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COMPARATIVE ECOLOGY OF THE CARDINALFISHES OF
THE BAHAMAS: A STUDY OF COMPETITION, SPECIES
DIVERSITY, AND RELATED FACTORS.

CITY UNIVERSITY OF NEW YORK, PH.D., 1978

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COMPARATIVE ECOLOGY OF THE CARDINALFISHES OF THE BAHAMAS: A STUDY OF COMPETITION, SPECIES DIVERSITY, AND RELATED FACTORS

by

GEORGE DALE

A dissertation submitted to the Graduate Faculty in Biology
in partial fulfillment of the requirements for the degree
of Doctor of Philosophy, The City University of New York.

1978

George Dale

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Abstract

Cardinalfishes (family Apogonidae) are a very prominent component of coral reef fish communities in the Bahamas and elsewhere. Clarification of the basis of their diversity and their avoidance of competitive exclusion, was sought by studying a series of rotenone collections of Bahamian reef fishes and by means of field and laboratory observations. The results obtained fall into several categories.

1. Typologic Factors. Bahamian cardinalfishes fit a lognormal species abundance curve, i.e., an overlapping, multidimensional niche hypothesis. Abundance-frequency patterns among all the species in Bahamian reef fish communities emphasize the prominence of cardinalfishes. Species association patterns, investigated by means of 2 x 2 contingency tables, include nine species pairs with a positive association and two species pairs with a negative association.

A new statistic, the omission effect index, is derived. It estimates the contribution of a taxon or other unit to the Shannon-Weaver species diversity index of a community. Apogon and Phaeoptyx are found, by using this statistic, to have prominent though opposite effects on calculated species diversity. A study of the relationship of apogonid species richness vs. community species richness reveals that apogonid species generally comprise about 8-10% of total species in rotenone collections.

Length-weight relationships and "coefficients of stoutness" are calculated for 14 species. Estimates of "adult length" and

"adult weight" are also made, and a negative correlation is discovered between adult length and stoutness at a given size. Allometromorphism is suggested as a name for this relationship, and its possible evolutionary significance is discussed. Comparison of adult body size data with the abundance and frequency data and with the species association results suggests that body size differences may play a role in interspecific competition avoidance. A frequent ectoparasitic infestation of *Apogon townsendi* is noted, as are two undescribed parasitic copepods.

2. Topographic factors. An investigation of the geographic distribution of different apogonid species within the Bahamas indicates that most, perhaps all, of the twenty species are found throughout that area. Based on relative abundance and frequency at different ranges of depth of capture, a certain depth association is shown for each species, ranging from a fairly clear "preference" for shallower water by *Phaeoptyx conklini* and *Astrapogon puncticulatus*, and for deeper water by *Apogon affinis*, *A. lachneri*, and *A. phenax*, to less pronounced tendencies among other species. Based on relative abundance and frequency in collections from different broad habitat categories, the most notable apparent "preferences" are by *Astrapogon puncticulatus* for the shoreline category, by *Apogon affinis* and *A. lachneri* for the dropoff category, by *A. binotatus* for the top of bank category, and by *A. townsendi* for the outer shelf category.

Among various microhabitat associations observed, facultative association with *Diadema antillarum*, recorded for three additional cardinalfish species, is the most widespread, and tends to

emphasize spatial overlap among the commonest species. Consideration of the lack of a clearly circumscribed spatial niche for most apogonid species led to proposal of a model of reef fish coexistence for explaining such instances. It is offered as an alternative to the "reef fish lottery" model, which does not (it is argued) provide a means of escaping competitive exclusion. In the proposed "money-in-the-bank" model (and financial analogy) two or more species ("investors") can continually coexist in some habitats ("stock market") because of excess larva production ("interest") in other habitats ("savings banks") in which they occur alone. Various features of this model are described and examples among cardinalfishes from the present results are suggested.

3. Temporal Factors. Tabulation, according to month, of several kinds of evidence of reproduction, including evidence of oral brooding and occurrence of recruit-sized individuals, indicates that apogonids tend to reproduce throughout the year, and do not avoid competition by a staggering of breeding season. Direct or indirect evidence of the oral brooding habit is obtained for 12 different species.

In situ observations of cardinalfish changeover patterns support previous reports of their species-specific and sequential nature, and of their mediation in some way by light. A new hypothesis is offered to explain the proximate cause of this behavior: differential phototaxis. Arguments are offered in favor of this hypothesis, in terms of its conformity to various observations, its greater parsimony, and its falsifiability.

Laboratory observations of cardinalfish changeover behavior corroborate the view of its species-specific, sequential, and light-mediated nature. Brain dissections indicate a kind of brain morphology-behavior correlation. Slight differences in relative optic lobe size are positively correlated with photophobic tendency among the three species for which the laboratory changeover data are most reliable.

In addition to the differential phototaxis hypothesis, which addresses the "how" of changeover behavior, a new explanation is proposed for the "why" of this behavior, i.e., for its ecological significance. This hypothesis, termed phototactic habitat partitioning, states that changeover is a space-sharing mechanism in which differences in photophobia or photophilia result in a passive partitioning of shelter space on the reef. It is argued that this explanation is parsimonious, is framed in terms of the resource that is widely considered limiting for most reef fishes (i.e., shelter space), is falsifiable, and has a plausible evolutionary basis.

4. Trophic factors. Stomach content analyses are described which utilize a new volumetric estimation method. In this technique the fraction of a stomach's contents that a given food item represents is multiplied by the fullness fraction of that stomach, giving a "fraction-of-full-stomach" value for that item. Adding and comparing such values to determine a species' food habits avoids certain misleading characteristics of other methods. Food habits determined by this method are tabulated for six species. Crustaceans dominate the food habits of all except _A. affinis_, in

which fish constitute more than half the diet.

Food overlap between two of the six species, *A. maculatus* and *P. conklini*, was studied with the $\hat{C}\lambda$ statistic. Although the calculated overlap between these species is high, it is argued that possible pooling artifacts render such results unreliable. An analytic approach is suggested for testing the possibility that the food habits of two such species are essentially identical. This approach, termed "interspecific-intracollection-overlap vs. intraspecific-intercollection-overlap", indicates whether species identity or collection identity is more of a determinant of diet. The pitfalls of relating food overlap to competition are discussed.

Field and aquarium observations support a view that cardinalfishes are voracious, opportunistic, generalized carnivores, whose somewhat awkward predatory behavior is offset by superior visual capability. Scanning electron photomicrographs of the premaxillary and dentary teeth of twelve species do not reveal any special modifications which can be shown to be related to feeding differences.

5. Taxonomic Factors. Examination of the characters separating *Phaeoptyx* from *Apogon* and *Astrapogon* tends to emphasize the relatedness of these genera. A summary of Atlantic apogonid distribution is presented.

In conclusion, the results of this study suggest several mechanisms, within the framework of the space-sharing hypothesis, which may reduce competition among the various apogonid species of the Bahamas and result in their notable diversity.

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CHAPTER ONE: Introduction

Coral reefs and tropical rain forests are, respectively, the most diverse marine and terrestrial communities on earth. Among vertebrate communities, the coral reef fish community is possibly the most diverse of all. In the Virgin Islands, for example, Smith and Tyler (1972) studied a small, isolated patch reef, about three meters in diameter, which had 53 resident and 22 transient fish species associated with it. Goldman and Talbot (1976) have collected 150 species in a single rotenone station at One Tree Reef on the Great Barrier Reef, and H. A. Fehlmann (pers. comm. cited in Goldman and Talbot, 1976:126) has obtained over 200 species in a similar collection in the Palau Islands.

Typically, a large component of this local species diversity, as well as of coral reef fish diversity on a geographic scale, is contributed by members of the family Apogonidae, the cardinalfishes. There are about 200 shallow water apogonid species, distributed in tropical and subtropical waters throughout the world. Twenty species are known from the Bahamas (Böhlke and Chaplin, 1968: Dale, 1977)

A remarkable degree of taxonomic and ecological similarity exists among the twenty Bahamian species. They all belong to the subfamily Apogoninae and fifteen belong to the same genus: _Apogon_. Three of the other five species belong to the closely related genus _Phaeoptyx_, and the remaining two are _Astrapogon_ species.

Broadly speaking, all or most of these twenty species apparently share many ecologically important characteristics — small in size, coral reef dwelling, nocturnal, carnivorous, and oral brooding - thus implying a contradiction of the ecological principle of competitive exclusion.

This apparent contradiction and the high diversity of Bahamian cardinalfishes together provide the raisons d'être of the present study.

COMPETITIVE EXCLUSION

The principle of competitive exclusion, or Gause's principle, has been called "the most important theoretical development in general ecology" (Hutchinson and Deevey, 1949). The author of a recent ecology text is perhaps even more extravagant in his comments: "...the discovery of a pair of related animals living together is sure to set an ecologist to finding out how; the exclusion principle is one of the few firm anchors in his diffuse science, and he can use it as a physicist uses his general principle of the conservation of mass; as a base from which he can make his assault on complexity" (Colinvaux, 1973: 344). The latter quote would aptly describe the rationale of many recent ecological studies. In the present study the "discovery" of <u>twenty</u> species of closely related cardinalfishes living together has set the author "to finding out how."

How may the principle of competitive exclusion be defined? In several recent ecology and population biology textbooks it is variously defined as follows: "The tendency for competition to bring about an ecological separation of closely related or otherwise similar species" (Odum, 1971). "No two species that are ecologically identical can long coexist" (Wilson and Bossert, 1971). "Two species cannot occupy the same niche simultaneously" (Emmel, 1973). "One species: one niche" (Colinvaux, 1973).

The principle is ultimately derived from the "Verhulst-Pearl" equation (Verhulst, 1838; Pearl and Reed, 1920), which describes the sigmoid growth curve of a single species population in a limited environment (Wilson and Bossert, 1971):

$$\frac{dN}{dt} = rN\left(\frac{K - N}{K}\right)$$

where r = reproductive capacity, N = population size, t = time, K = carrying capacity or maximum population that environment can support.

Two modified differential equations of this kind, the "Lotka-Volterra" equations (Lotka, 1925; Volterra, 1926) deal with the additional effect of competition in a two-species population (Wilson and Bossert, 1971):

$$\frac{dN_1}{dt} = r_1N_1\left(\frac{K_1 - N_1 - \alpha N_2}{K_1}\right)$$

$$\frac{dN_2}{dt} = r_2N_2\left(\frac{K_2 - N_2 - \beta N_1}{K_2}\right)$$

where α = competition coefficient of species 2 (i.e. inhibitory effect of species 2 on species 1), β = competition coefficient of species 1.

These equations specify that the species with the higher competition coefficient ultimately eliminates or excludes the other species.

Experimental evidence of such exclusion was first obtained in the laboratory by Gause (1934) with populations of Paramecium aurelia and P. caudatum, and the term "Gause's principle" came to signify the phenomenon. Park (1948, 1954) provided further experimental demonstration using cultures of flour beetles of the genus Tribolium, and Frank (1952, 1957) studied the phenomenon in cladocerans.

Perhaps the earliest stated application of Gause's principle to natural populations was by David Lack in studies of closely related bird species. He showed for example, that despite the superficially similar ecological characteristics of the cormorant Phalacrocorax carbo and shag P. aristotelis, subtle differences in feeding and nesting habits allowed them to coexist (Lack, 1945). This is the general approach of countless succeeding ecological studies "inspired" by Gause's principle. Robert MacArthur (1958) solved a far more puzzling contradiction of the principle implied in the near identity of nesting sites (spruce trees) and food habits (mainly spruce budworms) among five coexisting warbler species in New England. He showed they avoided competition by hunting in different parts of the same trees.

Recently, the validity of the principle has come under attack for two reasons. First, the possibility that there are exceptions to it has been raised by the findings of Ayala (e.g. 1969, 1971), who described conditions under which two Drosophila species could coexist indefinitely in culture, implying they have the same niche. The ensuing discussion in the literature has included the suggestion that the idealized Lotka-Volterra equations are inadequate to describe this real situation (Antonovics and Ford, 1972), and the suggestion that the competitive exclusion principle be redefined as: "two species competing for limited resources can only coexist if they inhibit the growth of the competing species less than their own growth" (Gilpin and Justice, 1972). Another explanation is that the two Drosophila species each occupy a series of niches that give one species the advantage at one ontogenetic stage, the other at another stage, etc., in such a way that the advantages cancel out (Colinvaux, 1973).

The prevailing view is that the principle has not been invalidated but rather that attempts to express it in a simple mathematical model may encounter difficulty.

A second more fundamental question regarding the principle's validity has been raised by various authors. In the same paper in which the term "competitive exclusion principle" was first proposed, Hardin (1960) suggested that the principle was actually tautological and untestable. Itô (1970) pointed out that if any difference in the ecology of closely related species can define different niches, then coexistence of these species and the competitive exclusion principle must always stand together. Colinvaux (1973) likened the principle to a mathematical theorem in which the requirements of the model specify the results.

The circularity inherent in this and several other ecological and evolutionary concepts is concisely reviewed by Peters (1976), who shows that competitive exclusion is indeed a tautology, since the argument is logically derived from the assumptions. The experiments of Gause thus reqresent "a post facto correspondency with the model, not its proof" (Peters, 1976).

To phrase this criticism in the language of Popperian philosophy (e.g. Popper, 1968), competitive exclusion cannot be considered a scientific theory because it is not falsifiable. Thus if we take the view that if two coexisting species appear to have the same niche it is only because we haven't looked hard enough - a widely held view, e.g. Hutchinson's (1959) view of Ross's (1957) demonstration of coexistence among leafhoppers - obviously we can never disprove the principle.

Is there some meaningful middle ground between acceptance of competitive exclusion as a law of high truth value, a dogma, or a "metaphysic" (Peters, 1976) and rejection of it as a circular, untestable, unfalsifiable model?

I assert that there is. Competitive exclusion does not require proof or disproof to be useful as a logical system for the ordering of our observations. I would further suggest that it is a valuable <u>gestalt</u>, in that it motivates a closer look at coexisting species, not for its verification but merely for generating observations helpful in understanding competition and species diversity.

SPECIES DIVERSITY

I. Cardinalfish diversity:

It could be argued that, superficially at least, cardinalfishes present an almost unprecedented challenge to the competitive exclusion principle, due to the multiplicity of closely related species involved. The twenty species known from the Bahamas are morphologically quite similar to one another - so much so that color pattern is almost indispensible for identification of some species. Yet in a given reef fish community sample they are quite often the most abundant family in number of species (as well as, quite often, in number of individuals).

The single genus Apogon, represented by fifteen species in the Bahamas, is the most speciose genus of the ichthyofauna of that area. In fact among all vertebrates known from the Bahamas only the warbler genus Dendroica exceeds Apogon in speciosenesss, but of the sixteen Dendroica species recorded in the Bahamas only three or four are nesting residents (Bond, 1971; Paterson, 1972). Among other vertebrate classes only several lizard genera are moderately speciose in the Bahamas, including Sphaerodactylus, with seven species; Anolis, with six; and Leiocephalus, with five (Schwartz and Thomas, 1975).

Several Bahamian reef fish genera approach Apogon in number of species, however, and it could of course be argued that the difference is as much an artifact of the prevailing taxonomy as anything else. This question will be considered in the course of this study.

The remarkable diversity of Apogon is not limited to the Bahamas.

According to Ida and Moyer (1974) approximately 30 of 50 apogonid species in 11 genera from Japan are Apogon. Smith (1975) lists 22 Apogon among 40 apogonid species of 13 genera from Southern Africa. According to Ehrlich (1975:212, citing Goldman, and Russel and Talbot) approximately 24 Apogon species are found in the Capricorn group at the southern end of the Great Barrier Reef.

In coral reef environments throughout the world apogonids in general and Apogon species in particular are very prominent components, in both abundance and diversity. The better known a given ichthyofauna becomes, the more dominated by Apogon the checklist of that area tends to become. Gerald R. Allen (personal communication) has recently made extensive collections of the reef fishes of western Australia, where the ichthyofauna was poorly known until now. He has increased the list of Apogon species of that area from 7 to 26 by collecting 17 new records and 2 new species, and increased the total apogonid species list to 43.

Besides the interest inherent in the diversity of apogonids in the Bahamas or elsewhere, it bears on coral reef fish diversity in general - an important problem in view of the unsurpassed richness, among vertebrates, of reef fish communities.

II. General explanations of high species diversity:

In the past twenty-five years or so there has been a great deal of interest in general explanations of high species diversity, particularly with reference to the so-called latitudinal diversity gradient, i.e. the increase in species diversity with decreasing latitude that is observed within many taxonomic groups (see e.g.

Dobzhansky, 1950; Fischer, 1960; Simpson, 1964; Connell and Orias, 1964; Pianka, 1966; Stehli et al., 1969). How do some of these concepts relate to coral reef fish diversity?

One factor proposed as the basis for the development and maintenance of high diversity is long-term environmental stability. In this interpretation tropical diversity results from a relative lack of climatic upheaval in the tropics through geological time (Fischer, 1960). Tropical communities may thus be older, with more opportunity for speciation. Newell (1971) has indeed shown that tropical reef structures date back at least to the Cambrian.

Stability over geological time is an intriguing general explanation, and dates back to Alfred Russell Wallace (1878), but there is evidence against it. For example, it might be expected that the diversity gradient would be greatest during periods of greatest climatic upheaval, e.g. Pleistocene and recent geological periods, and less during other epochs. Stehli et al. (1969) have shown that among fossil foraminifera and brachiopods no such pattern obtains.

Seasonal environmental stability is another proposed basis for tropical diversity, in that it provides less fluctuation in resources. This favors feeding specialization, restriction of niche size, and the opportunity for more species to coexist, or greater species packing (Klopfer and MacArthur, 1961; MacArthur and Levins, 1964; MacArthur, 1972). Environmental stability over time in a general sense, according to the stability-time hypothesis (Sanders, 1969; Slobodkin and Sanders, 1969), promotes diversity in deep-water benthic communities.

The rather narrow physical and chemical limits required for growth by reef-building corals (Wells, 1957) are ample evidence of the relatively stable environment of coral reef fishes. The role of seasonal or general stability in promoting their diversity is difficult to assess, however, since many of the most important reef fish families (including Apogonidae) are virtually limited to tropical (i.e. stable) areas.

High primary productivity is another suggested requisite of high species diversity (e.g. Connell and Orias, 1964; Pianka, 1966) and is certainly provided in the coral reef situation. Studies in the Marshall Islands and Hawaii have shown that coral reefs are among the most productive of all natural communities (Odum and Odum, 1955; Kohn and Helfrich, 1957). It has been suggested, however, that there are enough exceptions to the productivity-diversity correlation to warrant its rejection as a general explanation of diversity (Colinvaux, 1973: 543).

MacArthur (1955) and Hutchinson (1959), among others, have discussed the importance of the stability conferred by food web complexity as a basis for animal diversity, i.e. that trophically diversified communities are better able to persist. May (1973, 1974), however, has shown that increased complexity in model ecosystems tends to diminish stability.

The coral reef fish community seems to be characterized by trophic complexity. Hiatt and Strasburg (1960) broadly categorized the feeding habits of Marshall Islands reef fishes according to foraging method, and constructed an overall food web of the reef community. This summarized food web is itself quite complex and within each category there are wide differences in trophic habits.

The role of predation in maintaining diversity has long been recognized (Gause, 1934; Lack, 1949; Slobodkin, 1961). Slobodkin (1964) showed experimentally that a predator can help two similar species coexist. In the field, Connell (1961) demonstrated that predation reduces competition for space by barnacles, and Paine (1966), also studying a barnacle community, showed that predator removal can lead to local extinction of prey species. Parrish and Saila (1970) proposed a simple mathematical model of a two prey-one predator system, which has been shown (Cramer and May, 1972) to be stable in situations where a simple two-prey system would be unstable.

Fryer (1965) and Lowe-McConnell (1969) have argued that predator pressures are of prime importance in the speciation of tropical African and South American freshwater fishes. Lowe-McConnell (1969) has speculated that in certain very diverse fish communities of African lakes, heavy predation may help prey species coexist by keeping their populations below levels at which they might compete for food. Perhaps such a mechanism is also important in coral reef fish communities. The proportion of predatory fish species may in fact be higher in reef communities than in temperate communities (Hiatt and Strasburg, 1960; Bakus, 1964) as pointed out by Paine (1966).

Although the general factors discussed above may or may not prove to be ultimate explanations or at least ultimate correlates of high species diversity, their direct importance to coral reef fish diversity in general, or cardinalfish diversity in particular, is likely to remain speculative or ambiguous for some time. Insight in these matters is better gained by examining more proximate factors.

III. Spatial niche diversification:

Perhaps the general proximate correlate of high species diversity is fine subdivision of niches, or in a somewhat different sense, the saturation of available niches. According to Elton (1958) the introduction of new species is difficult in very diverse communities because all the niches are filled. This bears on the finding that the Suez Canal is a differential barrier to fish emigration (Marshall, 1966). Ten years ago more than twenty Red Sea species had become established in the eastern Mediterranean, while not one Mediterranean form was established in the Red Sea. Marshall suggested that this was due to the occupation of all available living spaces in the Red Sea reef communities.

In this interpretation living space is the key component of niche diversification. Spatial heterogeneity is indeed proposed as one of the main factors involved in latitudinal diversity gradients (Pianka, 1966).

Crombie (1947) demonstrated competitive exclusion of Oryzaephilus flour beetles by Tribolium in a simple flour medium, but coexistence if pieces of glass tubing were added. MacArthur and MacArthur (1961) and MacArthur (1964) showed that spatial diversity of foliage promotes bird species diversity. Regarding coral reef fish communities, even the casual observer notices that the physical intricacy of a given reef substrate is reflected in the diversity of the local fish fauna. Risk (1972) studied this correlation quantitatively.

Smith and Tyler (1972) have argued that space is a critical limiting resource to the fish residents of a coral reef, and that mechanisms for space sharing are essential in the evolution and maintenance of community diversity. The hypothesis is supported by the apparent saturation of space, lack of starvation, and lack of large fluctuations in the fish populations.

Perhaps the most obvious spatial aspect of niche diversification involves habitat. Habitat selection for some limited component of a species' activities has been shown in various groups of coexisting, closely related animals, e.g. for nesting in sympatric bird congeners (Lack, 1945), for spawning in sympatric freshwater fish congeners (Bartnik, 1970), and for foraging in alcid birds (Cody, 1973).

Broad habitat associations would also be important among species competing for space, and would promote what MacArthur (1965) termed "between-habitat diversity." Greater between-habitat diversity in regions with higher species diversity has been shown in birds (MacArthur et al., 1966; Orians, 1969; Karr and Roth, 1971), and lizards (Pianka, 1969, 1971).

The importance of habitat specializations in reef fish communities is indicated by the pronounced differences in species composition of different local habitats that have been demonstrated in the Marshall Islands (Hiatt and Strasburg, 1960), Hawaii (Hobson, 1974), Fanning Island (Chave and Eckert, 1974), and Great Barrier Reef (Goldman and Talbot, 1976). Clarke (1977) has shown, however, that the diversity of pomacentrids and chaetodontids in the Bahamas may be related more to factors operating within habitats than to habitat preferences.

"Within-habitat diversity" (MacArthur, 1965) would be enhanced in reef fish communities by a variety of space-sharing mechanisms involving foraging areas, shelter sites, activity cycles, symbiotic associations, seasonal reproductive cycles, and territoriality (Smith and Tyler, 1972, 1973).

Among these mechanisms perhaps symbiotic associations are the most spectacularly developed. It is noteworthy that Odum (1969) has suggested that a prevalence of symbiosis may be one of the fundamental characteristics of a community that is highly developed, in a successional sense. According to Goldman and Talbot (1976) "coral reefs are the epitome of mature biologically accommodated communities."

Reef fish symbiotic associations include the mutualism of certain shrimps with gobiid fishes (see Karplus et al., 1972), and the commensalism of various fish species with feeding goatfishes (Smith and Tyler, 1972; Collette and Talbot, 1972; Fricke, 1975). The association of pomacentrids of the genus Amphiprion with sea anemones has been extensively studied (see Allen, 1972). Cleaning symbioses have also been of wide interest (see Feder, 1966), but their relationship to high diversity is not entirely clear. Limbaugh (1964) suggested that cleaning symbioses were more common in the tropics, but this has been questioned by Hobson (1969). Limbaugh (1964) reported that removal of cleaners brought on a decrease in local fish diversity, but this result has not been repeatable (Youngbluth, 1968; Losey, 1972). Slobodkin and Fishelson (1974) have suggested that cleaning behavior promotes high "point diversity."

Several kinds of symbiosis are known among cardinalfishes, including associations with sponges (Smith, 1965; Tyler and Böhlke, 1972) and sea anemones (Colin and Heiser, 1973). One species, Astrapogon stellatus, is a commensal in the mantle cavity of the queen conch (Randall, 1964). Associations of many different apogonid species with sea urchins have been reported (Lachner, 1955; Whitley, 1959; Abel, 1960a, 1960b; Eibl-Eibesfeldt, 1961; Randall et al., 1964; Strasburg, 1966; Magnus, 1967; Fricke, 1970, 1975; Colin, 1974).

Territoriality is also very well developed among certain reef fishes, including damselfishes (Reese, 1964; Rasa, 1969; Low, 1971; Myrberg, 1972; Brockmann, 1973; Myrberg and Thresher, 1974) and acanthurids (Okuno, 1963; Rasa, 1969; Barlow, 1974), but its importance among cardinalfishes is unknown.

There is a wealth of descriptive information in the literature regarding the foraging areas and shelter sites of reef fishes. Tagging studies (e.g. Bardach, 1958; Randall, 1961; Springer and McErlean, 1962) and other studies (Smith and Tyler, 1972; Reese, 1973) indicate that most reef fishes have relatively limited home ranges. Extremely restricted home ranges have been described for a pomacentrid (Sale, 1971) and for several gobies and blennies (Smith and Tyler, 1972).

Descriptive information on the foraging areas and shelter sites of cardinalfishes is included in various studies (Hobson, 1965, 1968a, 1974; Starck and Davis, 1966; Livingston, 1971; Smith and Tyler, 1972; Collette and Talbot, 1972; Vivien, 1973, 1975; Colin, 1974; Ida and Moyer, 1974; Dale, 1975). Chave (MS) studied the importance of various environmental parameters, including salinity, temperature, water clarity, water movement, and light intensity on the distribution of six apogonid species in Hawaii.

Differences in activity cycles, which promote a temporal partitioning of space in the reef fish community, have also been widely studied (Schroeder and Starck, 1964; Hobson, 1965, 1968a, 1968b; Bertram, 1965; Starck and Schroeder, 1965; Starck and Davis, 1966; Fishelson et al., 1971; Livingston, 1971; Collette and Talbot, 1972, Smith and Tyler, 1972; Domm and Domm, 1973; Dale, 1975).

A final space-sharing mechanism that also has a temporal dimension is reproductive seasonality. There is a wealth of information in the literature on reef fish reproduction (see Ehrlich, 1975:217-223), but besides the study of Munro et al. (1973) on Caribbean reef fishes, there is very little comparative information on the spawning seasons of reef fishes and virtually none on cardinalfishes. Smith and Tyler (1972) have suggested that staggered recruitment of juveniles of different species to the reef may be an important aspect of space sharing.

The studies of Sale and others (Sale 1974, 1975; Russel et al., 1974; Sale and Dybdahl, 1975) on Great Barrier Reef fishes suggest that the randomness of recruitment and loss may actually be more important in promoting coexistence of related forms than space sharing mechanisms or any other niche specializations. Thus a patchy environment and the stochastic elements of a "reef fish lottery" (Sale, 1976) may be essential factors in the maintenance of high reef fish diversity. Levin (1974) has studied the theoretical basis of such a mechanism. A third hypothesis, somewhat intermediate between the space sharing and stochastic models, has also been suggested (Dale, 1978) and will be described in the present study.

IV. Trophic niche diversification:

Feeding specializations constitute another kind of niche diversification which has an essential bearing on competition and diversity in animal communities. Minor differences in the size and structure of the bill have been found to correlate with distinct differences in the diet of closely related birds (Lack, 1945, 1947; Bowman, 1961; Kear, 1962). Minor differences in other body dimensions and in locomotor ability have also been correlated with avian feeding habits (Davis, 1957; Hinde, 1959; Hamilton, 1961; Osterhaus, 1962). Schoener (1968) demonstrated feeding specializations in sympatric Anolis lizards.

Some studies have indicated a great apparent overlap in food habits among coexisting freshwater fishes. Forbes (1914) and Hartley (1948) suggested that they share a common stock of food resources. It has even been concluded that Gause's principle may not apply to freshwater fish communities (Hartley, 1948; Larkin, 1956). The findings of Keast and Webb (1966) differ with this conclusion. In a comprehensive study of a temperate fish community, they correlated mouth and body morphology with distinct, competition-reducing feeding habit differences, indicating that earlier studies may have been too superficial.

DeMartini (1969) showed that minor structural differences in the feeding apparatus are correlated with feeding specializations in the temperate marine surf-perches. Stephens et al. (1970) showed that differences in diet among sympatric California blennies were correlated with differences in feeding behavior and microhabitat associations. Zaret and Rand (1971) contended that the feeding habits of certain tropical stream fishes conform to the principle of competitive exclusion. Feeding specializations are apparently fundamental to the origin and maintenance of the extreme diversity of cichlids in African lakes (Lowe-McConnell, 1969; Fryer and Iles, 1972; Greenwood, 1973).

Several studies have analyzed the food habits of the entire reef fish faunas of certain regions, including the Marshall Islands (Hiatt and Strasburg, 1960), the Caribbean (Randall, 1967), Tuléar, Madagascar (Vivien, 1973), and Hawaii (Hobson, 1974). Austin and

Austin (1971) studied the feeding habits of juvenile fishes in mangrove areas of Western Puerto Rico, including many species that inhabit reefs as adults.

Other studies have concentrated on the food habits, as well as correlated morphological or behavioral factors, in some limited group e.g. pomacentrids (Emery, 1973), acanthurids (Jones, 1968), holocentrids (Vivien and Peyrot-Clausade, 1974). Chave (MS) studied the feeding habits of Hawaiian cardinalfishes and Vivien (1975) studied apogonid feeding habits at the reefs of Tuléar, Madagascar. Many additional studies have dealt with single reef species.

The results of all of these reef fish feeding habit studies seem to be consistent with the prevailing general assumption that competition for food is important in the reef fish community, but few if any of them are detailed enough or carried out in such a way that an alternative assumption — that food is, in general, not limiting — could be disproved. This alternative possibility is strongly suggested by the space sharing hypothesis of Smith and Tyler (1972, 1973).

The possibility that simple differences in body size, apart from any other trophic specializations, may allow coexistence of related forms was suggested by Hutchinson (1959, 1965). Such a mechanism may be important in rotifers (Pejler, 1956) certain mammals (Rosenzweig, 1966; McNab, 1971) lizards (Schoener, 1968; Rand and Williams, 1969; Williams, 1972), mites (Hurlbutt, 1968) and fishes (Barbour, 1973). According to Hutchinson (1959) a ratio of about 1.3 to 1 in body size is enough to allow coexistence. MacArthur (1972:23) suggests such a ratio in terms of weight and proposes an empirical definition of competitive exclusion related to it: "Species that differ only in size seem to require that the larger be about twice as heavy as the smaller in order to coexist."

The possibility that body size differences are of critical importance to reef fish community structure has been shown by Smith (1975, 1978).

In view of these considerations of the proximate correlate of high species diversity, i.e. fine niche subdivision, it would seem that one or more spatial, temperal, or trophic factors might be essential to cardinalfish diversity.

OBJECTIVES

The general objectives of the present study may be stated succinctly as follows:

I. To explain an apparent lack of competitive exclusion among the cardinalfishes of the Bahamas.

II. To clarify the nature of the high species diversity of Bahamian cardinalfishes.

III. By extension to clarify the nature of competition and species diversity in the coral reef fish community as a whole.

PHILOSOPHICAL APPROACH

The philosophical approach of this study includes two general considerations:

I. Perhaps the greatest single pitfall of ecological investigations of the kind undertaken here involves starting without an "open mind." As in any scientific study, *a priori* assumptions may predetermine the nature of our observations and conclusions. That is "the expectations of theory color perception to such a degree that new notions seldom arise from facts collected under the influence of old pictures of the world" (Eldredge and Gould, 1972). Or, as stated by S. Holmes (in Doyle, 1930): "It is a capital mistake to theorize before one has data. Insensibly one begins to twist facts to suit theories, instead of theories to suit facts."

For example, if we begin looking at an animal community with the assumption that food is a limiting resource in that community, it makes us see differences in dentition, gut anatomy, etc., as competition-reducing adaptations, thus in neatly circular fashion "proving" the assumption. Or it might make us complete an analysis of food habits with the demonstration that some interspecific differences are detectable, also "proving" the assumption, without requiring us to establish that the differences are not related to different collection sites, times, etc.

Perhaps "Innocent, unbiased observation is a myth" (Medawar, 1969:28). Certainly the scope of the present investigation was influenced by current ecological theory. Nevertheless an effort was made to minimize preconceived notions.

II. Although the factors underlying competition and species diversity among different taxonomic or ecological groups in the coral reef fish community may be multifarious and diffuse, certain general principles, perhaps as yet unknown, may be involved. This philosophical approach may be termed "nomothetic ecology" in the sense that Raup et al. (1973:p. 526) refer to "nomothetic paleontology", i.e. "the study of 'cases and events as universals, with a view to formulating general laws.' The conventional approach, on the other hand, is termed 'idiographic': 'The study of cases or events as individual units, with a view to understanding each one separately.'" Ecological science has perhaps always been somewhat more nomothetic than Raup and his coauthors contend paleontology has been. Nevertheless a great deal of observation and explanation has yet to provide a cohesive picture of reef fish community ecology. The space sharing model of Smith and Tyler (1972) and the stochastic model of Sale and Dybdahl (1975) are widely recognized as landmarks in this direction, but their very oppositeness is an indication of how tentative our understanding of coral reef fish communities is.

METHODOLOGICAL APPROACH

For the purpose of this investigation an extensive collection of Bahamian fishes in the Ichthyology Department of the American Museum of Natural History was made available to the author for examination and dissection. This collection comprises over two hundred quantitative rotenone samples made by Dr. C. Lavett Smith, primarily during the Bahamas Natural History Survey sponsored by the American Museum between 1964 and 1968, and includes several thousand cardinalfish specimens representing the genera _Apogon_, _Phaeoptyx_, and _Astrapogon_. The author also made several field trips to various parts of the Bahamas between 1973 and 1975, including Bimini, Grand Bahama, Nassau, and Eleuthera, during which _in situ_ observations were made and additional samples were taken. Finally, certain experimental studies were made possible by the opportunity to maintain laboratory populations of cardinalfishes in the Ichthyology Department of the American Museum and at the Museum's field station in Bimini, Bahamas.

Given these operational possibilities, a variety of approaches was employed, as outlined below. The categorization and sequence are not necessarily those followed during the investigation (some major aspects of the study were carried out more or less concurrently), but are considered, in retrospect, to be a logical means of presentation.

I. Typologic Factors:

An obvious primary task was precise identification of all the apogonid specimens present in the fish samples to be studied, i.e.

determination of the kinds or "types" of cardinalfishes present (whence the heading "typologic"). Length and weight determinations were also made, and any apparent ectoparasites were noted.

This information was used to study: (A) species abundance patterns (B) abundance-frequency patterns, (C) species association patterns, (D) species diversity patterns, (E) body size patterns (F) occurrence of ectoparasites

II. Topographic Factors:

To determine the extent of actual physical coexistence among the various species, certain spatial or topographic factors (in the broadest sense) related to the distribution of the various species were studied: (A) geography (B) depth (C) habitat (D) microhabitat.

III. Temporal Factors:

Certain aspects of the temporal dimension of coexistence were also considered relevant:

(A) The importance of reproductive seasonality was assessed.

(B) Circadian activity patterns were studied by means of <u>in situ</u> and laboratory observation, and the possible correlation of such patterns with brain morphology was investigated.

IV. Trophic Factors:

The importance of feeding specializations among the various species was estimated by studying:

(A) Feeding Habits.

(B) Morphological correlates to feeding.

Investigation of morphological correlates to feeding was arbitrarily limited to an SEM study of the teeth of the jaws. As the overall study progressed (including the food habit study) the possibility that feeding specialization was of overriding ecological importance appeared increasingly unlikely and more attention was devoted to other aspects of the study.

V. Taxonomic Factors:

Since the rationale of the present study hinges on the occurrence of twenty closely related species in the Bahamas, matters pertaining to the taxonomic relatedness of these species and to the interrelationships of the three genera were of obvious relevance. Certain discoveries in this regard, made during the study, led to the investigation of:

(A) Validity of the genus _Phaeoptyx_.

(B) Interrelationships of western Atlantic cardinalfishes

(C) Biogeography of western Atlantic cardinalfishes.

The wide-ranging nature of the methodological approach outlined above was partly a result of the philosophical considerations mentioned earlier, but was also dictated by the wide-ranging possibilities that the problem presented. This latter fact is due, no doubt, to the relative infancy of coral reef community studies. SCUBA and other recent technological advances enabling _in situ_ observations have uncovered a whole new biological world: the coral reef ecosystem. In this ecosystem the fishes are arguably the most conspicuous, colorful, and behaviorally interesting component. They have indeed been likened to "underwater birds", and there is much promise that reef fish studies will stimulate ecological thought as much in the next decade or two as avian studies did in the last few decades. The present study was aimed at making a small contribution in that regard.

CHAPTER TWO: Typologic Factors

I. METHODS

More than two hundred fish collections were made by Dr. C. Lavett Smith in the Bahamas between 1964 and 1973, and are deposited in the fish collections of the American Museum of Natural History. Most were made with the aid of emulsified rotenone (either Chemfish Collector or Pronoxfish). Since use of this ichthyocide allows relatively unbiased sampling (see Smith, 1973, for a discussion of the sampling efficiency of rotenone collecting) collections made by other means were not included in the present study. Inland rotenone collections were also omitted, as were repeat samples of the same stations if these were made less than four months after the first sampling, on the assumption that a reef or other habitat would have largely recovered after that amount of time.

After eliminating the non-rotenone collections, inland collections, and repeat samples, 152 collections remained. In addition, two large rotenone collections were made by the author in Bimini, in 1973. The total of 154 non-repeat marine rotenone collections is referred to in various places below as "total collections."

Among the 154 collections were 58 collections from patch reefs in three general habitat areas: top of bank, moat, and outer shelf. These designations are based on a classification of Bahamian fish habitats (C. L. Smith, unpublished). Because these collections tended to be the largest and most diverse, and because the patch reef fish community is in many respects a self-contained unit and is sampled very effectively, some calculations below are based on the pooled collections from these three patch reef habitats only (referred to as "patch reef collections").

Although most of the rotenone collections had been sorted and identified before the present study, the cardinalfish specimens in all cases were carefully reexamined and identified. Because many of the collections had been identified before the availability of Böhlke and Randall's (1968) key to western Atlantic cardinalfishes, and also because of the time required to make positive identifications of all juveniles, a large number of specimens had been misidentified. In the present study an effort was made to positively identify all apogonid specimens, including the smallest juveniles. In some of the analyses performed, information on the identity, abundance, and frequency of occurrence of non-apogonid species in the Bahamian collections was used. In most cases these data came directly from the notes of Dr. Smith or from the card catalog of the Ichthyology Department of the American Museum. A small number of specimens (apogonid and non-apogonid) were too small for positive species identification and were simply eliminated from consideration.

(A) Species abundance patterns

The information gained by simply counting and identifying the apogonid specimens (in "total collections") made possible the consideration of species abundance patterns. Abundance rank was tabulated for the totals of each cardinalfish species in all collections, and for totals of the cardinalfish species from the single most important habitat type (defined here as that from which the greatest number of cardinalfish specimens was collected): outer shelf patch reefs.

From these tabulations, species abundance curves were prepared, by plotting abundance against rank, the latter on a logarithmic scale. These curves permitted graphic comparison with various theoretical species abundance patterns.

(B) Abundance-frequency patterns

The overall structure of the reef fish communities in which cardinalfish were most abundant was studied by combining species abundance information with data on frequency of occurrence (i.e., number of samples in which a species occurs) to study abundance-frequency patterns. These patterns were tabulated according to a method of Mason and Bryant (1974). This method is derived graphically by plotting the logarithm of proportionate abundance (ordinate) against frequency of occurrence (abscissa) for each species. Proportionate abundance is a simple percentage, following Alevizon and Brooks (1975), eliminating the unnecessary "relative abundance index" of Mason and Bryant (1974).

The resulting graph is then subdivided along the frequency axis by drawing vertical lines at frequencies of 33.3% and 66.7%, thus forming three frequency categories:

A: species occurring in $>$66.7% of samples

B: species occurring in 33.3-66.7% of samples

C: species occurring in $<$ 33.3% of samples

and subdivided along the abundance axis by drawing horizontal lines such that four abundance categories result:

1: proportionate abundance $>$10%

2: proportionate abundance 1-10%

3: proportionate abundance 0.1-1%

4: proportionate abundance $<$ 0.1%

In this way each species may be placed in one of twelve categories of abundance-frequency: A1, A2, A3, A4, B1, B2, etc.

Tabulation by this method was carried out for all species in the "patch reef collections," as a means of summarizing the relative importance of apogonid species among all the fish species in this very important general habitat category. Since these data also permitted a calculation of the relative abundance of the different fish families, a table showing the abundance rank of the various families was prepared.

(C) Species association patterns

The frequency of occurrence of each apogonid species in the "total collections" was tabulated. In order to detect the existence of and enable evaluation of the significance of any positive or negative tendency for pairs of cardinalfish species to occur together, i.e., (as thus defined) any positive or negative association, a tabulation of observed apogonid species co-occurrence in these collections was also prepared. If the tendency for two species to occur together was entirely random, the "expected" frequency of co-occurrence of the two species would be the product of their respective frequencies of occurrence. On this basis expected frequencies of co-occurrence were added to the above tabulation. Comparison of observed and expected frequencies of co-occurrence would indicate either a positive or negative association which may or may not be statistically significant.

In each case, significance may be tested with a 2 x 2 contingency table (see Pielou, 1974:258-266). The form of such a table, with the cells of the table and the row and column sums labeled here with a, b, c, d, and N, is as follows:

		Species K		
		present	absent	Σ
Species J	present	a	b	a + b
	absent	c	d	c + d
	Σ	a + c	b + d	N = a+b+c+d

The following chi-square equation, designed for use with this table (see Pielou, 1974:260) could then be used to test the null hypothesis that any indication of positive or negative association was due to chance alone:

$$\chi_c^2 = \frac{\left(|ad - bc| - N/2\right)^2 N}{(a + b)\ (c + d)\ (a + c)\ (b + d)}$$

The subscript c in χ_c^2 indicates, following Pielou (1974:191) an adjusted formula for χ^2 which gives a closer approximation (by incorporating "Yates' correction for continuity" - see Sokal and Rohlf, 1969:590).

For a single, isolated, 2 x 2 contingency table determination, the null hypothesis may be rejected if the probability of the calculated chi-square value (for one degree of freedom) is 0.05 or less. As seen in a chi-square distribution table, 3.84 is the "critical value" for this level of significance. In other words, the association is deemed significant (at the 5% level) if its 2 x 2 contingency table yields a chi-square of 3.84 or greater.

If, however, the association of different pairs of a number of species is being investigated by this method (as in the present case), it is not permissable to conclude that there is significant association in each case where a 2 x 2 table yields $\chi^2 \geq 3.84$ (see Pielou 1974:262). Under these circumstances, one can compute a "supercritical value" for χ^2 such that the probability is only 0.05 that it will be exceeded, by chance alone, by <u>any</u> of the batch of calculated χ^2 values. If one is testing n different 2 x 2 tables (for n different species pairs), this supercritical value, denoted as $[\chi_o^2]_n$, is (for the 5% sifnificance level) approximately equal to the critical value for a single test at the $\frac{5}{n}$ % significance level (Cooper, 1968: cited in Pielou 1974:262).

Another important consideration is that the 2 x 2 table chi-square test is unreliable if the smallest "expected frequency" (computed in an "expected" 2 x 2 table: see Pielou 1974: 260) is less than 5 (Pielou 1974: 262-263). For this reason, testing of association was limited, in the present case, to species occurring in at least 10% of the samples. This 10% "cutoff point" was chosen arbitrarily, but proved, for the present case, to be just about exactly the level necessary to avoid calculating associations which could not be then deemed reliable due to the "small expected frequency consideration." Such useless calculations are important to avoid because of a trade-off involving the supercritical χ^2 value, i.e., the more pairs of species tested, the higher the χ^2 value needed for significance at the 5% level. It should be noted, however, that such a "cutoff point" must be chosen solely on the basis of the "small expected frequency consideration." To do so after the testing of the 2 x 2 tables, to an extent that reduces the supercritical χ^2 value enough to make certain calculated χ^2 values which are not quite significant become significant (as one might be tempted to do) would obviously be an invalid statistical procedure.

Limiting the association testing to species occurring in at least 10% of the samples resulted in the testing of eight species (see Table 6). Since, for k species, k (k-1)/2 different pairs are possible, 8(8-1)/2 = 28 different 2 x 2 tables were constructed and tested. The supercritical χ^2 value for the 5% significance level is thus approximately equal to the critical value for a single test at the $\frac{5}{28}$% level, i.e., for p = 0.0018.

In the absence of tables giving χ^2 values for increments of p small enough to obtain the χ^2 corresponding to $p = 0.0018$, a visual estimate made from a graphical projection of the χ^2 distribution (Herskowitz 1965:528) was deemed acceptable. This visual estimate indicated a χ^2 value of about 9.7 for $p = 0.0018$.

