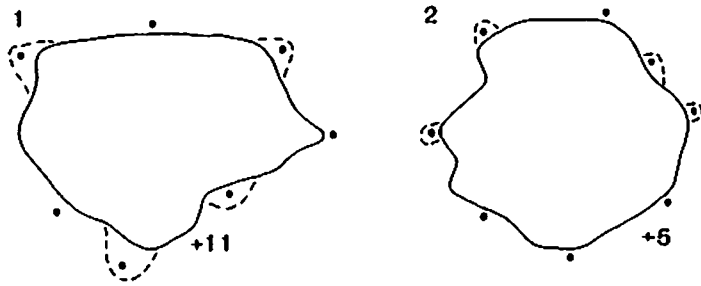
When conspecifics alone were placed around the territory, no changes in territory size were observed (Figure 40). The vigorous displays made by the experimental pair at the bottled fish resulted in increased chase rates. This defensive behavior was accompanied by redirected aggression in the form of intense feeding bouts on substrates near the bottled fish, and at least partially accounts for the increased in feeding rates (significant for the female) seen among this pair. This experiment showed that territory residents do not increase their

Figure 40. Changes in territory shape and area for concurrent increased food and competitor experiments. Dots represent positions of added corals. Squares indicate locations of bottled fish. NC = no change. Remaining legend as in Figure 31.

INCREASE FOOD AND COMPETITORS



FOOD ONLY



COMPETITORS ONLY

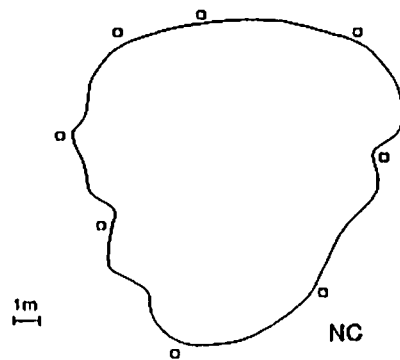
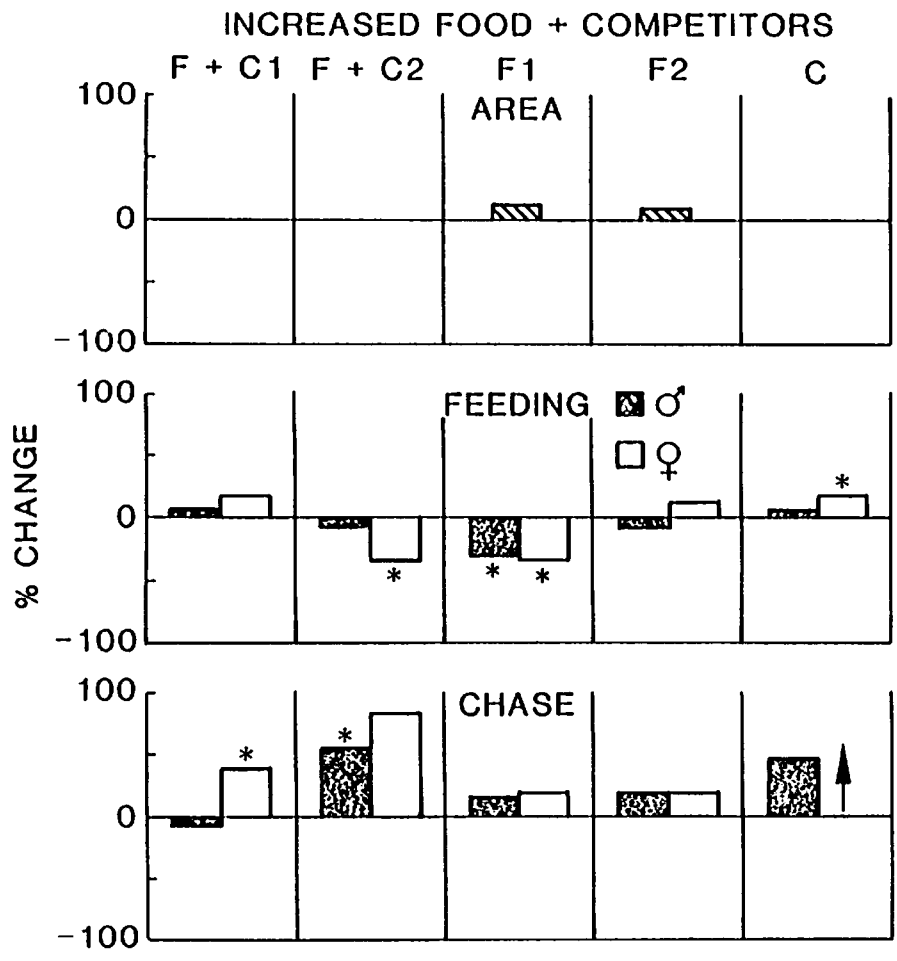


Figure 41. Summary of changes in butterflyfish feeding-territory area and activity budgets for increased food (F) and competitor (C) experiments. Legend as in Figures 30 and 32.



defended area as a result of attraction to conspecifics although it can significantly affect the animal's activities.