Following the procedure described above, a significant positive association was determined for 7 of the 28 species pairs. Several indications of negative association were not significant at the 5% level. Because of a special interest in comparing positive and negative associations (in order to evaluate the ecological significance of body size differences, as described earlier in this METHODS section), an effort was made to render some of these negative associations significant at a lower confidence level by testing at the 10% significance level. In this case the supercritical χ^2 is approximated by the critical value for a single test at the $\frac{10}{28}$ % level, i.e. for $p = 0.0036$. The best visual estimate from the χ^2 distribution graph indicated a χ^2 of about 8.4 for this p value. Using this lower confidence limit, significance was indicated for two negative associations, as well as for two additional positive associations.

The results of the 2 x 2 table testing were used in the preparation of a table giving, for the 28 species pairs, the expected and observed frequencies of co-occurrence and any statistically significant positive or negative associations, with probability values.

(D) Species diversity patterns

In 1. and 2., below, species diversity was calculated with the information theoretical measure known as the Shannon-Weaver index (Shannon and Weaver, 1949):

$$H' = -\sum p_i \log p_i$$

where p_i is the proportion of the i^{th} species. The use of this and other measures of species diversity is reviewed by Peet (1974).

In the present study the Shannon-Weaver index was determined by the method prescribed in Lloyd et al. (1968). Since the proportions p_i are, in practice, estimated as

$$p_i \approx \frac{n_i}{N}$$

where N is the total number of individuals, and n_i the number of individuals of the i^{th} species, the formula for H' is put directly in terms of the observed n_i's, avoiding the bother and rounding errors of calculating the proportions. Thus, for logs to base e:

$$H' = -\sum p_i \log_e p_i \approx \frac{1}{N} (N \log_e N - \sum n_i \log_e n_i)$$

To perform this calculation a program was prepared for use with a Hewlett-Packard HP-55 calculator.

1. "Diversity contribution" analysis: for pooled patch reef collections.

The relative contribution of apogonid species to the species diversity of Bahamian reef fish communities was estimated by calculating the species diversity of the "patch reef collections" and then repeatedly recalculating it after omission of one fish family at a time to rank families according to their relative contribution to "patch reef collections" diversity. That family whose removal from the calculation resulted in the greatest decrease in diversity for the total of remaining families was ranked number one, etc.

Since the genus is perhaps a less subjective taxonomic category than the family, and since the author was especially interested in the diversity contribution of the genus Apogon, a similar series of calculations was made of the species diversity of the "total patch reef collections" after omitting each genus, and the resulting data were used to rank genera according to their relative diversity contribution. An "omission effect index" (explained in 2., below) was also calculated for each family and each genus.

It should be noted that a family or genus could make a negative contribution to species diversity, and that its removal from the calculation could increase the diversity of the remaining total. This would occur, for example, if a family or genus included only one extremely abundant species.

2. "Diversity contribution" analysis: for the five richest collections of the "patch reef collections" - the derivation of a diversity contribution statistic.

To obtain at least a partial evaluation of the degree to which the above family ranking and genus ranking might be an artifact of the pooling of collections (or, more specifically, to determine if the relative importance of the diversity contributions of the family Apogonidae and of the apogonid genera is similar in high diversity local situations to what it is in the "total patch reef collections") family and genus ranking was carried out for each of the five richest patch reef collections.

That is, species diversity was first calculated for the single richest patch reef collection (the collection with the greatest total species number). Then the diversity of that collection after omission of each family and each genus was calculated. Note, again that it is possible for the species diversity to be increased by the omission of a family or genus.

From the resulting data an "omission effect index" for each family and each genus was calculated as follows:

$$C_{jk} = \frac{H'_{k-j} - H'_k}{H'_k}$$

where C_{jk} is the omission effect index of the j^{th} taxon in the k^{th} collection; H'_k is the diversity of the k^{th} collection; H'_{k-j} is the diversity of the k^{th} collection with the j^{th} taxon omitted. (For the calculation of omission effect index in 1., above, the pooled "patch reef collections" are treated as one collection, the k^{th} collection.)

What, in words, does the numerical value of C_{jk} represent? It is that proportion of the species diversity index of a collection which when added to that index gives the species diversity index of that collection with taxon j omitted; i.e., the proportion of H'_k which when added to H'_k gives H'_{k-j}. This can be seen by rearranging the above equation as follows:

$$(H'_k \cdot C_{jk}) + H'_k = H'_{k-j}$$

In most cases omission of a taxon from a collection will decrease the species diversity of the collection. Such a taxon will have a negative C_{jk} value between 0 and -1. (The value would be -1 if that taxon included the entire collection.) Multiplying H'_k, the species diversity of the collection, by this negative C_{jk} and adding the resulting negative product to H'_k yields the lowered species diversity of the collection with that taxon omitted, i.e., H'_{k-j}.

In the case of a taxon which includes an extremely abundant species, its removal will actually make a collection more diverse. Such a taxon will have a positive C_{jk} value. Multiplying H'_k by this positive C_{jk} and adding the product to H'_k yields the higher species diversity of the collection with that taxon omitted.

While negative C_x values can be no less than -1, positive C_{jk} values can be greater than +1. This would be the case for a taxon whose omission more than doubles the species diversity of the collection, as in the following hypothetical example. A collection with 11 species, 10 of which are represented by 10 individuals each and the 11th by 1000 individuals, would have a species diversity of

0.514. Omitting the abundant 11th species would change the species diversity of the collection, now consisting of 10 species represented by 10 individuals each, to 2.303. This effect is expressed by the C_{jk} of the 11th species: +3.480. Omitting one of the other 10 species would change the species diversity of the collection, now consisting of 9 species with 10 individuals each plus 1 species with 1000 individuals, to 0.466, as expressed by the C_{jk} value of -0.092.

The omission effect index is a measure of the contribution of a taxon to the species diversity of a collection, describing it in a clear and quantitative manner. Thus a C_{jk} value of -0.10 means, regardless of the size or diversity of a collection, that without that taxon the diversity of the collection is reduced by 10%; a C_{jk} value of 0 means that without that taxon the diversity remains the same; a C_{jk} value of +1.00 means that without that taxon the diversity is augmented by 100%; and so forth.

The omission effect index calculations described above for the single richest patch reef collection were then made, in turn, for the second, third, fourth, and fifth richest patch reef collections. All calculations were made with a program on the HP-55 calculator.

A mean omission effect index for any taxon present in one or more of the five collections could then be calculated as the following quantity:

$$\frac{\sum_{k=1}^{M} C_{jk}}{M}$$

where M is the total number of collections, in this case five. Note that the expression ΣC_{jk} for a taxon present in, e.g., only one of M collections is, in effect, the sum of the one calculated omission effect index plus M-1 zeroes.

Calculating a mean omission effect index in this way has one important disadvantage: that small collections would have the same effect on the result as large collections. To eliminate this problem, a weighted mean omission effect index may be calculated by multiplying each C_{jk} value by:

$$(\frac{t_k}{T})M$$

where t_k is the total number of individuals in the k^{th} collection, and T is the total number of individuals in all collections.

The equation for calculating the weighted mean omission effect index, $\bar{C}_j$, is thus:

$$\bar{C}_j = \frac{\sum_{k=1}^{M} \left[C_{jk} \cdot (\frac{t_k}{T})M \right]}{M}$$

$$= \sum_{k=1}^{M} \left[C_{jk} \cdot \frac{t_k}{T} \right]$$

It is important to note that calculating a mean omission effect index for a taxon in this way for, e.g., five collections, is not the same as calculating an omission effect index for a taxon in the pooled collections. For example, let us suppose that a taxon in one collection which has a positive C_{jk} (due to containing a very abundant species) is absent in the other four of five collections. The $\overline{C}_j$ for that taxon would still be positive, though lower in value. The omission effect index for that taxon in the pooled collections, however, would not only be different, but might well be negative since the abundant species would no longer be so dominant. Pooling would hide the effect of the taxon's actual proportionate occurrence in discrete collections (thus creating the kind of artifact mentioned earlier as the reason for developing this statistic).

The $\overline{C}_j$ values calculated for the families and genera included in the five richest patch reef collections were then used to rank families and genera according to their relative contribution to the diversity of these five collections. All calculations were again performed with the aid of a program on the HP-55 calculator.

3. Apogonid species richness vs. community species richness

One further aspect of "species diversity" was studied using simple richness (i.e., number of species) without any consideration of equitability (the Shannon-Weaver index includes both components). This simpler approach was considered meaningful for the following simple graphical calculation: for each collection of the "total collections," the number of cardinalfish species was plotted against the total number of species. The resulting graph would indicate the kind of correlation existing between the species richness of a community and the species richness of its apogonid component.

(E) Body size patterns

Standard length was measured for all apogonid specimens in "total collections", to the nearest tenth millimeter, using a Helios dial caliper. In samples where one or more specimens had been removed earlier for an alizarin preparation (in most cases for use in taxonomic studies by some other American Museum investigator) standard length was measured as well as possible on these alizarin specimens. *Astrapogon* *stellatus* and *Apogon* *leptocaulus* were omitted from the body size difference investigation because of their rarity in the collections being studied.

Fifty specimens of each of the other 14 species, from two or more different collections in each case (or the total number of specimens, except alizarin specimens, of that species if less than fifty), were weighed to the nearest hundredth gram on a Torbal model ST-1 triple beam balance. Collections were chosen such that the whole size range of specimens of that species was more or less represented. Obviously emaciated, damaged, or gravid specimens were not included.

These length and weight data were then used to study length-weight relationship in each species, to tabulate body size differences among the different species, and to evaluate the possible ecological significance of these body size differences.

1. Length-weight relationship

The relationship of length to weight is expressed in the equation $W = aL^n$. The length and weight data described above were used to obtain the empirical values of a and n for each apogonid species, by a method described in Lagler (1956: 164-165). A computational procedure was developed, for use with a Toshiba BC-1623G programmable calculator, and a work sheet was prepared for this procedure.

Using the equation $W = aL^n$ with the values of a and n for each species thus obtained, a table of calculated weight values for 5 mm standard length intervals (within the observed standard length range of a given species) was then prepared.

For each species these calculated weight values, together with the actual measured weights were plotted against the length intervals and actual measured lengths, respectively, on the same graph. A curve was fitted to the calculated length-weight points, and a subjective judgement was made as to whether or not this curve deviated from the actual data little enough so that the weight of a fish could always or nearly always be accurately estimated from its length alone.

One final length-weight datum was calculated for each species. Using the formula given in Lagler (1956: 159-162) for calculating coefficient of condition: $K = W/L^3$, and the length-weight relationship obtained in the above calculations, a "coefficient of condition", better termed "coefficient of stoutness", or s, for this purpose, was calculated for each species for a standard length of 35 mm (for all species this is within the size range represented in the length-weight determinations, except <u>Apogon</u> <u>mosavi</u>, whose range is just short of 35 mm).

2. Body size differences

As described above, standard length was measured for all specimens. From these data the mean standard length of the largest 10% of the specimens of each species was calculated. Using this value as an estimate of "adult length", the species were ranked in order of "adult length" in a table giving that value and also giving the standard length of the single largest specimen of that species.

From this table a second table was constructed ranking the species according to "adult weight". This statistic was estimated for each species by conversion of the "adult length" value, using the calculated length-weight relationship described in 1., above.

3. Ecological significance of body size differences

Some evaluation of the ecological significance of body size differences (specifically as a possible means of avoidance of interspecific competition) could be made by reference to the tables described above. For example, if the two or three most abundant species were widely different in body size, a possible underlying ecological basis would be suggested. If, however, they were very similar in body size, then a lack of ecological basis would be suggested.

A more meaningful and more reliable indication of the ecological significance of body size differences could perhaps be obtained with reference to the species association data obtained in (C), above. If species pairs that showed a positive association tended to differ in body size far more than those pairs showing a negative association, an ecological basis would be strongly suggested.

A simple method of assessing this possibility would be to calculate the average size difference (in "adult length" and "adult weight") between species showing a positive association, and likewise to calculate the average size difference between species with a negative association. The results would be interpreted as follows: if the average adult size difference for positive associations is greater than the average adult size difference for negative associations, then an ecological basis is suggested - the greater the disparity, the stronger the suggestion. If they are more or less the same, there is then no indication of an ecological basis.

Perhaps a far better evaluation of the ecological significance of body size differences would be one based on actual size differences of the specimens of different species present in the various collections. Because of the far greater difficulty of extracting that information, such an evaluation was not carried out in the present study.

(F) Occurrence of ectoparasites

Although no special study was made, ectoparasites (including, as defined here, parasites in the oral cavity or gill chambers) were noticed on numerous occasions during the identification and measurement of specimens, and all such instances were recorded.

II. RESULTS

One or more apogonid specimens were present in 125 of the 154 non-repeat marine rotenone collections ("total collections"). They totaled 4,209 specimens, of 16 different species, in 433 separate samples. (A sample is here defined as the specimens of a given species in a given collection.) The total number of different species and of specimens of all fish species were not calculated for "total collections". The 58 "patch reef collections" included a total of 11,981 fish specimens, of 214 different species, in 2,077 samples. Apogonids were present in 55 of the collections, and comprised 2,166 specimens of 13 different species in 194 samples. These data and some related statistics are summarized in Table 1.

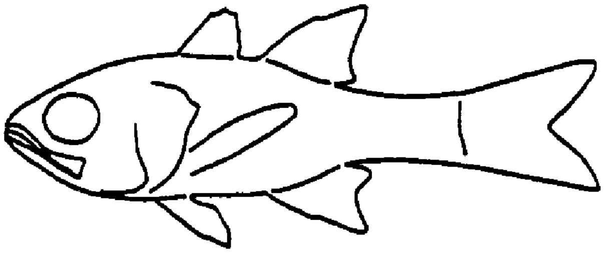
Among the apogonid specimens were two samples of a new species, Apogon mosavi Dale (1977), and one sample of a species previously unrecorded in the Bahamas, Apogon leptocaulus Gilbert (1972).

Outline drawings of the 20 apogonid species known from the Bahamas, which give a rough indication of their morphological similarity, are given in Figure 1. Photographs of live specimens of the three species which are probably the most abundant of apogonid species in shallow water in the Bahamas are shown in Figure 2. For these photographs the fish were held in a plastic chamber that proved to be ideal for photographing live fish of this size (Figure 2A).

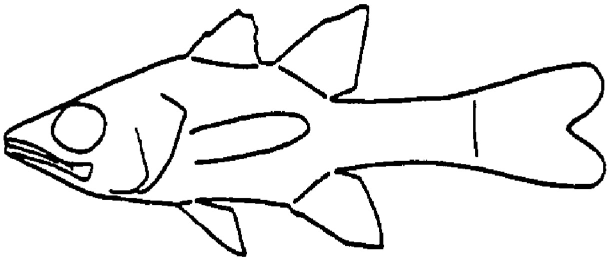
	Apogonids in "total coll'ns." (= 154)	All species in "total coll'ns." (= 154)	Apogonids in "patch reef coll'ns." (=54)	All species in "patch reef coll'ns." (=54)
Total specimens	4,209	-	2,166	11,981
Different species	16	-	13	214
Number of samples	433	4,885	194	2,077
Specimens per coll'n.				
Average	27.3	-	37.3	206.6
Range	0-336	-	0-366	-
Species per coll'n.				
Average*	2.81	31.7	3.34	35.8
Range	0-8	2-76	0-8	2-66

Table 1. Summary of specimen counts, species numbers, sample numbers, and related statistics for apogonid species and all fish species in 154 "total collections" and 58 "patch reef collections." Where no figure is given, the calculation was not made. (* number of samples / number of collections)

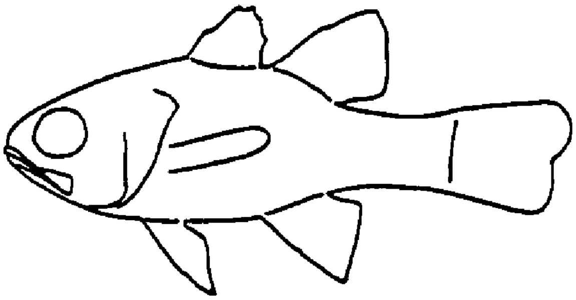
Figure 1. Outline drawings of the 20 cardinalfish species known from the Bahamas. All but two are after Böhlke and Chaplin (1968); Apogon leptocaulus and Apogon mosavi are adapted from photographs of the holotypes in the original descriptions (Gilbert, 1972; Dale, 1977).



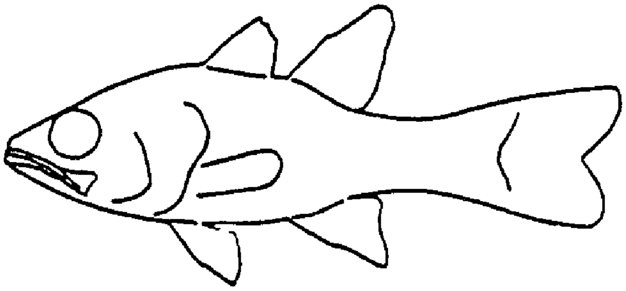
Apogon affinis



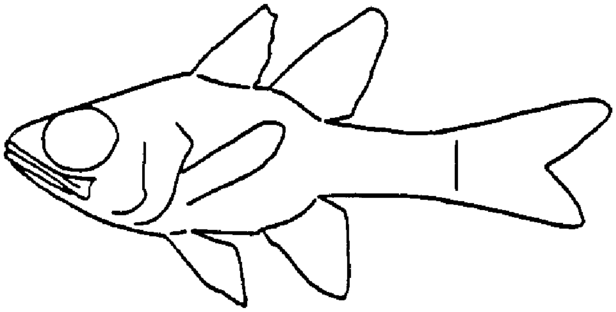
Apogon anisolepis



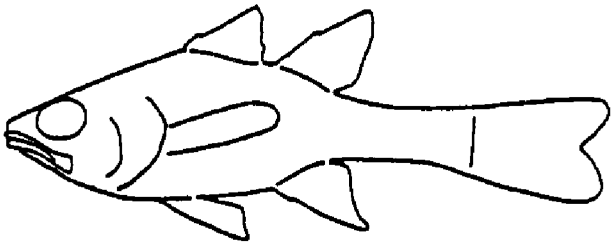
Apogon aurolineatus



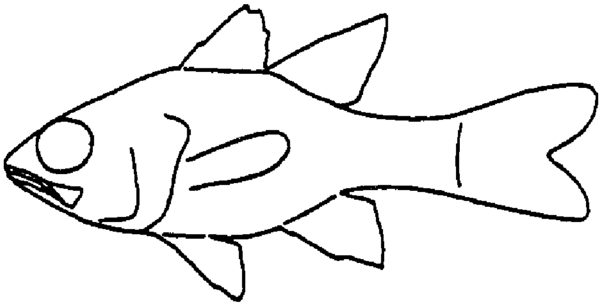
Apogon binotatus



Apogon lachneri



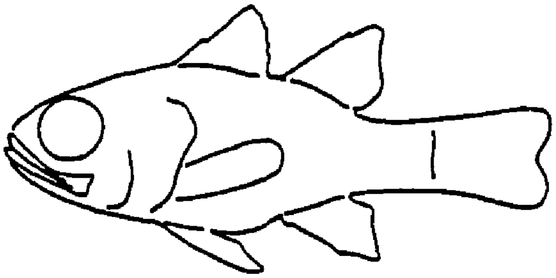
Apogon leptocaulus



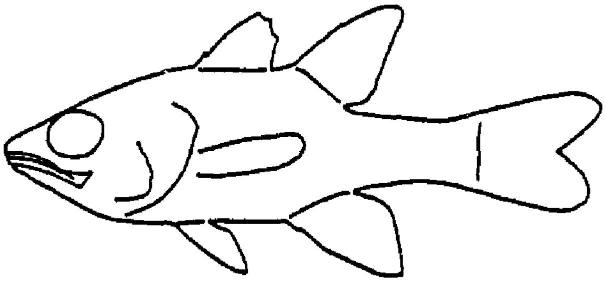
Apogon maculatus

FIGURE 1

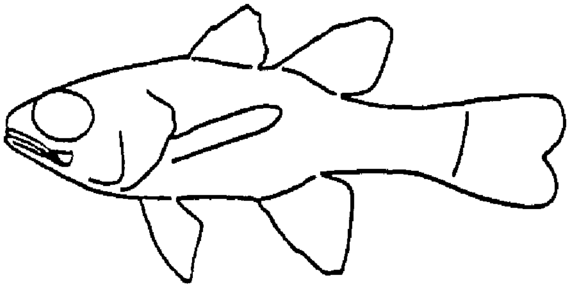
(1st of 3 pages)



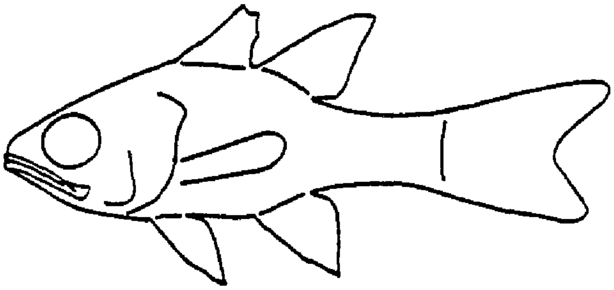
Apogon mosavi



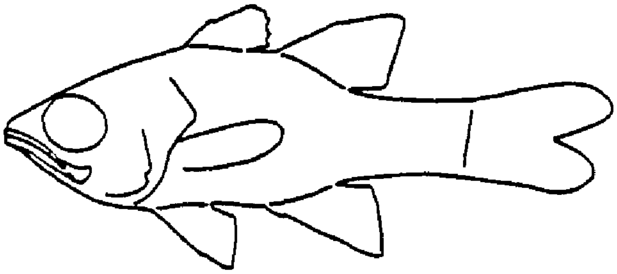
Apogon phenax



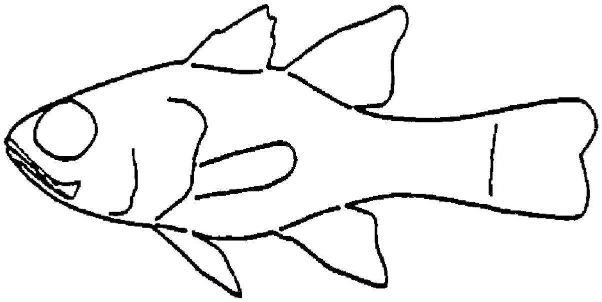
Apogon pillionatus



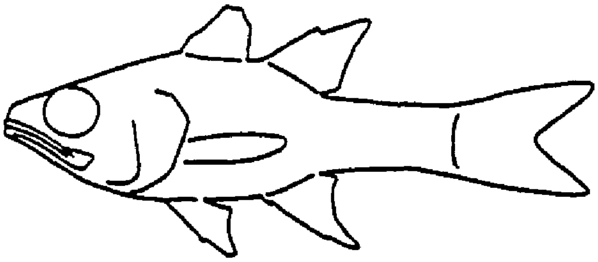
Apogon planifrons



Apogon pseudomaculatus



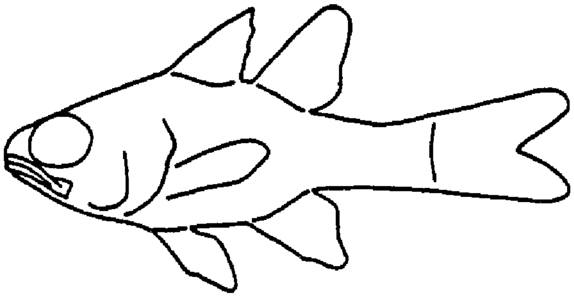
Apogon quadrisquamatus



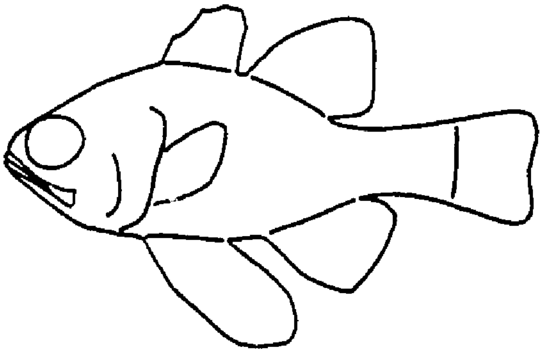
Apogon robinsi

FIGURE 1

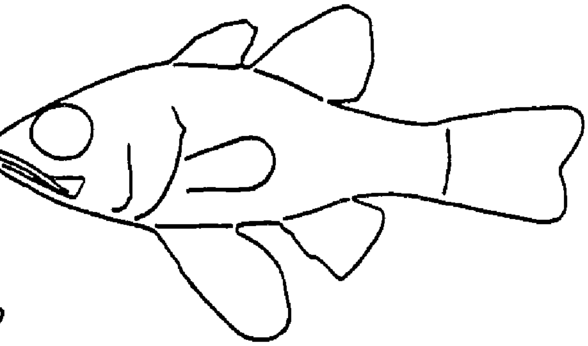
(2nd of 3 pages)



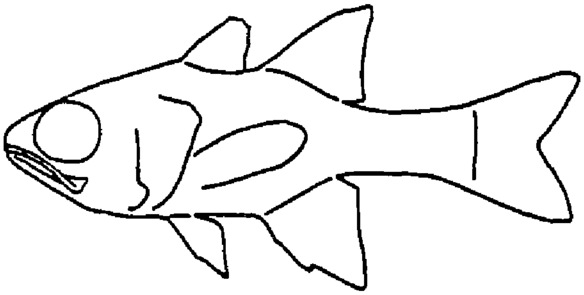
Apogon townsendi



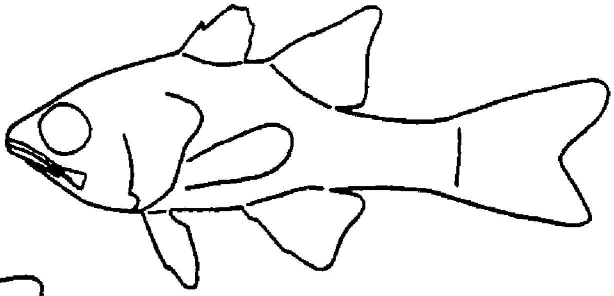
Astrapogon puncticulatus



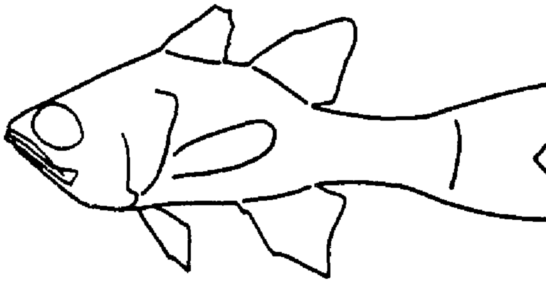
Astrapogon stellatus



Phaeoptyx conklini



Phaeoptyx pigmentaria



Phaeoptyx xenus

FIGURE 1

(3rd of 3 pages)

Figure 2. Photographs of live specimens of three species that are probably the most abundant apogonid species in shallow water in the Bahamas. (A) Diagram of the photographic chamber used. The top and bottom of a plastic Petri dish were glued together with silicone sealer, and a section was sawed off. White paper was taped on the outside of the Petri dish top for a background. The chamber was held with a three-prong extension clamp, which was attached to a support stand. (B) Phaeoptyx conklini. (C) Apogon maculatus. (D) A. townsendi. All specimens were collected off Turtle Rocks, south of Bimini, Bahamas.

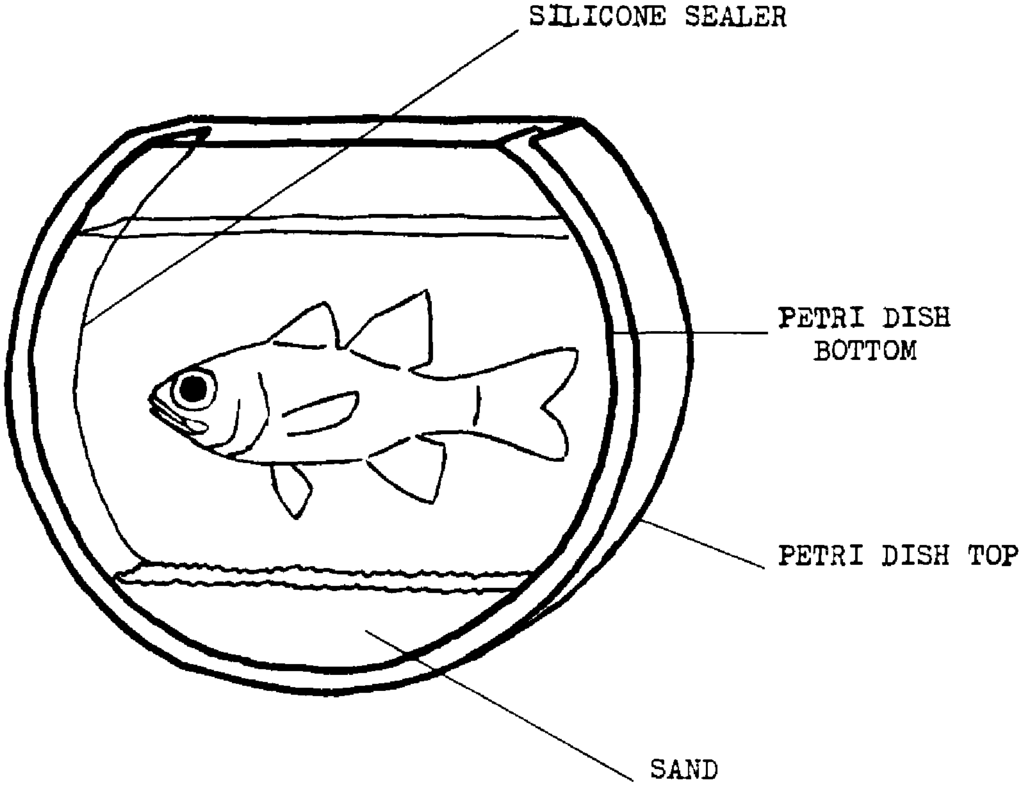


FIGURE 2 (A)

FIGURE 2 (B)

FIGURE 2 (C)

FIGURE 2 (D)

(A) Species abundance patterns

The abundance rank data for apogonid species in "total collections" and in outer shelf patch reef collections are given in Tables 2 and 3, and shown graphically in Figures 3 and 4

The single species Phaeoptyx conklini accounts for nearly half (48.6%) of the apogonid specimens in "total collections" (Table 2). Apogon maculatus accounts for 18.5% and A. townsendi for 9.1%. Together these three most abundant species comprise over 3/4 (76.3%) of the specimens of the 16 species present. The seven least abundant species (ranks 10 - 16 in Table 2) comprise less than 3.5% of the specimens. Between these two extremes are six species (ranks 4 - 9) of intermediate abundance (2.8 - 4.0%), whose combined numbers constitute 20.2% of the total specimens. The presence of the six intermediate abundance values among the otherwise more or less sharply declining abundance values results in a roughly sigmoid species abundance curve (Figure 3).

In outer shelf patch reef collections (Table 3), P. conklini again comprises nearly half (45.0%) of the apogonid specimens. A. maculatus (29.1%) and A. townsendi (14.4%) are again second and third most abundant. These three species together account for nearly 9/10 (88.6%) of the specimens of the 13 species present. The remaining species are moderate to rare in abundance, and although these two categories are not quite as apparent as in the "total collections", a more or less sigmoid species abundance curve results nevertheless (Figure 4).

Rank	Species	Number of specimens	Percent of total
1	*Phaeoptyx conklini*	2,046	48.6
2	*Apogon maculatus*	779	18.5
3	*Apogon townsendi*	384	9.1
4	*Apogon binotatus*	167	4.0
5	*Astrapogon puncticulatus*	165	3.9
6	*Phaeoptyx pigmentaria*	153	3.6
7	*Apogon mosavi*	128	3.0
8	*Apogon lachneri*	122	2.9
9	*Apogon affinis*	117	2.8
10	*Apogon phenax*	47	1.1
11	*Apogon planifrons*	45	1.1
12	*Apogon quadrisquamatus*	21	0.5
13	*Phaeoptyx xenus*	20	0.5
14	*Apogon robinsi*	11	0.3
15	*Astrapogon stellatus*	2	0.05
16	*Apogon leptocaulus*	1	0.02

Table 2. Abundance rank for the apogonid species in "total collections."

Rank	Species	Number of specimens	Percent of total
1	*Phaeoptyx conklini*	577	45.0
2	*Apogon maculatus*	373	29.1
3	*Apogon townsendi*	185	14.4
4	*Phaeoptyx pigmentaria*	40	3.1
5	*Apogon phenax*	30	2.3
6	*Apogon binotatus*	16	1.2
7	*Apogon planifrons*	15	1.2
8	*Apogon lachneri*	13	1.0
9-10	*Apogon affinis*	10	0.8
9-10	*Apogon quadrisquamatus*	10	0.8
11	*Astrapogon puncticulatus*	6	0.5
12	*Phaeoptyx xenus*	5	0.4
13	*Apogon robinsi*	1	0.1

Table 3. Abundance rank for the apogonid species in outer shelf patch reef collections.

Figure 3. Species abundance curve for the 16 apogonid species in "total collections." Number of individuals of each species is plotted against the species rank in the sequence from most abundant to least abundant.

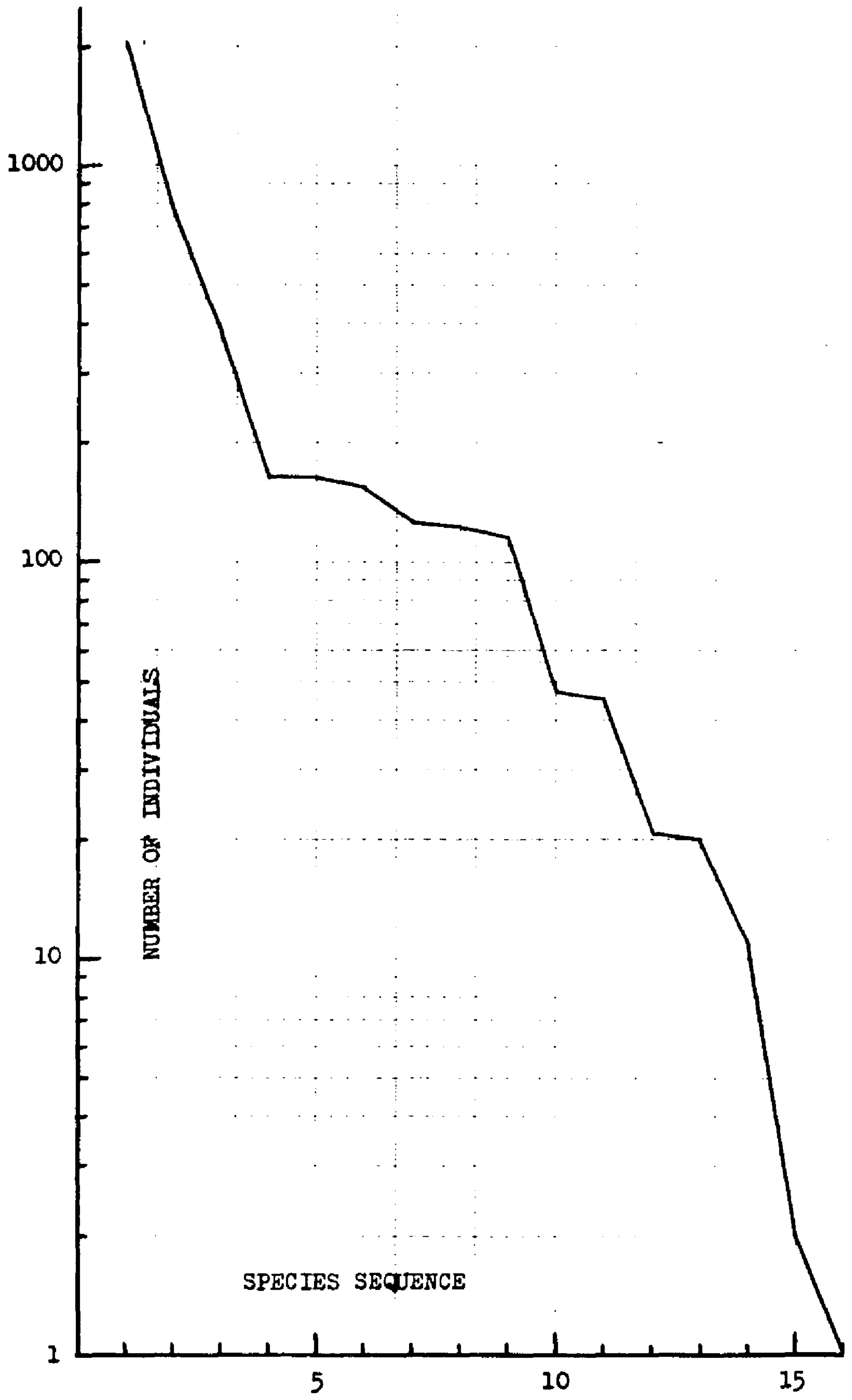
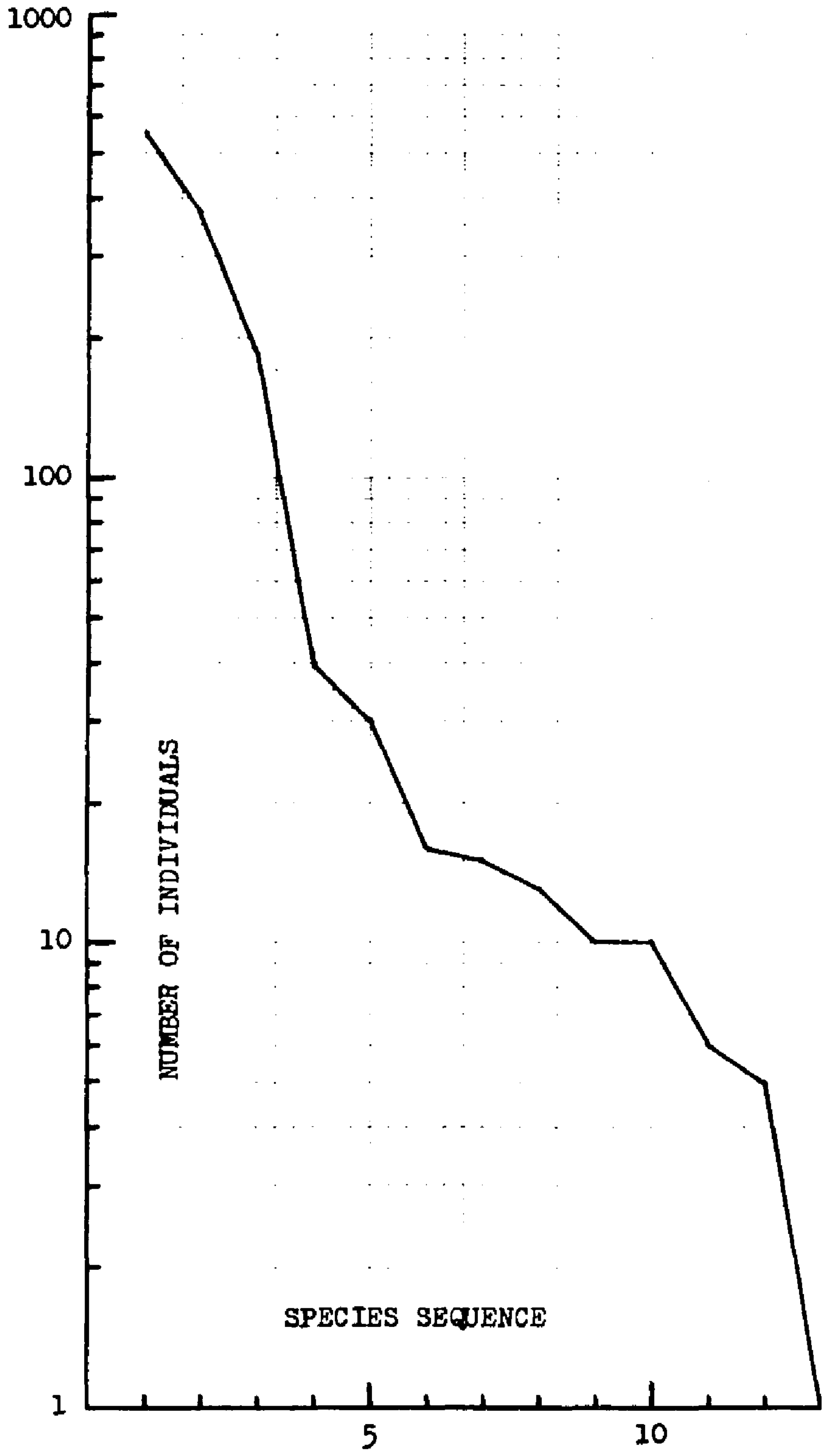

NUMBER OF INDIVIDUALS
SPECIES SEQUENCE
1000
100
10
1
5
10
15

Figure 4. Species abundance curve for the 13 apogonid species in outer shelf patch reef collections.


1000
100
10
1
NUMBER OF INDIVIDUALS
SPECIES SEQUENCE
5
10

(B) Abundance-frequency patterns

Table 4 gives a listing from the "patch reef collections" data, of the species in each abundance-frequency category. P. conklini, present in 74.1% of the collections, and comprising 10.45% of the total specimens, is alone in the A1 category. Only the bluehead wrasse Thalassoma bifasciatum exceeds P. conklini in frequency (93.1%), and heads the A2 category in abundance (6.01%). A. maculatus, also in the A2 category, has the third highest frequency (72.4%) and fifth highest abundance (3.44%). Of the six species in the high frequency, high abundance categories A1 and A2, two are apogonids. The other four are the sole representatives in these categories of their respective families.

The apogonid species in other abundance-frequency categories are: A. townsendi in B2, P. pigmentaria in B3, A. binotatus, A. phenax, A. planifrons, A. lachneri, A. affinis, and Astrapogon puncticulatus in C3, and Apogon robinsi, A. quadrisquamatus, and P. xenus in C4.

Thus apogonid species are found in various abundance-frequency categories, but tend to stand out in the high abundance, high frequency categories.

Table 5 gives the abundance rank of the various fish families present in the "patch reef collections." The family Apogonidae is seen to be the most abundant, accounting for 18.1% of all the specimens collected, followed by Clinidae (11.2%), Pomacentridae (10.8%), Labridae (8.7%), Tripterygiidae (6.5%), Holocentridae (5.1%), Grammidae (4.5%), Scaridae (4.0%), and Pomadasyidae (3.5%).

Table 4. Structure of Bahamian patch reef fish communities: abundance-frequency characteristics of the species present in 58 rotenone collections ("patch reef collections"). An asterisk indicates an apogonid species.

Abundance-frequency category	Species	Abundance (%)	Frequency (%)
A1	**Phaeoptyx conklini*	10.45	74.1
A2	*Thalassoma bifasciatum*	6.01	93.1
	Enneanectes altivelis	4.62	70.7
	Gramma loreto	4.39	67.2
	**Apogon maculatus*	3.44	72.4
	Canthigaster rostrata	1.23	69.0
A3	none		
A4	none		
B1	none		
B2	*Starksia atlantica*	3.09	51.7
	Eupomacentrus fuscus	2.86	50.0
	Quisquilius hipoliti	2.84	60.3
	Haemulon flavolineatum	2.76	36.2
	Chromis cyanea	2.13	48.3
	Scarus croicensis	2.04	43.1
	Myripristis jacobus	1.74	43.1
	Starksia lepicoelia	1.68	53.4
	**Apogon townsendi*	1.66	34.5
	Malacoctenus triangulatus	1.60	63.8
	Coryphopterus glaucofrenum	1.44	37.9
	Eupomacentrus pictus	1.44	43.1
	Halichoeres garnoti	1.19	58.6
	Ogilbia cayorum	1.17	62.1
	Pseudogramma bermudensis	1.07	62.1
	Sparisoma viride	1.05	50.0
	Holocentrus vexilliarus	1.04	43.1
	Malacoctenus macropus	1.01	37.9

(continued)

Abundance-frequency category	Species	Abundance (%)	Frequency (%)
B3	*Acanthurus coeruleus*	0.98	46.3
	Eupomacentrus variabilis	0.90	48.3
	Ophioblennius atlanticus	0.86	39.7
	Acanthurus bahianus	0.66	39.7
	Kaupichthys hyoproroides	0.83	56.9
	Labrisomus gobio	0.81	51.7
	Labrisomus haitiensis	0.72	41.4
	Scorpaenodes caribbaeus	0.68	51.7
	Holocentrus rufus	0.67	37.9
	Synodus synodus	0.64	46.6
	Plectrypops retrospinis	0.58	50.0
	**Phaeoptyx pigmentaria*	0.58	44.8
	Gobiosoma genie	0.54	41.4
	Epinephelus fulvus	0.53	37.9
	Moringua edwardsi	0.42	36.2
	Epinephelus cruentatus	0.40	37.9
B4	none		
C1	none		
C2	*Coryphopterus hyalinus*	2.65	10.3
	Chromis multilineata	1.65	31.0
C3	*Lythrypnes nesiotes*	0.95	24.1
	Coryphopterus personatus	0.95	10.3
	Gnatholepis thompsoni	0.88	31.0
	Enneanectes boehlkei	0.85	25.9
	**Apogon binotatus*	0.85	29.3
	Labrisomus guppyi	0.79	32.8
	Lythrypnus elasson	0.78	20.7
	Eupomacentrus partitus	0.68	5.2
	Holocentrus coruscus	0.60	31.0
	Halichoeres bivittatus	0.59	29.3
	Jenkinsia lamprotaenia	0.53	5.2
	Sparisoma aurofrenatum	0.50	32.8
	Enneanectes pectoralis	0.50	27.6
	Enchelychore carychroa	0.38	31.0
	Eupomacentrus leucostictus	0.38	17.2
	Dactyloscopus tridigitatus	0.38	15.5
	Holocentrus marianus	0.36	27.6
	Halichoeres maculipinna	0.33	17.2

(continued)

Abundance-frequency category	Species	Abundance (%)	Frequency (%)
C3	Priacanthus cruentatus	0.33	15.5
	Haemulon melanurum	0.33	3.4
	Coryphopterus dicrus	0.32	24.1
	Gillellus rubrocinctus	0.31	25.9
	Enneanectes atrorus	0.31	12.1
	Coryphopterus eidolon	0.28	12.1
	*Apogon phenax	0.28	10.3
	*Apogon planifrons	0.25	10.3
	Microspathodon chrysurus	0.23	24.1
	Eupomacentrus planifrons	0.22	25.9
	Lythrypnus heterochroma	0.22	20.7
	Eupomacentrus mellis	0.22	15.5
	Arcos artius	0.21	24.1
	Amblycirrhitus pinos	0.20	24.1
	Bodianus rufus	0.20	17.2
	Monacanthus tuckeri	0.18	22.4
	Rypticus subbifrenatus	0.18	20.7
	Muraena miliaris	0.18	17.2
	Sparisoma radians	0.18	15.5
	Starksia fasciata	0.18	12.1
	Starksia elongata	0.18	12.1
	Aulostomus maculatus	0.16	25.9
	Doratonotus megalepis	0.16	8.6
	Paraclinus marmoratus	0.15	8.6
	Enneanectes jordani	0.14	13.8
	Pempheris schomburgki	0.14	5.2
	Bothus ocellatus	0.13	13.8
	Opistognathus maxillosus	0.13	12.1
	Haemulon aurolineatum	0.13	1.7
	Acanthemblemaria maria	0.13	1.7
	Serranus tigrinis	0.12	15.5
	*Apogon lachneri	0.12	13.8
	Haemulon plumieri	0.12	8.6
	Dactyloscopus crossotus	0.12	8.6
	Gramma melacara	0.12	1.7
	*Astrapogon puncticulatus	0.11	13.8
	Ahlia egmontis	0.11	12.1
	*Apogon affinis	0.11	5.2
	Acanthemblemaria spinosa	0.10	12.1
	Malacoctenus boehlkei	0.10	8.6
C4	Pseudupeneus maculatus	0.09	13.8
	Starksia nanodes	0.09	13.8
	Paraclinus nigripinnis	0.09	12.1

(continued)

Abundance-frequency category	Species	Abundance (%)	Frequency (%)
C4	*Apogon robinsi	0.09	10.3
	Acanthemblemaria aspera	0.09	10.3
	Clepticus parrai	0.09	3.4
	Holacanthus tricolor	0.08	17.2
	Stathmonotus stahli	0.08	8.6
	Lythrypnus spilus	0.08	8.6
	Scorpaena albifimbria	0.08	8.6
	*Apogon quadrisquamatus	0.08	6.9
	Epinephelus striatus	0.08	5.2
	Equetus acuminatus	0.08	5.2
	Callionymus bairdi	0.08	5.2
	Acanthurus chirurgus	0.08	5.2
	Pseudemblemaria signifera	0.08	3.4
	Holocentrus ascensionis	0.07	13.8
	Enchelychore nigricans	0.07	12.1
	Chorististium rubre	0.07	10.3
	Haemulon sciurus	0.07	6.9
	Halichoeres pictus	0.07	5.2
	Sparisoma chrysopterum	0.07	5.2
	Risor ruber	0.07	5.2
	Holacanthus ciliaris	0.06	12.1
	Bothus lunatus	0.06	10.3
	Epinephelus guttatus	0.06	10.3
	Chaetodon capistratus	0.06	10.3
	*Phaeoptyx xenus	0.06	8.6
	Halichoeres radiatus	0.06	5.2
	Labrisomus nigricinctus	0.06	5.2
	Symphurus ommaspilus	0.06	3.4
	Antennarius multiocellatus	0.05	8.6
	Chaetodon striatus	0.05	6.9
	Coryphopterus thrix	0.05	6.9
	Abudefduf saxatilis	0.05	5.2
	Lucayablennius zingaro	0.05	5.2
	Gillellus uranidea	0.05	3.4
	Petrotyx sanguineus	0.04	8.6
	Micrognathus vittatus	0.04	6.9
	Lutjanus mahogoni	0.04	5.2
	Gobiosoma pallens	0.04	5.2
	Calamopteryx goslinei	0.04	3.4
	Scarus vetula	0.04	3.4
	Paraclinus fasciatus	0.04	3.4
	Gymnothorax moringua	0.03	6.9
	Parophidion lagochila	0.03	6.9
	Kaupichthys nuchalis	0.03	5.2
	Syngnathus dunckeri	0.03	5.2

(continued)

Abundance-frequency category	Species	Abundance (%)	Frequency (%)
C4	*Symphurus arawak*	0.03	5.2
	Lutjanus apodus	0.03	5.2
	Prognathodes aculeatus	0.03	5.2
	Scarus taeniopterus	0.03	5.2
	Sparisoma rubripinne	0.03	5.2
	Malacoctenus erdmani	0.03	5.2
	Emblemariopsis bahamensis	0.03	5.2
	Entomacrodus nigricans	0.03	5.2
	Hypleurochilus springeri	0.03	5.2
	Antennarius pauciradiatus	0.03	5.2
	Oligopus claudei	0.03	3.4
	Malacanthus plumieri	0.03	3.4
	Opistognathus aurifrons	0.03	3.4
	Haemulon chrysargyreum	0.03	1.7
	Conger triporiceps	0.02	3.4
	Hypoplectrus puella	0.02	3.4
	Epinephelus adscensionis	0.02	3.4
	Haemulon carbonarium	0.02	3.4
	Equetus punctatus	0.02	3.4
	Scarus guacamaia	0.02	3.4
	Opistognathus whitehursti	0.02	3.4
	Leurochilus acon	0.02	3.4
	Gobiosoma evelynae	0.02	3.4
	Lythrypnus okapia	0.02	3.4
	Scorpaena plumieri	0.02	3.4
	Arcos rubiginosus	0.02	3.4
	Haemulon striatum	0.02	1.7
	Scarus coeruleus	0.02	1.7
	Sparisoma atomarium	0.02	1.7
	Labrisomus bucciferus	0.02	1.7
	Acanthemblemaria chaplini	0.02	1.7
	Urolophus jamaicensis	0.01	1.7
	Synodus saurus	0.01	1.7
	Synodus intermedius	0.01	1.7
	Chilorhinus suensoni	0.01	1.7
	Rabula acuta	0.01	1.7
	Gymnothorax vicinus	0.01	1.7
	Ariosoma impressa	0.01	1.7
	Nystactichthys halis	0.01	1.7
	Tylosurus crocodilus	0.01	1.7
	Hemiramphus brasiliensis	0.01	1.7
	Atherinomorus stipes	0.01	1.7
	Otophidium dormitator	0.01	1.7
	Penetopteryx nanus	0.01	1.7
	Hypoplectrus nigricans	0.01	1.7

(continued)

Abundance-frequency category	Species	Abundance (%)	Frequency (%)
C4	Hypoplectrus unicolor	0.01	1.7
	Rypticus saponaceus	0.01	1.7
	Anisotremus virginicus	0.01	1.7
	Equetus lanceolatus	0.01	1.7
	Mulloidichthys martinicus	0.01	1.7
	Centropyge argi	0.01	1.7
	Chaetodon sedentarius	0.01	1.7
	Chromis insolatus	0.01	1.7
	Hemipteronotus splendens	0.01	1.7
	Hemipteronotus martinicensis	0.01	1.7
	Scarus coelestinus	0.01	1.7
	Dactyloscopus poeyi	0.01	1.7
	Gillellus greyae	0.01	1.7
	Malacoctenus aurolineatus	0.01	1.7
	Blennius marmoreus	0.01	1.7
	Hypleurochilus bermudensis	0.01	1.7
	Psilotris alepis	0.01	1.7
	Psilotris celsus	0.01	1.7
	Scorpaenodes tredecimspinosus	0.01	1.7
	Cantherhines pullus	0.01	1.7
	Lactophrys triqueter	0.01	1.7

Table 5. Abundance of the various fish families present in "patch reef collections," listed in order of abundance.

Family	Number of specimens	Percent of total
Apogonidae	2166	18.1
Gobiidae	1454	12.1
Clinidae	1344	11.2
Pomacentridae	1289	10.8
Labridae	1045	8.7
Tripterygiidae	774	6.5
Holocentridae	607	5.1
Grammidae	540	4.5
Scaridae	480	4.0
Pomadasyidae	418	3.5
Acanthuridae	230	1.9
Serranidae	156	1.3
Brotulidae	154	1.3
Grammistidae	151	1.3
Tetraodontidae	147	1.2
Blenniidae	116	1.0
Dactyloscopidae	106	0.88
Xenocongridae	105	0.88
Scorpaenidae	95	0.79
Muraenidae	81	0.68
Synodontidae	79	0.66
Clupeidae	64	0.53
Moringuidae	50	0.42
Priacanthidae	39	0.33
Chaetodontidae	35	0.29
Gobiesocidae	27	0.23
Cirrhitidae	24	0.20
Bothidae	22	0.18
Balistidae	22	0.18
Opistognathidae	21	0.18
Aulostomidae	19	0.16
Pempheridae	17	0.14
Sciaenidae	13	0.11
Ophichthidae	13	0.11
Mullidae	12	0.10
Syngnathidae	10	0.08
Cynoglossidae	10	0.08
Callionymidae	10	0.08
Antennariidae	10	0.08
Lutjanidae	8	0.07
Ophidiidae	5	0.04
Congridae	4	0.03
Branchiostegidae	4	0.03
Urolophidae	1	0.01
Belonidae	1	0.01
Hemiramphidae	1	0.01
Atherinidae	1	0.01
Ostraciidae	1	0.01

These nine families include a total of 8,663 or 72.3% of the specimens. The other thirty-nine families account for the remaining 3,318 specimens, or 27.7% of the total.

(C) Species association patterns

The frequency of occurrence of each of the 16 different cardinalfish species present in "total collections" is given in Table 6. Not surprisingly, perhaps, the order of frequency rank is rather similar to that of abundance rank (Table 2). <u>Phaeoptyx conklini</u> and <u>Apogon maculatus</u> rank first and second, respectively, in both frequency of occurrence and abundance. <u>Phaeoptyx pigmentaria</u>, <u>Apogon townsendi</u>, <u>Astrapogon puncticulatus</u>, and <u>Apogon binotatus</u> occupy ranks 3 to 6 in both frequency and abundance though in somewhat different order. The abundance and frequency ranks of the remaining species are somewhat less similar.

Table 7 gives, for the eight apogonid species present in at least 10% of the collections, the expected and observed co-occurrence data and significant positive and negative associations. Even though significance testing was described in METHODS for the 10% and 5% levels only, a p value of $< .01$ is indicated in some cases. This was determined with the appropriate supercritical X^2 value (≈ 12.8). In many cases (indicated with "$p \ll .01$") these associations had X^2 values apparently corresponding to p values <u>far</u> lower than $p = .01$, but no table or graph was available to compute the supercritical X^2 value necessary to specify, e.g., $p < .001$.

As seen in Table 7, a significant association (as defined above) was determined for eleven species pairs. Nine of these

Table 6. Frequency of occurrence of different apogonid species in 154 rotenone collections ("total collections"), in order of decreasing frequency. Asterisks indicate those species included in the species association testing.

Species	Number of samples	Frequency of occurrence
**Phaeoptyx conklini*	89	.578
**Apogon maculatus*	77	.500
**Phaeoptyx pigmentaria*	60	.390
**Apogon townsendi*	44	.286
**Astrapogon puncticulatus*	34	.221
**Apogon binotatus*	33	.214
**Apogon lachneri*	23	.149
**Apogon phenax*	16	.104
Phaeoptyx xenus	13	.084
Apogon planifrons	12	.078
Apogon quadrisquamatus	11	.071
Apogon affinis	9	.058
Apogon robinsi	7	.045
Apogon mosavi	2	.013
Astrapogon stellatus	2	.013
Apogon leptocaulus	1	.006

	CON	MAC	PIG	TOW	PUN	BIN	LAC	PHE
CON	—	E= .289 O= .390	E= .225 O= .331	E= .165 O= .247	E= .128 O= .156	E= .124 O= .201	E= .086 O= .091	E= .060 O= .078
MAC	$p \overset{+}{\ll} .01$	—	E= .195 O= .266	E= .143 O= .169	E= .110 O= .162	E= .107 O= .156	E= .075 O= .039	E= .052 O= .019
PIG	$p \overset{+}{\ll} .01$	$p \overset{+}{<} .05$	—	E= .111 O= .162	E= .086 O= .130	E= .083 O= .156	E= .058 O= .058	E= .040 O= .045
TOW	$p \overset{+}{\ll} .01$	nsa	nsa	—	E= .063 O= .039	E= .061 O= .117	E= .043 O= .084	E= .030 O= .058
PUN	nsa	$p \overset{+}{<} .10$	nsa	nsa	—	E= .047 O= .071	E= .033 O= 0	E= .023 O= .006
BIN	$p \overset{+}{\ll} .01$	nsa	$p \overset{+}{\ll} .01$	$p \overset{+}{<} .05$	nsa	—	E= .032 O= .032	E= .022 O= .026
LAC	nsa	nsa	nsa	$p \overset{+}{<} .10$	$p \overset{-}{<} .10$	nsa	—	E= .016 O= .058
PHE	nsa	$p \overset{-}{<} .10$	nsa	nsa	nsa	nsa	nsa	—

Table 7. Co-occurrence and association of apogonid species in 154 "total collections." CON = *Phaeoptyx conklini*. MAC = *Apogon maculatus*. PIG = *Phaeoptyx pigmentaria*. TOW = *Apogon townsendi*. PUN = *Astrapogon puncticulatus*. BIN = *Apogon binotatus*. LAC = *Apogon lachneri*. PHE = *Apogon phenax*. The data in the upper right half of the table are the expected co-occurrence (E), calculated as the product of the frequencies of occurrence of the two species concerned (see Table 6) and the observed co-occurrence (O), which represents the number of collections in which the two species occur together divided by the total number of collections, i.e., by 154. In the lower left half of the table, any instance of significant positive or negative association is indicated by a + or –, together with the p value. No significant association is signified by nsa.

associations are positive, and 2 are negative. Phaeoptyx conklini and Apogon maculatus are each members of 4 of the 11 associated pairs: P. pigmentaria, A. townsendi and A. binotatus are each members of 3 pairs; Astrapogon puncticulatus and Apogon lachneri of 2 pairs: and A. phenax of 1 pair.

(D) Species diversity patterns

1. "Diversity contribution" analysis: for pooled patch reef collections.

The Shannon-Weaver species diversity index (H') of the pooled "patch reef collections" is 4.1589.

A list of fish families in the pooled "patch reef collections", ranked in order of their "diversity contribution", is given, with related data, in Table 8 and a similar list of genera is given in Table 9. In each case, only families or genera for which C_{jk} has an absolute value of at least .0050 are included.

Among families, the greatest "diversity contribution", as indicated by the largest negative C_{jk} value, is made by the Clinidae. The only family with a positive C_{jk} (of any absolute value) is the family Apogonidae.

Among genera, the greatest "diversity contribution" is made by Eupomacentrus, followed by Apogon. Thalassoma and Phaeoptyx are the only genera with positive C_{jk} values (of any absolute value).

Familial designations in these and other calculations are those of Böhlke and Chaplin (1968). Generic designations are also in

Family	Number of species represented	Number of individuals	C_{jk}	H' with this family omitted
Clinidae	26	1344	-0.0394	3.9950
Gobiidae	19	1454	-0.0366	4.0066
Pomacentridae	12	1289	-0.0294	4.0366
Holocentridae	7	607	-0.0193	4.0766
Scaridae	12	480	-0.0142	4.1000
Pomadasyidae	9	418	-0.0088	4.1223
Serranidae	10	156	-0.0087	4.1226
Labridae	11	1045	-0.0084	4.1242
Tripterygiidae	5	774	-0.0081	4.1253
Acanthuridae	3	230	-0.0076	4.1273
Dactyloscopidae	7	106	-0.0062	4.1331
Grammistidae	3	151	-0.0051	4.1377
Brotulidae	4	154	-0.0050	4.1381
Apogonidae	13	2166	+0.0080	4.1921

Table 8. List of families in pooled "patch reef collections" with absolute value of omission effect index $C_{jk} \geq 0.0050$.

Genus	Number of species represented	Number of individuals	C_{jk}	H' with this genus omitted
Eupomacentrus	7	801	−0.0188	4.0807
Apogon	9	825	−0.0165	4.0903
Coryphopterus	6	682	−0.0150	4.0965
Holocentrus	5	328	−0.0124	4.0786
Labrisomus	5	287	−0.0105	4.1152
Halichoeres	5	269	−0.0099	4.1176
Starksia	5	625	−0.0099	4.1178
Lythrypnus	5	245	−0.0093	4.1204
Sparisoma	6	222	−0.0089	4.1219
Malacoctenus	5	329	−0.0087	4.1226
Haemulon	8	417	−0.0087	4.1228
Enneanectes	5	774	−0.0081	4.1253
Acanthurus	3	230	−0.0076	4.1273
Chromis	3	454	−0.0075	4.1276
Epinephelus	5	130	−0.0065	4.1317
Scarus	6	258	−0.0051	4.1378
Thalassoma	1	720	+0.0058	4.1830
Phaeoptyx	3	1328	+0.0234	4.2561

Table 9. List of genera in pooled "patch reef collections" with absolute value of omission effect index $C_{jk} \geqq 0.0050$.

accordance with these authors, except for differences within the following families as given by the indicated authors: Apogonidae (Fraser and Robins, 1970); Serranidae (Smith, 1971); Holocentridae (Bailey et al., 1971).

2. "Diversity contribution" analysis: for the five richest collections of the "patch reef collections."

Table 10 gives some of the pertinent locality data and other statistics, including species diversity, for the five richest collections of the "patch reef collections."

A list of the fish families in these five collections ranked in order of their "diversity contribution" is given, with related data, in Table 11, and a similar list of genera is given in Table 12. In each case, only families or genera for which $\overline{C}_j$ has an absolute value of at least .010 are included ($\overline{C}_j$ = .0098 for Phaeoptyx rounds off to .010).

Among families, the greatest "diversity contribution" is made by the Clinidae, as was the case for the pooled "patch reef collections." The Apogonidae, with a positive C_{jk} in the previous calculations, have the seventh greatest negative $\overline{C}_j$, i.e. a positive contribution to diversity in this case. The Pomadasyidae is the only family with a positive $\overline{C}_j$ value (of any absolute value).

Among genera, Apogon has the greatest negative $\overline{C}_j$ value, indicating the greatest average contribution to the species diversity of these collections. Phaeoptyx, Quisquilius, and Haemulon are the only genera with positive $\overline{C}_j$ values (of any absolute value).

Field number	S65-83	S68-10	S68-19	GD73-1	S66-85
Locality	Little Ragged Island, West Point	Ragged Islands, Nurse Cay	Aoklin's Island, Salinas Point	Bimini, Turtle Rocks	Grand Bahama, off High Rock Settlement
Date	10-VII-65	12-I-68	16-I-68	24-VII-73	22-XI-66
Time	0830-1030	0930-1030	1230-1400	1400-1500	0800-0945
Depth	15 feet	to 8 feet	to 9 feet	to 40 feet	35 feet
Number of species	66	56	54	53	53
Number of individuals	620	829	453	381	165
No. of apogonid species	5	6	5	6	8
No. of apogonid individuals	158	239	120	56	22
Species diversity (H')	3.5005	2.6777	3.1345	3.0505	3.6639

Table 10. The five richest collections of "patch reef collections": locality data, etc.; total species and apogonid species number and abundance; species diversity.

Family	$\overline{C}_j$
Clinidae	-0.0666
Labridae	-0.0365
Gobiidae	-0.0357
Pomacentridae	-0.0298
Scaridae	-0.0235
Holocentridae	-0.0221
Apogonidae	-0.0215
Tripterygiidae	-0.0157
Pomadasyidae	+0.0179

Table 11. List of families in five richest collections of "patch reef collections," with absolute value of weighted mean omission effect index $\overline{C}_j \geqq 0.010$.

Genus	$\bar{C}_j$
Apogon	-0.0302
Coryphopterus	-0.0252
Eupomacentrus	-0.0234
Halichoeres	-0.0178
Holocentrus	-0.0175
Malacoctenus	-0.0170
Starksia	-0.0169
Labrisomus	-0.0157
Enneanectes	-0.0157
Thalassoma	-0.0145
Scarus	-0.0123
Sparisoma	-0.0106
Lythrypnus	-0.0100
Phaeoptyx	+0.0098
Quisquilius	+0.0122
Haemulon	+0.0179

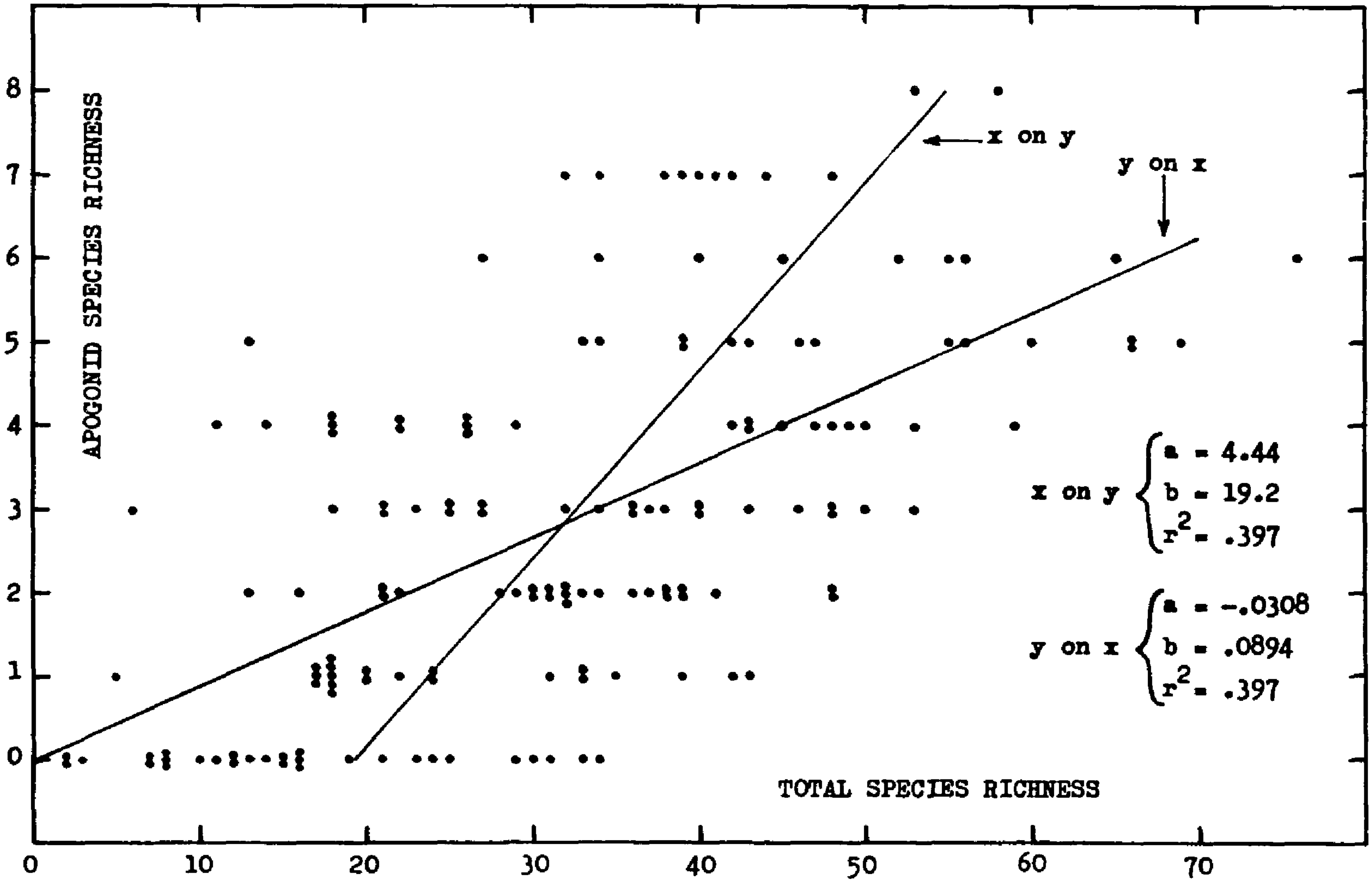
Table 12. List of genera in five richest collections of "patch reef collections" with absolute value of weighted mean omission effect index $\bar{C}_j \geqq 0.010$

3. Apogonid species richness vs. community species richness.

Figure 5 shows the relationship between apogonid species number and total number of species in the collections of "total collections." Also shown are the regression lines for y on x and for x on y, for reasons given in the DISCUSSION section of this chapter.

Ignoring these regression lines for the moment, it is fairly obvious from visual inspection of the data points that there is an association between apogonid species richness and total species richness. The correlation coefficient (r) is .630, which (for n - 2 = 152 degrees of freedom) is significant at well below the 1% level (Table Y in Rohlf and Sokal, 1969). This correlation is not surprising, and is not very informative. Another possible correlation, between collection richness and apogonid species proportion, is of interest and will be discussed in the DISCUSSION section.

Figure 5. The relationship between apogonid species richness and total species richness in the 154 collections of "total collections." The reasons for calculating the regression of x on y as well as of y on x are explained in the text. The values of the slope (a), y-intercept (b), and coefficient of determination (r^2) for each regression are indicated.


APOGONID SPECIES RICHNESS
TOTAL SPECIES RICHNESS
0
1
2
3
4
5
6
7
8
0
10
20
30
40
50
60
70
x on y
y on x
x on y
a = 4.44
b = 19.2
r2 = .397
y on x
a = -.0308
b = .0894
r2 = .397

(E) Body size patterns

1. Length-weight relationship

Table 13 gives the values of a and n, in the equation $W = aL^n$, for each of the 14 species. Curves prepared for each species, fitted to length-weight points calculated from these a and n values, were judged (subjectively) to conform fairly closely to the actual data points. The curve for Phaeoptyx conklini is typical and is given in Figure 6, as an example.

Thus a reasonably accurate estimate of weight was judged to be possible by converting from length (or vice versa), using the calculated a and n values.

Figure 7 shows a logarithmic transformation of the calculated length-weight curves for several representative species, including the species with the highest length/weight ratio (in the range considered here): Apogon robinsi; the species with the lowest length/weight ratio: Astrapogon puncticulatus; and two intermediate examples: Phaeoptyx conklini, and Apogon binotatus.

Table 14 gives the calculated weight for each species at 35 mm S. L. (a length within or nearly within the length range of the specimens examined for each species), as well as "s", the "coefficient of stoutness," calculated with the coefficient of condition equation $K = W/L^3$ for each species at 35 mm S. L. Astrapogon puncticulatus and Apogon mosavi are by far the stoutest (i.e., heaviest) at this length, over twice as heavy as Apogon robinsi, which is the least heavy at that standard length. The other 11 species range in stoutness between these extremes. Thus a considerable variability

Species	Number measured	Size range (mm S.L.)	a	n
Apogon affinis	50	22.5-53.4	3.4095×10^{-6}	3.4953
Apogon binotatus	50	11.0-74.9	1.1302×10^{-5}	3.2255
Apogon lachneri	50	14.0-46.1	1.5957×10^{-6}	3.7721
Apogon maculatus	50	12.5-75.4	9.5439×10^{-6}	3.3037
Apogon mosavi	50	18.6-33.6	1.5335×10^{-6}	3.8829
Apogon phenax	50	13.3-54.3	5.8478×10^{-6}	3.4141
Apogon planifrons	45	12.8-68.2	4.8675×10^{-6}	3.4545
Apogon quadrisquamatus	21	16.2-41.0	9.8794×10^{-6}	3.3233
Apogon robinsi	10	15.7-88.0	2.0954×10^{-6}	3.5950
Apogon townsendi	50	13.8-40.5	3.9332×10^{-6}	3.5218
Phaeoptyx conklini	50	11.1-49.8	2.5538×10^{-6}	3.6471
Phaeoptyx pigmentaria	50	11.2-48.8	5.5996×10^{-6}	3.4096
Phaeoptyx xenus	20	14.0-42.6	3.0643×10^{-6}	3.5102
Astrapogon puncticulatus	50	9.7-49.8	2.7469×10^{-6}	3.7250

Table 13. Length-weight relationship: calculated values of a and n in the equation $W = aL^n$, for fourteen apogonid species.

Figure 6. Length-weight relationship of *Phaeoptyx conklini*: data points and calculated curve.

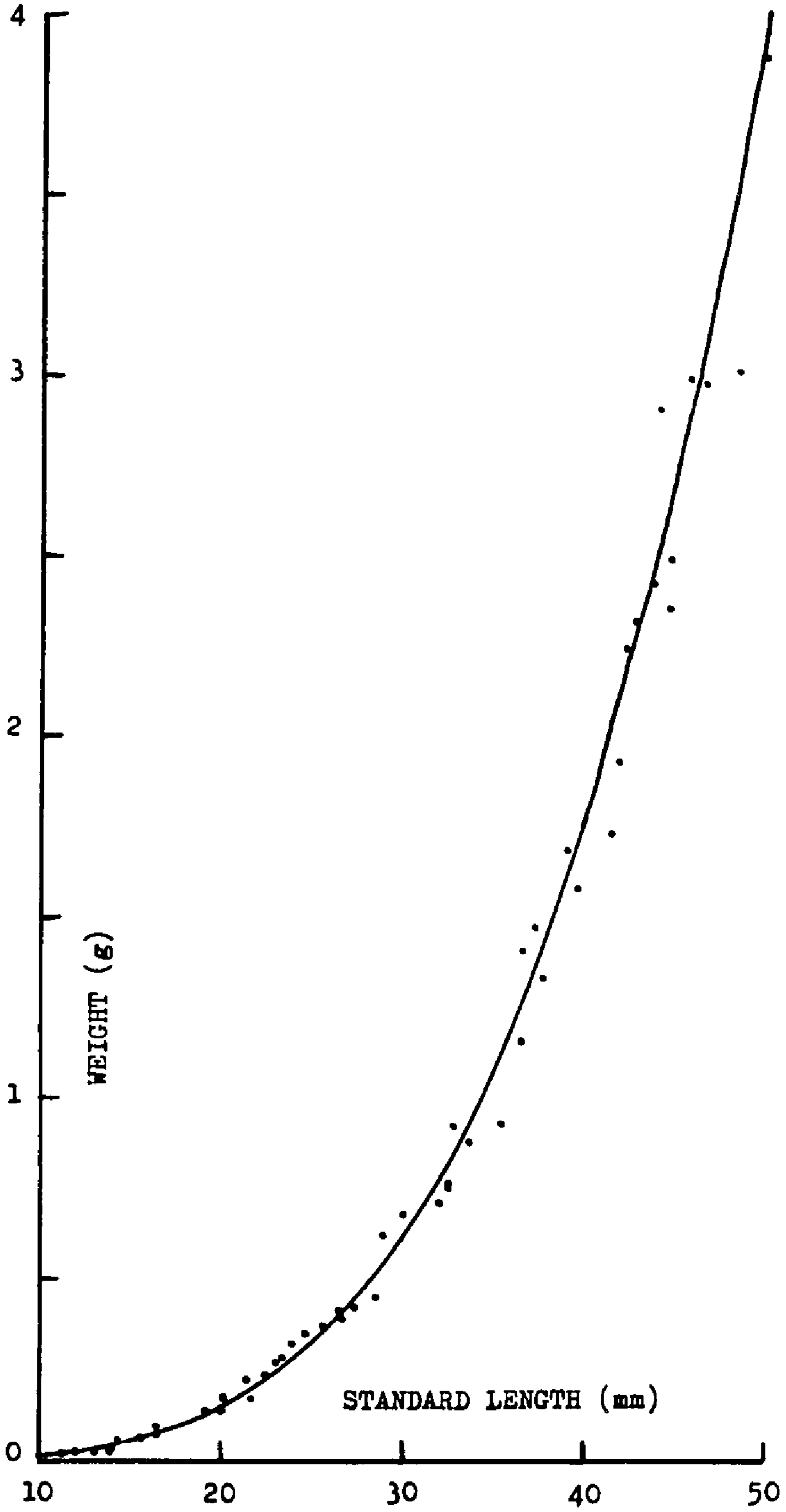
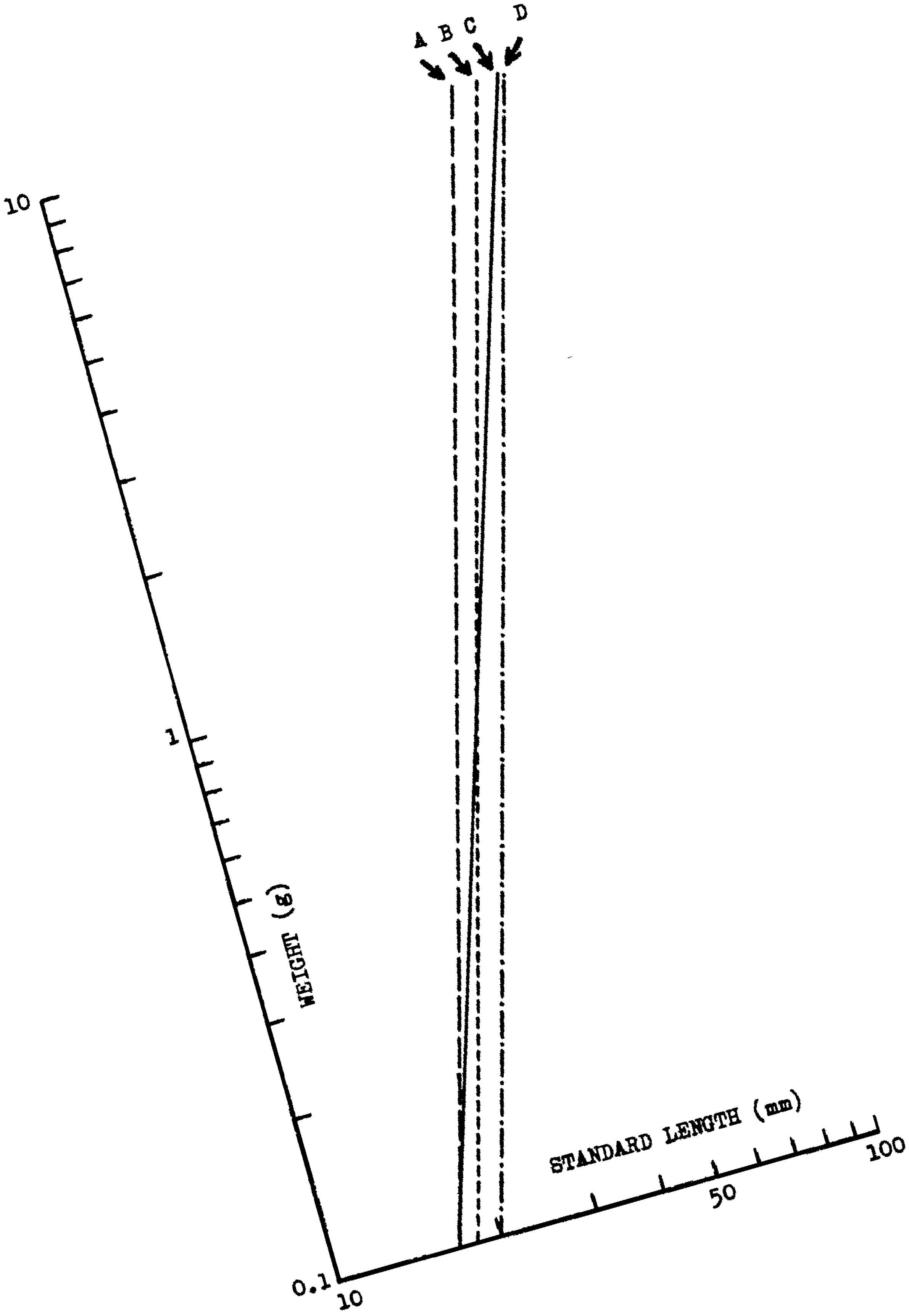

WEIGHT (g)
STANDARD LENGTH (mm)
0
1
2
3
4
10
20
30
40
50

Figure 7. Length-weight relationship: logarithmic transformation of calculated length-weight curves. A = <u>Astrapogon puncticulatus</u>. B = <u>Phaeoptyx conklini</u>. C = <u>Apogon binotatus</u>. D = <u>Apogon robinsi</u>.


A
B
C
D
10
1
0.1
WEIGHT (g)
STANDARD LENGTH (mm)
10
50
100

Species	Weight (g)	s
Astrapogon puncticulatus	1.5506	3.6165×10^{-5}
Apogon mosavi	1.5176	3.5395×10^{-5}
Apogon quadrisquamatus	1.3370	3.1184×10^{-5}
Apogon maculatus	1.2047	2.8097×10^{-5}
Apogon phenax	1.0929	2.5491×10^{-5}
Phaeoptyx conklini	1.0928	2.5489×10^{-5}
Apogon binotatus	1.0803	2.5197×10^{-5}
Apogon townsendi	1.0781	2.5144×10^{-5}
Apogon lachneri	1.0650	2.4839×10^{-5}
Apogon planifrons	1.0502	2.4495×10^{-5}
Phaeoptyx pigmentaria	1.0299	2.4022×10^{-5}
Apogon affinis	0.8505	1.9837×10^{-5}
Phaeoptyx xenus	0.8060	1.8798×10^{-5}
Apogon robinsi	0.7506	1.7378×10^{-5}

Table 14. Length-weight relationship: calculated weight and coefficient of stoutness $s = W/L^3$ at 35.0 mm, in order of decreasing stoutness.

exists among the different species in this body size charasteristic.

2. Body size differences

"Adult length" and "adult weight", calculated as described in the METHODS section of this chapter, are given (with some related data) for each species in Tables 15 and 16. Apogon robinsi has the highest values for each of these parameters and Apogon mosavi has the lowest values.

Because Apogon robinsi is the least stout species (Table 14) and is also the species with the largest adult size (Tables 15 and 16), and because Astrapogon puncticulatus and Apogon mosavi are the stoutest species and tend to have the smallest adult size, an intriguing possible relationship suggested itself: a negative correlation between stoutness at a given length and adult size.

This was investigated by calculating the coefficient of correlation (r) between weight at 35 mm S. L. (from Table 14) and "adult length" which equals -0.546. This value for r, for n-2 = 14-2 = 12 degrees of freedom, is significant at the 5% level.

The relationship is shown graphically in Figure 8. A regression line (coefficient of determination r^2 = .298) and a logarithmic curve (r^2 = .314) were calculated. Neither fits the data very well, but the logarithmic curve fits slightly better and is shown in Figure 8, for illustrative purposes.

The coefficient of correlation between weight at 35 mm S. L. (from Table 14) and "adult weight" (from Table 16) was also calculated, but its value, -0.445, is not significant at the 5% level.

3. Ecological significance of body size differences.

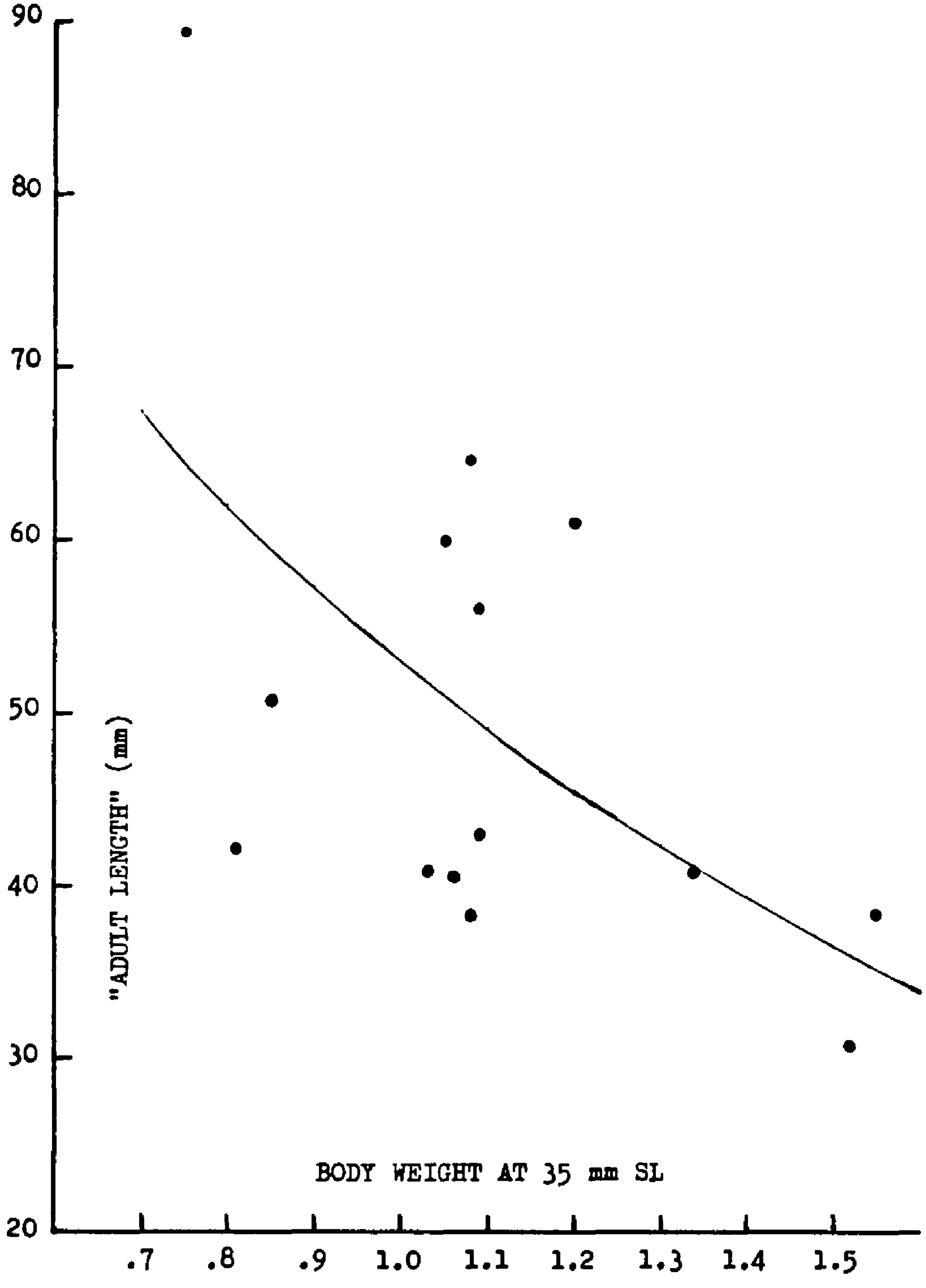
Species	Number Measured	"Adult length" = mean of largest 10% (in mm S.L.)	Largest specimen (mm S. L.)
Apogon robinsi	11	89.5	89.5
Apogon binotatus	167	64.6	74.9
Apogon maculatus	779	~61.	75.4
Apogon planifrons	45	59.9	68.2
Apogon phenax	47	56.0	62.0
Apogon affinis	117	50.6	55.0
Phaeoptyx conklini	2046	~43.	50.0
Phaeoptyx xenus	20	42.1	42.6
Phaeoptyx pigmentaria	153	40.8	48.8
Apogon quadrisquamatus	21	40.8	41.0
Apogon lachneri	122	40.5	46.1
Astrapogon puncticulatus	165	38.3	49.8
Apogon townsendi	384	38.3	41.2
Apogon mosavi	128	30.7	34.0

Table 15. "Adult length": mean of largest 10 percent of all specimens of each species and size of single largest specimen of each species, in order of increasing "adult length."

Species	"Adult weight" (g)
Apogon robinsi	21.78
Apogon binotatus	7.80
Apogon maculatus	7.55
Apogon planifrons	6.72
Apogon phenax	5.44
Apogon affinis	3.08
Phaeoptyx conklini	2.32
Apogon quadrisquamatus	2.23
Astrapogon puncticulatus	2.17
Apogon lachneri	1.85
Phaeoptyx pigmentaria	1.74
Phaeoptyx xenus	1.54
Apogon townsendi	1.48
Apogon mosavi	0.91

Table 16. "Adult weight": conversion of mean length of largest 10 percent of specimens ("adult length") to weight using calculated values of a and n in equation $W = aL^n$. In order of decreasing "adult weight".

Figure 8. The relationship of weight at 35 mm S. L. to "adult length," with fitted logarithmic curve, in 14 apogonid species.


90
80
70
60
50
40
30
20
"ADULT LENGTH" (mm)
BODY WEIGHT AT 35 mm SL
.7
.8
.9
1.0
1.1
1.2
1.3
1.4
1.5

The three most abundant species, Phaeoptyx conklini, Apogon maculatus, and A. townsendi (see Table 2) differ substantially in adult body size (see Tables 15 and 16). The largest of these three, A. maculatus, is 42% longer and 225% heavier than the second largest, P. conklini, which is 12% longer and 57% heavier than the third largest, A. townsendi.

These three species occur together quite commonly, all three being present together in 25 of the 154 "total collections." Two of the three possible species pairings among them, P. conklini-A. maculatus and P. conklini-A. townsendi, show a significant association (Table 7).

These size differences may well be of great importance in allowing the coexistence of the three species.

A comparison of the average adult size difference between positively associated species and that between negatively associated species is shown in Table 17, based on associations among the eight species occurring in at least 10% of the 154 collections. The per cent length differences and per cent weight differences are computed because these may be averaged more meaningfully than simple absolute values of length or weight (since, for example, an "adult weight" difference of less than a gram makes P. conklini more than 50% heavier than A. townsendi, while a difference of over 2 grams makes A. maculatus only about 40% heavier than A. phenax).