The concurrent presentation of corals and bottled competitors produced an immediate change in foraging patterns of resident fish that resulted in increased chase rates (significantly for 2 of 4 fish) but no change in territory size (Figures 40 and 41). During the early post-manipulation period, experimental pairs dashed rapidly between corals (both indigenous and added), fed by quick intense bites, and were highly aggressive when they encountered bottled fish. Most feeding time, however, was spent near the center of the territory, with peripheral defensive forays made to bottled fish. By the third day, residents had reduced attacks on bottled fish, and almost all aggression was now directed at neighboring free-swimming conspecific pairs feeding on the supplemental coral heads. In spite of the intense competition over the new food resources, fish did not establish exclusive use of heads in the presence of bottled fish. These experiments demonstrated that the continuous presence of a conspecific can inhibit access to food.

DISCUSSION

Chaetodon multicinctus: a Territorial Energy Maximizer

The widespread distribution patterns and high abundance of Hawaiian corals promotes their defendability as a food resource for C. multicinctus. Although the coral community at Puako is dominated by only three species, total living coral cover is very high and forms an extensive benthic food substratum. As a result, fish are distributed across a relatively uniform habitat with a comparatively low localized

variability in coral density and species composition. In addition, the extreme longevity of corals (Connell, 1973; Maragos, 1977) makes them a potentially stable temporal and spatial food source. Since only the surface tissues are cropped by C. multinctus, corals represent a renewable resource that can be maintained to supply energetic and nutritional requirements. These characteristics collectively make corals an economically defensible food resource (sensu Brown, 1964) that promotes the evolution of territorial social systems among corallivorous reef fishes (Tricas, 1985). For C. multinctus, undisturbed territories are highly stable in space and time, and may persist for many years.

In spite of the temporal and spatial stability of coral food resources, their nutritional quality to foraging butterflyfishes is not high. The soft tissues of Porites spp. corals are composed primarily of lipid and protein, but they have a water content in excess of 95% (Chapter III). Given the low energy content of food corals on an ash-free-dry-weight basis (Tricas, 1985), living coral tissues available to fish represents an extremely low energy source to foragers. As a result, fish must invest large amounts of time feeding to obtain adequate energy. Both male and female C. multinctus compensate for the low-energy content of coral tissue by spending over 92% of their time budget in feeding activities (Table XIV). This high portion of the total time budget devoted to feeding is extreme compared to that of 9% for the herbivorous redlip blenny, Ophioblennius atlanticus, (Nursall, 1981), 18% for drift-feeding yearling brook charr, Salvelinus

fontinalis, (McNicol et al., 1985), and 23% for the herbivorous reef damselfish, Parma victoriae (Norman and Jones, 1984).

The short term costs of establishing an exclusive foraging area can be extremely high for C. multinctus. This was best demonstrated when food enhancement resulted in the attraction of conspecific food competitors (Figures 34 and 35). When small additions of food were made to territories, fish were able to accommodate the moderate increase in defense costs and still increase feeding rates. But when large amounts of food were added (Figures 33 and 34), fish could not successfully defend against the markedly higher number of intrusions. This high defense cost ultimately reduced time available for feeding and residents reduced the size of their defended area, which re-established normal feeding rates (Figure 35). Thus, it appears that the use of space by C. multinctus is strongly influenced by the time available for feeding, and defense costs are modified through spatial adjustments of the territory perimeter.

Although the initial costs of establishing new territory boundaries may be expensive, the long term payoff for the highly aggressive behavior is clear. Once territorial disputes stabilize, usually within a few days or weeks in the present experiments, the well defined borders among neighboring pairs are maintained primarily through advertisement and displays, and overt chases are infrequent (Tricas, 1985; Tables XIV and XV). The low levels of agonistic interactions among C. multinctus and other chaetodontids apparently are a result of individual familiarity and agonistic bouts reinforce their territorial behavior (Reese, 1975). This 'dear enemy' phenomenon (Wilson, 1975) provides

mutual stimulation for the maintenance of territories between neighbors but reduces time and energetic costs of defense, and the risk of injury.