Table 17 shows that positively associated species differ by an average 39.0% in "adult length" and 214.9% in "adult weight", while negatively associated species differ by 7.3% in "adult length" and 28.1% in "adult weight." Thus species that tend to occur together tend to differ far more in size than species that tend not to occur together.

Association	Difference in "adult length"		Difference in "adult weight"	
Positive	in mm	in %	in g	in %
CON-MAC	18.0	41.9	5.23	225.4
CON-PIG	2.2	5.4	0.58	33.3
CON-TOW	4.7	12.3	0.84	56.8
CON-BIN	21.6	50.2	5.48	236.2
MAC-PIG	20.2	49.5	5.81	333.9
MAC-PUN	22.7	59.3	5.38	247.9
PIG-BIN	23.8	58.3	6.06	348.3
TOW-BIN	26.3	68.7	6.32	427.0
TOW-LAC	2.2	5.7	0.37	25.0
		351.3		1933.8
		$\bar{X}$ = 39.0		$\bar{X}$ = 214.9
Negative				
MAC-PHE	5.0	8.9	2.11	38.8
PUN-LAC	2.2	5.7	0.32	17.3
		14.6		56.1
		$\bar{X}$ = 7.3		$\bar{X}$ = 28.1

Table 17. Comparison of average differences in "adult length" and in "adult weight" between positively and negatively associated species. CON = *Phaeoptyx conklini*, MAC = *Apogon maculatus*, PIG = *Phaeoptyx pigmentaria*, TOW = *Apogon townsendi*, BIN = *Apogon binotatus*, PUN = *Astrapogon puncticulatus*, LAC = *Apogon lachneri*, PHE = *Apogon phenax*. Values in the "in %" columns represent the percent larger (in "adult length" or "adult weight") that the larger species is than the smaller species.

(F) Occurrence of ectoparasites

The most frequently noticed external parasitic infestation of the apogonid specimens examined was a copepod infestation of the body of Apogon townsendi. Twenty-nine of the 304 specimens of that species, in 11 of the 44 samples of that species in "total collections" had from 1 to 4 copepods attached to the body. All of these copepods appear to be the same type, a species of Cardiodectes, probably new (Roger Cressey, pers. comm.). This copepod parasite apparently infests A. townsendi in areas besides the Bahamas, including Puerto Rico (Ernest Williams, pers. comm.).

The same infestation was frequently observed in the field. On one occasion it made possible the recognition from day to day of a specific individual of A. townsendi, while another individual was recognized by the presence of an isopod attached to one gill cover (Dale, 1975).

Another instance of copepod infestation was observed on one individual in the type collection of A. mosavi (from Cat Island, Bahamas - part of one of the 154 collections of "total collections"). This copepod parasite was attached to the tongue of the host with two hook-like appendages, and oriented with its cephalic end toward the anterior of the fish mouth cavity and its caudal end, with egg sacs, toward the posterior of the mouth cavity. Roger Cressey (pers. comm.) has identified this parasite as Caritus sp. (new). One additional specimen was found similarly attached to the tongue of one specimen of A. mosavi in an Academy of Natural Sciences of Philadelphia collection of that species from Grand Bahama.

The size and site of attachment of this parasite are such that normal feeding or oral brooding by the host would seem to be impossible.

The only other observed instances of ectoparasitic infestation of the apogonid specimens in "total collections" are:

1. large shrimp-like parasite on one *A. lachneri* specimen.
2. isopod (?) under left opercles of two *Phaeoptyx conklini* specimens.
3. isopod (?) on head of one *A. maculatus* specimen.
4. isopod (?) under right opercle of one *P. pigmentaria* specimen.

(Only a small percentage of the mouths and gill chambers of most species were examined.)

In the course of dissecting and removing stomachs from specimens of various species during the food habits study, a curious cyst-like internal parasite was noticed in several specimens of *A. maculatus*. It was identified as an isopod by Dr. Horace Stunkard (pers. comm.).

III. DISCUSSION

Only four apogonid species that are known from the Bahamas are not represented in the collections studied here: *Apogon anisolepis*, *A. aurolineatus*, *A. pillionatus*, and *A. pseudomaculatus*.

A. anisolepis is known from only two specimens, including one from the Bahamas. It is evidently either very rare or at least very rare or absent in the habitats and depths normally sampled.

A. aurolineatus is only rarely collected in the Bahamas. Böhlke and Chaplin (1968) cite only one Bahamian specimen. *A. pillionatus* is also very uncommon in Bahamian collections, and tends to occur in fairly deep water (65-150 feet).

A. pseudomaculatus is also collected only rarely in the Bahamas (Böhlke and Chaplin, 1968, cite only two collections, from shallower water than it tends to habituate elsewhere; one small specimen is present in a 1974 collection made by C. Lavett Smith, which is not included in "total collections"). It is, however, very widespread and often quite common elsewhere. In addition to the West Indies, it is known from the Florida Keys (Starck, 1968, called it "frequent" at Alligator Reef; Longley and Hildebrand, 1940, reported it as more common than *A. maculatus* in deep water in the Dry Tortugas), and eastern Gulf of Mexico, where it is very common (G. B. Smith, 1976), and occasionally strays as far north as New England (Böhlke and Chaplin, 1968). It is also known from the faunistically isolated coral reefs of Brazil (Gilbert, 1977), and from Bermuda (Böhlke and Chaplin, 1968).

One conceivable explanation for the apparent rarity of

A. pseudomaculatus in the Bahamas is that it is ecologically replaced there (from its preferred deeper water habitat) by some other species such as *A. townsendi* or *Phaeoptyx pigmentaria*. These two species are common and abundant in the Bahamas (see Tables 2 and [illegible]) but are only "occasional" at Alligator Reef in Florida and may be absent in the eastern Gulf of Mexico (G. B. Smith, 1976, assigned previous records of *P. pigmentaria* from that area to *P. xenus*) - two places where *A. pseudomaculatus* is quite well represented.

Astrapogon alutus is the only apogonid species known from the Florida-Caribbean area that has not been recorded in the Bahamas. (No speculation on the reason for this apparent distribution will be offered here). In addition, *Apogon americanus*, recently redescribed by Gilbert (1977), is known only from Brazil: and the new Bermudan species mentioned above is known only from that area. *A. powelli*, included in Böhlke and Randall's (1968) key to western Atlantic cardinalfishes, has been synonymized with the eastern Atlantic and Mediterranean species *A. imberbis* and its western Atlantic record (Newport, Rhode Island) deemed erroneous (Fraser and Robins, 1970). *Synagrops bella*, a common offshore species in Florida (Starck, 1968) and not known from the Bahamas, is no longer placed in the family Apogonidae (Fraser, 1972, removed the entire subfamily Synagropinae, placing it in the Percichthyidae).

The known range of each of the 16 species included in the present study extends beyond the Bahamas. Most or all of them probably occur throughout much of the tropical western Atlantic. The range of two of them, *Phaeoptyx pigmentaria* and *A. affinis*, extends to the eastern Atlantic (Fraser and Robins, 1970).

(A) Species abundance patterns

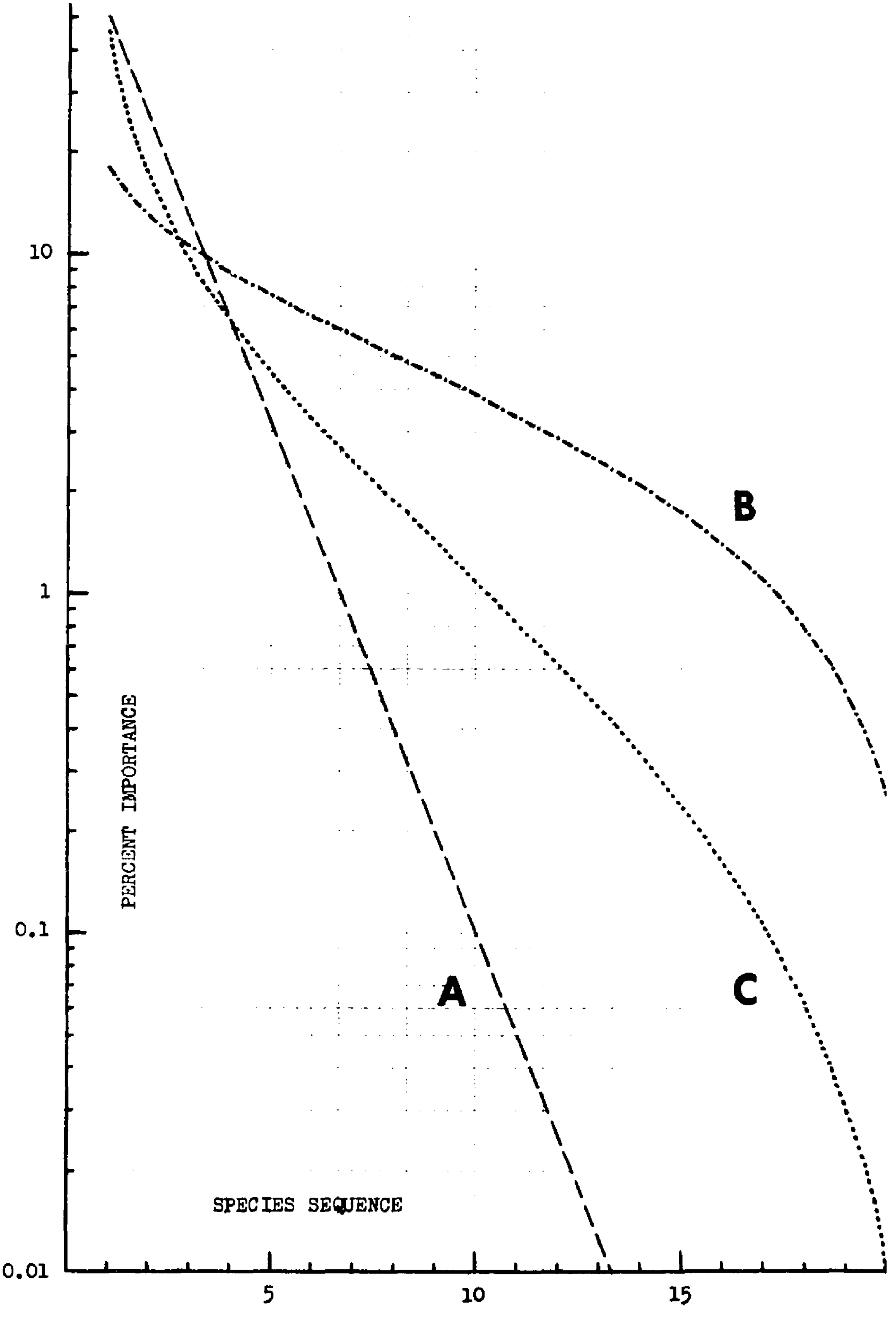
Much discussion in the ecological literature has been devoted to patterns of species abundance, because of the generally accepted view that such patterns reveal something about niche relationships among the species concerned. This approach has been taken in the study of species within trophic levels, taxonomic groups, and whole communities. The general idea is that the way a species divides up the n-dimensional niche hypervolume will be reflected by its relative abundance.

There are several hypotheses regarding species abundance, including the logarithmic distribution of species (Fisher, Corbet and Williams, 1943: Williams, 1964), the negative binomial model (Brian,1953), the niche preemption hypothesis (Motomura, 1932: Whittaker, 1965, 1970, 1972), the nonoverlapping random niche hypothesis (MacArthur, 1957, 1960), and the lognormal hypothesis (Preston, 1948, 1960, 1962a, 1962b; Whittaker, 1965, 1970, 1972).

The last three of these five hypotheses have been the most widely discussed and will be compared with the cardinalfish species abundance patterns obtained in the present study.

According to the niche preemption hypothesis, the dominant species preempts the most niche space, the next most dominant species preempts part of the remaining niche space, and so forth, resulting in a geometric series. If species sequence (importance rank order) is plotted against importance, the latter on a logarithmic scale, a straight line results (see "curve" A in Figure 9, calculated for a distribution in which the most abundant species is twice as abundant

Figure 9. Curves of species importance, after Whittaker (1965). A = Niche preemption hypothesis (geometric series). B = Nonoverlapping random niche hypothesis (broken stick model). C = Lognormal distribution.


PERCENT IMPORTANCE
SPECIES SEQUENCE
0.01
0.1
1
10
5
10
15
A
B
C

as the next most abundant species, which is twice as abundant as the next, etc). Whittaker (1965) found some distributions that approximate such a curve among plant communities in harsh environments.

The nonoverlapping random niche hypotheses, or "broken stick model", supposes that niche space is randomly divided into contiguous, nonoverlapping segments. When plotted logarithmically as above, species importances would describe a curve resembling B in Figure 9. The curve is calculated for 20 species (as in Whittaker, 1965) using MacArthur's (1957) formula for the expected abundance of the r^{th} rarest species:

$$\frac{m}{n} \sum_{i=1}^{r} \frac{1}{n - i + 1}$$

where there are n species (n = 20 in the present calculation) and m individuals (m treated as a per cent, i.e., 100 per cent, for the present calculation).

This type of curve was first shown to fit certain forest bird species samples (MacArthur, 1960), and later to fit lake mud microfossil samples (Goulden, 1966; Tsukada, 1967). Cohen (1966, 1968), however, showed that other, entirely different sets of assumptions could lead to the same mathematical equation that MacArthur (1957) derived for the broken stick model. Hairston, (1969) showed that a fit to the broken stick curve could be an artifact of sample size. Smart (1976) used statistical tests to show that agreement between observed and broken stick theoretical species abundance patterns, in certain breeding bird censuses, was unsatisfactory. For these reasons the broken stick hypothesis is now generally considered unrealistic.

According to the reasoning of the lognormal hypothesis, a species' niche space is determined by a multiplicity of niche dimensions affecting its competitive success, resulting in a normal distribution of importance values (i.e. abundances, for similarly sized species). The important and unimportant species will be few in number, while species of intermediate importance will be numerous. Plotted logarithmically, a curve results which tends to fall between the broken stick and geometric curves (see curve C in Figure 9, drawn after Whittaker, 1965). Many natural distributions have been shown to approximate such a curve (e.g. Whittaker, 1965).

Figure 10 shows the logarithmic curve of per cent importance of the 16 apogonid species in "total collections"(per cent values converted from abundance data - thus this is the same curve as in Figure 3, but the units on the ordinate are per cent instead of raw numbers) plotted together with a 16-species broken stick curve (i.e., calculated for n = 16), and a geometric series curve (calculated as in Figure 9). Clearly, the cardinalfish species distribution fits a lognormal interpretation better than either a niche preemption or broken stick interpretation. In Figure 11 the logarithmic curve of per cent importance of the 13 apogonid species in outer shelf patch reef collections (again with converted abundance data and in this case equivalent to Figure 4) plotted together with a 13-species broken stick curve (n = 13) and a geometric series curve (as before). Again, a lognormal distribution is approximated.

The pooling of samples collected from a wide geographic area for studying species abundance patterns (as in the present case) is not normally done and might be criticized as invalid. Although done out

Figure 10. Percent importance of the 16 apogonid species in "total collections" (C), plotted with geometric series curve (A), and 16-species broken stick curve (B).

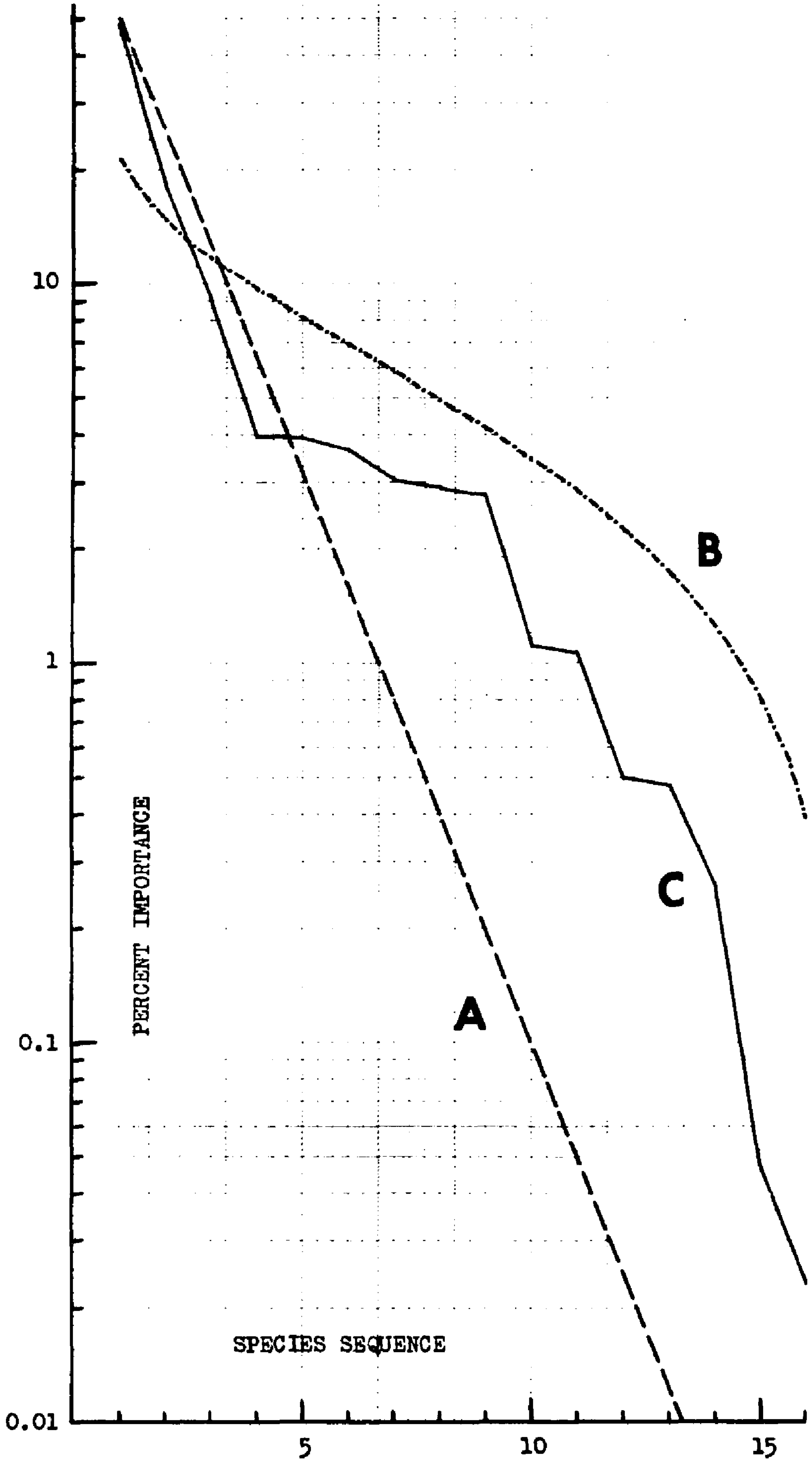
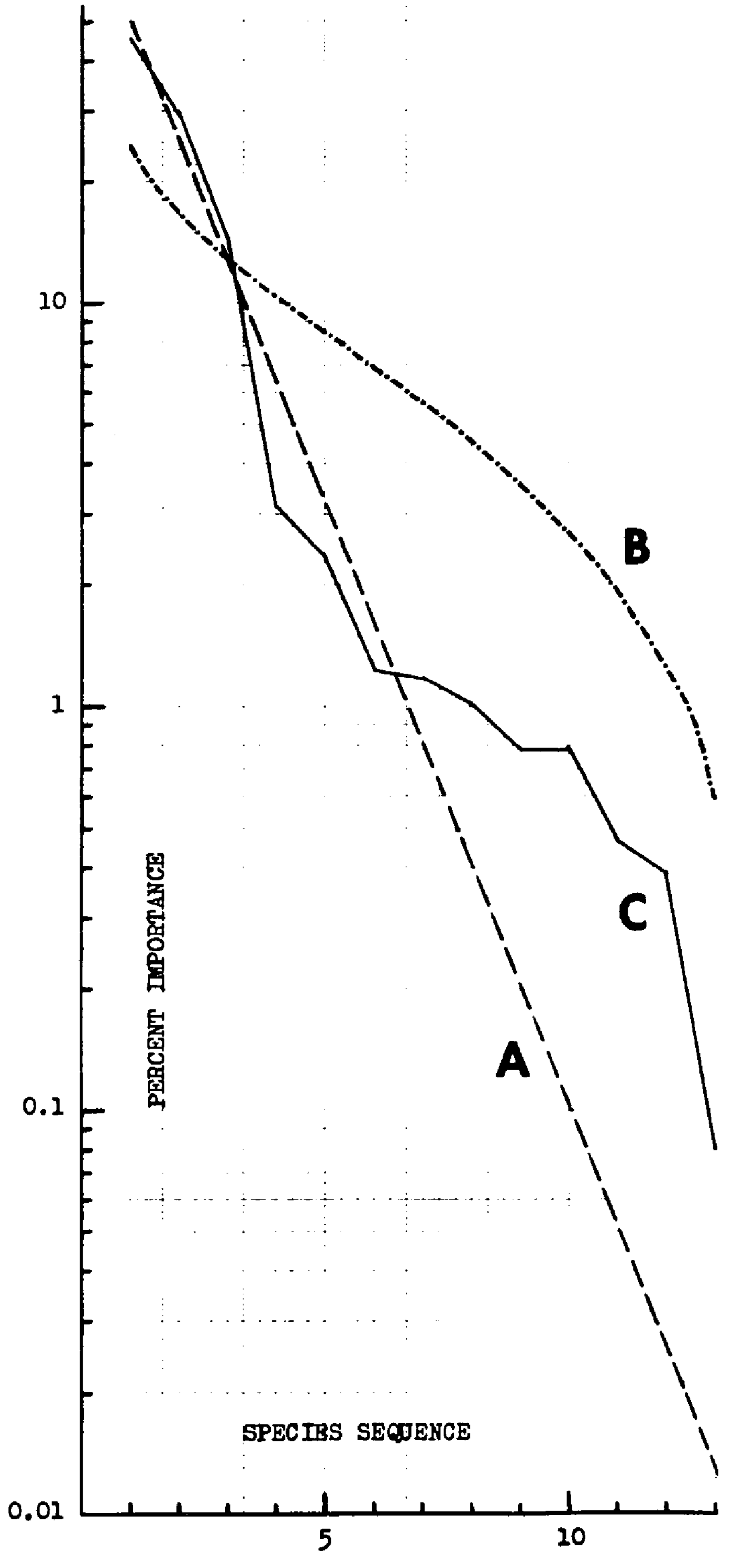

PERCENT IMPORTANCE
10
1
0.1
0.01
SPECIES SEQUENCE
5
10
15
A
B
C

Figure 11. Percent importance of the 13 apogonid species in outer shelf patch reef collections (C), plotted with geometric series curve (A), and 13-species broken stick curve (B).


PERCENT IMPORTANCE
10
1
0.1
0.01
SPECIES SEQUENCE
5
10
A
B
C

of necessity to provide adequate sample sizes, certain considerations argue in favor of its validity:

1. In terms of the far greater geographic area that forms the range of most, perhaps all, of these species, the Bahamas are only a small part.
2. More or less the same variety of reef fish habitats is present throughout this small part of the range, i.e. throughout the Bahamas (this point is supported by geographic distribution data given in Chapter 3).
3. Any given local habitat is potentially available for recruitment to the pelagic apogonid larvae.
4. The particular set of local conditions that allows or promotes the settling and survival to breeding adulthood of a given species is what essentially defines the niche of that species.
5. Therefore, the whole range of niche dimensions present in the Bahamas represents, in a sense, a niche hypervolume unit that is divided in different ways by different cardinalfish species.

I believe that a similar argument would justify the pooling of samples (for the same purpose) from a similar, more or less homogeneous fraction of the range of any group of reef fish species with pelagic larvae (or of any group of species with widely dispersing propagules).

To get back to the particular results at hand, the implication of the two cardinalfish species abundance curves is that cardinalfish species abundance patterns are consistent with a view that cardinalfishes define their niches in terms of many niche dimensions that affect their competitive abilities, and that their niches are thus extensively overlapping rather than discrete.

This finding is not momentous, or even perhaps very surprising - but it is not trivial either in view of the paucity of information on reef fish niche dynamics.

(B) Abundance-frequency patterns

The results of treating the abundance and frequency data from patch reef collections in the manner described clearly emphasize the importance of apogonids in patch reef communities. It could quite reasonably be argued, on the basis of Table 4, that apogonid species predominate in "abundance-frequency" over all other fish families sampled in these rotenone collections. Although such an argument is necessarily somewhat subjective, (in the absence of an objective assignment of relative importance to each of the 12 categories), it would seem far more difficult, on this basis, to argue that any other family predominates.

In Alevizon and Brooks' (1975) study of abundance-frequency patterns in two reef fish assemblages, an entirely different species structure was obtained. This is largely due to the fact that their data are "cinetransect" censuses (using motion picture photography) which reveal and emphasize many species that would be frightened away during rotenone collecting, and which do not reveal many small species and many diurnally inactive species of various sizes. Thus, for example, scarids, acanthurids, and pomadasyids are highly emphasized in their results, while apogonids, clinids, gobiids, and tripterygiids (among others) are entirely absent. In the present results these latter groups are emphasized, while scarids, acanthurids, and pomadasyids are relatively unimportant. One notable exception to this sampling difference is Thalassoma bifasciatum, which is sampled by both methods and is shown to be quite important in each case.

In the absence from the literature of any similar abundance-frequency study of data from rotenone collections, no meaningful comparisons with the present results can be made. The significance of the results to the present overall study lies in their clear indication of the importance of cardinalfishes relative to other fishes in this crucial habitat. When similar studies on other habitats or from other geographic areas are available, some very interesting comparisons will be possible.

Perhaps the ideal kind of data to use in abundance-frequency studies of this kind would be data of the kind collected by Smith and Tyler (1972). Their use of a visual census as well as a rotenone collection allowed a far more accurate estimate of species populations than either technique alone would permit.

(C) Species association patterns

As described in the RESULTS section, a number of different statistically significant positive and negative associations were determined among the eight species tested in this regard. Two important comments should be made about these results.

First, the tendency involving both an incidence of more positive than negative associations (9 vs 2) and a rather low confidence level (10%) of the only two negative associations, is difficult to interpret. This tendency may result, in part, from the nature of the data - specifically, from the inclusion, among the 154 collections the study is based on, of 29 collections containing no apogonid specimens at all. Inclusion of these collections might be considered to overemphasize positive associations, since it is possible to view the 29 collections as lacking cardinalfishes because they were from unsuitable habitats, and to view positive associations, in part, as a simple result of the common occupation of a "cardinalfish habitat". (Hypothetically, if one included additional, irrelevant collections in the calculation, containing no apogonid specimens, an increase in the occurrence and significance of positive associations could be obtained, and negative associations could be eliminated.)

An alternative way of treating the data would have been to eliminate the 29 collections containing no apogonids and study only those 125 collections which included at least one apogonid species. These 29 collections were, however, not irrelevant collections, and in no case were they made in habitats known or considered to be absolutely unsuitable for apogonids. Eliminating these collections would, in a sense artificially, overemphasize negative associations.

The first alternative, testing apogonid association in the 154 collections, was deemed less manipulative than the second. Moreover, it is identical to the testing of apogonids that would occur as part of a wider study of association among <u>all</u> the species in the 154 collections (which would be interesting to carry out, but would require testing about two orders of magnitude more 2 x 2 contingency tables).

Nevertheless, the positive association tendency should perhaps be viewed, in part, as simply reflecting a broad preference of apogonids in general for certain habitats.

A second (perhaps more obvious) comment, concerns the fact that the different number of significant associations that different species are involved in may simply be a statistical phenomenon reflecting the greater sample size of, e.g. <u>Phaeoptyx conklini</u> than <u>Apogon phenax</u>.

Despite these reservations, the results were considered useful in connection with the investigation of the ecological significance of body size differences. They will also be discussed in connection with various topographic factors.

(D) Species diversity patterns

1. and 2. "Diversity contribution analysis.

It should be noted that the concept of diversity contribution developed here is quite different from what Dickman (1968) referred to as "partial diversity contribution." That quantity is simply $p_i \log p_i$ for a given species. A ranking on that basis for species would not differ from a ranking based on relative abundance. Thus in a sample with one very abundant species, that species would rank number one in partial diversity contribution even though its abundance results in a low species diversity index for that sample. A ranking of genera or families, based on the sum of the partial diversity contributions of the component species, would reflect an ambiguous combination of abundance and richness. The concept of species-diversity within taxa developed by Pielou (1967, 1969, 1974) is also not useful for the kind of diversity contribution determination proposed here since, again, it does not consider the reductive effect on diversity that a highly abundant component has.

Before discussing the specific results of the diversity contribution analyses done in the present study, it might be appropriate to ask: what worthwhile application, if any, does the "omission effect index" have? In view of the profusion of widely differing concepts, definitions, and measures of species diversity (see Peet, 1974) and the profusion of explanations for high species diversity (see Chapter 1), and in view of the contention of Hurlbert (1971) that "diversity per se does not exist", this is not an unduly skeptical question.

A tentative answer, justifying its use in the present study, is offered as follows. Whatever the causes of high species diversity are, they should obviously be having their greatest effect in those components of the community which contribute most to that diversity. If diversity is being considered in terms of an information theoretical measure like the Shannon-Weaver index, then it is logical to consider contribution to diversity in terms of a statistic derived from the Shannon-Weaver index. The omission effect index is such a statistic.

In other words, if one is interested in the causes of high species diversity and assumes that they may be found by examining high diversity communities, then one's effort should be concentrated on the components contributing most to the diversity. The omission effect index provides a quantitative estimate of which components these are. It is impossible to identify the components in any rigorous fashion without the use of some such statistic.

Although presented in the context of the Shannon-Weaver diversity index the omission effect index (C_{jk} or $\overline{C}_j$) could be calculated in an identical manner with virtually any species diversity measure. It could also be applied with a Shannon-Weaver or other index calculated in terms of, e.g., biomass or productivity, rather than numerical abundance. Furthermore, C_{jk} or $\overline{C}_j$ could be computed for any taxa above and including species, or for any non-taxonomic groupings of species such as guilds or trophic levels.

The omission effect index could be used to compare the diversity contribution of a particular species group in one habitat type or geographic area to the diversity contribution of the same species group in another habitat or area.

It could also be used as the measure of a particular species group's contribution to alpha, beta, and gamma diversity (Whittaker, 1960) or to within-habitat and between-habitat diversity (MacArthur, 1965), by simply using data appropriate for these diversity measures. It might, for example, be of interest to compare the ratio of within-habitat diversity contribution to between-habitat diversity contribution for one taxon to the same ratio for another taxon. With such a comparison one could say, regardless of the absolute value of their respective diversity contributions (i.e., of their omission effect indices) that taxon x is more of a within-habitat diversity contributor than taxon y. Such a comparison could be a rigorously quantitative ecological comparison that could then be related to other ecological or evolutionary differences between the two taxa.

It would seem that there are as many different applications of the omission effect index as there are ways of thinking about and measuring species diversity, but further speculation in this regard will not be made in the present paper.

The application of the concept of diversity contribution to the present study is perhaps of the simplest variety. A clear quantitative analysis of the contribution of apogonid species to the rather high fish species diversity of Bahamian patch reefs was needed, and the omission effect index clearly meets this need.

The results indicate that the genus <u>Apogon</u> makes a predominant positive contribution in terms of its omission effect index (C_{jk}) in pooled patch reef collections, as well in terms of its weighted mean omission effect index ($\overline{C}_j$) in the five richest patch reef collections. <u>Phaeoptyx</u>, on the other hand, because of the extreme abundance of P. conklini, makes a substantial negative contribution in each of these computations.

Thus cardinalfishes have a two-sided effect on Bahamian patch reef fish species diversity (the relative rarity of Astrapogon specimens makes their contribution relatively unimportant). The diversity contribution of the family as a whole is a kind of balance between the opposite effects of Apogon and Phaeoptyx. In pooled patch reef collections the preponderance of P. conklini is such that the entire family has a positive C_{jk}, i.e., makes a negative contribution. In the five richest patch reef collections the balance is such that the family as a whole has a negative $\overline{C}_j$, i.e., makes a positive contribution.

The importance of adequate sampling for omission effect computations can hardly be overemphasized, especially because of the kind of effect that one uncharacteristically large sample of a species may have on the calculated omission effect of its genus or family.

For example, in the calculations based on the five richest patch reef collections, a single sample of 220 Haemulon flavolineatum is at the basis of the very large positive $\overline{C}_j$ values of Haemulon and the family Pomadasyidae. In the pooled patch reef collections calculations, the effect of this sample is greatly diluted, and the negative C_{jk} indices of Haemulon and Pomadasyidae are not extremely different from what they would be without that sample.

There is, however, a clear disadvantage to such a pooling of data, because of the possibility of "pooling artifacts." The following simplified hypothetical example illustrates one possibility of such an artifact. Suppose that a given single patch reef tends to support a moderate population of only one of several different congeric species which occur in different collections from this broad habitat type. Pooling such data would result in a much greater effect on diversity by that genus than it has in any single collection. Unless one is interested in between-habitat diversity, (in which case collections made in a variety of habitat types would be more appropriate) this greater effect is misleading. A more meaningful view of the diversity contribution of the genus would consider its typical local contribution. This is accomplished by the weighted mean omission effect index.

Based on the above arguments, it would thus seem that the computation based on the five richest patch reef collections, i.e. the weighted mean approach, is the better approach but is subject to considerable sampling error if only a few collections are analyzed, as in the present case.

An obvious next step in the treatment of the data at hand would be to calculate $\bar{C}_j$ for each genus and family in the "total rotenone collections." This would provide a more meaningful statistic for the diversity contribution of each genus and family to overall Bahamian reef fish diversity than either of the two approaches employed.

3. Apogonid species richness vs. community species richness.

As described in the RESULTS section, the data shown in Figure 5 indicate that apogonid species richness and total species richness are significantly correlated. In the absence of any notion of causation, it did not seem altogether unreasonable to calculate the linear regressions of both y on x (y as a function of x) and x on y (x as a function of y), as shown in Figure 5. Although the coefficient of determination for each of them is the same, a rather low value of .397, the regression of x on y seems somehow to fit the data better, i.e. it is closer to the line one would draw subjectively. For this rather arbitrary reason (i.e., despite the fact that the regression of y on x is more logical), the x on y regression was examined more closely.

If one inspects the values of x at different intervals of y, there might seem to be an indication in Figure 5 that the relative proportion of apogonid species increases with increasing collection size, since according to either the x on y regression line or to a simple average, collections with one apogonid species have about 24 total species (i.e. apogonids = 4%), collections with eight apogonid species have about 55 total species (i.e. apogonids = 15%), and in between these extremes a similar trend obtains (Table 18). This interpretation would certainly reveal a very interesting and important relationship between cardinalfish representation and community richness.

If, however, the data are summarized in a different way, it is evident that the trend described above is merely an artifact of the other interpretation. Thus if the apogonid percentage of collections of different richness is calculated, no such trend is indicated, as seen in Table 19. (This is certainly a simpler and more logical way to interpret the data.) Viewed in this way, apogonids are seen to comprise generally about 8 to 10% of the species in collection of various total species richness. The calculated correlation coefficient (r) for species richness range (entered in the calculation as the central number of the range, e.g. 3 for the 1 - 5 range, etc.,

	A		B	
Number of apogonids	Total species (regression)	Percent apogonids	Total species (average)	Percent apogonids
0	19.3	0	16.0	0
1	23.7	4.2	24.4	4.1
2	28.1	7.1	32.0	6.3
3	32.6	9.2	33.7	8.9
4	37.0	10.8	33.5	11.9
5	41.5	12.1	46.5	10.7
6	45.9	13.1	47.8	12.6
7	50.4	13.9	39.8	17.6
8	54.8	14.6	55.5	14.4

Table 18. Total species richness of collections of various apogonid species richness, and their apogonid species percentage. A) Total species richness estimated as the regression line value for a given apogonid species richness. B) Total species richness estimated as average of species richness of those collections with a given apogonid species richness

Richness range of collections	Apogonid species samples	Total species samples	Average apogonid species percentage
1-5 (4)	1	12	8.3
6-10 (7)	3	54	5.6
11-15 (11)	15	143	10.5
16-20 (19)	27	336	8.0
21-25 (17)	32	386	8.3
26-30 (13)	36	364	9.9
31-35 (21)	54	688	7.8
36-40 (19)	68	728	9.3
41-45 (14)	60	599	10.0
46-50 (13)	49	623	7.9
51-55 (6)	32	321	10.0
56-60 (5)	28	289	9.7
> 60 (5)	27	342	7.9

Table 19. Percentage of apogonids in collections of different total species richness, the latter classed in ranges of species richness. The number in parenthesis following the richness range is the number of collections falling in that class.

and 68.5 for the 60 range, which extends from 61 to 76) vs. average apogonid percentage, is 0.272. This value, for n-2 = 13-2 = 11 degrees of freedom, is insignificant at the 5% level (Table Y in Rohlf and Sokal, 1969), hence there is no significant correlation between apogonid percentage and collection richness.

The other regression line in Figure 5, for y on x (y as a function of x) is thus a more appropriate representation of the relationship of the two variables, indicating that apogonids tend to comprise about 9% of the species in any sized collection. The original reason for arbitrarily favoring the other, inappropriate regression line, i.e., the fact that that line appeared to fit better, may be a peculiarity of data which includes a large number of points at y = o.

The error in the first interpretation exemplifies a kind of pitfall that is difficult to define. Perhaps another example illustrates it more clearly. If one were to calculate, let's say, for maternity ward nurseries in American hospitals on a given day, the percentage of total babies that boys constitute in nurseries with only one boy, it would obviously be low, while boys would constitute a higher percentage of total children in nurseries that included 25 boys. This change in percentage would correlate with total nursery population size, since it would only be in relatively large nursery populations that you could have as many as 25 boys, and since the likelihood of having only one boy at a given time is far greater for small nursery populations. It certainly could not, however, be said on this basis that the larger a nursery population is, the higher the percentage of boys tends to be.

A full account and explanation of the erroneous interpretation of the species richness relationship has been included here because it seems to be so easily made. Moreover, in a case where this kind of interpretation fits one's preconceptions, it may not be immediately recognized as erroneous - a case of twisting facts, albeit unknowingly, to suit theories.

In the present case the author was, let us say, not dissatisfied with evidence that might correlate diversity with apogonid species proportion. A proper interpretation, however, indicates the complete lack of such correlation.

(E) Body size patterns

1. Length-weight relationship.

The length-weight calculations per se were not of as much interest as the adult body size considerations enabled by them.

"Coefficient of stoutness", the statistic suggested and used for summarizing the length weight relationship of a given species in a single arbitrary figure, probably has a certain limited usefulness. However, since such coefficients from different species can only be compared for a given length, it really provides no more information than a simple statement of the estimated weight of that species at that length. This latter statistic is more straightforward, and was used in certain computations in 2., discussed below.

2. Body size differences.

The relationship discovered between stoutness and adult size is reminiscent of the tendency, discovered by Lindsey (1975) and called pleomerism, for vertebral number to be correlated with maximum body-length within different groups related fishes. It remains to be seen if the stoutness-length negative correlation can also be shown among different groups of related species.

The following term is suggested for this phenomenon: allometromorphism (Gr. allos: other; + Gr. metron: measure; + Gr. morphe: form: + ism: noun-forming suffix), signifying the variation in form (i.e. stoutness) that is related to variation in length.

Why is the phenomenon of special interest? First, (assuming for the moment that this relationship may prove to occur in other groups of related fish species) it may have some simple predictive value, i.e., one could predict the maximum adult size of a species based on its stoutness as a juvenile. This might, for example, help a taxonomist to recognize adult specimens of a species he is attempting to describe from juvenile specimens. In the context of the present study, one is led to the prediction that Apogon leptocaulus, known from 4 specimens ranging in size from 23.5 to 51.5 mm S. L. (Gilbert, 1972; Dale, 1977) and notably slender in this range, is a rather large species, its maximum size greatly exceeding 51.5 mm S. L.

Second, the phenomenon may reflect an underlying evolutionary mechanism, specifically a speciation mechanism. It is not unreasonable that an interspecific difference in juvenile stoutness might involve a fairly small genetic difference. It is also conceivable that this genetically determined juvenile stoutness might somehow predetermine the maximum size. Perhaps there is some "ideal adult stoutness" for the "generalized" adult cardinalfish. This would be reached by normal, allometric (i.e., non-cubic) growth. Thus a fish that is very slender as a juvenile, like A. robinsi, would keep on growing until it reached the "ideal" stoutness.

The idea of an "ideal adult stoutness" is supported by the general observation that the various apogonid species are, at their "adult size", of a similar stoutness. Thus, for example, A. mosavi is estimated (using Table 13 values) to be 0.834 g. at 30 mm (its "adult length" is 30.7mm). If, hypothetically, it were of exactly the same stoutness but 90 mm in length it would weigh 22.52 g. The computation is based on the cube law. This can be seen most simply as follows (see Lagler, 1956:161): if 30 mm is considered 1 length unit and 0.834g is considered 1 weight unit, then a fish of 3 length units (=90 mm) will weigh 27 weight units (=22.52 g). This is almost exactly the estimated weight (using Table 13 values) of a 90 mm specimen of A. robinsi (whose "adult length" is 89.5 mm), i.e., 22.22 g.

If, on the other hand, the hypothetical 90 mm A. mosavi were of a stoutness determined by its calculated length-weight relationship (Table 13), it would weigh 59.40 g, making it quite unlike the typical cardinalfish in body form, and certainly far stouter than any western Atlantic cardinalfish.

Of what connection are these growth patterns to an evolutionary mechanism? Returning to the first point of this argument, it is not unreasonable to suggest that juvenile stoutness patterns, and hence adult size patterns, may involve fairly small genetic differences. If so, such differences could presumably arise fairly easily (i.e. without extensive evolutionary change) between two allopatric populations of an ancestral species, and could result in body size differences sufficient to permit coexistence of the two forms if and when they became sympatric. To speculate a bit further, it could easily be imagined that the stoutness-size change might also involve a size-at-reproductive-maturity change which would serve to reproductively isolate the two forms.

It should be noted that the argument does not really hinge on the smallness of the genetic change that might cause these differences, but the possibility that the change could be small makes the mechanism of greater potential importance.

The question of whether or not body size differences have a role in permitting coexistence among these species, will be discussed in 3., below.

The entire argument above, regarding the possible evolutionary importance of allometromorphism, may also be relevant in terms of pleomerism (Lindsey, 1975).

3. Ecological significance of body size differences.

Size difference is perhaps the simplest kind of specialization among related species that allows resource sharing. Hutchinson (1959, 1965) showed that a ratio of about 1.3 to 1 in bill size apparently provides a degree of trophic specialization sufficient to allow coexistence among similar bird species. Other studies have indicated a similar ecological role for size differences among carnivora (Rosensweig, 1966), anoline lizards (Rand and Williams, 1969; Williams, 1972), tropical bats (McNab, 1971) and freshwater atherinid fishes (Barbour, 1973).

MacArthur (1972:23) used this kind of coexistence permitted by size difference (in terms of weight) as the basis for a definition of the competitive exclusion principle: "species that differ only in size seem to require that the larger be about twice as heavy as the smaller in order to coexist."

In the case of apogonid or other coral reef fishes, body size differences may function to reduce competition for spatial resources rather than for trophic resources, or perhaps for some complex combination of the two.

Among the three commonly co-occurring and most abundant apogonid species in the present study, the size differences in terms of ratios are, between the largest and intermediate species (Apogon maculatus and Phaeoptyx conklini): 1.42 to 1 in "adult length" and 3.25 to 1 in "adult weight; between the intermediate and smallest species (P. conklini and A. townsendi): 1.12 to 1 in "adult length" and 1.57 to 1 in "adult weight." Thus in one case the 1.3 to 1 size ratio and 2 to 1 weight ratio are exceeded, but in the other case they are not attained.

Far more suggestive than these differences are the results of the comparison of average adult size difference between positively associated species and that between negatively associated species (Table 17). Species tending to occur together differ in "adult length" by 1.39 to 1, and in "adult weight" by 2.15 to 1, while species tending not to occur together differ in "adult length" by only 1.07 to 1 and in "adult weight" by only 1.28 to 1. These findings provide strong support, although not proof by any means, for a view that body size differences are important in competition avoidance among these species. They also, therefore, lend support to the possibility that allometromorphism is a speciation mechanism among cardinalfishes.

(F) Occurrence of ectoparasites

The only observed parasitic infestation of particular importance to the present study is that of Apogon townsendi by copepods, which seems common enough to be a very important aspect of the biology of that species. On several occasions quite small individuals (20 - 25 mm S. L.) were observed carrying several of the copepods, whose length (with trailing egg sacs) approached that of the host. It would seem that such a fish must be appreciably slowed down, and presumably under physiological stress, to an extent that its survival for long enough to be noticed by a curious diving biologist is an improbable event. It thus seems likely that many others succumb to predators, and that these copepods are therefore a major factor limiting the population of A. townsendi.

On several occasions in the field, copepod-infested A. townsendi individuals were observing to be residing in very close proximity to, i.e., sharing the same small microhabitat with, other uninfested cardinalfish species, especially A. maculatus. One possible reason for the difference would be that the uninfested species are cleaned by one or more cleaner species that do not perform this service for A. townsendi. On one occasion at a patch reef off Grand Bahama, a large A. maculatus individual was closely inspected by a cleaning goby, Gobiosoma genie, but no actual cleaning was observed (Dale, 1975).

CHAPTER THREE: Topographic Factors

I. METHODS

(A) Geography

An essential consideration in the context of Bahamian cardinalfish coexistence is whether or not they have the same geographic range within the Bahamas, i.e., whether or not all the species are indeed sympatric.