Behaviors other than those related to feeding and defense comprise less than 4% of the total time budget. C. multincinctus probably spawns at least 1-2 egg clutches per month during the spring season (Chapter II). Courtship is brief and gametes are shed by pairs into the water column at sunset (Lobel, 1978). Thus, reproductive activities are ephemeral and there is no parental care. The lack of any observed predation on adult C. multincinctus during this study, the long term duration of territory residency, and the small proportion of time spent sheltering indicate that predation pressure on adults is also a minor factor in structuring daily activity budgets. The large amount of time spent foraging further indicates that the territory functions primarily to defend food resources rather than spawning sites or shelter as reported for other reef fishes (e.g. Warner and Hoffman, 1980).

Because C. multincinctus feeds almost continuously and spends relatively little time at other activities, it is best classified as an energy maximizer (Schoener, 1971; Hixon, 1982). Furthermore, its foraging appears to be constrained by time (sensu Schoener, 1983). This was seen in numerous experiments where decreases in feeding rates were associated with increased defense costs and vice versa (Figures 34, 35, and 39). It is not possible, however, to reject the coexistence of a processing constraint (sensu Belovsky, 1981; Schoener, 1983) since this species has a very long gut (> 9 times body length; Tricas, unpublished data) that becomes packed with coral tissue early in the day.

Although the activity budget of males involves less feeding and more defense time than their mates, there appears to be little justification to classify males as time minimizers even in a relative sense. The magnitude of the sex-based differences is slight and are of only minor energetic consequence in relation to territorial defense and feeding. In fact, males are probably under strong selection to maximize food intake since their fitness may be related to body size, fat storage, and energy available for territory defense.

From a theoretical perspective, the behavioral biology of C. multincinctus points out fundamental qualities critical to understanding the major factors that regulate its territory size. To summarize, this species is obligatively dependent upon food corals that are spatially and temporally stable in distribution. Because of the low energy value of living corals however, fish must spend large amounts of time feeding to obtain food rations. Thus C. multincinctus behaves as an energy maximizer constrained by time available for feeding. Monogamous pairs maintain exclusive access to food resources and insure its availability by defending feeding territories primarily against conspecifics that hold contiguous territories. Although reproduction and refuge from predation are also served by the territory, they are relatively minor proximate factors that structure their defense of the feeding territory.

Determinants of Territory Size

Ecological correlates

Territory size within the C. multincinctus population at Puako was inversely related to percent coral cover but not to any other single

variable (Table XIII). This negative relationship, however, is not surprising in view of the extreme disparity in coral abundances between the two habitats and the dependence of C. multicoloratus on coral as its primary food resource. The size of fish territories on the shallow reef flat averaged almost 3 times that of territories in the deeper coral rich habitat. A similar 3-fold difference in mean territory size between coral poor lagoon and coral rich reef slope habitats was reported for the corallivorous butterflyfish C. trifasciatus on the Great Barrier Reef (Sutton, 1985).

When the 5 territories from the shallow habitat were omitted and only those from the coral rich habitat analyzed, male length was the only significant correlate of territory size. Norman and Jones (1984) reported a lack of association between territory size and food abundance for natural populations of the temperate damselfish, P. victoriae. The only significant correlates were the number of conspecifics that shared common borders and the proportion of territory border shared with neighbors. The inverse relationship between territory size and adjacent competitors, and the lack of association with food supply in their system was further supported by field manipulation experiments. The importance of male size for C. multicoloratus is probably related to fighting ability but perhaps more importantly to advertisement since territories are normally maintained by low levels of overt aggression.

The significant relationship between food abundance and territory size in the pooled-habitat sample was highly influenced by a few large territories within the shallow coral-depauperate habitat. While low

food abundance may be a primary factor for large territories on the shallow reef, it would be inappropriate to attribute food supply as the critical determinant of territory size in all habitats. Furthermore, partial correlation analyses, in which measures of food abundance and intrusion pressure were statistically controlled, failed to change the significant associations between variables and territory size. This result is in contrast to that demonstrated for sanderlings by Myers et al. (1979). The results of experimental analyses of territory size for C. multicinctus (discussed below) show different relationships with food supply than would be predicted by the above statistical treatments of correlative data, and emphasize the importance of experimental analyses within natural populations.