The simplest approach to this question would be to divide the total area of the Bahamas into several units and tabulate locality information, from the literature and from the collections being studied, according to these divisions.

In the author's judgement the possibility that deep water would somehow serve as a distributional barrier seemed as reasonable a possibility as any. Therefore an attempt was made to find a natural division of the Bahamas, into units that might possibly be zoogeographically meaningful, by inspecting maps of the area that included depth information.

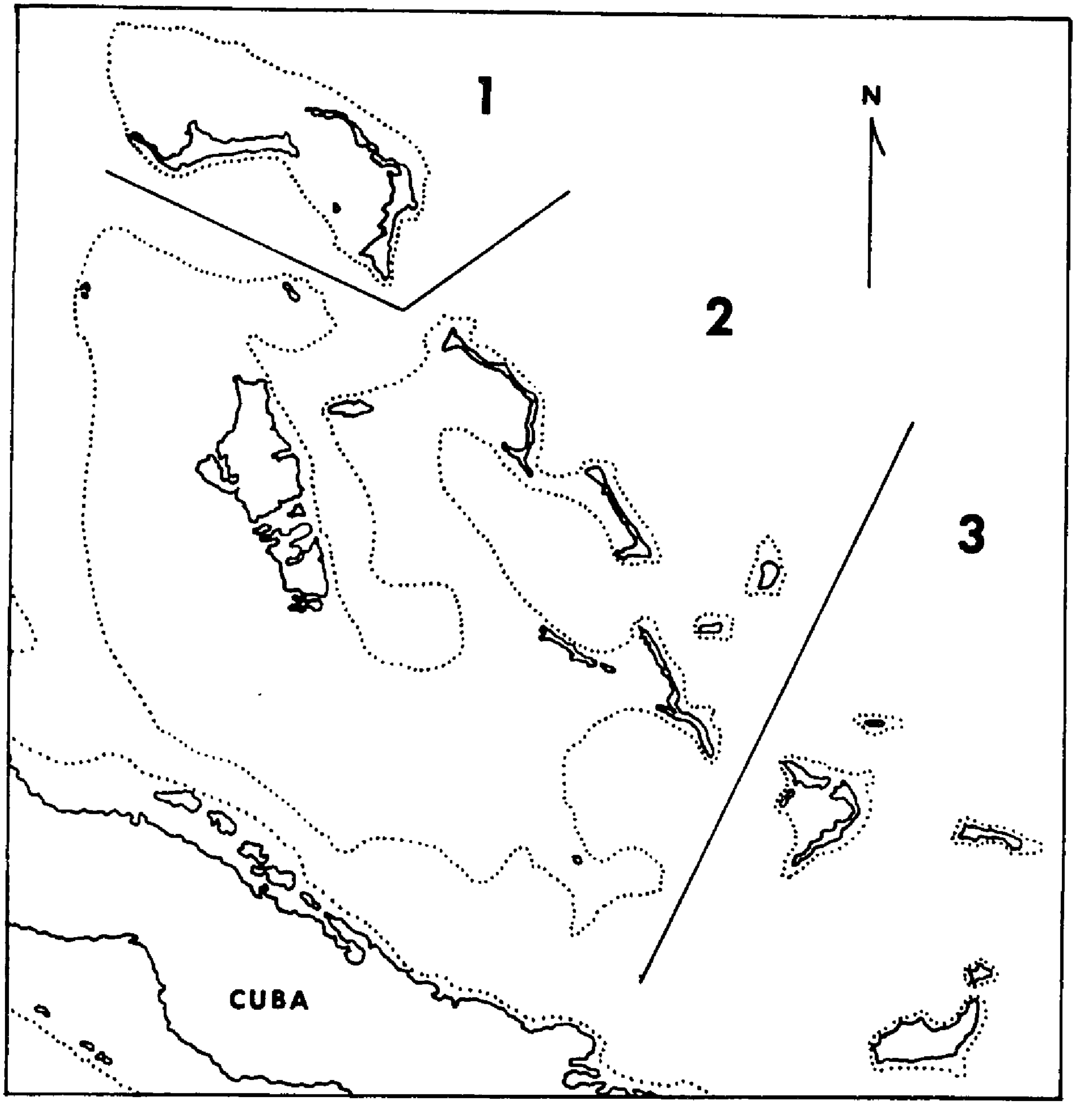
One of the most striking aspects of the bathymetry of the Bahamas region is the presence of two large banks, the Little Bahama Bank, on which the northernmost islands of the Bahamas are located, including Grand Bahama and Great Abaco, and the much larger Great Bahama Bank, on which Bimini, Andros, New Providence, Eleuthera, Cat Island, Great Exuma, Long Island, and numerous smaller islands are located. These two banks are separated from each other by the deep water of Northwest Providence Channel and Northeast Providence Channel (several hundred to several thousand meters).

The Great Bahama Bank is separated from nearly all of the remaining islands to the southeast by the deep water of the Crooked Island Passage (over two thousand meters). Rum Cay and San Salvador, southeast of Cat Island, may be lumped together with the Great Bahama Bank islands because of their proximity to it. An additional area to the west of the Great Bahama Bank, the Cay Sal Bank, does not include any sizeable islands. Although Bohlke and Chaplin made some collections there, they did not obtain apogonid records that were not also obtained in the nearby Great Bahama Bank. For this reason, and because no Cay Sal Bank collections are included in the present study, this area was omitted from the present analysis.

Thus three broad subdivisions of the Bahamas may be easily recognized, based on depth information, as shown in Figure **12**. The Little Bahama Bank is designated as region 1, and the Great Bahama Bank + Rum Cay + San Salvador as region 2. The remaining islands to the southeast, including Crooked Island, Acklin's Island, Great Inagua, Little Inagua, Samana Cay and Mayaguana Island, are assigned to region 3. A tabulation of cardinalfish distribution was prepared in accordance with these subdivisions.

By coincidence, the boundaries based on depth are similar to the boundaries one might make using another parameter of possible zoogeographic significance: surface water temperatures. On Colin's (1975:276) map of the distribution of surface temperature in the tropical western North Atlantic Ocean during January, the 23.5° C. and 25° C. isotherms divide the Bahamas into almost the identical three regions.

Figure 12. Three broad subdivisions of the Bahamas, separated by deep water areas. The dotted lines represent 100 fathom isobaths.


1
2
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(B) Depth

Another important consideration is whether or not there are any differences in depth distribution among the various cardinalfish species. In other words, is there any vertical zonation which might result in an avoidance of competition between some of the species?

Since the collection data for all of the Bahamian fish samples being studied included information on depth of capture, both frequency of occurrence and numerical abundance of each species at different depth ranges could be obtained. Because of the large number of collections made at various depths between 0 and 40 feet, and the relative paucity of collections from below 40 feet to a maximum of 140 feet, the following series of depth ranges (in feet), in which to tabulate and graph the data, proved to be convenient: 0-10, 11-20, 21-30, 31-40, 41-90, 91-140.

From the data for "total collections", tables giving the number of samples and the total abundance of each apogonid species at each depth range were prepared.

(C) Habitat

A third spatial or "topographic" parameter that is relevant to cardinalfish coexistence is habitat preference. Are there differences in broad habitat preference that might result in interspecific competition avoidance?

To answer this question the author made use of a classification of Bahamian fish habitats (C. L. Smith, unpublished). All of the samples being studied were classified in one or another of five broad habitat categories in this classification: shoreline, top of bank, moat, outer shelf, and drop-off.

Tabulation of habitat distribution data was carried out for these five categories in the same way that depth distribution data had been tabulated for six different depth ranges, as described earlier.

(D) Microhabitat

A final pertinent spatial parameter to be considered is microhabitat preference. What special associations with the immediate biotic or abiotic environment are demonstrable which would help define the niche of one or more cardinalfish species?

A partial answer to this question was available in the literature. Additional data were sought by the author by means of direct in situ observation during field trips to various parts of the Bahamas.

II. RESULTS

(A) Geography

Table 20 shows the occurrence in the three suggested subdivisions of the Bahamian region, of each of the 20 apogonid species known from the Bahamas. Included in the tabulation are records given by Böhlke and Chaplin (1968), records included among the 154 rotenone collections examined in the present study, and additional records among specimens cataloged at the American Museum.

Fourteen of the 20 species are seen to occur in all three regions. Apogon mosavi is recorded in only two regions. Records for the remaining five species occur in only one of the three regions.

Species	Region 1	Region 2	Region 3
Apogon affinis	+	x +	+
Apogon anisolepis		x	
Apogon aurolineatus	x		
Apogon binotatus	x +	x +	+
Apogon lachneri	x	x +	x +
Apogon leptocaulus			+
Apogon maculatus	x +	x +	x +
Apogon mosavi	+	+	
Apogon phenax	x +	x +	+
Apogon pillionatus		x	
Apogon planifrons	x	x +	+
Apogon pseudomaculatus		x +	
Apogon quadrisquamatus	x +	x +	+
Apogon robinsi	x	x +	+
Apogon townsendi	x +	x +	x +
Phaeoptyx conklini	x +	x +	x +
Phaeoptyx pigmentaria	x +	x +	x +
Phaeoptyx xenus	x +	x +	+
Astrapogon puncticulatus	x +	x +	x +
Astrapogon stellatus	+	x +	+

Table 20. Occurrence of apogonid species in three subdivisions of the Bahamas: Region 1 = Little Bahama Bank; Region 2 = Great Bahama Bank + Rum Cay + San Salvador; Region 3 = remaining islands to southeast, including Crooked Island, Acklin's Island, Great Inagua, Little Inagua, Samana Cay, and Mayaguana Island. x = records of Böhlke and Chaplin (1968). + = records in collections of present study plus other American Museum records.

(B) Depth

Tables 21 and 22 give frequency and abundance data, for six different depth ranges, for each apogonid species present in "total collections." There seem to be various depth preference tendencies among the various species.

With the data in this form, however, between-depth comparisons of either frequency or abundance for a given species are difficult, since the collecting effort at the different depths varied widely. To begin with, fewer collections were made at the greater depth ranges. Moreover, the deeper collections tend to be smaller and less diverse because of the bottom-time limitations that curtail the diver's collecting effort.

With these considerations in mind, both the frequency and abundance data were converted into percentages. Figure 13 is a series of bar graphs giving, for each species, the percent of the total apogonid samples from a given depth range. Figure 14 is a series of bar graphs giving, for each species, the percent of the total apogonid abundance from a given depth range. A clearer idea of the "depth preference" of each species may be obtained with reference to these two series of graphs.

Apogon affinis has an apparent preference for the deepest of the six depth ranges, both in terms of frequency and abundance. It is uncommon and sparse, or absent, elsewhere.

A. binotatus tends to be moderately frequent and abundant in all depth ranges except the deepest, where it is absent.

A. lachneri is highly frequent and abundant in the two deepest categories, and rare and sparse, or absent, in the shallower ranges.

Species	Depth Range (feet) 0-10	11-20	21-30	31-40	41-90	91-140
Apogon affinis	2	3	1	1	-	2
Apogon binotatus	11	10	5	5	2	-
Apogon lachneri	1	-	3	4	6	9
Apogon leptocaulus	-	-	-	-	1	-
Apogon maculatus	30	23	13	8	3	-
Apogon mosavi	-	-	-	1	-	1
Apogon phenax	-	-	2	5	6	3
Apogon planifrons	4	3	2	1	1	1
Apogon quadrisquamatus	1	2	2	4	2	-
Apogon robinsi	2	3	1	-	-	-
Apogon townsendi	7	9	11	8	6	3
Phaeoptyx conklini	36	21	13	13	4	2
Phaeoptyx pigmentaria	20	15	11	9	3	2
Phaeoptyx xenus	1	1	2	3	3	3
Astrapogon puncticulatus	21	9	-	4	-	-
Astrapogon stellatus	1	-	-	1	-	-

Table 21. Number of samples of different apogonid species taken at different depth ranges, in "total collections."

Species	0-10	11-20	21-30	31-40	41-90	91-140
Apogon affinis	6	46	8	12	-	45
Apogon binotatus	88	43	11	22	3	-
Apogon lachneri	1	-	7	12	32	70
Apogon leptocaulus	-	-	-	-	1	-
Apogon maculatus	210	203	268	95	3	-
Apogon mosavi	-	-	-	1	-	127
Apogon phenax	-	-	4	13	26	4
Apogon planifrons	11	17	3	1	9	4
Apogon quadrisquamatus	2	7	2	8	2	-
Apogon robinsi	6	4	1	-	-	-
Apogon townsendi	32	114	122	85	19	12
Phaeoptyx conklini	1151	570	206	102	8	9
Phaeoptyx pigmentaria	51	56	17	23	4	2
Phaeoptyx xenus	1	3	2	4	3	7
Astrapogon puncticulatus	142	16	-	8	-	-
Astrapogon stellatus	1	-	-	1	-	-

Table 22. Total abundance of different apogonid species taken at different depth ranges, in "total collections."

Figure 13. Apogonid occurrence at various depths, based on "total collections" data. For each species, in a given depth range, the percent of the total number of apogonid samples taken in that depth range, is given. Each small vertical division of the grid equals 2%: each large division equals 10%. Thus, for example, 8.0% of all the apogonid samples taken in the 0-10 feet depth range were *Apogon binotatus*.

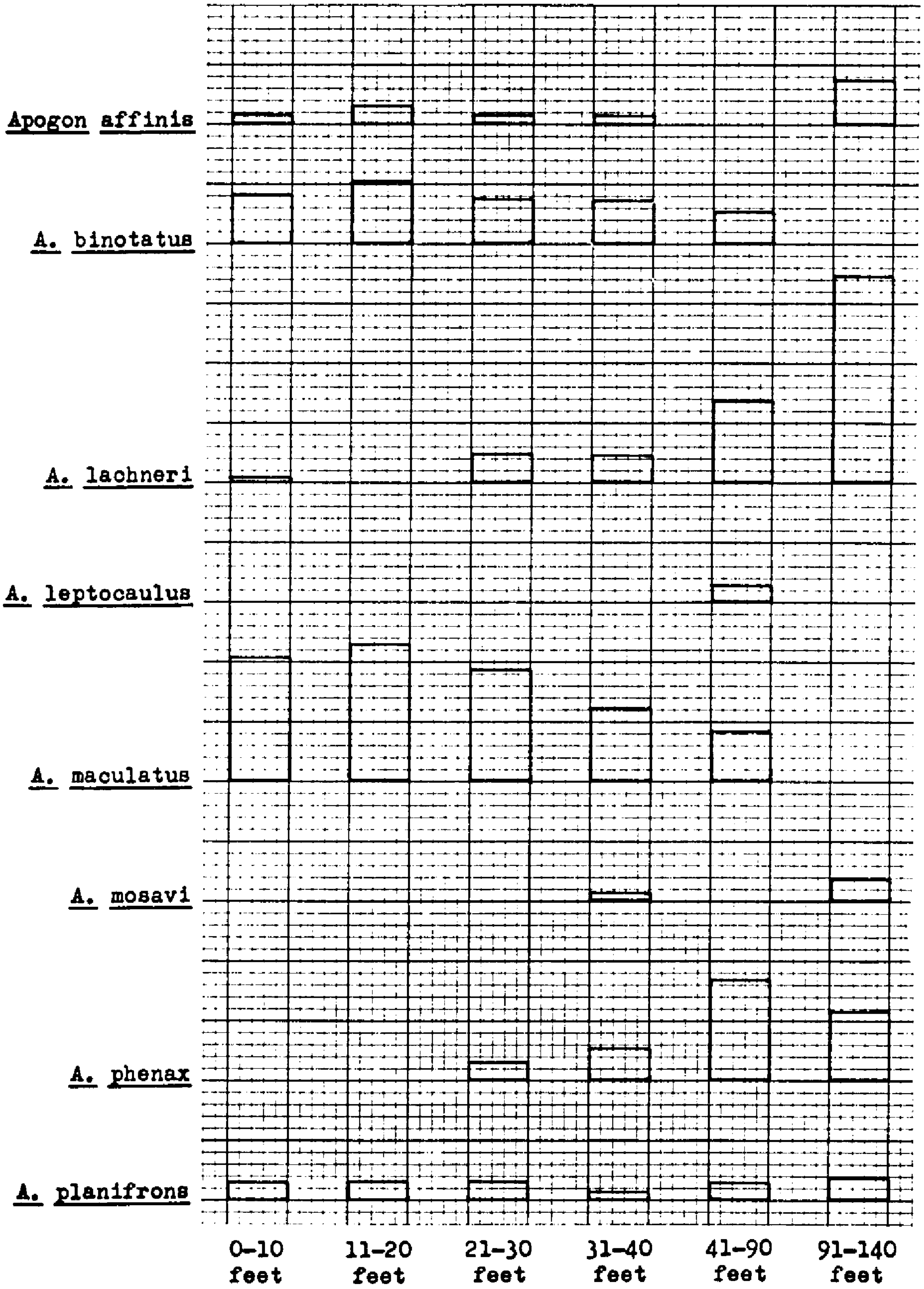


FIGURE 13 (1st of 2 pages)

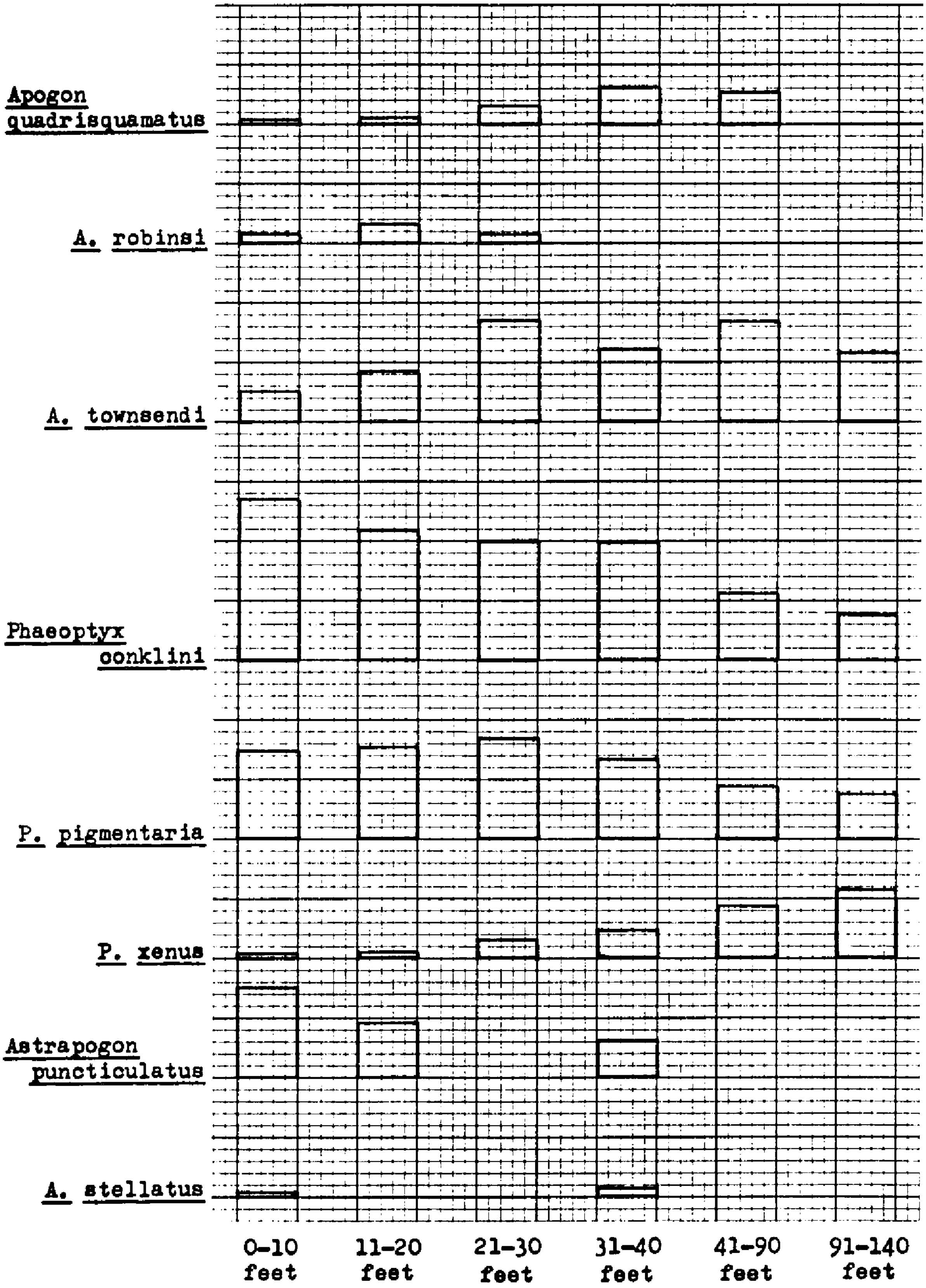


FIGURE 13 (2nd of 2 pages)

Figure 14. Apogonid species abundance at various depths, based on "total collections" data. For each species, in a given depth range, the percent of the total number of apogonid specimens taken in that depth range, is given. Each small vertical division of the grid equals 2%; each large division equals 10%. Thus, for example, 12.3% of all the apogonid specimens taken in the 0-10 feet depth range were *Apogon maculatus*.

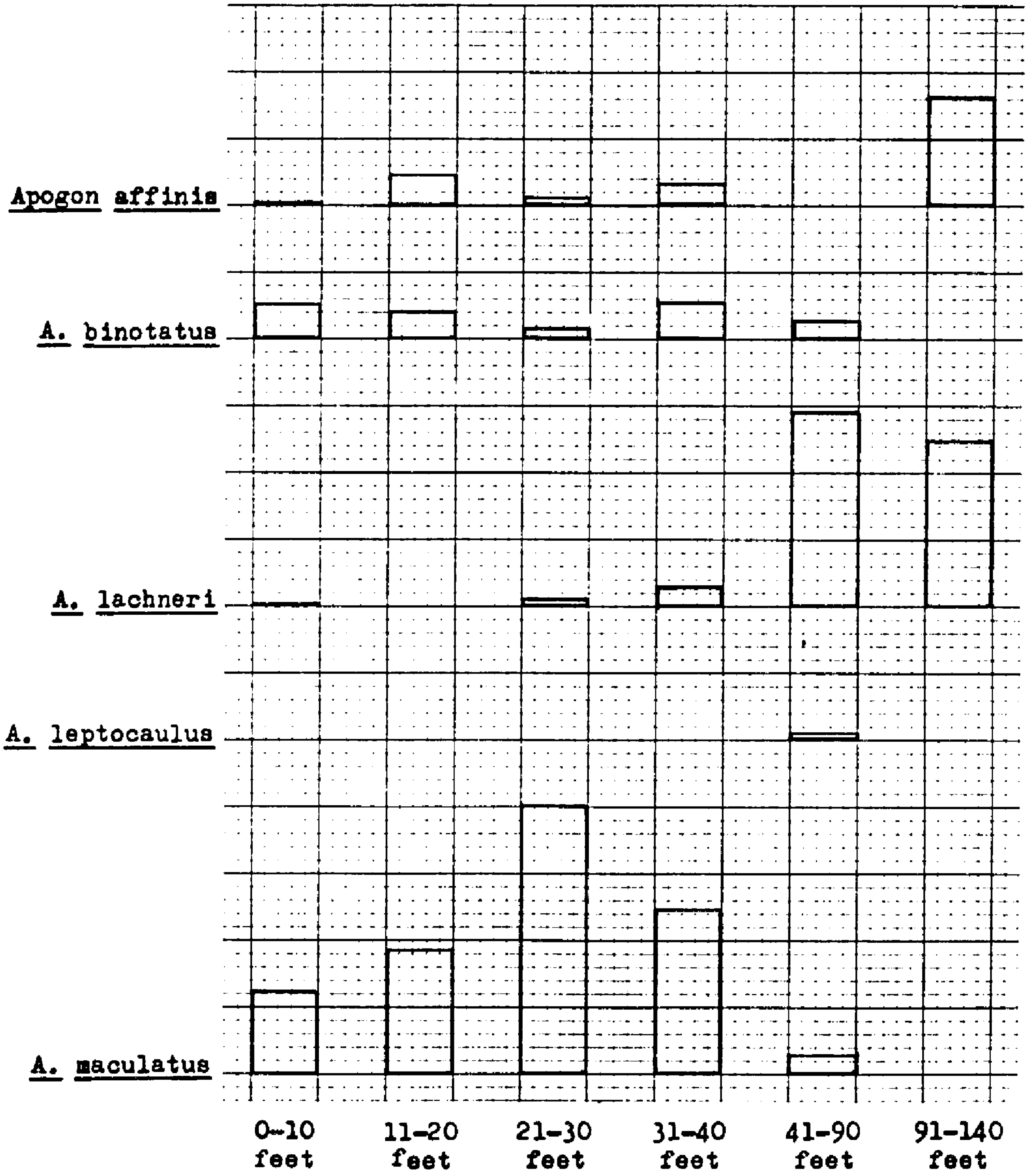


FIGURE 14 (1st of 3 pages)

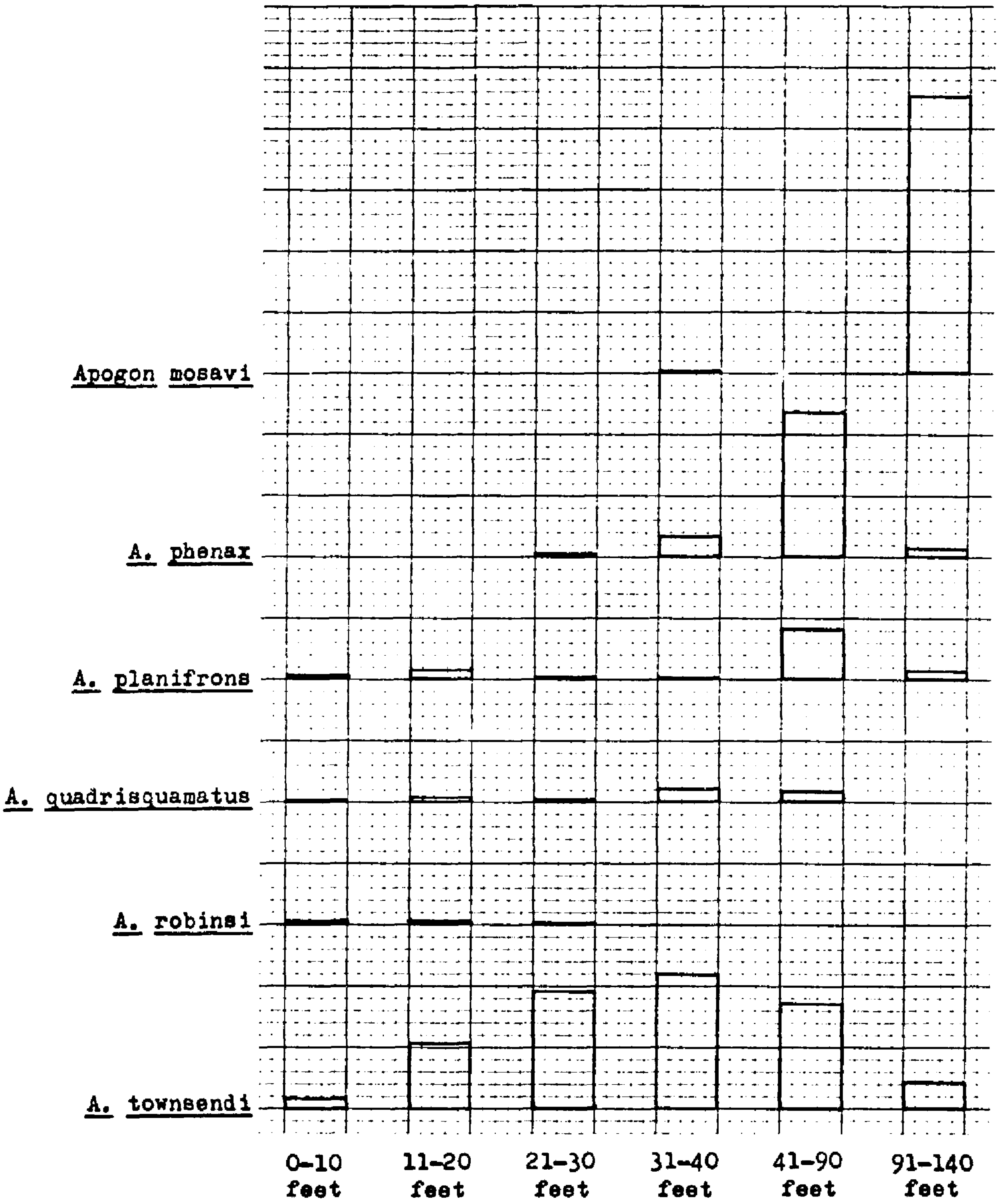


FIGURE 14 (2nd of 3 pages)

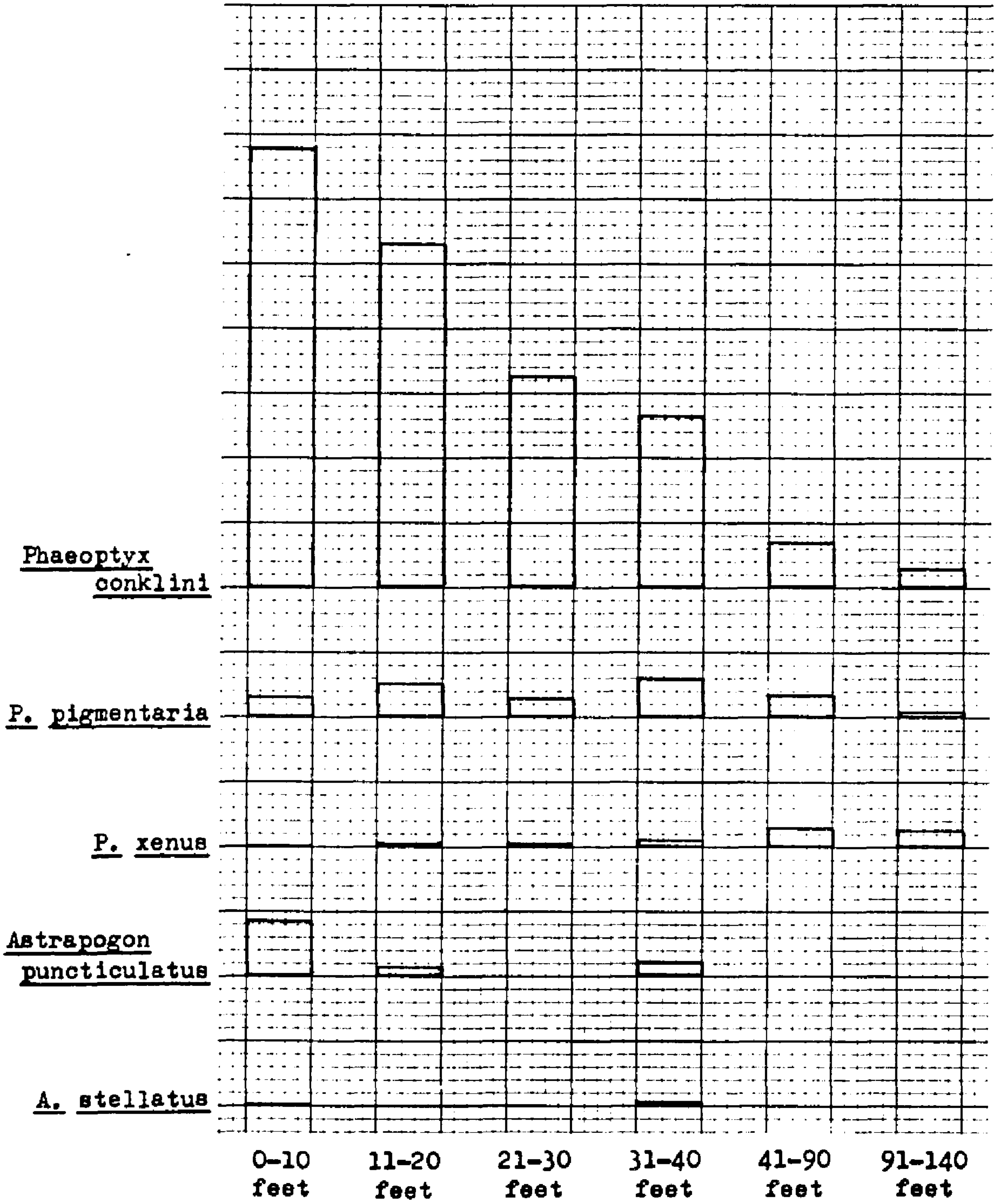


FIGURE 14 (3rd of 3 pages)

The single specimen of A. leptocaulus falls in the 41-90 feet range (actually taken at 70-80 feet). The depth of capture of the three type specimens: 65-70, 95-100, and 70-100 feet (Gilbert, 1972), and a "photograph record" from 80 feet (Colin, 1974: see Dale, 1977), together with the present record, indicate that this species prefers fairly deep water.

A. maculatus is moderately to highly frequent and abundant in the five shallower ranges, and is absent in the deepest range.

The depth records included here for A. mosavi, as well as the depth records of the other three known samples (Dale, 1977), together comprising a range of 40-135 feet, indicate a preference by this species for relatively deep water.

A. phenax is moderately to highly frequent and abundant in the deeper ranges, and absent in the two shallowest categories.

A. planifrons is present in fairly low frequency and abundance at all depth ranges.

A. quadrisquamatus is present in fairly low frequency and abundances at all depth ranges except 91-140 feet, where it is absent.

A. robinsi is rare and sparse in the shallower ranges and absent in the deeper ranges.

A. townsendi occurs in all ranges, but is especially frequent and abundant in the intermediate depth ranges.

Phaeoptyx conklini is present in all six depth ranges, and predominates in frequency and abundance over other species in the shallower ranges. There is a steady decline in its commonness and numbers from the shallowest to the deepest categories.

P. pigmentaria tends to be moderately frequent and abundant at all ranges, and seems to show a slight preference for intermediate depths.

P. xenus is present at all depth ranges, but is frequent and fairly abundant only in the deeper ranges.

Astrapogon puncticulatus is very common and fairly abundant in the 0-10 feet range, present in some intermediate depths, and absent in the deepest categories.

Little can be said about the depth preference of A. stellatus based on the depth of capture of the two specimens in the present data. This species lives as a commensal in the mantle cavity of the queen conch Strombus gigas (and occasionally in the pen shell Atrina rigida), and is only rarely collected apart from this association. The depth preference of A. stellatus would presumably parallel that of its usual host, which is fairly wide-ranging.

(C) Habitat

Tables 23 and 24 give frequency and abundance data, for five different broad habitat categories, for each apogonid species present in "total collections." Although some habitat association tendencies are apparent among the different species, interpretation of between-habitat differences in frequency or abundance, for a given species, is difficult with the data in this form. As with the depth ranges, the collection effort differed widely for the different habitat categories.

Therefore the data were again converted to percentages, which were then used to prepare bar graphs. Figure 15 gives, for each species, the percent of the total apogonid samples from a given habitat category. Figure 16 gives, for each species, the percent of the total apogonid abundance from a given habitat category. A more meaningful idea of the "habitat preference" of each species is obtained by examining these two series of graphs.

Apogon affinis shows an apparent "preference" for the drop-off zone, and is uncommon and sparse, or absent, elsewhere.

A. binotatus is quite common and abundant in the top of bank category, moderate in frequency and abundance in three other areas, and absent at the drop-off.

A. lachneri is highly frequent and abundant at the drop-off, and rare and sparse, or absent, elsewhere.

The single _A. leptocaulus_ specimen was taken at the drop-off. Two of the three specimens on which the description is based are also from drop-off areas (Gilbert, 1972).

Species	Shore-line	Top of bank	Moat	Outer shelf	Drop-off
Apogon affinis	-	1	-	6	2
Apogon binotatus	3	8	5	17	-
Apogon lachneri	-	1	-	12	10
Apogon leptocaulus	-	-	-	-	1
Apogon maculatus	17	8	7	45	-
Apogon mosavi	-	-	-	1	1
Apogon phenax	-	-	-	11	5
Apogon planifrons	2	3	-	6	1
Apogon quadrisquamatus	-	-	-	10	1
Apogon robinsi	-	2	3	1	-
Apogon townsendi	1	3	3	33	4
Phaeoptyx conklini	16	9	11	49	4
Phaeoptyx pigmentaria	9	8	6	33	4
Phaeoptyx xenus	1	1	1	7	3
Astrapogon puncticulatus	15	1	2	16	-
Astrapogon stellatus	1	-	-	1	-

Habitat Category (spanning header over Shore-line through Drop-off)

Table 23. Number of samples of different apogonid species taken in different habitat categories, in "total collections."

Species	Shore-line	Top of bank	Moat	Outer shelf	Drop-off
Apogon affinis	-	3	-	69	45
Apogon binotatus	8	89	14	56	-
Apogon lachneri	-	1	-	32	89
Apogon leptocaulus	-	-	-	-	1
Apogon maculatus	95	24	17	643	-
Apogon mosavi	-	-	-	1	127
Apogon phenax	-	-	-	41	6
Apogon planifrons	5	20	-	16	4
Apogon quadrisquamatus	-	-	-	20	1
Apogon robinsi	-	3	7	1	-
Apogon townsendi	11	8	7	344	14
Phaeoptyx conklini	430	651	190	764	11
Phaeoptyx pigmentaria	23	40	13	72	5
Phaeoptyx xenus	1	1	3	10	5
Astrapogon puncticulatus	129	1	5	31	-
Astrapogon stellatus	1	-	-	1	-

Table 24. Total abundance of different apogonid species taken in different habitat categories, in "total collections."

Figure 15. Apogonid species occurrence in various broad habitat categories, based on "total collections" data. For each species, in a given habitat category, the percent of the total number of apogonid samples taken in that category, is given. Each small vertical division of the grid equals 2%; each large division equals 10%.

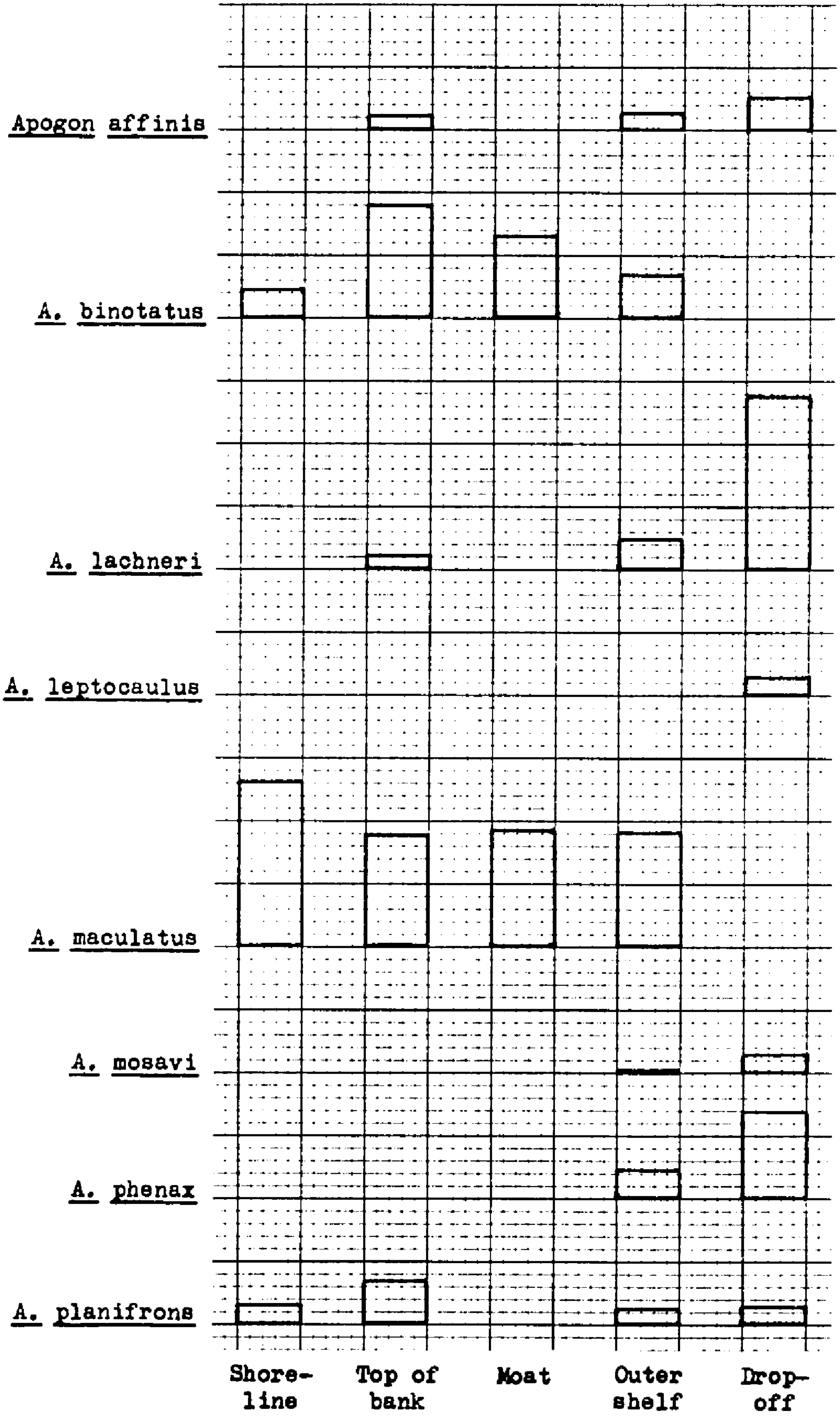


FIGURE 15
(1st of 2 pages)

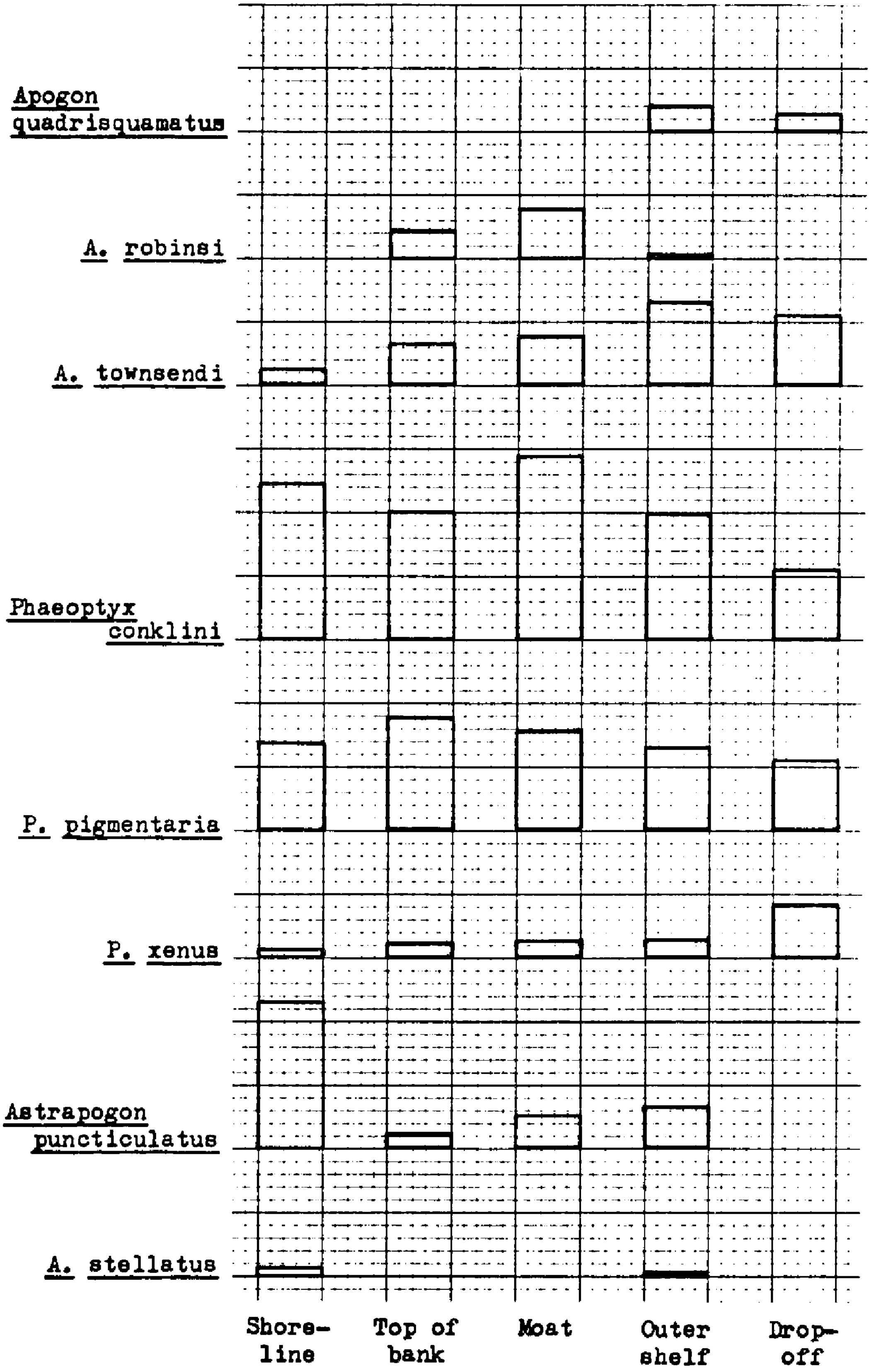


FIGURE 15
(2nd of 2 pages)

Figure 16. Apogonid species abundance in various broad habitat categories, based on "total collections" data. For each species, in a given habitat category, the percent of the total number of apogonid specimens taken in that category, is given. Each small vertical division of the grid equals 2%: each large division equals 10%.

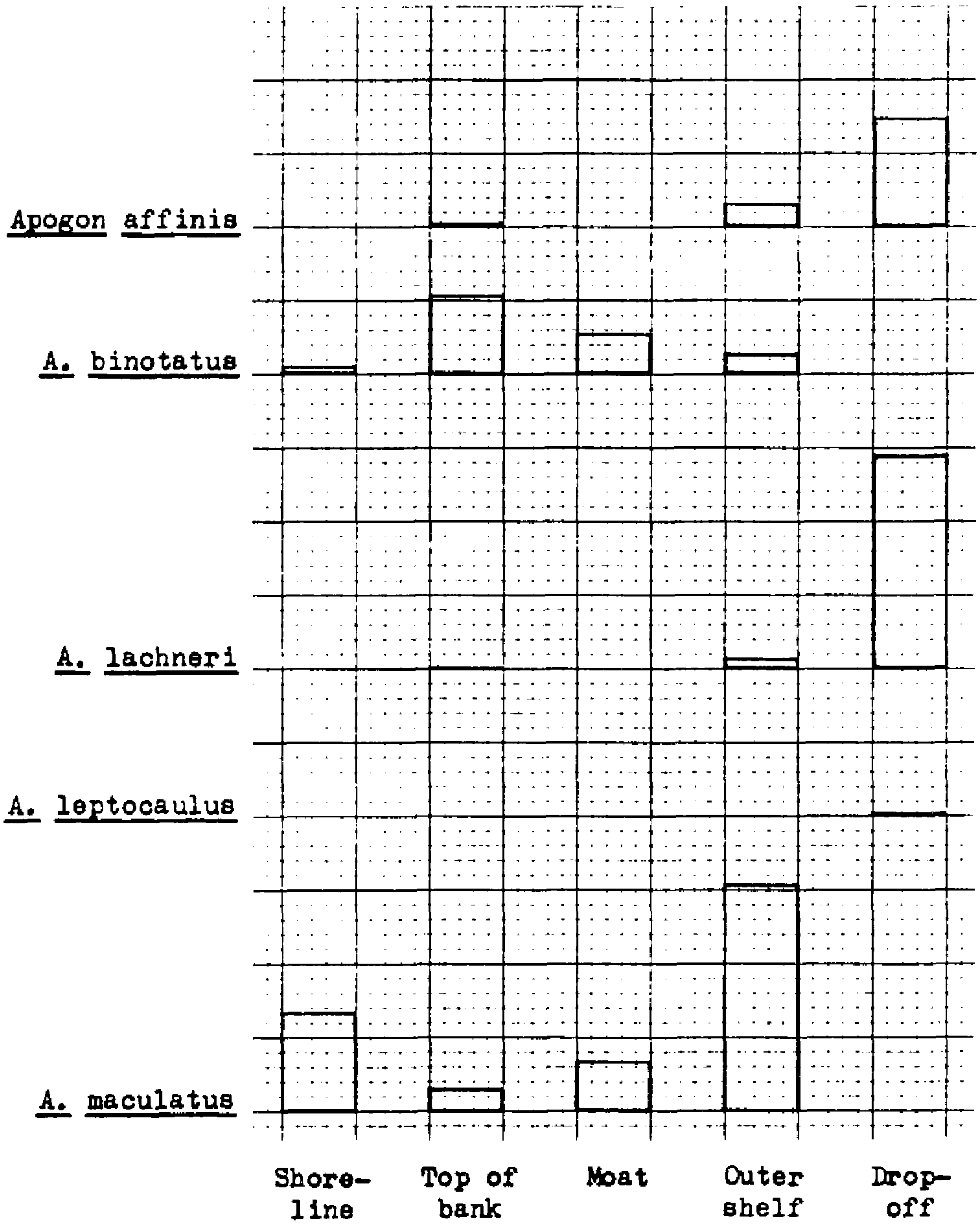


FIGURE 16 (1st of 3 pages)

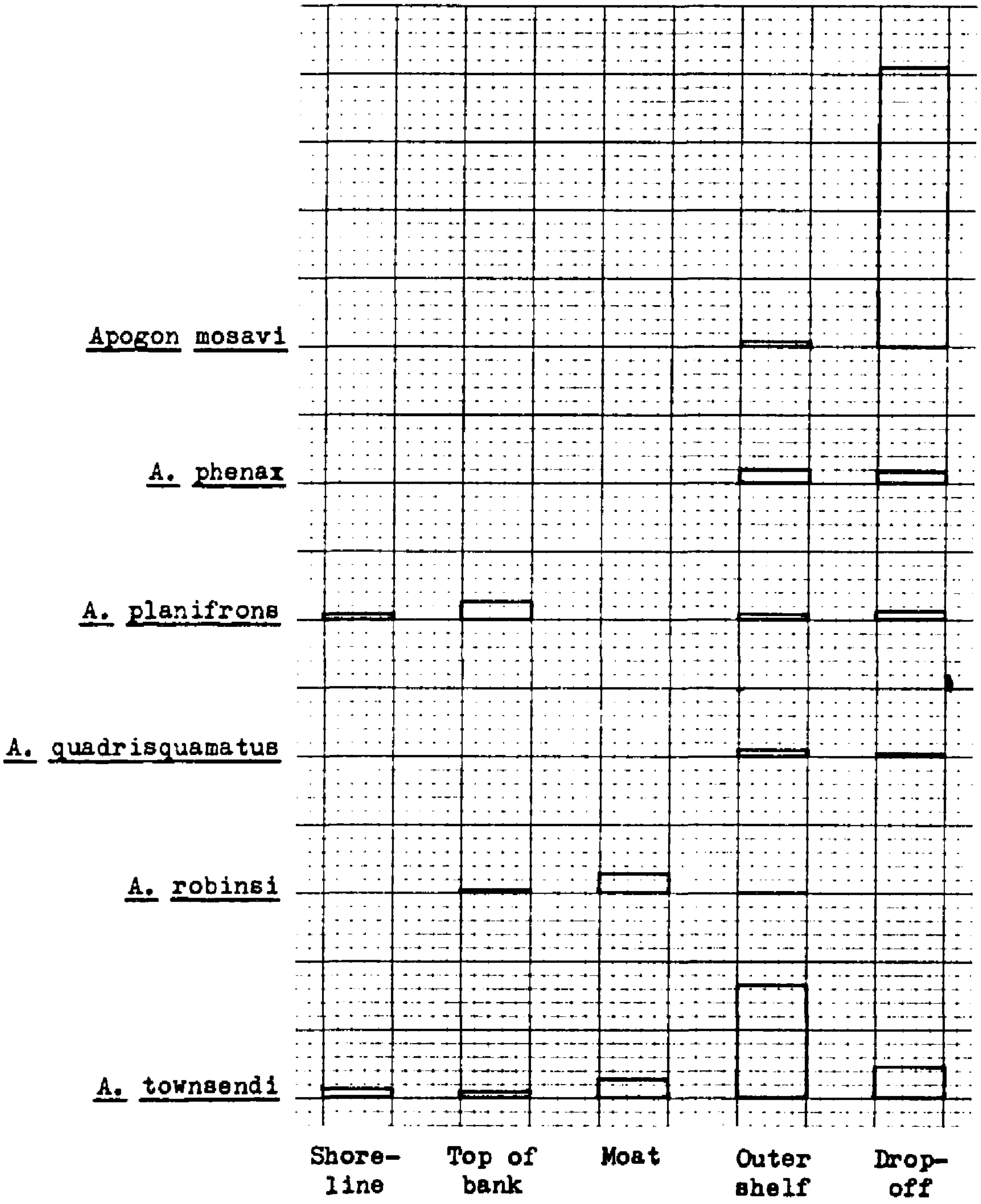


FIGURE 16 (2nd of 3 pages)

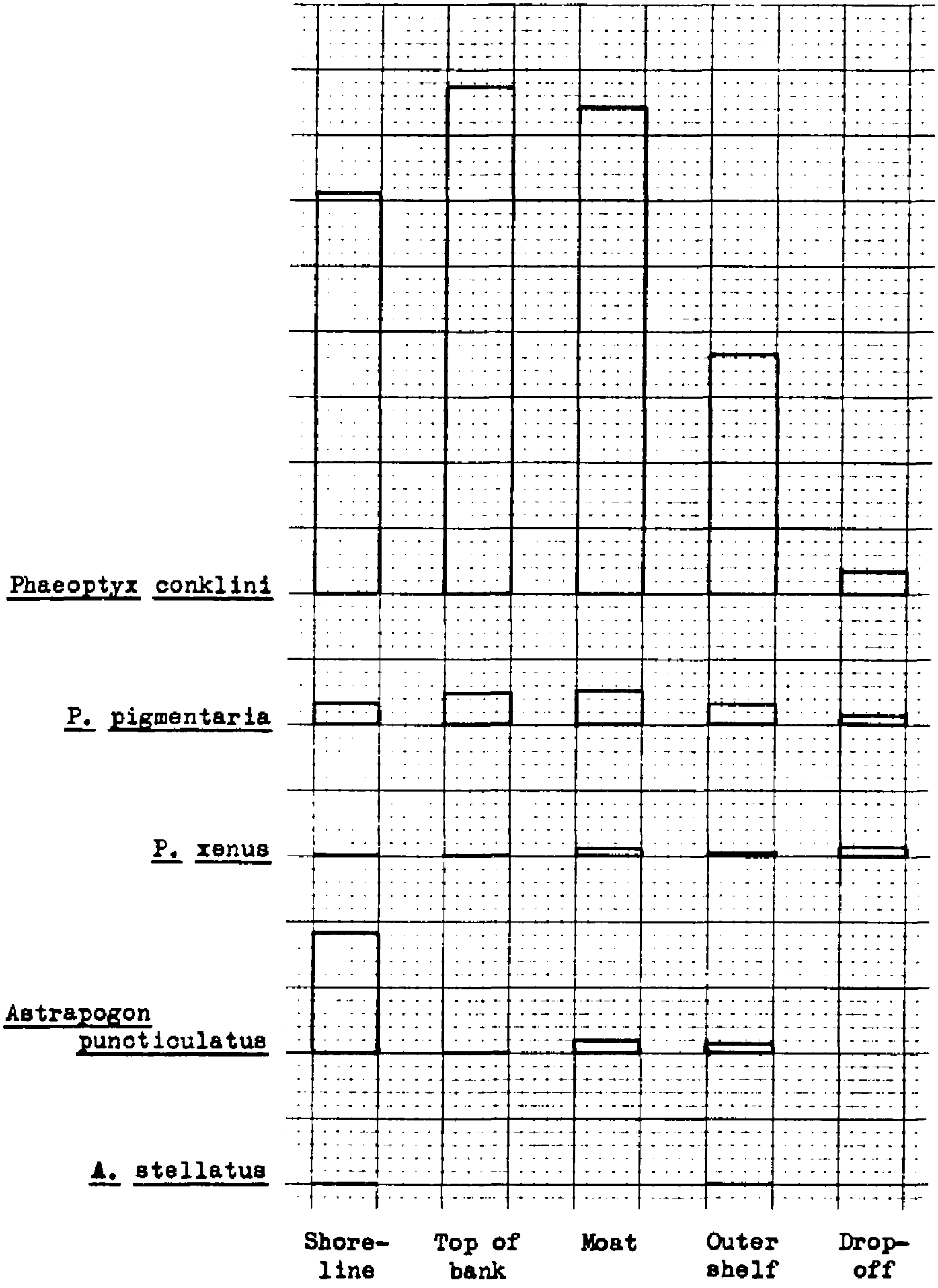


FIGURE 16 (3rd of 3 pages)

A. maculatus occurs very frequently, and also tends to be abundant in all areas except the drop-off, where it is absent.

The two samples of *A. mosavi* were taken in the outer shelf and drop-off categories.

A. phenax is frequently present, in low numbers, at the drop-off; rare and sparse in the outer shelf category, and absent in the other areas.

A. planifrons is present in low frequency and abundance in all areas except the moat, where it is absent.

A. quadrisquamatus is uncommon and sparse in the outer shelf and drop-off categories and absent elsewhere.

A. robinsi is absent in the shoreline and drop-off categories and present in very low frequency and abundance in the other three.

A. townsendi is present in low to moderate numbers in four categories, and is very frequent and abundant at the outer shelf.

Phaeoptyx conklini equals or surpasses all other species in frequency and abundance in all categories except the drop-off, where it is fairly frequent, but in low numbers.

P. pigmentaria is rather frequent in all categories, in fairly low numbers in each case.

P. xenus is very rare and sparse in all categories except the drop-off, where it is slightly more common.

Astrapogon puncticulatus is highly frequent and abundant in the shoreline category, and fairly uncommon and sparse, or absent, elsewhere.

The two *A. stellatus* specimens were taken in the shoreline and outer shelf categories. Again, however, this provides little information on the real habitat associations of this species, for reasons discussed in connection with its depth distribution.

(D) Microhabitat

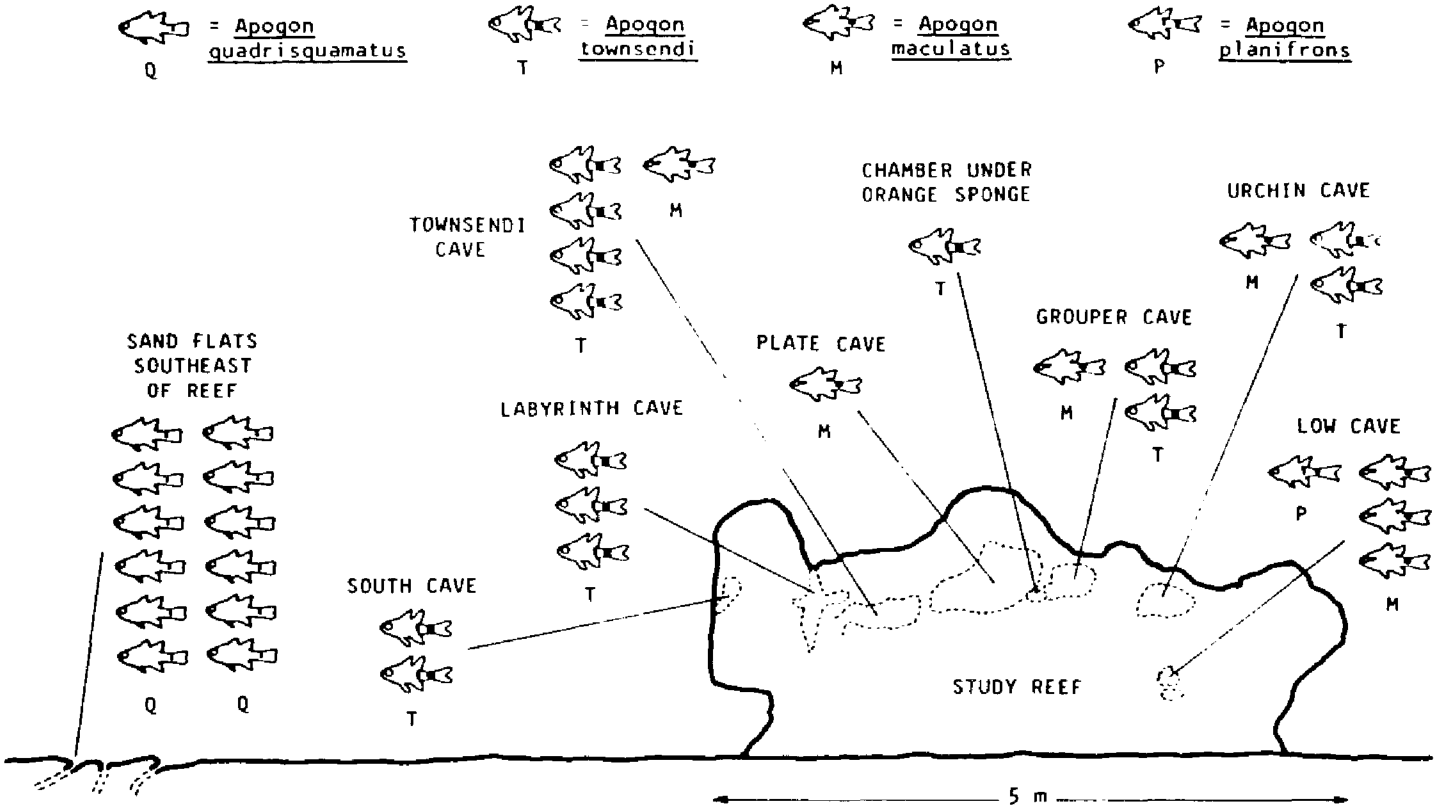
In March, 1973, the author took part in a seven-day saturated diving mission from the underwater habitat "Hydrolab", off Grand Bahama, together with C. Lavett Smith and Marvin Greenbaum. A few of the details of this mission will be described in the Temporal Factors chapter. A small patch reef at a depth of about 15 meters was chosen on the first day and studied for the rest of the week. An account of various observations on cardinalfishes seen on or near that reef has been published (Dale, 1975). A few of the observations are pertinent to a consideration of cardinalfish microhabitat preferences, and may be summarized as follows.

Three apogonid species: Apogon maculatus, A. planifrons, and A. townsendi, were diurnal residents of the reef and one species, A. quadrisquamatus, inhabited crevices in the bottom nearby. Figure 17 shows the study reef and the daytime locations of these species.

The locations containing A. townsendi, the most numerous cardinalfish species on the reef (14 individuals), were mostly cave-like spaces with multiple entrances, and ranged in size from several hundred to several thousand cm^3. The consistent occurrence of recognizable individuals in the same daytime places indicated that, at least for the duration of this study, each individual resided in the same limited location on the reef from day to day. One of the A. townsendi individuals in "urchin cave" was observed resting between the spines of a Diadema antillarum sea urchin that resided in that cave.

Seven individuals of A. maculatus were resident on the study reef. No consistent differences between its microhabitats and those

Figure 17. Typical daytime distribution of four cardinalfish species on and near a patch reef at 50 feet depth off Grand Bahama. Caves were named after some descriptive feature to facilitate note-taking and comparison (from Dale, 1975).



= Apogon quadrisquamatus
Q
= Apogon townsendi
T
= Apogon maculatus
M
= Apogon planifrons
P
TOWNSENDI CAVE
T
M
CHAMBER UNDER ORANGE SPONGE
T
URCHIN CAVE
M
T
GROUPER CAVE
M
T
PLATE CAVE
M
SAND FLATS SOUTHEAST OF REEF
Q
Q
LABYRINTH CAVE
T
LOW CAVE
P
M
SOUTH CAVE
T
STUDY REEF
5 m

FIGURE 17

of A. townsendi were discerned. In three cases a cave was shared by the two species. A. maculatus was more mobile than A. townsendi, tending to roam between adjacent caves. One individual was observed on one occasion between the spines of the D. antillarum in "urchin cave".

Photographs of A. maculatus and A. townsendi, taken at the study reef, are given in Figure 18.

At least twelve individuals of A. quadrisquamatus apparently resided in crevices between partially buried rocks in the sandy area near the study reef.

In July, 1973 the author spent two weeks at the Lerner Marine Laboratory of the American Museum, in Bimini, Bahamas. A number of observations were made, related to cardinalfish microhabitats, during numerous diving trips in the vicinity of Turtle Rocks, just south of the Bimini island group.

In several small caves in a more or less vertical rocky wall just off the northernmost of the Turtle Rocks islands, an interesting association was observed. One to several A. maculatus specimens, plus one long-spined sea urchin Diadema antillarum, and often also one red-banded coral shrimp Stenopus hispidus, shared an otherwise essentially barren space. In each case the caves were quite exposed, i.e. had entrances as wide as the caves themselves, so that the Diadema individual was evidently the major protection against predators for A. maculatus (and possibly also for the shrimp). If closely approached, the fish sought shelter in the spines of the sea urchin.

Among several coral reef formations in the Turtle Rocks area

Figure 18. Cardinalfishes in diurnal microhabitat, on study reef near Hydrolab, off Grand Bahama. (A) Two *Apogon maculatus* individuals in small cave-like space within the reef. The walls of the cave are partially covered with encrusting and filamentous algae. (B) *A. townsendi* in similar cave-like space. An encrusting sponge (mustard-colored in life) is seen at the right. Several patches of encrusting red algae are also prominent in the color slide from which this conversion was made. (Photographs by M. Greenbaum)

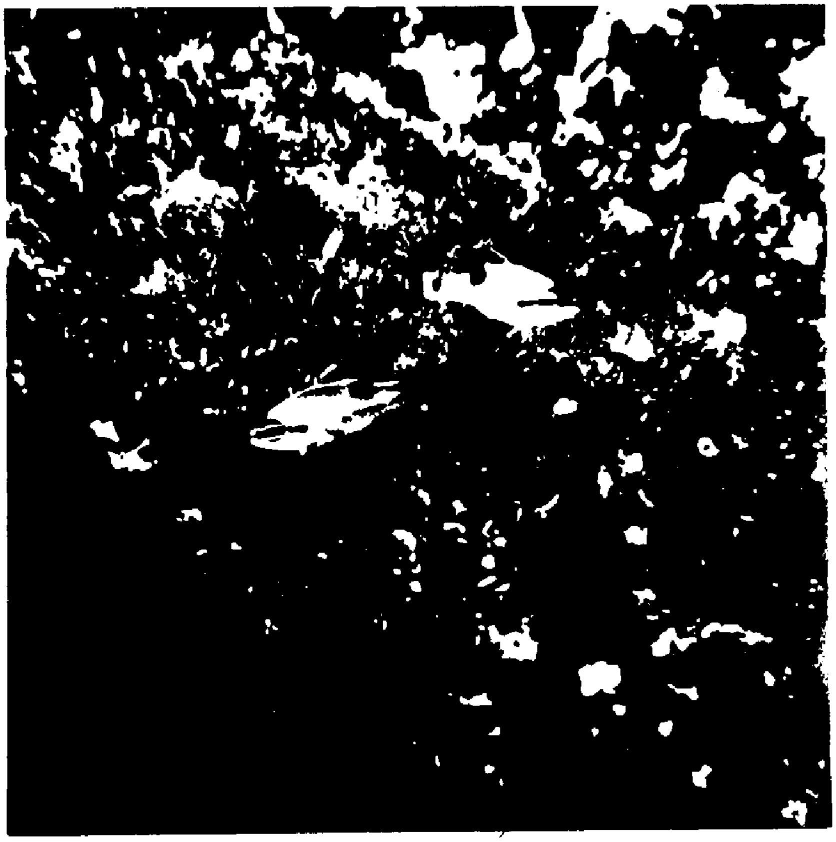


FIGURE 18 (A)

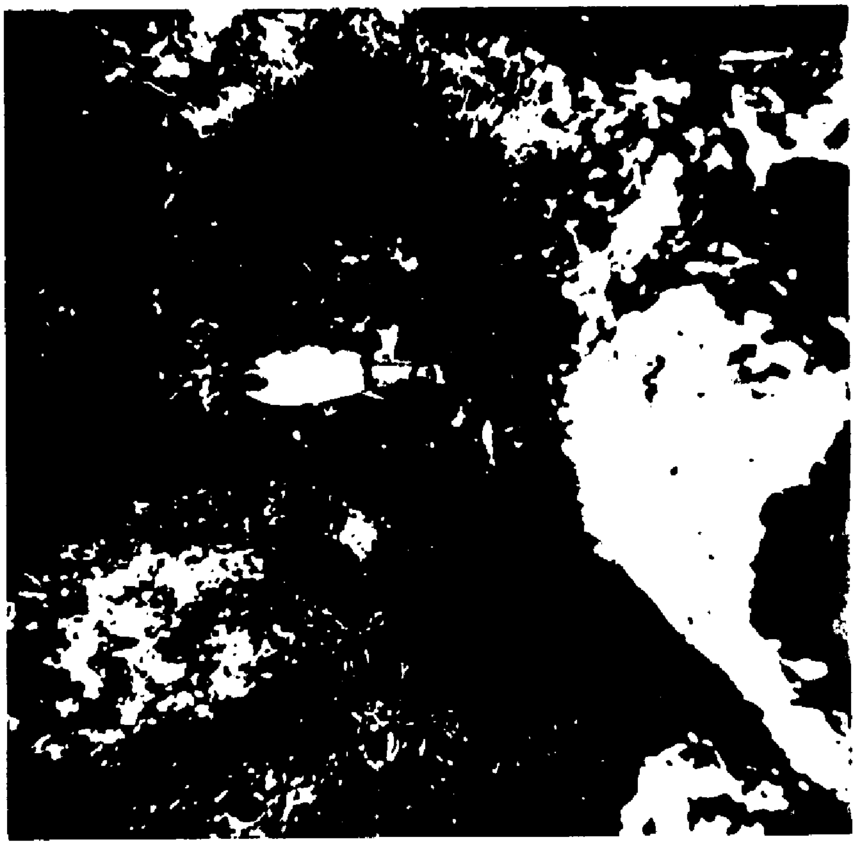


FIGURE 18 (B)

whose cardinalfish residents were observed, one patch reef was especially scrutinized (Figure 19). It was a dome-shaped reef at about 10 meters depth, constructed almost entirely of *Montastrea annularis* coral and completely penetrated by a large cave. This same reef later served as the example of an intermediate stage in the model of Montastrea dome reef succession proposed by Smith and Tyler (1975). It was chosen by the author for close observation and for a rotenone station because of its highly diverse and abundant cardinalfish population. Special interest was also provided by one large, oddly-pigmented cardinalfish, quite possibly an undescribed species, residing within the reef.

This individual was a pale olive-gray in color, and in body and fin shape very much like an *Apogon* species. It had no dark markings at all, and had one anteroposteriorly elongated white spot just below the posterior half of the second dorsal fin. This spot was as wide as the pupil and 1½ times as long. The fish also had two iridescent, white, parallel and horizontal lines on the iris, similar to those of *A. maculatus*.

Numerous attempts (by the author and by several diving companions, including Dr. James C. Tyler) were made to capture this individual with a slurp-gun or net, during several different dives to this patch reef - without success. The largest opening into the hollow reef permitted only partial entry by a SCUBA-wearing diver, making the capture effort difficult. Eventually, after careful notes had been taken on this fish, several (rather poor) color photographs taken, and the rest of the cardinalfish population observed, the reef was poisoned with rotenone. The "pale cardinalfish" did not, unfortunately, turn

Figure 19. Dome-shaped, hollow patch reef at 10 m depth off Turtle Rocks, south of Bimini, Bahamas. The dome is approximately 2.5 m in diameter and rises about 1.3 m from the bottom. It is constructed almost entirely of *Montastrea annularis* coral. Several gorgonians and several brown sponges (*Agelas sparsus*?) are also prominent on the surface of the dome. Small patches of *Agaricia* and *Porites* coral, and several small tubular sponges are scattered around the perimeter. (Photograph by C. L. Smith)

FIGURE 19

up among the specimens collected.

Although it seems likely that this fish was an undescribed species, another more intriguing speculation will be offered here. Its presence among a large population of *A. maculatus*, (114 specimens of that species were collected) and its similarity to that species in several respects – including overall form, the iris lines, and the dorsal spot location (but not color – it is a dark spot in *A. maculatus*) – suggest the possibility that it represents a distinct color phase of *A. maculatus*. Perhaps it is a high male or terminal male phase, as known among many fish groups. Such a situation is, however, unknown in the family Apogonidae, and therefore seems unlikely. The possibility that this fish was merely an aberrant *A. maculatus*, i.e., an anomaly, also seems improbable, in view of the extreme difference in pigmentation from the very uniform normal pattern. No equivalent anomaly has, to the author's knowledge, ever been noted among apogonids.

To return to the consideration of cardinalfish microhabitats, two important observations were made at this dome reef in that regard. First of all, the observation of the "sharing" of one very large *Diadema antillarum* individual – apparently for protection – by no less than five different cardinalfish species, is of interest. These species were: *Apogon maculatus*, *A. binotatus*, *A. townsendi*, *Phaeoptyx conklini*, and *P. pigmentaria*. Two of these species are visible in Figure 20, a photograph of this cardinalfish-*Diadema* association at the dome reef.

Secondly, the apparent preference of cardinalfish species for this kind of hollow, dome-shaped reef, as judged by their great diversity and abundance in the fish community of the reef, is also

Figure 20. Association of cardinalfishes with a long spine sea urchin, inside dome-shaped patch reef at 10 m depth off Turtle Rocks, south of Bimini, Bahamas. Although five different apogonid species were observed to associate with this *Diadema antillarum* individual, only two are visible in this photograph. All but one are *Apogon maculatus*. Of the two fish at the top of the photograph, the one at the right (in postero-ventral aspect) is *A. townsendi*. (Photograph by M. Greenbaum)

FIGURE 20

of interest. The total fish specimen count of the rotenone collection was 558 individuals, of 39 different species - a fairly large and diverse collection. Apogonids accounted for 336, or about 60% of the individuals, and 7 or about 18%, of the species (not including the uncollected "pale cardinalfish"). These seven species (and the number collected) were: *P. conklini* (166), *A. maculatus* (114), *A. townsendi* (45), *A. binotatus* (6), *A. planifrons* (2), *P. pigmentaria* (2), and *A. lachneri* (1). The only other families in the collection approaching this abundance or diversity were pomacentrids (102 individuals of 6 species), wrasses (40 individuals of 5 species) and gobiids (39 individuals of 5 species).

The preference of apogonids for large, protected cave-like areas in reefs was observed on numerous other occasions at Bimini and elsewhere in the Bahamas. The particular type of patch reef described here in detail was simply a pre-eminent example of this tendency, and perhaps represents an ideal apogonid shelter site.

Some final observations of apogonid microhabitats were made by the author and by Mitch Alvo at New Providence, Bahamas, while he and I were involved in teaching a marine biology course there in summer, 1975. The symbiotic association between *Apogon quadrisquamatus* and the sea anemones *Bartholomea annulata* and *Condylactis gigantea*, first described by Colin and Heiser (1973), was extensively observed in shallow water at various locations off this island, in most cases involving *B. annulata*. Although Colin and Heiser reported that the cardinalfish (*A. quadrisquamatus* as well as *A. aurolineatus*, for which they also described the anemone association) were often stung by the anemones, this was not observed at New Providence, and the white spots or lesions caused by contact with tentacles, reported to be common by these authors, were absent from over 70 *A. quadrisquamatus* specimens collected and a similar number observed but not collected.

On one occasion, as the author was attempting to capture an *A. quadrisquamatus* individual associated with a *B. annulata* anemone, a specimen of the clinid blenny *Malacoctenus macropus* turned up instead in the slurp gun. It had not been observed before then, but there seemed to be some possibility, because of the manner of capture, that it had been associating with the anemone.

Also observed at New Providence by Mitch Alvo (pers. comm.) was the use of empty tests of the sea biscuit *Meoma ventricosa* by *Astrapogon puncticulatus* as diurnal shelters. Twenty-one specimens were collected from a total of 60 tests examined. One *Apogon quadrisquamatus* was also found inhabiting a *M. ventricosa* test. An additional *Astrapogon puncticulatus* specimen was taken from one of three empty tests of *Clypeaster rosaceus* (?) examined.

III. DISCUSSION

(A) Geography

Among the six species not present in all three subdivisions of the Bahamas (according to Table 20) three are species known from only a very few collections from any locality. Thus Apogon anisolepis is known from only two specimens, one Bahamian; A. leptocaulus is known from only four specimens, one Bahamian; A. mosavi is known from five collections, three made in the Bahamas. It is reasonable to speculate that if more collections were made, at the appropriate depths and in the appropriate habitats, the gaps in distribution in the Bahamas would be filled.

Among the other three species, A. aurolineatus and A. pillionatus are fairly uncommon among collections from any locality and might also be recorded in all three regions with more collecting. A record in "region 3" (West Plana Cay) for A. pillionatus is included among the paratypes for that species (Böhlke and Randall, 1968), so it is only region 1 that lacks a record.

The rarity of A. pseudomaculatus in Bahamian collections may well represent a real distributional barrier between that area and other areas where it is very common. It was suggested earlier (in DISCUSSION of Chapter 2) that it may be ecologically replaced in the Bahamas by A. townsendi or Phaeoptyx pigmentaria. Perhaps the records in region 2 represent strays from areas where it is abundant.

Thus most, if not all, of the twenty species are probably found throughout the Bahamas, with the possible exception of A. pseudomaculatus.

(B) Depth

Reexamination of the species association data (Table 7) in light of these depth data reveals a tendency for significantly positively associated species to have similar depth preferences. This is not surprising, of course, since positively associated species are, by definition, collected together. There is no indication of whether the depth preference similarity causes the association; or if some actual mutual attraction causes the association and the depth preference is secondary; or if the two species are independently selecting a similar habitat or microhabitat that tends to occur at certain depth ranges; or if some combination of these factors is involved.

Species which are not significantly positively associated even though they show a more or less parallel depth distribution, may be selecting different habitats in the same depth range; or may somehow be actively excluding each other; or might indeed be demonstrably associated in larger sample sizes.

There is a clear tendency for negatively associated species to have very different depth preferences. Here depth may have a primary or secondary role in causing the negative association; or it may reflect a habitat selection; or a combination of factors may be involved.

(C) Habitat

The broad habitat categories used here are more or less qualitatively distinct, though no effort will be made here to characterize them in any detail. Because they are arranged in an order which corresponds to the sequence from nearest to furthest from land, they may also be assumed to vary in some roughly directional sense in certain quantitative respects, most obviously in depth. Thus the frequency of occurrence and abundance of different species in different habitats in the shoreline to drop-off sequence may be expected to bear some similarity to that in the depth range sequence from shallowest to deepest. Comparison of the depth and habitat data reveals that such a similarity does indeed obtain.

As with the depth data, positive associations (Table 7) are more or less reflected by similar habitat preferences, and negative associations by different habitat preferences. It is again difficult to infer any causal relationships.

One of the possibly erroneous implications of speaking in terms of depth or habitat "preferences", is that adult fish actively seek such sites. In the case of apogonids, and perhaps many other fish groups, it may be a "seeking" or preferential settling at the larval recruitment stage that brings a species permanently to a particular site. This is indicated by the total absence of cardinalfish and near absence of other fish species from the dome reef at Bimini for at least 10 days after the rotenone collection was made (J. C. Tyler, pers. comm.).

Indeed it is at recruitment or earlier, in the pelagic larval period of the life history of cardinalfishes (and many other species), that many crucial competitive mechanisms and competition-avoiding mechanisms may be operative, but there has been very little investigation in this area.

(D) Microhabitat

Certain of the microhabitat associations observed, as well as certain others described in the literature, may certainly play an important part in the avoidance of competition among the various cardinalfish species.

The association of A. quadrisquamatus and A. aurolineatus with sea anemones (Colin and Heiser, 1973) observed for the former species during the present study, not only protects these species from predators, but also provides them with shelter space distinct from that of other species.

The intimate symbiotic association of Astrapogon stellatus with the live queen conch Strombus gigas (Randall, 1964) and sometimes with the bivalve mollusk Atrina rigida (Livingston, 1971) provide it with a unique type of shelter.

Although Phaeoptyx xenus has been observed to be a sponge dweller in the Bahamas and West Indies (Tyler and Böhlke, 1972), evidently leaving its sponge microhabitat only for nocturnal foraging (Smith and Tyler, 1972), it has been observed apart from this association in the eastern Gulf of Mexico (G. B. Smith, 1976). This difference is revealing in terms of the competition-avoiding role of the association, since apogonids are far less diverse in the latter area and the congeners of *P. xenus* may even be absent (G. B. Smith assigned previous eastern Gulf records of *P. conklini* and *P. pigmentaria* to *P. xenus*). The more highly competitive milieu of Caribbean reefs may be what sometimes promotes the occurrence of *Apogon quadrisquamatus* in tubular sponges (Tyler and Böhlke, 1972).

The role of the apogonid-sea urchin association in terms of interspecific competition is not as clear. The observation of this habit for *A. binotatus*, *A. maculatus*, *A. townsendi*, *P. conklini* and *P. pigmentaria* adds three species to the list of apogonids showing the association in the Western Atlantic. Previously it had been recorded for *A. maculatus* (Livingston, 1971), *P. pigmentaria* (Smith and Tyler, 1972), and questionably for *A. quadrisquamatus* (Smith and Tyler, 1972). Since this list now includes most of the more common and abundant species (Tables 2 and 6), it seems quite possible that the list will grow as more observations are made of the less common species, and that perhaps this behavioral capability is the rule rather than the exception for cardinalfishes.

This suggests that microhabitat specificity may not be the crucial mechanism promoting cardinalfish coexistence in general, although it may be important for a certain few species. Also minimizing the role of such specificity is the apparent non-specificity of *A. quadrisquamatus*, which has been recorded in association with sea anemones, sponges and sea urchins and also apart from any associations. The failure by the author to detect any microhabitat differences between *A. maculatus* and *A. townsendi* during the week-long Hydrolab observations argues further against microhabitat specificity.

Thus, although the depth and habitat analyses showed that these parameters may contribute to a spatial separation of certain species, there is evidently no such thing as a clearly circumscribed spatial niche for each cardinalfish species, with a few possible exceptions such as *Astrapogon stellatus* and *P. xenus*.

A similar situation among species of the territorial pomacentrid guild on Australian reefs led Sale (1974, 1975, 1976) and Sale and Dybdahl(1975) to propose a model of reef fish coexistence that emphasizes stochastic factors rather than the orderly space-sharing mechanisms emphasized by Smith and Tyler (1972).

An alternative hypothesis for instances of coexistence without apparent spatial niche partitioning has been proposed by the author (Dale, 1978) and will be described in the section that follows.

IV. MONEY-IN-THE-BANK: A MODEL FOR CORAL REEF FISH COEXISTENCE

A) Background

The space sharing hypothesis of Smith and Tyler (1972, 1973) is a comprehensive explanation of the coexistence of species in coral reef fish communities. In their view the fineness of niche subdivision, in terms of various spatial parameters, is at the basis of the numerical stability of the highly diverse reef fish community. This view is consistent with the competitive exclusion principle and provides an important perspective for understanding many of the adaptations of reef species.

According to Sale (1974, 1975) some instances of reef fish coexistence do not conform to this orderly explanation, particularly among species of the territorial pomacentrid guild that inhabit rubble patches. These species coexist despite the facts that space is apparently the limiting factor and that they apparently have identical space requirements. Moreover, there is no tendency for a patch to revert to its original species composition after experimental disruption, as might occur if the species composition resulted from a systematic partitioning of living space. Sale and Dybdahl (1975) attempted to detect small-scale patterns of species distribution in simple habitats (units of live _Acropora_ coral and of dead coralline rock), but failed to find any temporal (seasonal) partitioning of space, any subtle microhabitat specializations, or any evidence of species mutually excluding each other from such units.

These finding led Sale (1974, 1975, 1976) and Sale and Dybdahl (1975) to propose an explanation of reef fish coexistence that emphasizes stochastic factors rather than orderly resource partitioning. In this view chance colonization and chance mortality determine small-scale distribution of species and promote coexistence. The important factors that would allow this are:

1. vacant living space becomes available randomly;
2. there is uncontrolled dispersal of pelagic larvae;
3. vacancies are filled on a first come, first served basis;
4. once recruited, reef fish tend to be sedentary.

The overall mechanism may be viewed as a reef fish lottery (Sale, 1974, 1975) in which superabundant pelagic larvae are tickets in a lottery for space on the reef - a lottery won by first arrivals. Coexistence continues because no species wins or loses all the time.

This model has provided a valuable new perspective for understanding reef fish ecology. Certain considerations, however, may argue against its general applicability.

The relative impossibility of making, in complex habitats, the kinds of quantitative observations or doing the kinds of elegant experiments that Sale (1974, 1975) and Sale and Dybdahl (1975) made and did in simpler habitats perhaps dictated their choice of these simpler habitats. Nevertheless, both rubble patches (Sale, 1974, 1975) and small, isolated, living or dead coral colonies (Sale and Dybdahl, 1975) may be qualitatively different in some important respects from larger reef formations that support more diverse fish assemblages. I would assert that, most importantly, the latter habitats seem to be somewhat more predictable and more stable (Smith, 1973; Smith and Tyler, 1975), although direct comparison of the two habitat extremes by the same methods is needed to substantiate this assertion.

There may be a more fundamental flaw in the lottery model related to its basis in the superabundant production of dispersive pelagic larvae that is apparently typical of many reef fish species. If the general features ascribed to this larva production are true, and I am not arguing otherwise, then the population of larvae from which recruits are drawn may be viewed as a multispecific pool, drifting over fairly wide geographic areas. Random recruitment from this pool would, statistically, have to reflect the relative proportions of the different larval species in the pool, as emphasized by Sale and Dybdahl (1975: 1354): "The species composition of a number of adjacent patches will be a reflection of the relative abundance of colonists of different species." The larval proportions, in turn, reflect adult proportions, as emphasized by Sale (1974: 205): "...the number of recruits potentially available for settlement within a patch of rubble is dependent on the total population of animals of that species in the region, and is independent of the numbers in that particular patch."

I would argue that this framework precludes the possibility of avoiding competitive exclusion between two closely related (or intraguild) species. Either each species somehow always has an average larva population (average in spatial and temporal terms) in this pool that is precisely the proportion necessary to continually renew the adult population proportions, or one species will, based on even the slightest competitive advantage, have a tendency to progressively enhance its proportions in the larval pool, resulting inexorably in the competitive exclusion of the other species.

Attainment of the first condition, or avoidance of the second, would require the existence of some counterbalancing mechanism or negative feedback control.

Sale (1974) cites Beverton and Holt (1957) in support of one possibility, that high mortality of pelagic larvae has some homeostatic effect on relative recruitment proportions, but how this would work is not explained. Perhaps there is preferential predation on the more abundant larval species. That larvae of closely related species might differ enough for such predator selectivity is supported by McPhail's (1969) demonstration that larvae of two genetic varieties of stickleback show behavioral differences affecting their vulnerability to predation.

In terms of the lottery analogy, if one species can buy at least a few more tickets than another, or, more precisely, if one species can have more tickets in the drum at the moment of drawing, then that species' statistically inevitable greater number of wins will, by positive feedback, eventually eliminate the other species from the game.

If the "larval pool" scenario is more or less valid, then the whole geographic range of two sympatric species may be viewed more or less as a closed system. In that case, if the two species are strongly competing for the limiting resource, competitive exclusion will result. Again, if this scenario is valid, local spatial and temporal unpredictability is irrelevant - it would only add some "noise" to the system.

Sale and Dybdahl (1975: 1354) have asserted that "The species composition of the fishes occupying small areas on a reef will be best understood in terms of chance colonization and chance mortality.

Competitive interactions between residents seem likely to be important only in so far as they affect either of these processes." This may be true, but competition in these terms is all that is necessary to bring about competitive exclusion.

In the alternative model (and financial analogy) presented below, two or more species ("investors") can coexist in some habitats ("stock market") because of excess larva production ("interest") in other habitats ("savings banks") in which they occur alone.

(B) Analogy

At yearly intervals, investors a, b, and c convert all their investments into cash, which they then reinvest. At each reinvestment time investors a, b, and c put $10,000 into 5% annual interest accounts at savings banks A, B, and C, respectively, and a variable amount in the stock market (X). A year later each investor converts his bank account ($10,500) and stocks into cash. He then reinvests $10,000 in the bank and the remainder in the stock market. Each year be plays the stock market with an amount equivalent to the money obtained from selling last year's stocks plus his bank interest. No matter how badly his stocks do in any year, he always has at least $500 to invest in stocks the next year. The continued presence year after year in a fluctuating stock market of investors a, b, and c, whose luck and investment wisdom may noticeably differ, will puzzle the observer who is unaware of the bank accounts, and who looks only where all three investors are found together, i.e., the stock market.

(C) Model

In the model, investors a, b, and c represent three sympatric reef fish species. Institutions A, B, and C are habitats into which only species a, b, and c, respectively, can recruit successfully and grow to maturity. X is a habitat type that can and often does support all three species. Luck and investment wisdom are analogous to chance and competitive advantage. X habitats may be more common; consequently we would tend to conclude that the co-occurring species have very similar habitat preferences. It is the diversity observed in X habitats that we usually try to explain.

(D) Assumptions

This system could maintain a dynamic equilibrium if:

1. The planktonic larvae of these three species constitute a "pool" within which at least some of the larvae disperse over a fairly wide geographic area.

2. The species in question are sedentary after recruitment.

3. Adults of a species living in its monospecific habitat produce enough larvae to insure repopulation of that habitat, plus a sufficient excess to enter into competition with other species in the multispecific habitats.

Assumptions 1. and 2. are more or less similar to assumptions made by Sale (1974, 1976) for the reef fish lottery model, and probably apply to a wide variety of reef fish species. Assumption 3. is an extension of assumption 1.

(E) Features

1. The relative success of *a*, *b*, and *c* in repopulating *X* habitats could be variable, depending on chance and differences in competitive advantage in *X* habitats. If the *a*-*A*, *b*-*B*, and *c*-*C* relationships did not exist and only *X* was available to *a*, *b*, and *c*, these two factors would promote competitive exclusion. The model allows a large stochastic element to operate in *X* habitats without upsetting the dynamic equilibrium.

2. *A*, *B*, and *C* could be rare habitats if a great excess of larva production is assumed, or less rare if less excess is assumed.

3. There are two possible relationships between *a* and *A*, etc.:

   a) *A* is a marginal habitat for *a*, *b*, and *c*, all of which settle there, but only *a* survives.

   b) *A* is the "preferred" habitat of *a*, and selection has promoted its tendency to recruit there; *b* and *c* do not recruit there successfully.

Natural selection would tend to drive condition a) to condition b), leading to greater and greater differences in habitat preference, and less and less coexistence. Ultimately *a*, *b*, and *c* would not be competitors; selection could lead to adaptation and a decrease in what Slobodkin and Fishelson (1974) have termed "point diversity."