The distribution of food resources

Careful consideration must be given to the distribution pattern of supplemental foods during experimental manipulations in order to elicit realistic responses from test animals. For example, Rubenstein (1981) found that male pygmy sunfish (Elassoma evergladei) established territories at all food densities when food was clumped, but only at intermediate densities when food was randomly distributed. In the present study, the responses of territorial fish were also highly dependent upon the distribution of supplemental food. In all food enhancement experiments, fish were presented with distributions that altered their normal foraging patterns to varying degrees. Since defensive behaviors are most likely to occur near foraging sites, it is not surprising that territory size changed according to the placement of supplemental food at the random, central, and peripheral sites. In the

former two experiments, fish increased their feeding rates by decreasing travel time between coral heads. Defense costs did not increase in the central distribution experiment because new food was located far from the original border and there were fewer interactions with neighbors. Thus, an unrealistic food enhancement pattern may produce erroneous support for a particular food supply model because it affects foraging routes and reduces opportunities for agonistic encounters as a result of its distribution. Such point-source food enhancements in systems where natural food is distributed much differently (e.g. Simon, 1975) must be carefully interpreted in terms of spatial adjustments to feeding area.

What constitutes a realistic increase in food availability? The answer ultimately depends upon the natural distribution of food in relation to the test animal's foraging behavior and the particular model being tested. Theoretical measures of food supply are usually expressed in terms of distribution (Horn, 1968), density (Dill, 1978; Ebersole, 1980) or production (Hixon, 1980). Because of differences between natural systems and logistic constraints, field studies generally use more conveniently manipulated or quantified measures of food supply such as weight (Fransblau and Collins, 1980), percent body weight (McNicol and Noakes, 1984), density (Norman and Jones, 1984), daily production of energy (Norton et al., 1982), and number of flowers per territory (Gill and Wolf, 1975; Kodric-Brown and Brown, 1978). Although such measures may adequately account for changes in food supply, careful comparison between experimental systems and their application to various models must be made particularly when density or areal units are used. In

order to control for confounding factors of localized manipulation, food should be manipulated in ways that approximate the natural distribution pattern across the entire habitat. In systems where food is abundant and widely distributed, increases in food supply can be reasonably approximated by the introduction of food in random or uniform distribution patterns that extend ideally throughout the habitat and minimally at sufficient distances beyond the boundaries of an experimental territory to buffer attraction of competitors. In this way, spatial responses will be subject to reduced bias from the foraging patterns induced by the localized distribution of supplemental food.

Food abundance

Since all food energy for C. multinctus must come from within its feeding territory, there must exist some minimum renewable food level that can satisfy short term metabolic requirements. A supply of food below that amount would not be replaced at a rate equal to food removal and eventually resources would be depleted. The results of the food reduction experiments indicate that fish were able to assess decreased food availability and compensate by increasing territory size. Similar reports of increased territory size in response to experimentally decreased food supplies were reported for juvenile rainbow trout, Salmo gairdneri, (Slaney and Northcote, 1974) and adult black surfperch, Embiotoca jacksoni, (Hixon, 1981). As in the present study, Hixon (1981) found a sequential increase in feeding area associated with stepwise reductions in food supply. Unfortunately, too little is presently known about the physiological energetics of C. multinctus to conclude whether territory expansion was a response to food reductions

below some level required for maintenance or an alternative energy maximization strategy.

In contrast to the food reduction experiments, the addition of corals at low densities (Figure 33A) resulted in no decrease in territory size over a 1-month period, even when accompanied by a moderate increase in defense costs from attracted conspecifics (Figure 34). Instead, residents successfully repelled intruders from their territories and even secured a few additional corals beyond original borders. The failure of C. multicolor to reduce territory size when presented additional food indicates that the low density food enhancement could be economically defended and net benefits increased. A similar lack of territory contraction when food supply was experimentally increased was reported for other fishes. Increased territory size was reported for the beaugregory, Eupomacentrus leucostictus, (Ebersole, 1980) and juvenile brook char, S. fontinalis, (McNicol and Noakes, 1984). Symons (1971) found that increased food supply in juvenile Atlantic salmon (Salmo salar) caused no change in territory size for dominant fish.

The defense of excess food by energy maximizers like C. multicolor (best seen in the low-density enhancement experiments) has both short and long-term selective advantages. Exclusive access to more total food could increase daily energy intake through increased feeding rates at a higher self-renewing standing crop. In addition, associated increases in territory productivity or standing biomass of food may function as a hedge against calamitous environmental events (Salomonson

and Balda, 1977; Myers et al., 1981; Dugan, 1982; Millington and Grant, 1983; Lima, 1984) which on Hawaiian reefs is associated with winter storms (Dollar, 1982; Walsh, 1983) or the potential depletion of food resources by other fishes and invertebrates such as the starfish Acanthaster planci. Increased food supply can directly increase reproductive benefits for fishes through higher female fecundity (e. g. Tyler and Dunn, 1976; Hirschfield, 1980). Both male and female C. multinctus may benefit from increased food since both store large amounts of body fat during the non-spawning season (Chapter II). In addition, energy partitioned to growth may provide benefits associated with size-related fecundity (Bagenal, 1966), social dominance (Jenkins, 1969; Constanz, 1975), reproductive success (Kodric-Brown, 1977), or interspecific competitive dominance (Robertson, 1984). Male C. multinctus experience increased reproductive output with increased body size because large females are usually paired with slightly larger males, and fecundity is related to female body size (Chapter II). In addition, since larger males have access to more total food (Table XIII), egg production by their mates may be further increased.

Although territory size for C. multinctus pairs increased when food supply was reduced (Figure 33), that response was not complemented by decreases in defended area when food supply was increased at low density. Thus, the major prediction of the food maintenance hypothesis, that territory size is adjusted inversely to local food supply, is not fully supported by experimental manipulations of food resources in the territorial system of C. multinctus. The failure of the prediction is due in large part to the energy maximization strategy of C.

multicinctus. Although rarely formally addressed, the hypothesis may be best applied to animals with a time minimization strategy or even perhaps energy maximizers with spare time due to a processing constraint. In such cases, the defense of extra food should have no short term value.

Competitor abundance

In contrast to the gradual and subtle responses of fish to manipulation of food resources, changes in the abundance of conspecific neighbors had much more immediate and extreme effects on territory size. Strong evidence that territorial neighbors limit spatial use and access to food resources was seen when residents foraged well beyond their original territory almost immediately after removal of adjacent pairs (Figure 37). Similar expansion of territory area following removal of territorial neighbors was reported for other fishes (Nursall, 1977; Larson, 1980; Norman and Jones, 1984) and indicate that conspecifics often constrain territories below some larger size. In other systems, however, removed fish were rapidly replaced by new individuals and no change in territory size of neighbors was observed (Clarke, 1970; Hixon 1981).

When C. multicinctus residents were subjected to increased intrusions simulated with bottled fish, total territory area decreased (Figure 37). In these experiments, intruder persistence forced residents to modify their spatial use as a result of increased defense costs. While decreased intruder pressure has been demonstrated to increase territory size in fishes (e.g. Norman and Jones, 1984), it is

much more difficult to simulate increased competitor density in natural populations since introduced fish are very likely to be chased away by territory holders (e.g. Nursall, 1977). A good, but generally impractical, means to accomplish this would be to introduce a large number of conspecific adults within the entire study area.

The responses of residents to increased competitors were independent of changes in food supply because bottled fish could not feed during their introduction. If intruders were able to consume large amounts of food under more natural conditions before being expelled, this could have the same effect as decreasing food density and territories might be expected to expand (Hixon, 1980). Given the high aggressiveness towards conspecifics, however, it is more probable that C. multinctus would contract its territory to a size at which all intruders could be successfully expelled and exclusive rights to food corals maintained.

As described by Meyers et al. (1979), the competitor constraint hypothesis will operate if increased food availability results in increased competitor abundance. This condition was met in the current system as all uniform food enhancement experiments attracted large numbers of C. multinctus and resulted in increased costs of defense (Figure 34). In the high density food enhancement experiments, time budgets of residents were radically altered by increased chase rates and resultant decreases in time spent feeding. It is very unlikely that fish would limit their foraging area to the extent seen in the field had competitor intrusion rates been controlled or eliminated in conjunction with an increase in food abundance. This reasoning is supported by the

competitor removal experiments, where foraging areas greatly increased in size (Figures 37A, 38) and indicates that total spatial use is limited by competitors in natural populations. Further support comes from the low density enhancements where residents experienced increased defense costs but still expanded their defended area (Figures 33A and 34), and contrasts the intruder-induced contraction seen in the high-food density experiments (Figures 33, 34, and 35). These experiments indicate that fish will forage over a very large area, and adjust territory size according to costs of defense against intruders. Thus, the major prediction of the competitor constraint hypothesis, that territory size is adjusted in response to levels of competitors rather than food supply, is supported by the experimental manipulations in C. multicinctus territories.