4. If we look at the species in question only in *X* habitats (where we would tend to concentrate our observation, in an effort to understand that diversity), the apparent identity of their habitat requirements would seem to be the proximate factor resulting in coexistence of the three species. This coexistence ultimately

depends, however, on the niche differences operating in *A*, *B*, and *C* habitats – differences we would not tend to see in *X*. Thus habitat similarity is required for the coexistence to be observable at a point in space and time, but would promote competitive exclusion in the long run, in the absence of *A*, *B*, and *C* habitats.

5. Production of superabundant larvae over a prolonged breeding season seems to be a characteristic that has evolved in many reef fish families, and this characteristic would allow the great diversity we observe in these groups. In fact, excess recruitable larva production would be selected for in this model.

6. The larval pool would act as a buffer, insuring that local extinctions are only temporary, since such extinctions would have little effect on the number of recruits available to repopulate that area.

7. In a variant of the model, two species could coexist in *X* habitats even if only one had a bank account habitat, as long as the other species had a decisive competitive advantage in *X* habitats.

8. *A*, *B*, and *C* habitats could take several different forms:
   a) a suboptimal microhabitat: perhaps some facultative symbioses serve this purpose
   b) a marginal, broad habitat type or depth range
   c) a geographic refugium: e.g., if the upcurrent edge of the range of species *a* is beyond that of *b* (perhaps *a* can tolerate some environmental extreme better than *b*) then this fringe area would be the *A* habitat or bank account of species *a*.

(F) Examples

Certain patterns in the habitat and depth data discussed earlier seem to fit the money-in-the-bank model. For example, in terms of broad habitat types (Figures 15 and 16) Apogon lachneri is absent from the shoreline habitat but common and abundant at the drop-off, while A. maculatus is absent at the drop-off and common and abundant at the shoreline. In a third habitat category, the outer shelf, both species are present, often in the same sample. This habitat tends to have the greatest apogonid species richness (as well as the highest overall fish diversity) of the three. The money-in-the-bank interpretation would be that the shoreline and the drop-off are the A and B habitats of A. maculatus (a) and A. lachneri (b), respectively, and that the outer shelf is the X habitat. A. lachneri and A. maculatus also differ markedly in their depth preference, and since these three habitat types tend to occur at different depths, depth could be the overriding factor.

Another pair of species may serve to exemplify the model in terms of depth (Figures 13 and 14). In the 0-10 and 11-20 feet ranges, A. phenax is absent from all samples, while A. binotatus is fairly common. In the 91-140 feet range A. binotatus is absent and A. phenax is present. At intermediate depth ranges both species occur, sometimes together. The interpretation here is that shallow water or deep water may provide bank account habitats for species that coexist at intermediate depths.

Facultative symbioses among western Atlantic apogonid species might also be interpreted in terms of the model. A. quadrisquamatus and A. aurolineatus are each found in a variety of habitats, but both associate in some cases with sea anemones (as described earlier), an association which may function as a bank account. The facultative associations of some apogonid species with Diadema antillarum might also represent bank accounts vis-à-vis other species lacking this habit (unless, as speculated earlier, the ability to enter such an association is shared by most or all of the species).

The examples given above are not offered as any kind of definitive demonstration of the model, which would require far more extensive evidence.

G) Summary and concluding remarks

The money-in-the-bank model may be summarized as follows. Two or more species among which there is no apparent spatial resource partitioning in the habitats in which they coexist, avoid competitive exclusion because of other habitats in which they occur alone. Excess larva production from the monospecific habitats insures a continual supply of recruits for the multispecific habitats.

This model represents a variety of niche overlap, and the variant (Feature 7., above) is a variety of niche inclusion (see, e.g., Pianka, 1974 and Colwell and Fuentes, 1975 for discussions of these). In either case, in the present application, the tendency toward competitive exclusion in the superimposed region is mitigated by dispersal from the non-superimposed region(s). Levin (1976a, 1976b) emphasizes the importance of dispersal and of fugitive strategies in facilitating a similar kind of coexistence of competitors. The reef fish larval pool represents the "bath" of his calculations.

An underlying assumption of the model is that larvae of the species in question are ecologically identical. It is possible, however, that one or more mechanisms operating at this stage provide the negative feedback necessary to prevent competitive exclusion. As mentioned earlier, differential predation on the larval species might have this function. Various other kinds of niche separation in the pelagic stage or at settling might also override the effects of postlarval competition. In the virtual absence of information on the ecology of reef fish larvae, one can only speculate on these matters.

Another somewhat tenuous underlying assumption concerns the applicability of the competitive exclusion principle. In instances where predation keeps competing prey populations below carrying capacity, the principle may not apply, as has been shown in numerous field studies (e.g., Connell, 1961) and laboratory studies (e.g., Slobodkin, 1964), as well as theoretically (Parrish and Saila, 1970) and by simulation (Cramer and May, 1972). This effect may be relevant in the present context. Alternatively, a network of interference competition among similar species may allow coexistence without any heavy predation (Jackson and Buss, 1975).

With or without these cautionary considerations I do not propose the money-in-the-bank model as a comprehensive explanation of reef fish coexistence and diversity. It may, however, help explain some apparent exceptions to the space sharing hypothesis. Perhaps other apparent exceptions will prove, upon closer inspection, not to be exceptions. On the other hand, in many cases the mechanics of short-term species distribution patterns may indeed be best understood in purely stochastic terms.

Even communities that are stable over long periods may have a largely stochastic basis. I would suggest that the "urn and ball game" (Cohen, 1976; May, 1976) is an apt metaphor for explaining some of the apparent order and determinism of larger reef fish communities. In this game an urn initially contains one black and one white ball, and then one ball is randomly removed at a time and put back with another of the same color. After a large number of turns the proportion of white balls will tend to converge on some steady, limiting value. This value, however, is equally likely to be anywhere between 0 and 1, and essentially depends on the vagaries of the first few turns. If only one run of the game is witnessed, there is a strong illusion of determinism, even though the result depends on a purely stochastic process. In the coral reef context, the long term stability of the total biotic community of a reef may ultimately depend on the statistical accidents of early colonization. Russel et al. (1974) demonstrated the importance of chance factors in the colonization of artificial reefs by coral reef fishes.

It is unlikely that coexistence of species in the coral reef fish community, among the most diverse and complex of vertebrate communities, will be completely explainable by any one general model. As pointed out by Clarke (1977), different mechanisms may even operate among different species within a single genus. It is possible, however, that several simple, interacting mechanisms may adequately account for the greater part of the coexistence and diversity in this community. The money-in-the-bank model is here proposed as one of these mechanisms.

CHAPTER FOUR: Temporal Factors

I. METHODS

(A) Reproductive seasonality

One possible means of competition avoidance among the various apogonid species would be differences in reproductive season. This might function in several ways. For example, more territory or more of a special kind of shelter might be required during courtship or during the brooding of eggs. Staggering of reproductive season would reduce interspecific competition for such territory or shelter. Another possibility would be avoidance of spatial or trophic competition between newly recruited juveniles of different species.

One simple way of assessing the possibility of reproductive season differences would be to record evidence of reproductive condition in the adult specimens being studied, and tabulate these data according to month of capture. This was done using, as evidence, mouth in brooding condition (i.e., greatly expanded buccal cavity), or eggs actually found in the mouth. Several instances of oral brooding observed in the field were added to this tabulation, as were records from the literature.

A second kind of evidence would be seasonal differences in the occurrence of recruit-sized individuals of the different species. Such evidence was sought by tabulating the occurrence of specimens under 15 mm standard length according to month of capture. This criterion is approximately equivalent to "$\leq$ 20 mm total length", which Luckhurst and Luckhurst (1977) used to designate recruit-sized apogonids.

(B) Circadian activity patterns

1. In situ observation

Cardinalfishes in general are considered nocturnal in habits, and there are no known exceptions to this in the western Atlantic (although some diurnal species occur elsewhere). Nevertheless, the classification "nocturnal" may obscure more subtle differences in activity cycles that could be important in the avoidance of competition. Perhaps because of the difficulties and hazards involved in night diving, few field observations of cardinalfish nocturnal habits have been made. Some of the most useful and detailed information was collected by Collette and Talbot (1972) during their saturated diving mission from the Tektite underwater habitat. The numerous advantages of diving under such conditions made possible the prolonged *in situ* observations that enabled these investigators to document subtle differences in nocturnal-diurnal changeover among various reef fish species, including several apogonid species.

Collection of changeover data for the present study was carried out by the author during the seven-day saturated diving mission (from the underwater habitat Hydrolab, off Grand Bahama, in March, 1973) that was mentioned earlier. During this week, the author and the two other aquanauts, C. Lavett Smith and Marvin Greenbaum, made a total of 26 excursions, two men at a time, from the habitat to a selected patch reef at a depth of 15 m. Figure 17 shows the typical daytime distribution of apogonid species on and near this study reef.

The excursions averaged about 1 hour and 25 minutes each, and the author took part in 17 of them, including four during evening changeover, two during morning changeover, and two night dives. Activity pattern observations made during these dives are described in Dale (1975) and this chapter.

2. Laboratory observation

During the summer of 1974 the author was able to spend about 3½ months at the Lerner Marine Laboratory, the American Museum's field station in Bimini, Bahamas. One of the projects initiated during this time was a laboratory investigation of cardinalfish changeover behavior.

Live specimens of six different apogonid species were collected, using SCUBA, with the fish anesthetic quinaldine. Several collecting trips were made to each of two locations:

Location #1: a curved rocky ledge about 75 m in length, at a depth of 3 to 7 m, in the Bimini lagoon about 250 m east of the desalination plant on North Bimini.

Location #2: a coral-rock ledge at about 7 m depth, about 15 m west of the western side of the northern end of the northernmost island of Turtle Rocks, south of South Bimini.

Because of the initially high mortality of specimens during and shortly after collections were made, several changes and improvements were made in the collecting technique, which virtually eliminated this problem:

a) At first, 20% quinaldine in acetone, carried in a small plastic dishwashing detergent bottle with closable squirting top, was used for collecting several fish at a time. This concentration was far higher than necessary (and may have contributed to the loss of specimens), but since the quinaldine-acetone solution was diluted with incoming water after each squeeze, it seemed suitable to start with a high concentration so that this dilution did not render the mixture ineffective after the first few squeezes. This problem was solved by the invention of a simple device for squirting the anesthetic without any dilution (Figure 21A). With the aid of this device, 10% quinaldine in acetone could be used.

b) Anesthetized fish or stunned fish (only partially anesthetized and still able to evade capture) were collected with a dip net or slurp gun and transferred to a mesh bag (the standard yellow nylon "goody bag" commonly available in dive shops). Since the bag was not held open in any way after the metal ring at the mouth was closed, fish collected soon after the beginning of a dive were rubbed around quite a bit in the folds of the bag during the rest of the dive, sustaining damage to fins and scales. A kind of frame device, placed inside the bag to hold it open, was made by cutting sections out of a plastic five-gallon bucket (Figure 21B), and this problem was minimized.

c) Because apogonids have a physoclistous swim bladder, which adjusts buoyancy rather slowly, it is possible that in spite of the relative shallowness of the collecting locations, specimens were injured as a result of swim bladder expansion during ascent to the surface at the end of a collecting dive. Therefore a practice of ascending very slowly with the

Figure 21. Two devices used in collection of live fish specimens. (A) Plastic bottle used for squirting quinaldine anesthetic solution, without dilution occurring during use. (Bottles of a suitable size - about 200 to 400 ml - with flip-top nozzles or similar tops, are used for various household products. The bottle should be flexible but not soft, and flat in shape rather than cylindrical). A polyethylene bag large enough, when fully expanded, to fill the inside of the bottle and extend out and over the neck, is placed inside and filled with the quinaldine solution. The cap is screwed on over that part of the bag that extends over the neck (some vaseline or silicone grease facilitates this). For use underwater the nozzle is opened and the bottle is squeezed while covering the hole with the thumb. When the nozzle is closed and the thumb removed, an amount of water enters the bottle, outside the bag, that is equivalent to the amount of solution that was expelled from the bag. This can be repeated until the bag is empty. (B) Frame device, placed inside nylon mesh collecting bag, to reduce injuries to collected fish. Four sections from the sides, and a circular section from the bottom, are removed from a flexible plastic five-gallon bucket.

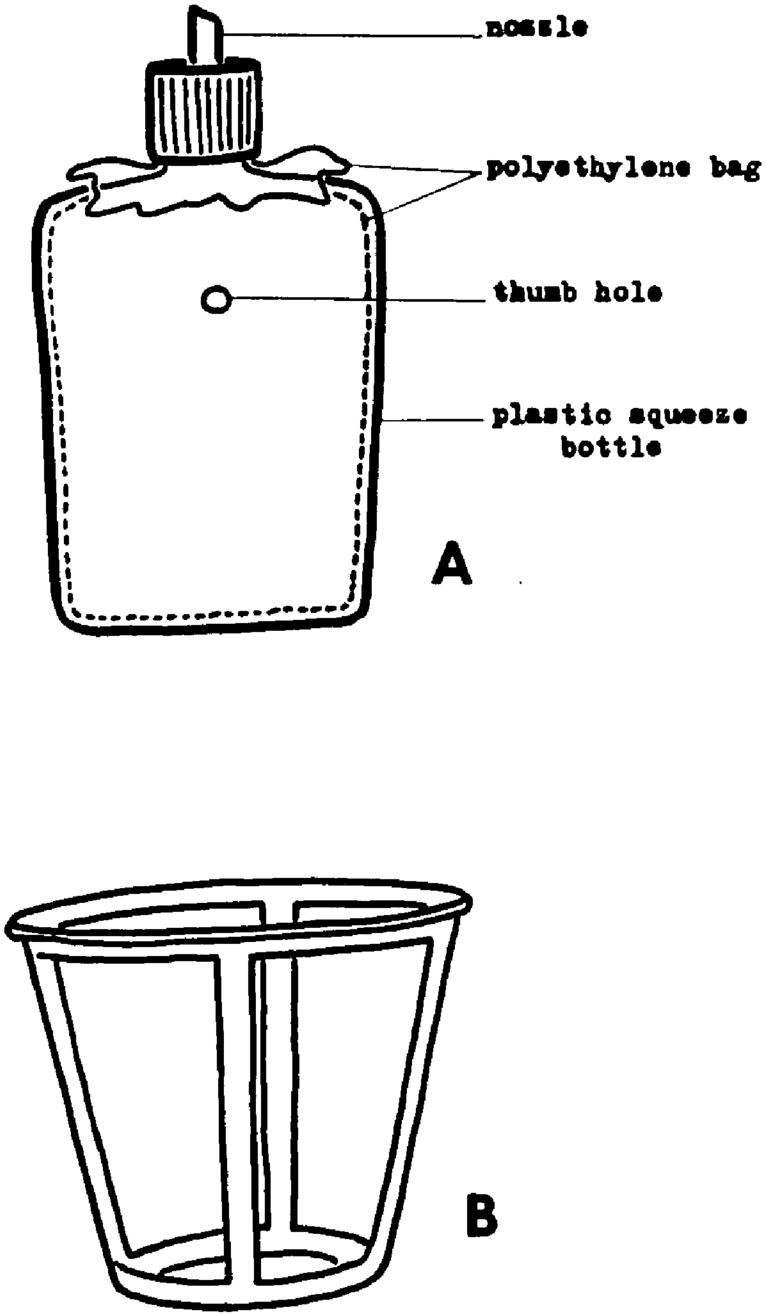

nozzle
polyethylene bag
thumb hole
plastic squeeze bottle
A
B

FIGURE 21

collected specimens (roughly two or three meters per minute) was soon adopted.

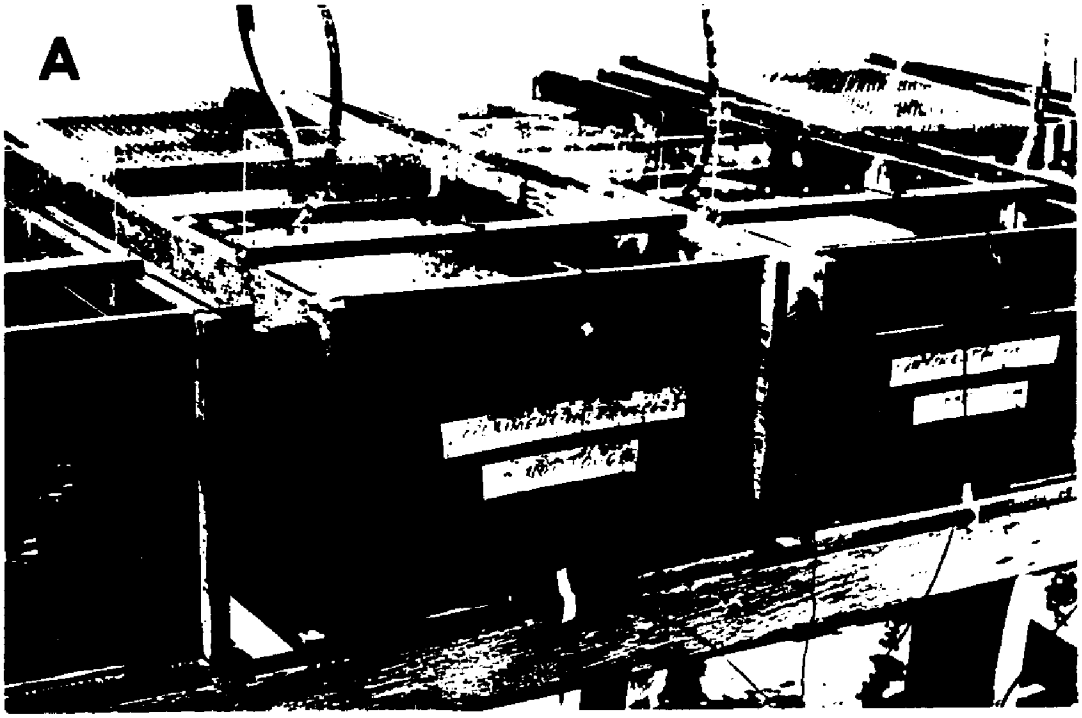
The fish were maintained for at least a day after capture in one of the large outdoor concrete tanks at the Lerner Lab in flowing sea water. They were then transferred to a series of eight glass and plywood aquaria, also outdoors, which were provided with flowing sea water. The configuration of these experimental tanks is shown in Figure 22.

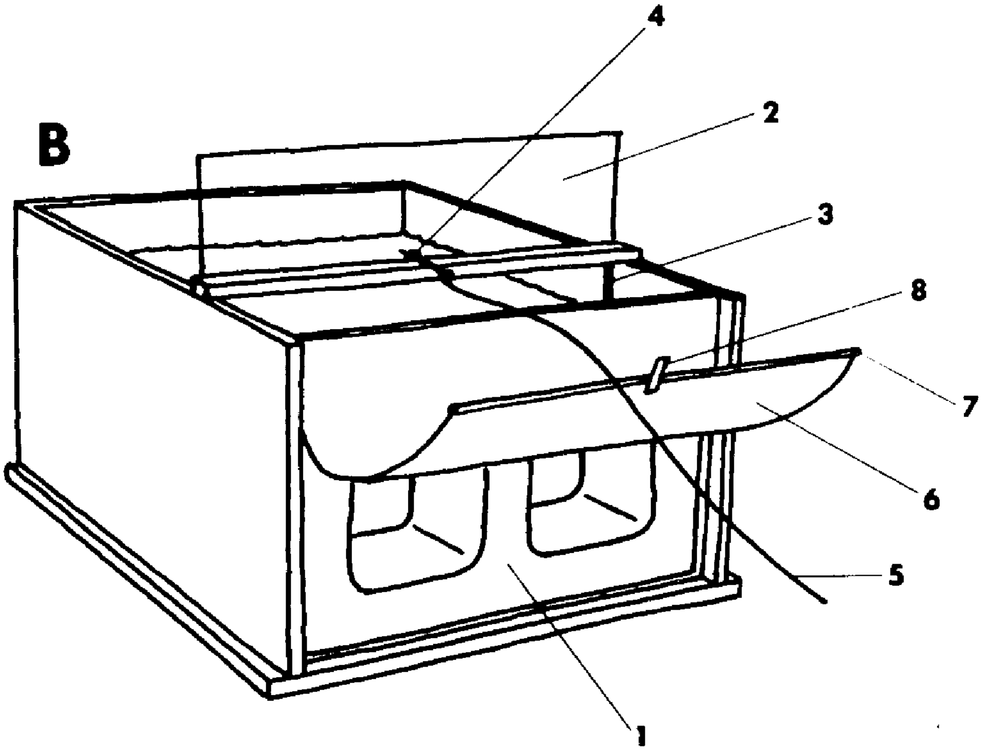
As many as 12 individuals of a given cardinalfish species were kept in a given tank. Each tank was provided with an open area and a shelter space (cinder block). The time of entrance into and exit from the shelter spaces of each species in the morning and evening was monitored for 3 days and again for 6 days with a second series of populations. This was done by dropping a plexiglas partition between the open area and the shelter space, and then counting individuals in the two areas. The partition was then raised until the next count. Counts were made at 15 minute intervals during the morning and evening monitoring periods. In most cases the monitoring covered the period between 0530 and 1200 hours and between 1700 and 2100 hours. The resulting data were analyzed in an attempt to detect species-specific differences in changeover time.

Changing light levels during the course of these observations were monitored with a Photovolt light meter (model #200, Photovolt Corp., N. Y. C.) which gave readings on four scales: 5, 25, 100, and 500 foot-candles. A reading was taken once during each monitoring period, immediately after the partitions were dropped in the tanks.

Although each of the tanks was identical in construction and

Figure 22. Outdoor flowing sea water aquaria at the Larner Marine Laboratory. (A) Tanks as modified for changeover observations. Each tank is about 50 cm wide x 65 cm long x 35 cm deep, and is constructed of plywood, with a glass front. (B) Diagram showing tank modifications. 1. Cinder block inside tank, just behind glass front. 2. Plexiglass partition, shown in raised position, allowing passage of fish between open area in rear of tank and the cinder block spaces. When dropped this partition separates the two areas. 3. One of two slots in sides of tank in which partition slides up and down. 4. Hole in plexiglass partition in which nail is placed to hold partition in raised position. 5. Wire connected to this nail which permits dropping the partition without closely approaching the tank, thus minimizing the possibility of disturbing fish in the tank with a noise, shadow or reflection from the approaching observer. 6. Black plastic curtain covering the tank glass. 7. Metal rod taped into lower edge of curtain to hold it flat against glass. 8. Tab made of plastic tape, for raising curtain (after partition is dropped) to observe and count fish in cinder block spaces.


A


B
4
2
3
8
7
6
5
1

orientation, the fish population in each tank was transferred each night at the end of the evening monitoring period to the tank on its right, or, in the case of the population in the last tank to the right, to the first tank on the left. This minimized the possible influence on the results of undetected differences between the tanks.

Fish populations were fed, daily, with either freeze-dried brine shrimp or freshly caught live zooplankters. The latter were collected in the evening at the Lerner Lab dock during incoming or outflowing tides, at which time there was ample tidal current in the Bimini lagoon for such collection without the need for towing a net. A waterproof lantern, with 100 watt bulb (to attract zooplankton) was suspended in front of the mouth of a standard zooplankton net, which was dropped to just below the surface. In this way, enough tiny shrimps, copepods, fish larvae, etc., were collected in a few minutes to feed the fish populations in the eight tanks. Because the fish were fed far more successfully on this live food than on the freeze-dried food, use of the latter was avoided if possible.

3. Brain morphology

The possibility that brain morphology might in some way reflect differences in changeover behavior was then investigated. A preliminary survey had suggested that a certain pattern might indeed be demonstrable, namely that species which left the shelter site later in the evening and returned earlier in the morning, under darker conditions in both cases than other species, had larger optic lobes (relative to the rest of the brain) than the earlier-in-evening, later-in-morning species. A simple way of collecting data to test this possibility was decided on. After dissecting away the integument and muscle from the dorsal surface of the head, and the thin roof of the skull, measurements were made with a dial caliper, to the nearest tenth millimeter, on the dorsal aspect of the brain. "Size of optic lobes" was measured as the sum of the length + width of those lobes; "rest of brain" was measured as the sum of the lengths + widths of the cerebrum, cerebellum, and medulla (Figure 23).

Several alternative ways of collecting this data, which might seem more direct, had certain disadvantages. For example, comparing optic lobe size with the linear dimensions of the whole brain was not suitable because of the varied degree of bending and compactness of the brain among different species. These variations seem to represent a sort of anatomical accommodation to different-sized eyes, which occupy a large part of the volume of the head in the species examined in this study. Another alternative, dissecting out the whole brain and making the comparison on a weight basis, was rejected because of the far greater difficulty of the technique.

Several minor details of the brain measurement technique should be mentioned:

a) Because of a slight assymetry of the cerebrum, i.e., the left hemisphere tended to be slightly larger than the right one, length of the cerebrum was arbitrarily measured as the length of the right hemisphere. Width of the cerebrum was measured across both hemispheres at the widest point, viewed dorsally.

b) Length of the optic lobes was also arbitrarily measured as length of the right lobe, although no assymetry was noticed in this case. Width was again measured across both lobes at

Figure 23. Camera lucida drawing of the dorsal aspect of the brain of *Apogon maculatus*. The specimen dissected is 39.4 mm SL, from collection no. GD73-2, taken off Turtle Rocks, south of Bimini, Bahamas.

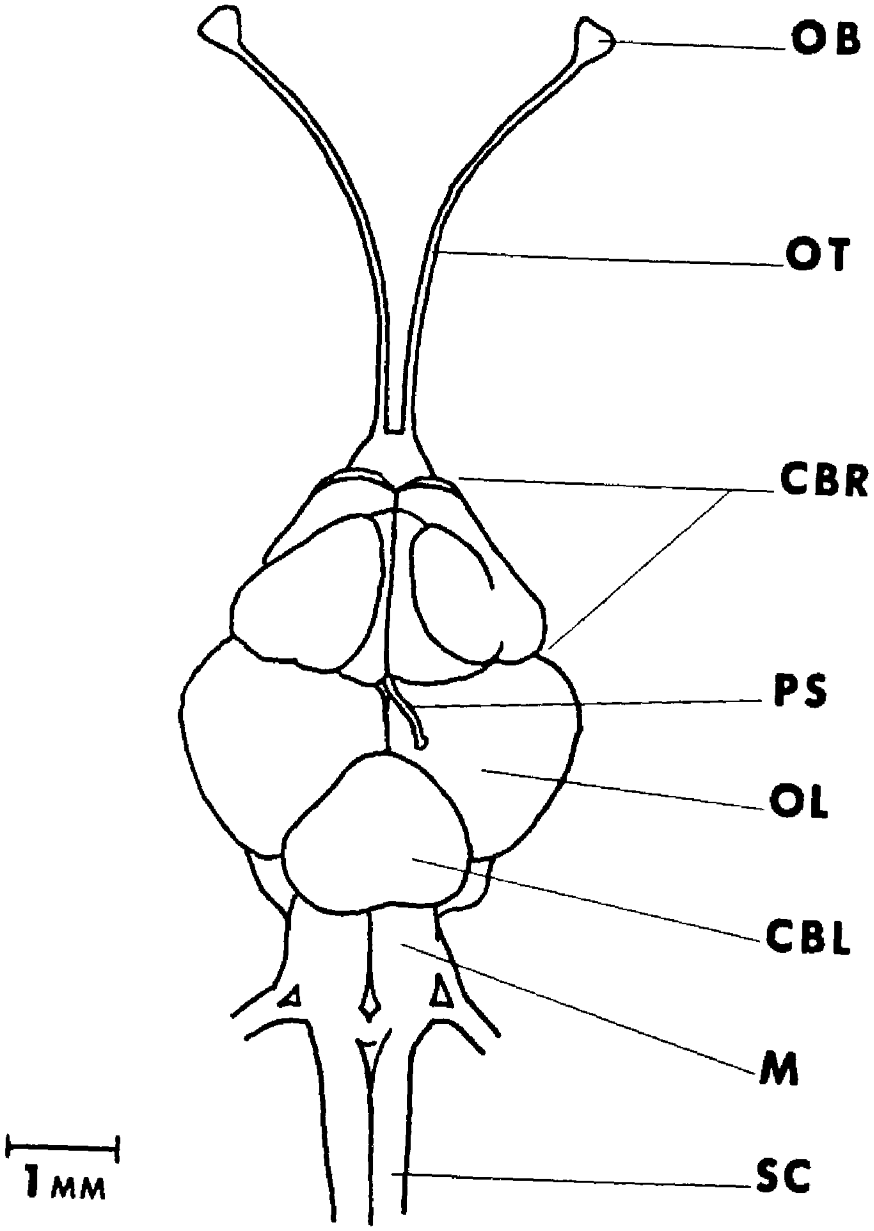


Figure 23

the widest point, in dorsal aspect.

c) The long axis of the cerebrum varied from more or less anterior-posterior in its orientation in some specimens, to an orientation with a noticeable antero-ventral tilt in other specimens. This variation occurred among different-sized individuals of the same species and among similar-sized specimens of different species. A more reliable measurement of the length of the cerebrum was therefore achieved by measuring its long axis, even if that required tilting the specimen so that an anterodorsal aspect was being viewed.

d) Although the medulla did not stand out as a distinct lobe or bilobed structure, and therefore its length would seem difficult to measure, it had a distinct dorsal bulge in all species examined. The measurement was arbitrarily made between the anterior and posterior edges of this bulge.

One additional possibility of an anatomical correlation was also briefly investigated in the present study. Since nocturnal fishes, like other nocturnal vertebrates, tend to have larger eyes as an adaptation to this habit than their diurnal counterparts, it seemed reasonable to suppose that differences in eye size among the different nocturnal apogonid species might show some correlation with changeover behavior. That is, a species which left shelter later in the evening and returned earlier in the morning, in greater darkness in each case than other species, might be in some sense "more nocturnal" than the other species, and have slightly larger eyes. Eye diameter measurements were made on series of specimens of different species, but no apparent pattern or correlation was obtained, and the results are not presented.

II. RESULTS

(A) Reproductive seasonality

Table 25 gives the number of samples of each species that included one or more specimens with expanded buccal cavities, and the number that included one or more specimens under 15 mm SL, according to month of capture. Also in the table are records of oral brooding observed by the author in preserved specimens or in the field, and records of this habit made by other investigators for apogoniis from the Bahamas.

(B) Circadian activity patterns

1. *In situ* observation

The evening changeover period of the cardinalfishes, the period when they leave their diurnal microhabitats for nocturnal feeding areas, was observed at the study reef on March 14, 15, 16 and 17. Arbitrarily defining the limits of this period as the earliest observed emergence from the reef and the latest observation of an individual still in its diurnal place, the evening changeover period of *A. townsendi* was estimated to be 1810-1840, and that of *A. maculatus* to be 1835-1850. A single *A. planifrons* was observed within the reef as late as 1845, but was never seen leaving or hovering outside the reef. It is suspected that its changeover period came after that of *A. townsendi* and *A. maculatus* .

The time of sunset, calculated from tables in the *American Ephemeris and Nautical Almanac*, was about 1823 for these four days

Table 25. Reproductive data for cardinalfishes in the Bahamas, according to month. May, September, and October are omitted from the vertical column headings because no collections made in these months were examined in the present study, and because of a lack of oral brooding records in the Bahamas for these months (except an October record for A. affinis in Smith et al., 1971). The horizontal column heading "UNDER 15 mm" gives the number of samples, of a given species, that included one or more specimens less than 15 mm SL. "B.C. EXPANDED" gives the number of samples of a given species which include one or more specimens with the buccal cavity expanded, indicating oral brooding. "O.B. EVIDENCE" gives one of the following kinds of evidence of oral brooding: a- eggs observed by author in buccal cavities of preserved specimens examined in this study; b- field observations, by author at Bimini, of oral brooding; c- Charney, 1976; d- Smith et al., 1971; e- Breder, 1948; f- Mitch Alvo, pers. comm.; g- Dale, 1975; h- Dale, 1977.

SPECIES (SAMPLES OF THIS SPECIES)	MONTH (COLLECTIONS MADE IN THIS MONTH THAT INCLUDED AT LEAST ONE APOGONID SPECIES)								
	JAN(33)	FEB(7)	MAR(30)	APR(6)	JUN(7)	JUL(13)	AUG(2)	NOV(22)	DEC(5)
Apogon affinis (9)									
UNDER 15 mm	-	-	-	-	-	-	-	-	-
B.C. EXPANDED	-	-	-	-	-	-	-	1	-
O.B. EVIDENCE	-	d	-	-	d	-	-	a	-
Apogon binotatus (33)									
UNDER 15 mm	2	-	1	1	-	1	-	1	1
B.C. EXPANDED	-	-	-	-	-	-	-	1	-
O.B. EVIDENCE	-	-	-	-	-	-	-	-	-
Apogon lachneri (23)									
UNDER 15 mm	-	-	-	-	-	1	-	-	-
B.C. EXPANDED	-	1	-	-	-	-	-	-	-
O.B. EVIDENCE	-	-	-	-	-	-	-	-	-
Apogon leptocaulus (1)									
UNDER 15 mm	-	-	-	-	-	-	-	-	-
B.C. EXPANDED	-	-	-	-	-	-	-	-	-
O.B. EVIDENCE	-	-	-	-	-	-	-	-	-
Apogon (77) *maculatus*									
UNDER 15 mm	2	1	-	1	-	-	-	1	-
B.C. EXPANDED	3	1	1	1	-	-	1	-	-
O.B. EVIDENCE	c	-	-	-	-	a,b,c	-	-	-

Table 25 (continued)

	JAN(33)	FEB(7)	MAR(30)	APR(6)	JUN(7)	JUL(13)	AUG(2)	NOV(22)	DEC(5)
Apogon mosavi (2)									
UNDER 15 mm	-	-	-	-	-	-	-	-	-
B.C. EXPANDED	1	-	-	-	-	-	-	-	-
O.B. EVIDENCE	a,h	-	-	-	-	-	-	-	-
Apogon phenax (16)									
UNDER 15 mm	1	-	1	-	-	-	-	-	-
B.C. EXPANDED	-	-	1	-	-	-	-	-	-
O.B. EVIDENCE	-	-	-	-	-	-	-	-	-
Apogon planifrons (12)									
UNDER 15 mm	-	1	1	-	-	1	-	-	1
B.C. EXPANDED	-	-	-	-	-	-	-	-	-
O.B. EVIDENCE	-	-	-	-	-	-	-	-	-
Apogon quadrisquamatus (11)									
UNDER 15 mm	-	-	-	-	-	-	-	-	-
B.C. EXPANDED	2	-	1	-	-	-	-	1	-
O.B. EVIDENCE	-	-	-	-	f	-	-	-	-
Apogon robinsi (6)									
UNDER 15 mm	-	-	-	-	-	-	-	-	-
B.C. EXPANDED	-	-	-	-	-	-	-	-	-
O.B. EVIDENCE	-	-	-	-	-	-	-	-	-
Apogon townsendi (44)									
UNDER 15 mm	3	-	6	1	1	1	-	-	-
B.C. EXPANDED	-	-	3	-	-	1	-	-	-
O.B. EVIDENCE	-	-	g	-	-	a,b	-	-	-

Table 25 (continued)

	JAN(33)	FEB(7)	MAR(30)	APR(6)	JUN(7)	JUL(13)	AUG(2)	NOV(22)	DEC(5)
Astrapogon puncticulatus (34)									
UNDER 15 mm	6	2	5	2	2	1	-	4	1
B.C. EXPANDED	-	1	-	-	-	-	-	-	1
O.B. EVIDENCE	-	-	-	-	-	-	-	-	-
Astrapogon stellatus (2)									
UNDER 15 mm	-	-	-	-	-	-	-	-	-
B.C. EXPANDED	-	-	-	-	-	-	-	-	-
O.B. EVIDENCE	-	-	-	-	-	-	e	-	-
Phaeoptyx conklini (89)									
UNDER 15 mm	7	2	9	2	-	6	1	5	2
B.C. EXPANDED	2	1	6	3	-	5	-	5	-
O.B. EVIDENCE	c	-	c	-	-	b	-	c	-
Phaeoptyx pigmentaria (60)									
UNDER 15 mm	2	-	-	-	-	2	-	-	-
B.C. EXPANDED	-	-	-	-	-	1	-	1	-
O.B. EVIDENCE	-	-	-	-	-	-	-	-	-
Phaeoptyx xenus (13)									
UNDER 15 mm	-	-	-	1	-	-	-	-	-
B.C. EXPANDED	-	-	1	-	-	-	-	-	-
O.B. EVIDENCE	-	-	-	-	-	-	-	-	-

Table 25 (continued)

(a minute or so earlier on March 14, and a minute later on March 17). In their study of reef fish activity patterns in the Virgin Islands, Collette and Talbot (1972) determined that the evening changeover period (defined in their work as the earliest observed onset of activity) of A. townsendi was 1740-1845, or from shortly before to shortly after sunset (1758-1812 during their 17 day study in September and October). This relation to sunset roughly coincides with the present findings, further indicating that, as these authors suggested, this behavior is light-mediated. Collette and Talbot (1972) also reported that the evening changeover period of A. maculatus followed that of A. townsendi. Based on more limited data, they calculated that A. maculatus became active at about 1840, or roughly 30 to 40 minutes after sunset (somewhat later in relation to sunset than found in the present study).

A. townsendi emerged from the reef in the evening in a characteristic manner. After slowly leaving their caves with approaching darkness, they seemed to assemble in a loose group over the south end of the reef, and then moved down the side of the reef and out to the adjacent sandy areas, a meter or less from the bottom, where they apparently spent the night feeding. Livingston (1971) reported that A. townsendi in the Florida Keys foraged individually or in groups, close to the bottom, near its diurnal habitat. Smith and Tyler (1972) found that the nighttime feeding of A. townsendi took place 2.5 m and higher above the sand flats adjacent to its daytime patch reef habitat. Collette and Talbot (1972) described the nocturnal feeding location of this species as 25-30 cm above the reef.

A. maculatus, at least the smaller individuals, seemed to leave their caves and congregate near the base of the reef, a few inches from the bottom, hiding in crevices if approached. Whether or not they moved further from the reef later on was not determined, but it is suspected that they also spend the night feeding over the sand flats. Starck and Davis (1966) and Livingston (1971) found that _A. maculatus_ in the Florida Keys feeds close to the bottom, near its daytime habitat, and Smith and Tyler (1972) described similar habits for this species in the Virgin Islands. Collette and Talbot (1972) reported that _A. maculatus_ stayed low over the reef at night. Both _A. maculatus_ and _A. townsendi_ have been observed to feed to a limited extent during the day (Livingston, 1971).

Numerous individuals of _A. quadrisquamatus_ were observed several times hovering over the sand flats southeast of the test reef. These observations were made, on the average, shortly after sunset, and before and after sunrise. No attempt was made to judge how long they remained in this area, but they were not seen there during the day or during one visit to the reef at night. Collette and Talbot (1972) reported that _A. quadrisquamatus_ was active from about 1820 (shortly after sunset) generally until 0515 to 0535, and on one occasion until 0550, apparently due to a storm-caused increase in turbidity. Sunrise occurred at 0609 to 0612 during their study.

The morning changeover period of _A. townsendi_ and _A. maculatus_, that is, the time when they return to the reef from their nocturnal feeding areas and reenter their diurnal microhabitats, was observed on two occasions (March 16 and 19). Defined as the period from the time of earliest observed occupying of a daytime cave to the latest time an individual was observed outside the reef structure, the morning changeover period of A. townsendi was estimated to be 0550-0620, and of A. maculatus to be 0550-0615. These times are based on too few observations to be reliable, but the overall impression, difficult to quantify, was that the morning changeover periods of these two species were substantially overlapping. The time of sunrise on these two mornings was 0623 (March 16) and 0620 (March 19). The manner in which the reef was approached and entered by these two species in the morning seemed to be the reverse of the emergence pattern of the evening changeover period.

Collette and Talbot (1972) found that morning changeover (time of last observation of an active individual) for A. townsendi generally occurred between 0505 and 0615 and was delayed about 45 minutes during the storm-caused turbidity period. They estimated the changeover period for A. maculatus, for which they again had less data, to be 0540-0550. Thus the data of the present study, which indicate that these two species both resume their diurnal activity regime shortly before sunrise, more or less reflect the findings of Collette and Talbot (1972).

2. Laboratory observation

Table 26 shows the numbers of individuals in the tank populations during the two monitoring periods. Because of the fact that only three species were represented by sizable populations during both periods, the results for these species are emphasized.

Figure 24 shows the laboratory "changeover" data for these three species. The three species were: P. conklini, collected at Turtle Rocks; A. binotatus, collected in the Bimini lagoon; and A. maculatus

	Collection locality		Tank population size	
Species	Turtle Rocks	Bimini lagoon	1st monitoring period	2nd monitoring period
*Apogon maculatus**	x		9	10
		x	9	4 + 12
*Apogon binotatus**		x	6	11
Apogon townsendi	x		1	9
*Phaeoptyx conklini**	x		8 + 9	12 + 12
Phaeoptyx pigmentaria	x		2	3
Phaeoptyx xenus	x		1	-

Table 26. Numbers of individuals of different apogonid species in tank populations of changeover experiments. Where two numbers are given, they represent populations in two separate tanks. * The results for these three species are described in greater detail since they were represented by appreciable numbers during both periods.

Figure 24 (A-I). "Changeover" data for outdoor tank populations of apogonid species in an experiment performed at the Lerner Marine Laboratory in Bimini, Bahamas, August 1-3, 10-15, 1974. Each curve represents a "5-point moving average" of the percentage of individuals in the open areas of the tanks (left ordinate). Data were taken at 15 minute intervals. MAC-BL = *Apogon maculatus* from Bimini lagoon. MAC-TR = *A. maculatus* from Turtle Rocks. BIN = *A. binotatus*. CON = *Phaeoptyx conklini*. + = photometer light reading in foot-candles (right ordinate). See text for further explanation.