Further evidence that competitors inhibit access to food resources was provided by the experiments in which additional food was presented in association with competitors (Figures 40 and 41). These showed that the presence of a conspecific near a food coral was sufficient to disrupt normal access to food resources independent of any intruder induced decrease in food availability. Furthermore, they show that the simple presence or advertisement of conspecifics, rather than overt aggressive acts that involve body contact, can inhibit access to food resources. Similar behavioral responses of territorial fish were observed when dead fish were placed in bottles (Tricas, unpublished data). Aggressive exclusion of test fish from supplemental food by neighbors or heterospecific fishes was not a major factor in these

tests. Instead, the lack of territory expansion was due to residents spending large amounts of time displaying at bottled conspecifics and little time spent feeding on the associated coral heads.

The competitor constraint hypothesis was originally proposed as an alternative explanation to the inverse relationship between territory size and food abundance (see Myers et al., 1979; 1981 for reviews) and does not literally address the effects of competitor abundance independent of food supply, although the present and other studies (e. g. Norton et al., 1982) have attempted to test this more critical question. In ideal tests of the hypothesis, both food and competitor abundance should covary in some proportionate manner that approximates realistic situations of the system. This approach in itself, however, is problematic since any increase in competitor density that reduces food abundance would make it difficult to identify which variable was responsible for changes in territory size. This was also the case in the present study where increased food abundance attracted additional competitors. Thus, in tests of the competitor constraint hypothesis as presently stated in which each variable is independently manipulated, the direct relationship between competitors and food abundance should also be demonstrated and the interactions considered.

Complex Models of Territory Size

Comprehensive tests of complex theoretical models are extremely difficult for many reasons. In the present study, I attempted to examine the effects of only two variables (food and competitors) by manipulating their abundances in two directions (increases and

decreases). I examined the effect of distribution patterns on food enhancement and show this can affect outcomes of spatial changes in territory use. Those experiments show that it is extremely important to approximate the assumptions of each model examined. Beyond such caveats inherent to model testing lie difficulties in meeting model predictions. Most theoretical models in behavioral ecology (and biology in general) are deterministic, that is they predict one and only one outcome given a specific set of conditions. Understandably, they often lack sufficient depth to account for individual variability or stochastic processes. Further, statistical tests are often limited by the practicality of an experimental system, and trade-offs must be made between sample sizes and number of experimental replicates. As a result we must rely upon experimental test from a limited number of individuals to make inferences about the behavior of a population or species. This in itself should not be forgotten when attempts are made to characterize whole systems.

Although manipulations of competitors had rapid and dramatic effects on territory size for C. multicinctus, fish also made clear spatial adjustments to altered food abundance, thus the importance of food as a determinant of territory size must not be discounted. The interrelationships between food abundance and competitor density have been addressed by more comprehensive models that predict optimal feeding territory size based upon different energetic and time constraints of energy maximizers (reviewed by Schoener, 1983). Below, I review changes associated with food and competitor manipulations for the C.

multicinctus system and discuss them in relation to more complex theoretical models.

The responses of C. multicinctus to manipulations of food and competitors can be qualitatively summarized for each treatment (Table XVI). Although statistical analyses often failed to verify significant changes in direction for activity budgets, general directional trends can be identified for most treatments. The clearest examples are responses to increased food (Figure 34) and increased competitor (Figure 39) manipulations. In the decreased food experiments (Figure 36), the chase rates of fish in 2 sites decreased while increasing in the third. As previously discussed, the low post-manipulation rates of aggression resulted from a slow process of expansion into territories of smaller fish pairs. Higher levels of food reduction (>50%) in C. multicinctus territories elicited increased chase costs associated with expansion into neighboring territories (T. Hourigan, personal communication). Thus, changes in chase rates associated with decreased food may be related to the amount of food reduction. The most equivocal trend was for feeding rates associated with decreased competitor abundance (Figure 38). These changes were of small magnitude, showed no predominant direction, and thus are concluded to reflect no change. Associated increased chase rates were due to interactions with immigrating fish, and would decrease in an experimental environment free of conspecific interactions.

Most critical assumptions of Hixon's (1980) model for optimal feeding territory size for an energy maximizer operating under a time constraint are met by the C. multicinctus system. Food is evenly

Table XVI. -- Qualitative summary of experimental field manipulations for C. multicinctus.

| Environmental Change | Territory Size | Feeding Rate | Chase Rate |
|----------------------|-----------------|-----------------|------------|
| Food | | | |
| Decrease | increase | increase | decrease** |
| Increase | | | |
| Low Density | slight increase | slight increase | increase |
| High Density | decrease | decrease | increase |
| Competitors | | | |
| Decrease | increase | no change* | decrease |
| Increase | decrease | decrease | increase |

* indeterminate with respect to direction of changes.

** increase at higher level of food reduction.

distributed, immobile, continuously renewing, and harvested at a sustainable yield. Territories are approximately circular where occupants can survey the entire area from any one point and no transport of food to a central area is involved (as occurs in many birds and small mammals). The major predictions of the model are that territory area should vary inversely with both competitor and food densities. He also provided predicted changes in time budgets for feeding and defense.

When compared with results of experimental manipulations of food and competitors in the C. multincinctus system (Table XVI), Hixon's original model fails primarily for responses to increased food abundance at low densities. Territory size was predicted to decrease with increased food abundance because of an increase in time required to consume the daily production of food. In the low-density food enhancement experiments, fish increased their feeding rates (functionally equivalent to increased feeding time as predicted), but territories also increased slightly in size. In addition, fish accommodated the increased food supply concurrently with a moderate increase in time allocated to defense. Thus, it appears that C. multincinctus is not as tightly constrained by tradeoffs between time spent feeding and territory defense as required by the model. The acquisition of additional food resources at only a nominal increase in defense cost would only increase net foraging benefits and provide no driving mechanism to decrease foraging area. The decrease in territory size seen in the high density food enhancements also was not a direct response to increased time required to consume the daily production of food, but rather was due to increased time spent chasing intruders

attracted to the supplemental food resources. While this latter point does not fit the original prediction set, it is not entirely inconsistent with implicit predictions for a system where food and competitor abundances covary in such a manner. Schoener (1983) and Hixon (in press) have addressed this problem in greater detail.

Two additional assumptions of Hixon's original model can be addressed with respect to the observed changes in territory size and activity budgets for C. multicinctus. First, the assumption that intruders are primarily non-territorial individuals can be relaxed to include territorial neighbors as long as defense time remains an increasing function of territory size. The relationship between territory size and time required for defense appears to be a monotonically increasing function, since a larger territory perimeter would elicit more agonistic interactions as it infringed more tightly with neighboring pairs. However, whether it is the assumed linear relationship of Hixon's model or a nonlinear increasing function that may reverse predictions of increased food supply (Schoener, 1983) is difficult to assess because of the variable responses of individuals over a relatively small range of area changes. Intuitively, it would seem that over small increases in territory area, defense time would change in an approximately linear fashion, since conflicts normally occur in the buffer zone between familiar neighbors at constant low levels. But as increased territory area begins to impinge upon neighboring territories, agonistic encounters accelerate in a much more rapid manner because neighbors do not tolerate intrusions into their

territory. Thus, defense costs as a function of territory radius may involve a two segment curve: an approximately linear segment with a relatively low slope that operates across the small interterritory buffer zone, and a second steeper (and possibly exponential) segment that operates when the expanding perimeter abuts and crosses borders of neighboring pairs.

Finally, the changes associated with spatial manipulations of food supplies may also affect the movement patterns of foraging individuals. Thus, foraging efficiency (defined as food intake per unit foraging time) may have varied directly with food abundance rather than remained constant. In the food reduction experiments, fish experienced increases in search and travel times between foraging sites which resulted in a decreased foraging efficiency. Fish increased mean feeding rates, however, by swimming faster between feeding sites. Conversely, fish showed decreased feeding rates when coral abundance was increased. Increased feeding efficiency under food enhancement conditions may have resulted from decreased travel time, differential energy content, or morphological variations between food corals (see Tricas, 1985). Hixon (in press) will address the affect of changes in foraging efficiencies in relation to his original model and the predictions are more consistent with results of these experiments. However, additional indicators of changing foraging efficiency, such as duration of feeding bouts, feeding intensity, search/handling times, and prey selectivity are required to validate this last assumption.

Ebersole (1980) modelled the effects of food density on territory size for various types of energy maximizers. In the version most

relevant to the C. multincinctus system (his equation set 5 for insectivorous birds), he predicted the effects of food supply and associated covarying competitors attracted to high levels of food on territory size. At a given food density, territory size was determined by the total time that could be spent foraging in the territory (a constraint similar to Hixon's model), and was influenced by both travel time to a central nest (that can be ignored in the present system) and time spent in defense of the territory perimeter. The model predicted that optimal territory size should vary inversely with competitor abundance as well as food supply when accompanied by high levels of attracted competitors. While Ebersole's model can account for decreased territory size when defense costs are independently high or vary directly with increased food supply, it fails to explain the increase in territory size when food supply was decreased. His model predicts that territory size should vary directly with food abundance if competitor intrusion rates remain constant. It is unlikely that decreased defense costs that accompanied food reduction were responsible for the increase in area because fish slowly encroached upon territories of smaller neighboring pairs over a long period of time. Higher levels of food reduction performed on C. multincinctus resulted in a similar increased territory size but at increased defense cost with neighbors (T. Hourigan personal communication). It is more probable that fish expand their territory because food was reduced below a level to support long-term food requirements of the pair. Fish do not totally abandon the territory under extreme food shortage probably because the cost of

establishing a new site would be much higher than contending with neighbors, and the probability of lost breeding opportunity or decreased reproductive output would be great. Deterministic models would benefit from incorporation of explicit functions to account for minimum levels of food that set lower bounds to the range of predicted responses.

In summary, territoriality for C. multicinctus functions to ensure long term availability of a dispersed, predictable, and self-renewing food supply. Because fish are site attached, food resources within the territory must supply all energetic and nutritional needs of residents. The smallest permanent territory must contain enough renewable food to meet minimum energetic requirements. Surplus food that can be economically defended may be partitioned to additional growth or reproduction. Conspecific competitors directly influence the time available for feeding, mediate the amount of total food resources defended within the territory, and therefore are a major force that limits spatial use and food-dependent reproductive output. Thus, both food supply and competitor abundance influence the use of space in the territorial system of C. multicinctus.

SUMMARY

Chaetodon multicinctus is an obligate coral feeder endemic to the Hawaiian Islands and Johnston Atoll. Adults form long-term monogamous pairs that together defend a single feeding territory from intrusion by other corallivorous fishes, especially neighboring pairs.

Fish undergo sexual differentiation, maturation, and form pairs during their first year of life. Both sexes are predominantly gonochoristic, although some females may change sex prior to reproductive maturity. This phenomenon is viewed as an adaptation to ensure a heterosexual mate in a monogamous mating system where social contact between sexes is constrained by strong selection for early site attachment.

Oocyte development is similar to that described for other teleost fishes. Specific histological criteria were used to mark reproductive events, and show that fish spawn approximately from September through May with peak activity during spring months. Reproductive output and growth are two important aspects of individual fitness for this species. Large males defend the largest feeding-territories, and have the largest female mates. For females, fecundity increases rapidly with body length. Females are highly fecund, and spawn multiple egg batches on a semi-lunar period during the week prior to the new and full moon phases. Both sexes deposit large visceral fat stores during the short non-reproductive summer season, which coincides with the period of maximum growth of their food corals. It is suggested that spawning in this and other coral-feeding fishes may be limited by food availability. The peak spring spawning is most likely an adaptive strategy to maximize

reproductive output, enhance larval survival, and maximize growth of newly settled juveniles in the first year of life.

Living tissues of food corals for C. multicoloratus are high in water content but relatively low in energy. As a result, fish invest over 90% of their time budget feeding, and selectively forage on corals that are the most energetically profitable. The strong preference for rose coral, Pocillopora meandrina, is explained by its relatively high energy content. In contrast, the preference for the massive coral, Porites lobata, over finger coral, Porites compressa, is explained by handling costs associated with their different gross morphologies. Searching for coral polyps on finger coral returns energy at the lowest rate. Furthermore, differences between nematocyst quality and abundance may also structure coral preference patterns, although this remains to be investigated in more detail.

Both food abundance and competitor density are important determinants of feeding-territory size. Territoriality functions to ensure long-term availability of a dispersed, predictable, and self-renewing food supply. Because this species is site-attached, food resources within the territory must supply all energetic and nutritional needs of residents. Field experiments show that territory area changes as an inverse function of food competitor abundance. When coral food supply is decreased, fish increase territory size. In contrast, fish maintain or expand their territories when food abundance is increased and levels of attracted food competitors remain low. When high densities of competitors are attracted to increased food resources, territory holders contract their borders so that exclusive use of food

resources is maintained. This energy-maximizing species will defend the largest amount of food possible, and adjust its territory size according to costs associated with border defense. Thus, both food supply and competitor abundance influence the use of space in the territorial system of C. multicinctus.

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