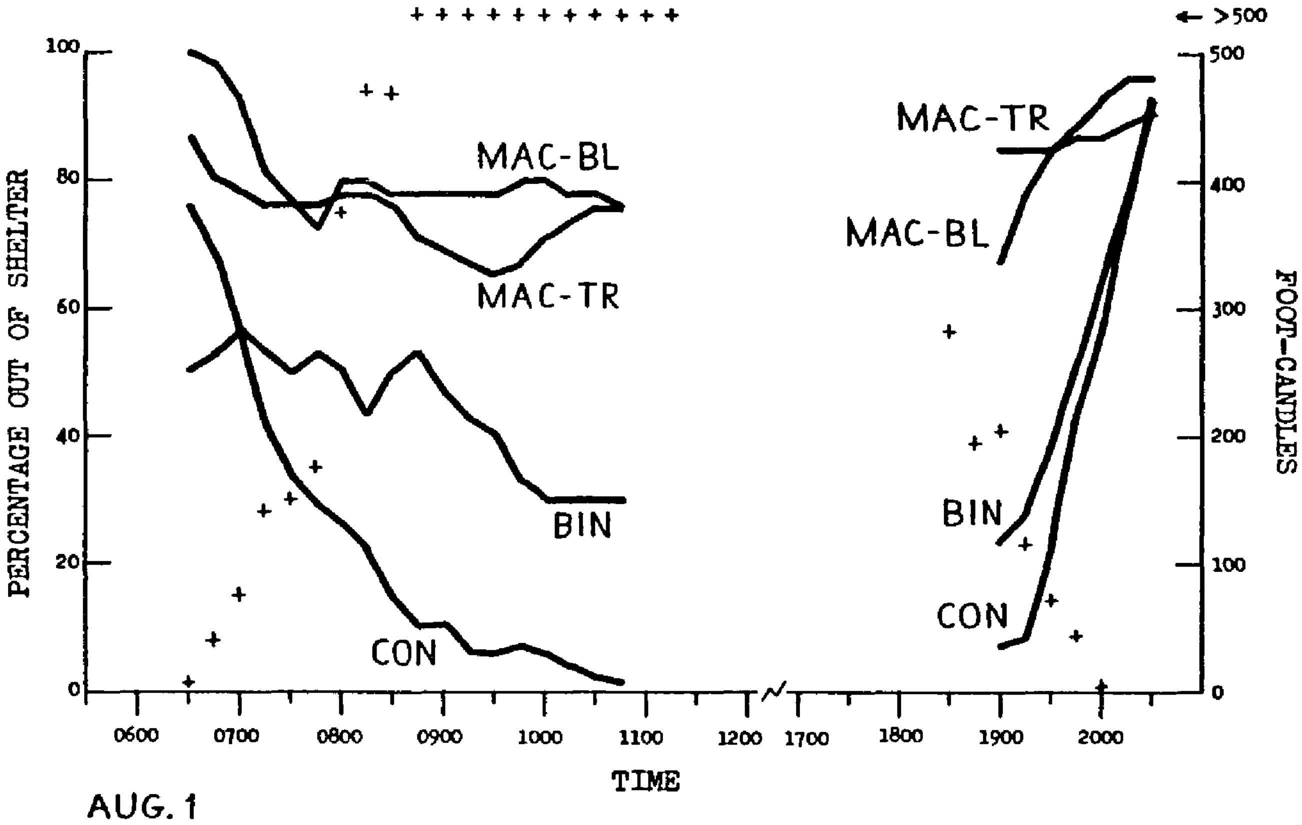

PERCENTAGE OUT OF SHELTER
FOOT-CANDLES
TIME
MAC-BL
MAC-TR
BIN
CON
MAC-TR
MAC-BL
BIN
CON
← >500
100
80
60
40
20
0
500
400
300
200
100
0
0600
0700
0800
0900
1000
1100
1200
1700
1800
1900
2000
AUG. 1

FIGURE 24 (A)

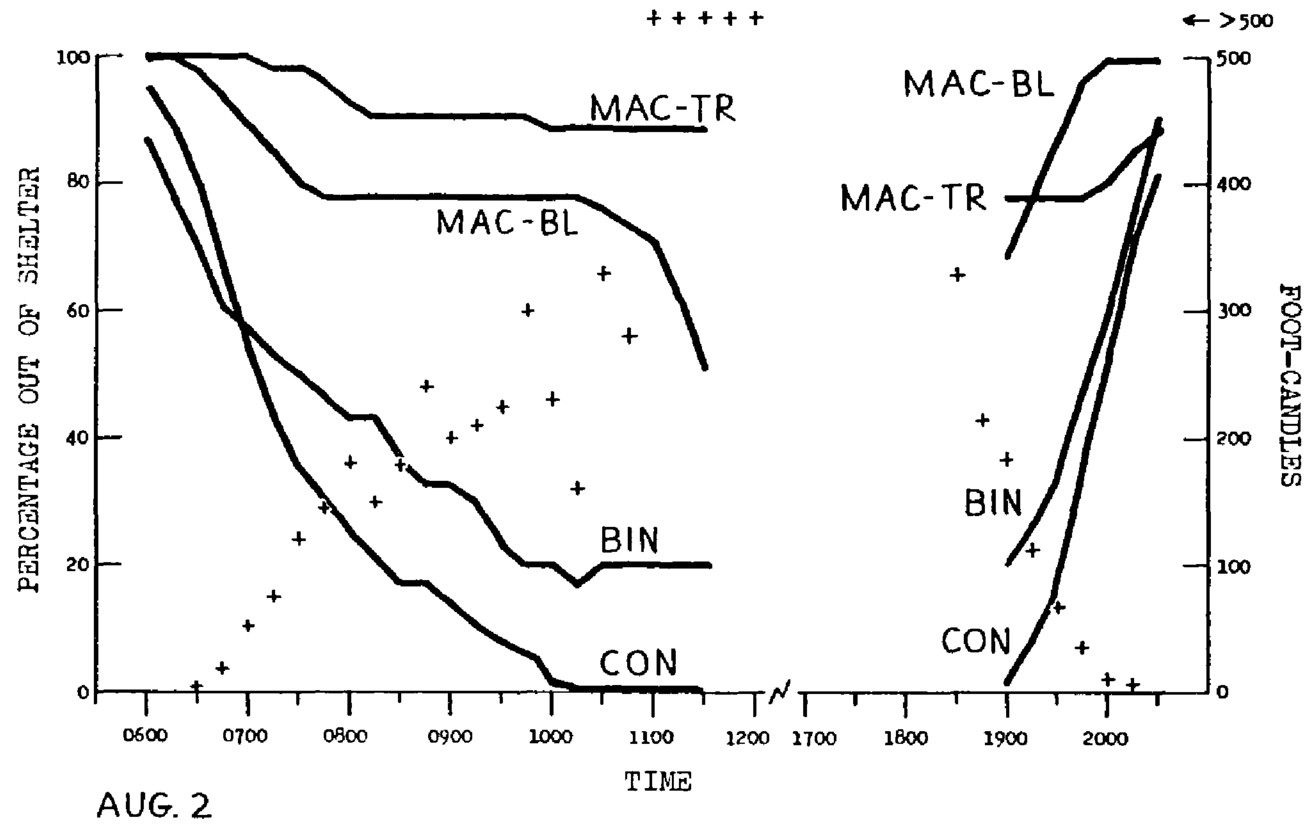

+ + + + +
← >500
100
80
60
40
20
0
PERCENTAGE OUT OF SHELTER
500
400
300
200
100
0
FOOT-CANDLES
MAC-TR
MAC-BL
BIN
CON
MAC-BL
MAC-TR
BIN
CON
0600
0700
0800
0900
1000
1100
1200
1700
1800
1900
2000
TIME
AUG. 2

FIGURE 24 (B)

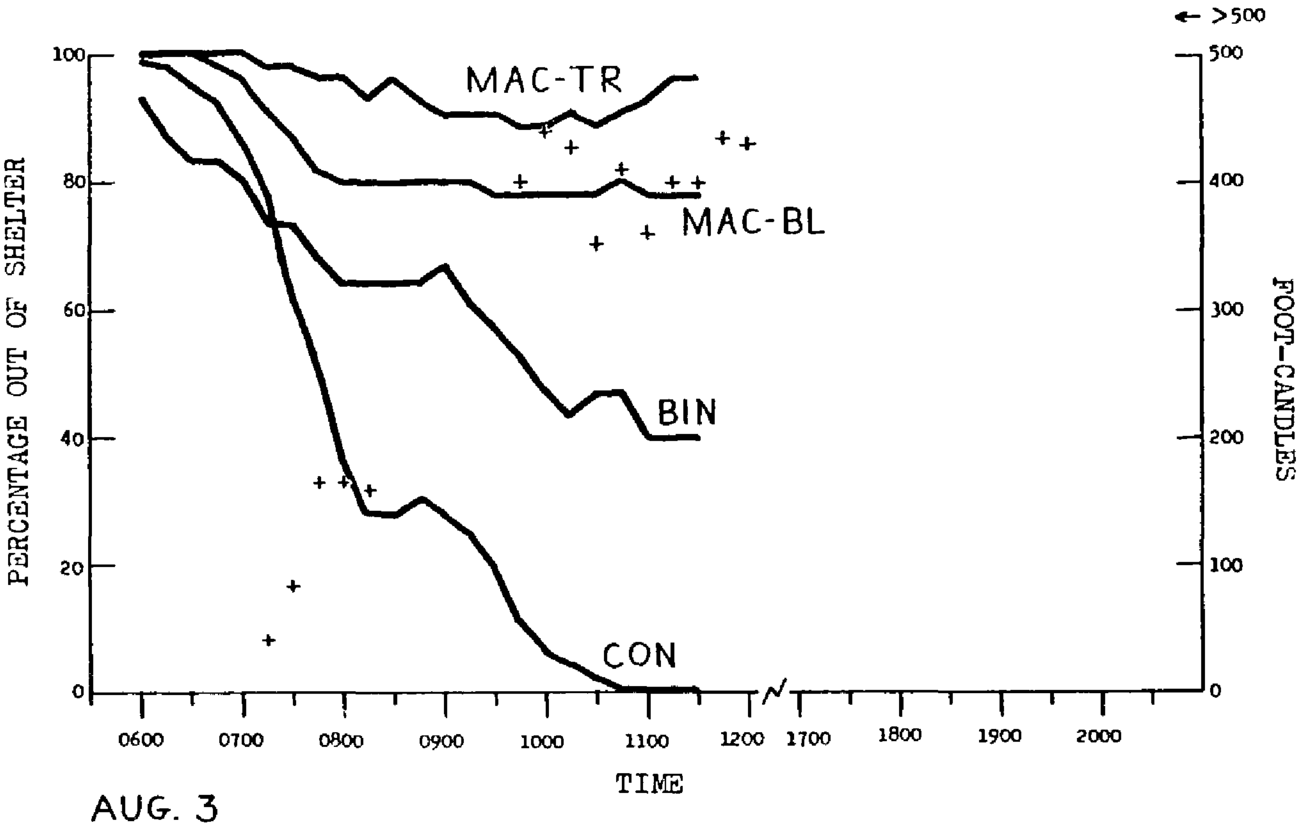

← >500
MAC-TR
MAC-BL
BIN
CON
PERCENTAGE OUT OF SHELTER
100
80
60
40
20
0
FOOT-CANDLES
500
400
300
200
100
0
0600
0700
0800
0900
1000
1100
1200
1700
1800
1900
2000
TIME
AUG. 3

FIGURE 24 (C)

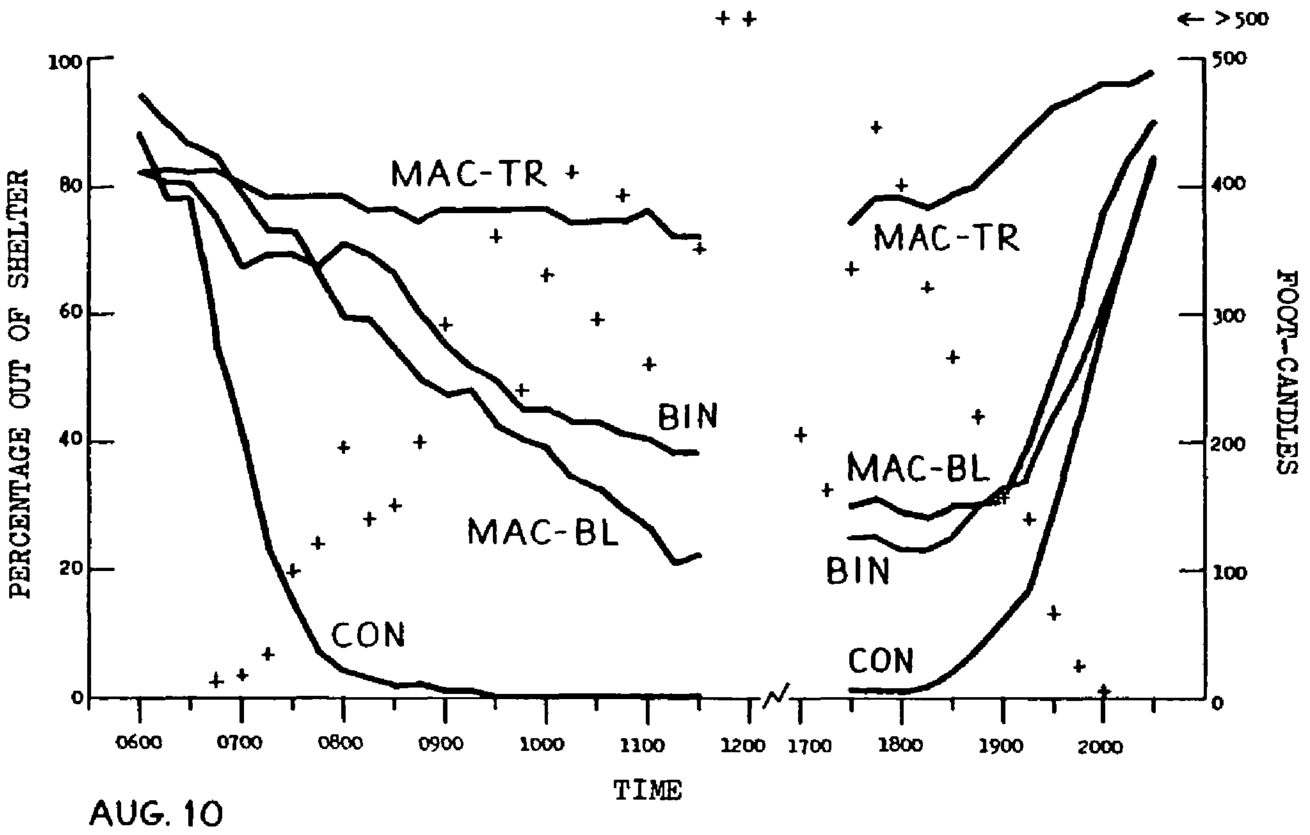

PERCENTAGE OUT OF SHELTER
100
80
60
40
20
0
FOOT-CANDLES
← >500
500
400
300
200
100
0
MAC-TR
BIN
MAC-BL
CON
MAC-TR
MAC-BL
BIN
CON
0600
0700
0800
0900
1000
1100
1200
1700
1800
1900
2000
TIME
AUG. 10

FIGURE 24 (D)

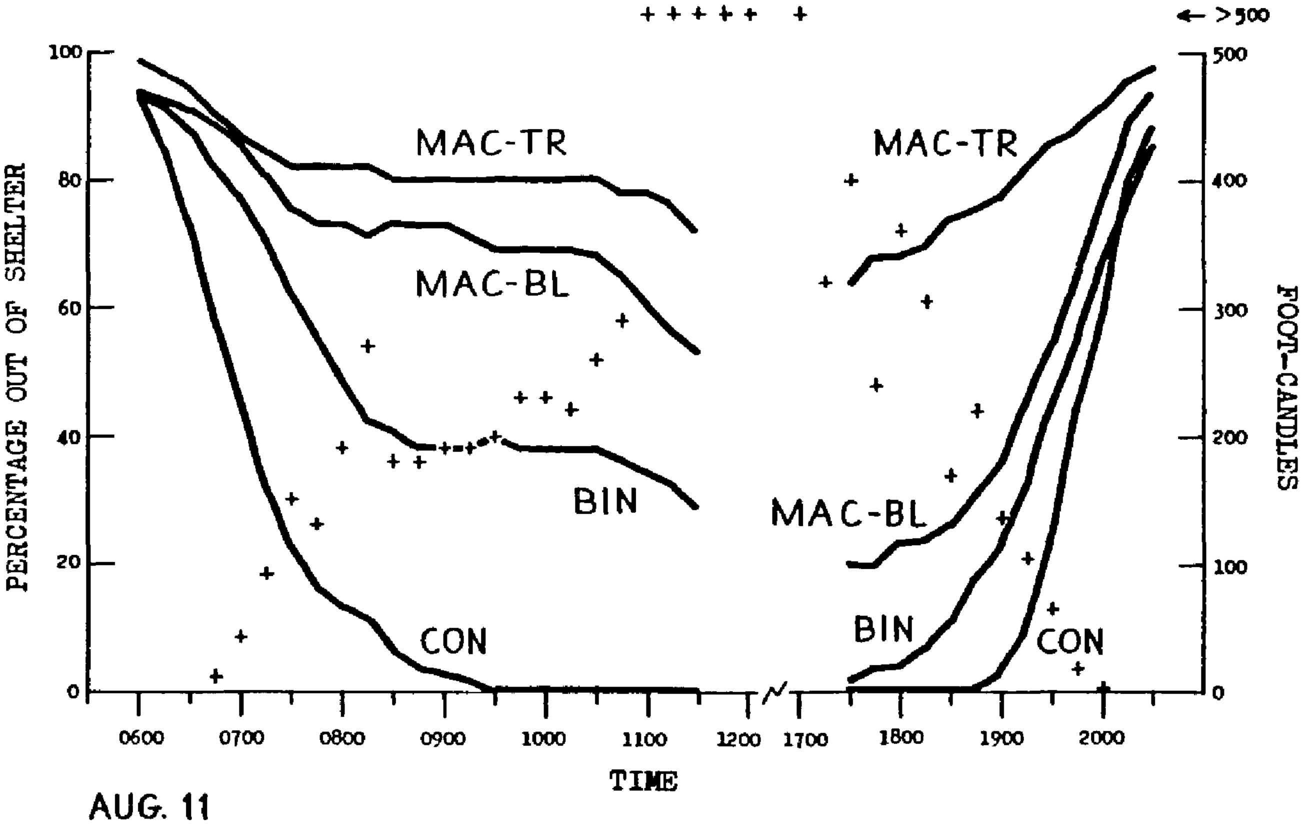
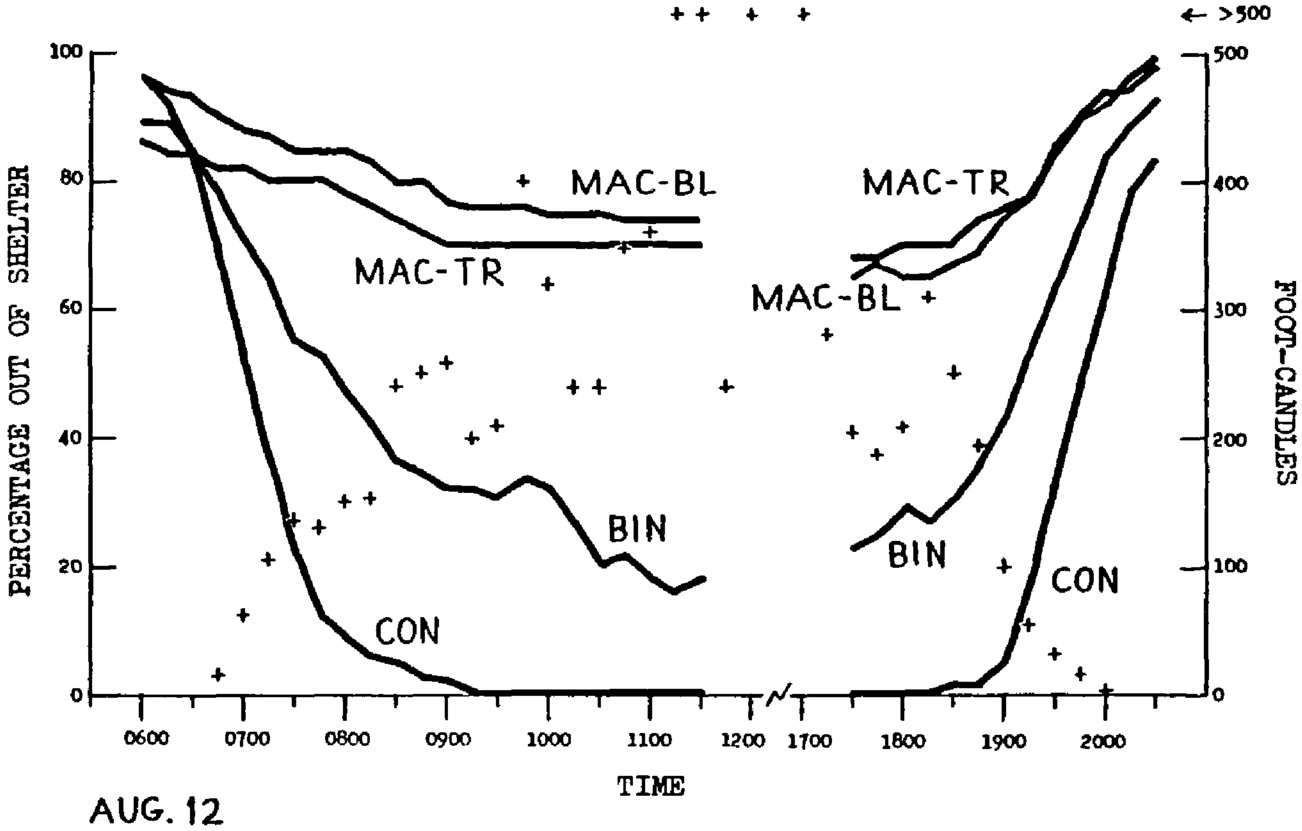

PERCENTAGE OUT OF SHELTER
100
80
60
40
20
0
FOOT-CANDLES
>500
500
400
300
200
100
0
MAC-TR
MAC-BL
BIN
CON
MAC-TR
MAC-BL
BIN
CON
0600
0700
0800
0900
1000
1100
1200
1700
1800
1900
2000
TIME
AUG. 11

FIGURE 24 (E)



← >500
100
80
60
40
20
0
PERCENTAGE OUT OF SHELTER
500
400
300
200
100
0
FOOT-CANDLES
MAC-BL
MAC-TR
MAC-TR
MAC-BL
BIN
BIN
CON
CON
0600
0700
0800
0900
1000
1100
1200
1700
1800
1900
2000
TIME
AUG. 12

FIGURE 24 (F)

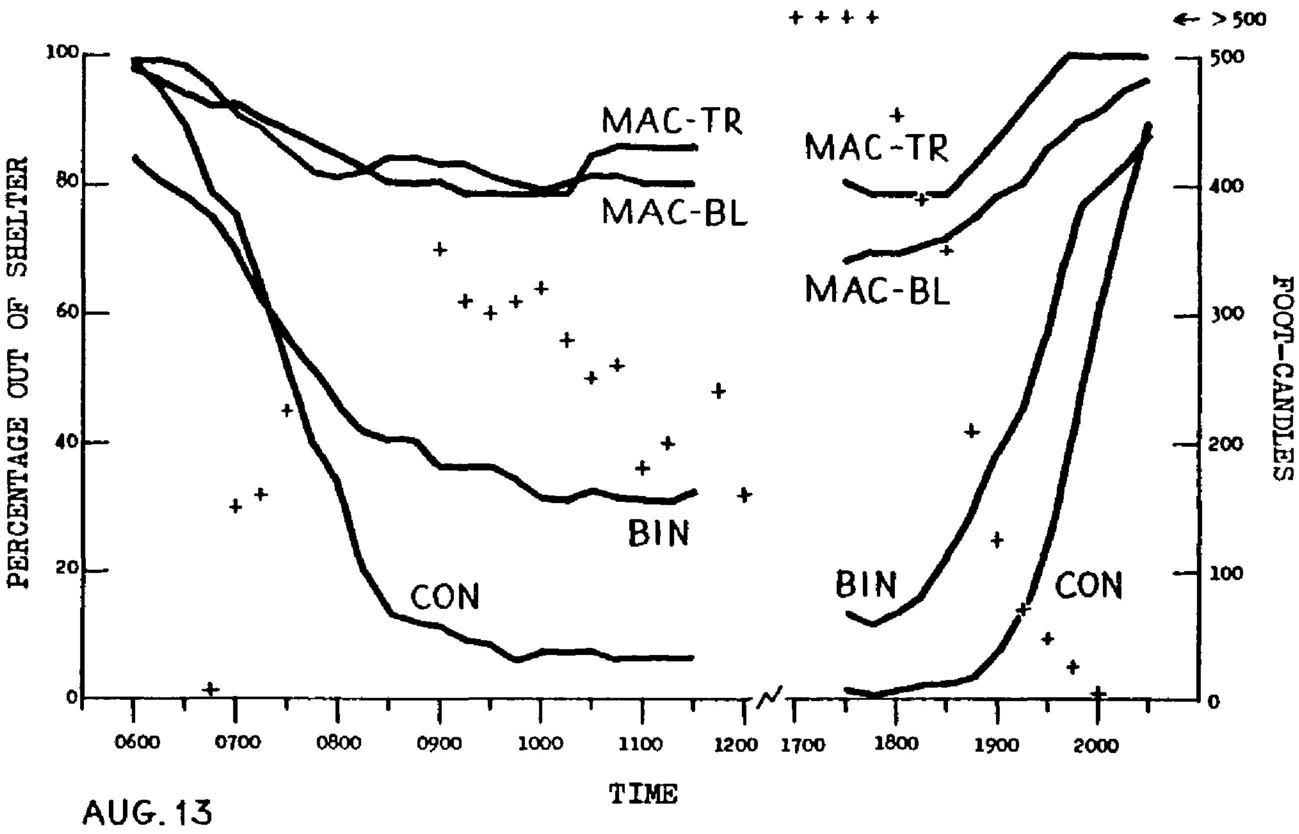
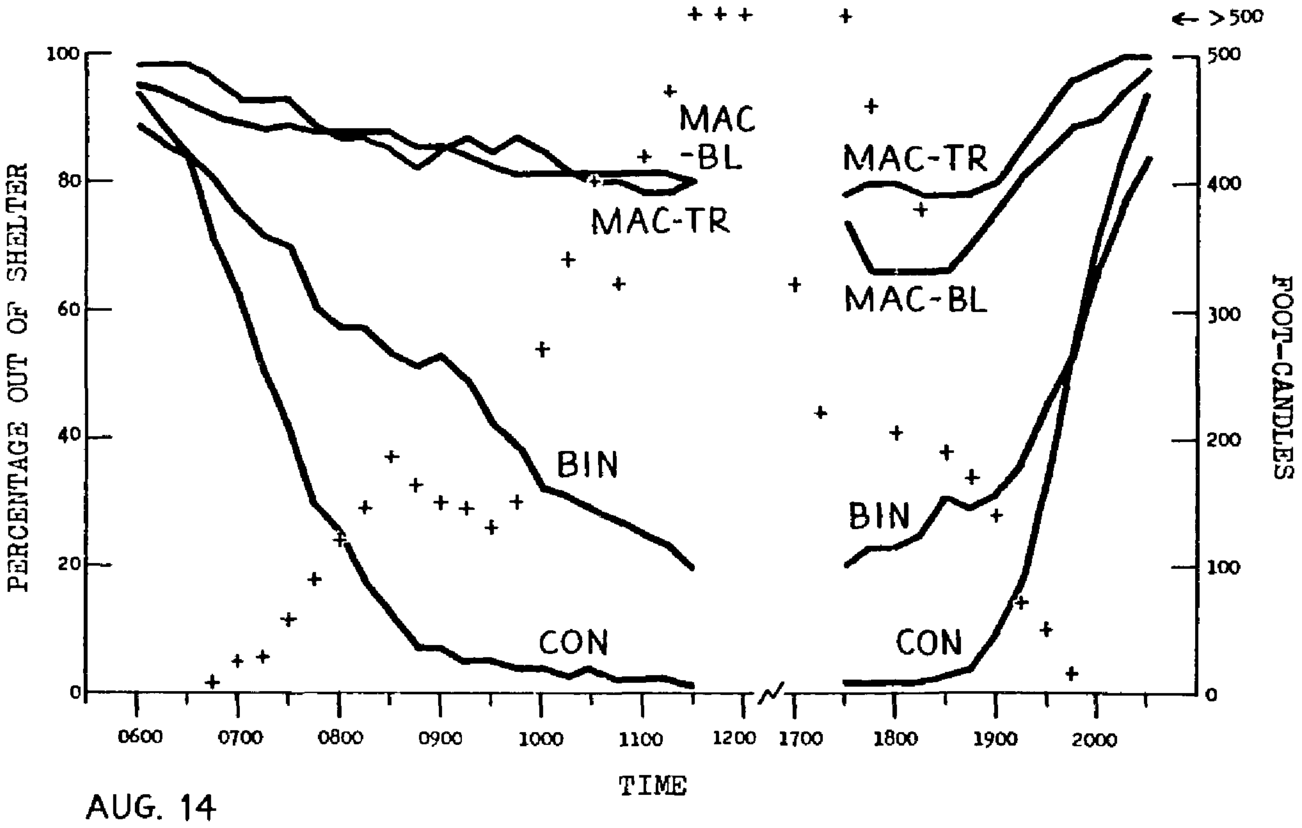
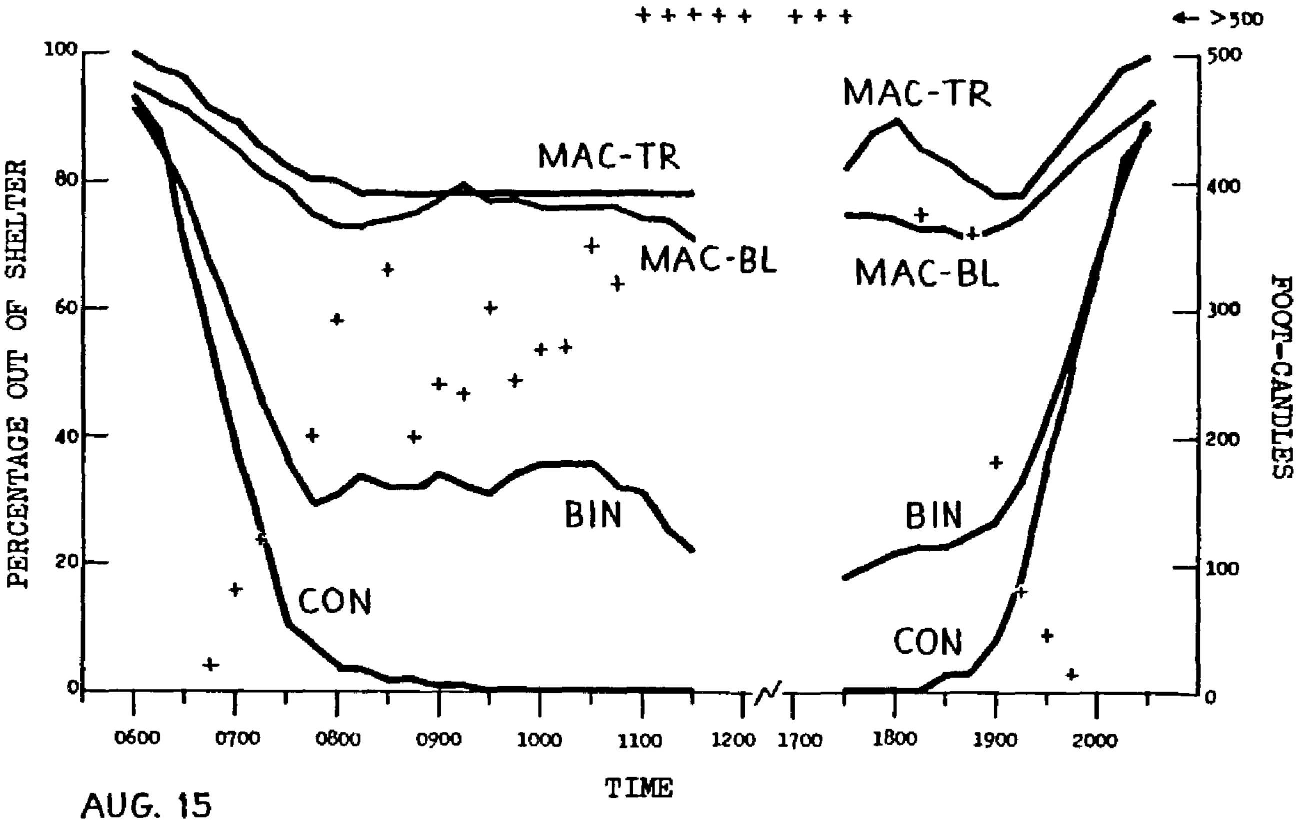

++++
← >500
100
80
60
40
20
0
PERCENTAGE OUT OF SHELTER
500
400
300
200
100
0
FOOT-CANDLES
MAC-TR
MAC-BL
BIN
CON
MAC-TR
MAC-BL
BIN
CON
0600
0700
0800
0900
1000
1100
1200
1700
1800
1900
2000
TIME
AUG. 13

FIGURE 24 (G)



PERCENTAGE OUT OF SHELTER
FOOT-CANDLES
TIME
100
80
60
40
20
0
500
400
300
200
100
0
← >500
0600
0700
0800
0900
1000
1100
1200
1700
1800
1900
2000
MAC
-BL
MAC-TR
BIN
CON
MAC-TR
MAC-BL
BIN
CON
AUG. 14

FIGURE 24 (H)



PERCENTAGE OUT OF SHELTER
FOOT-CANDLES
TIME
100
80
60
40
20
0
500
400
300
200
100
0
← >500
0600
0700
0800
0900
1000
1100
1200
1700
1800
1900
2000
MAC-TR
MAC-BL
BIN
CON
MAC-TR
MAC-BL
BIN
CON
AUG. 15

FIGURE 24 (I)

collected from both places.

During both monitoring periods there were two tanks with P. conklini. In each case changeover was remarkably similar in the two tanks and the data for P. conklini were therefore pooled for each day. Only one tank had A. binotatus in it during each monitoring period, so no pooling of data was required.

In the case of A. maculatus there was one tank each of individuals from the two localities during the first monitoring period. In this case the 2 populations behaved somewhat differently and the data were not pooled. Thus the changeover of Bimini lagoon fish is graphed separately from that of Turtle Rocks fish. For the second monitoring period, the data from two tanks containing A. maculatus from the Bimini lagoon was pooled and graphed separately from the data from one tank containing Turtle Rocks individuals of that species.

The ordinate on the left in each of the nine graphs of Figure 24, labeled "percentage out of shelter", indicates the percentage of the individuals of a given species that was seen to be in the open area(s) of the test tank(s) of that species, i.e. out of the cinder block shelter area(s).

Each of the curves in a given graph represents a "5-point moving average" for that species on the given day. Thus a point on a curve for a given time represents the average of the "percentage out of shelter" for that time, 30 minutes before, 15 minutes before, 15 minutes after and 30 minutes after. This is why, for example, the morning curves (except for August 1) start at 0600, even though data were collected starting at 0530. Although computation of the 5-point moving averages was very tedious (over a thousand averages were computed) a presentation of the data for the three species on one graph would have been very difficult, both to draw and to interpret, without the use of this curve-smoothing technique. The computation was somewhat facilitated by developing a simple program on a Toshiba BC-1623G programmable calculator.

A more or less consistent pattern of shelter-seeking in the morning is apparent for each of the three species. P. conklini tended to seek the shelter of the cinder block openings earliest, and most if not all individuals were in the shelter by mid-morning. A. binotatus sought shelter later, and by the end of the morning monitoring period roughly 1/4 of the individuals remained out in the open area. A. maculatus sought shelter latest, and in nearly all cases a sizeable majority of the individuals remained in the open area at the end of the morning period. In most cases the Turtle Rocks populations of A. maculatus were somewhat less shelter-oriented than the Bimini lagoon populations.

A more or less opposite pattern of emergence-from-shelter in the evening is apparent for each of the three species. In the case of P. conklini, no appreciable emergence occurs until about 1900 hours. By that time about 1/3 of the A. binotatus individuals were in the open area of their tank, and in most cases roughly 3/4 of the individuals in the A. maculatus populations were in the open areas. The Turtle Rocks populations of that species again tended to be less shelter-oriented at a given time than the Bimini lagoon populations.

Among the species not included in the graphed results, A. townsendi was somewhat erratic in its changeover behavior in relation to the other species, but tended to approximate the "schedule" of A. maculatus.

P. pigmentaria tended to be most similar to *P. conklini*. The single specimen of *P. xenus* studied in the first monitoring period was perhaps the most shelter-oriented of all the species. At about 0630 each morning it literally disappeared from view, at a time when most individuals of the other species were still in the open areas. It reappeared in the open area, on the two evenings of this monitoring period, at 2045 and 2000 - a time when most individuals of the other species were out in the open areas again. Only after the end of the morning monitoring on August 3, when the cinder block was removed from its tank, was it discovered that it had been hiding in a thin space between the cinder block and the plywood of the side of the tank. Although this *P. xenus* specimen was rather small (about 25mm S.L.) it had evidently been hiding in a crevice that was very little wider than its body.

Whatever effect differences in tank-population size among the different species may have had on the results is impossible to estimate, but any such effect is believed to be minimal. In the first place, there is no evident trend in the results to indicate such an effect. Secondly the degree of crowding in the cinder block shelters (which might be supposed to delay entry by individuals still outside) did not exceed the degree of crowding sometimes seen in the natural diurnal habitats of these species.

The effect if any, of differences in average body size among the different tank-populations is also impossible to estimate, but is assumed to be secondary to the importance of species identity. The *A. maculatus* and *A. binotatus* specimens (averaging roughly 50-60mm S.L.) were somewhat larger than the *P. conklini* and *P. pigmentaria* specimens

(35-45mm S.L.), which were larger than the A. townsendi specimens (30-35mm S.L.). The single P. xenus individual was about 25mm S.L., as noted above. (More precise measurements are not possible since the specimens, preserved after the study, were later lost during shipment from Bimini to New York).

The slight difference in changeover behavior between the A. maculatus individuals from the two different collection sites may perhaps reflect an average size difference, since the Turtle Rocks specimens tended to be somewhat larger than the Bimini lagoon specimens.

Figure 24 also shows, in addition to the changeover data, the intensity of the light impinging on the tanks during the monitoring periods. The ordinate on the right of each graph indicates foot-candle readings taken with the photometer sensor aimed at the sky. Light intensities exceeding 500 foot-candles are indicated on a line above the 0-500 scale, labeled > 500, because the photometer had a maximum upper range of 500 foot-candles. In most cases where a light reading is missing, it was raining at that point in the monitoring, and the photometer was not used, to protect if from rain damage. In a few cases a light reading was inadvertantly omitted. Light levels that registered zero on the photometer, taken in early morning and late evening, are not included on the graphs.

Figure 24 shows that, roughly speaking, most of the morning changeover activity of the three species occurs before the light intensity reaches 200-250 footcandles, and very little of the evening changeover occurs until the light intensity again reaches that level. If a comparison is made between the progress of morning changeovers and evening changeovers at a given light intensity, such as 200 foot-candles, there is evidence of a lag in the phototactic response. This is seen by the fact that, in general, substantially greater proportions of individuals are still "out" at that light intensity in the morning than the proportions of individuals that have emerged at that light intensity in the evening.

The fact that the evening changeover curves are more or less consistently steeper than those of the morning seems to reflect, at least partly, a similar steepness difference between the evening and morning changes in light intensity, which in turn is the result of a tendency toward intermittent cloudiness, overcast, or even rain during the middle or latter part of the monitoring periods. Skies were clearer, in general, during the evening monitoring periods.

Also discernible in Figure 24, but difficult to quantify, are the effects of certain day to day changes in the light regime. For example, on the morning of August 13 (Fig. 24G), a period of rain (from 0745 to 0845, when no readings were taken) was followed by heavy overcast and the morning monitoring period ended at a rather low light intensity - below 200 foot-candles. On that day each species was less shelter-oriented than usual during the later morning monitoring. This effect was especially pronounced for A. townsendi, which is not included in Figure 24. No more than one of the nine individuals of that species was ever seen to be in the sheltered area during that entire morning, whereas there were usually several individuals in the shelter by late morning on other days.

One final pertinent consideration is whether the morning changeover data for a given species represents a progressive loss of specific individuals from the shelter which do not then return to the shelter, and whether the evening changeover represents a progressive gain, with individuals staying in the shelter once they enter it. Alternatively the data could represent statistical trends during which the fish are frequently "changing places". Obviously the first possibility is not strictly true, otherwise there would be no small upward jumps in the morning curves, or downward dips in the evening curves, many of which are apparent in Figure 24. Without the use of five point moving averages these jumps and dips would be even greater in frequency and magnitude.

Nevertheless, there seemed to be a certain tendency for individual fish to be more or less consistent, i.e., to remain in the shelter area for the morning once they entered it or to remain out of the shelter for the evening once they left it. This impression was permitted by the fact that many of the individuals of a given species became recognizable (due to size, markings, parasites, etc.) over the course of the monitoring period.

3. Brain morphology

Figure 25 shows clear differences in relative optic lobe size among the three species emphasized previously in the laboratory study, over a wide size range. Figure 26 shows a positive correlation between relative optic lobe size and photophobic tendency. Thus Phaeoptyx conklini has the largest "optic lobes/rest of brain" ratio and is the most photophobic; Apogon binotatus is intermediate in this brain ratio and in photophobia; and A. maculatus has the smallest ratio and is the least photophobic of the three. Representative brain

Figure 25. Differences in relative size of optic lobes in three cardinalfish species. ● = *Apogon maculatus*. X = *Apogon binotatus*. ○ = *Phaeoptyx conklini*. Lines drawn are visual estimates. The size ranges of specimens dissected are (in mm SL): *Apogon maculatus*: 24.6–71.4; *Apogon binotatus*: 20.7–68.9; *Phaeoptyx conklini*: 20.7–49.8.

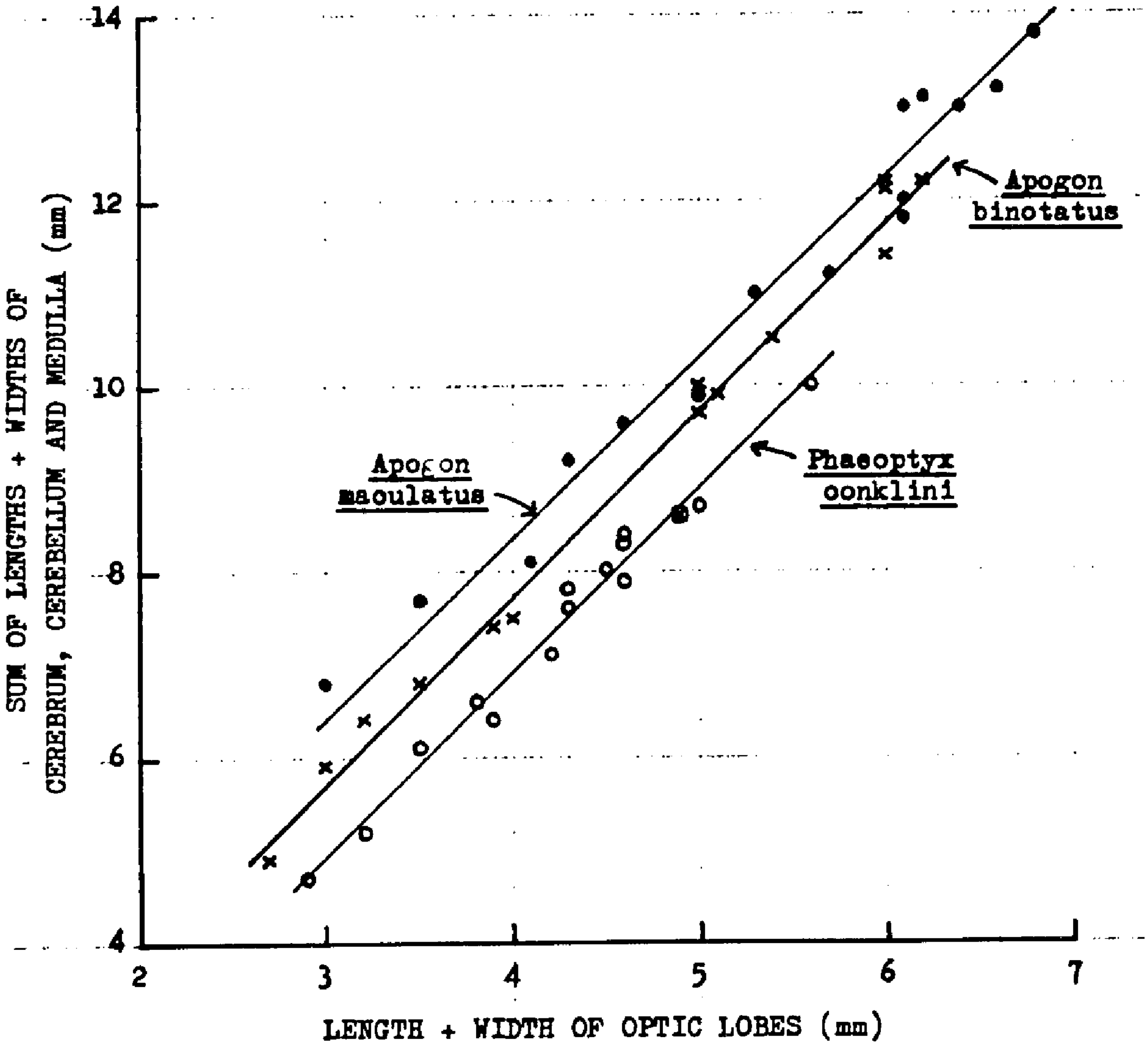
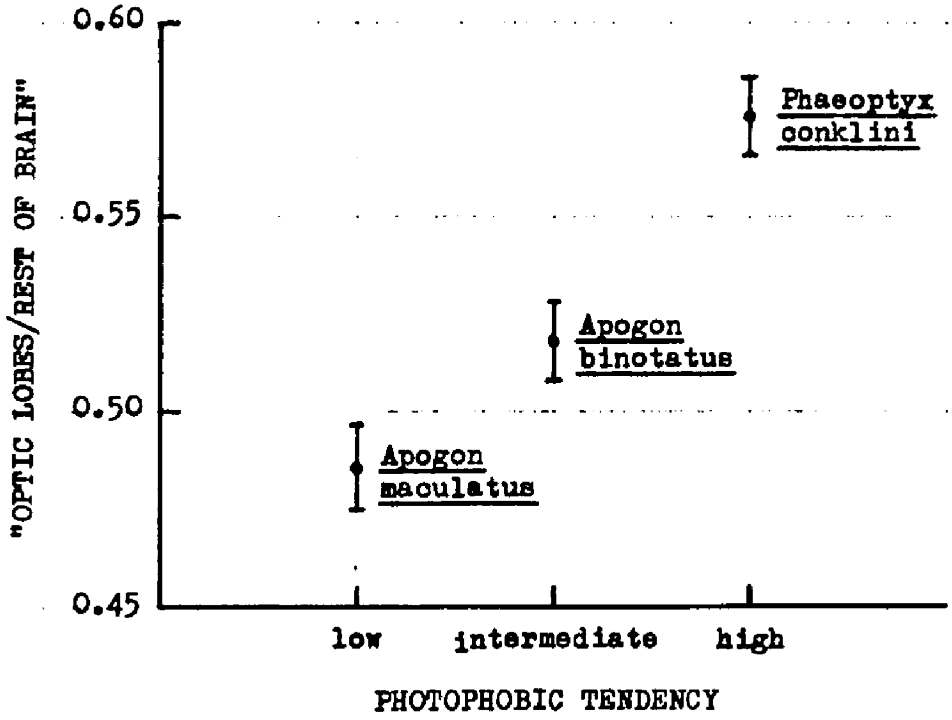

SUM OF LENGTHS + WIDTHS OF CEREBRUM, CEREBELLUM AND MEDULLA (mm)
LENGTH + WIDTH OF OPTIC LOBES (mm)
4
6
8
10
12
14
2
3
4
5
6
7
Apogon maculatus
Apogon binotatus
Phaeoptyx conklini

Figure 26. Relationship of relative optic lobe size to photophobic tendency in three cardinalfish species. "OPTIC LOBES/REST OF BRAIN" represents the length + width of the optic lobes divided by the sum of the lengths + widths of the cerebrum, cerebellum and medulla. The mean and 95% confidence limits of the mean are shown for each species.


"OPTIC LOBES/REST OF BRAIN"
0.60
0.55
0.50
0.45
Phaeoptyx conklini
Apogon binotatus
Apogon maculatus
low
intermediate
high
PHOTOPHOBIC TENDENCY

dissections of the three species are shown in Figure 27.

Brain measurements on the other three species studied in the laboratory changeover experiments partly conform to and partly contradict this trend. Table 27 summarizes the brain measurement data for all six species. Both _P. pigmentaria_ and _P. xenus_, apparently rather highly photophobic, have relatively large optic lobes. _A. townsendi_ also has large optic lobes but is relatively low in photophobic tendency.

Figure 27. Representative brain dissections of three cardinalfish species. From left to right: *Phaeoptyx conklini*, *Apogon binotatus*, *Apogon maculatus*.

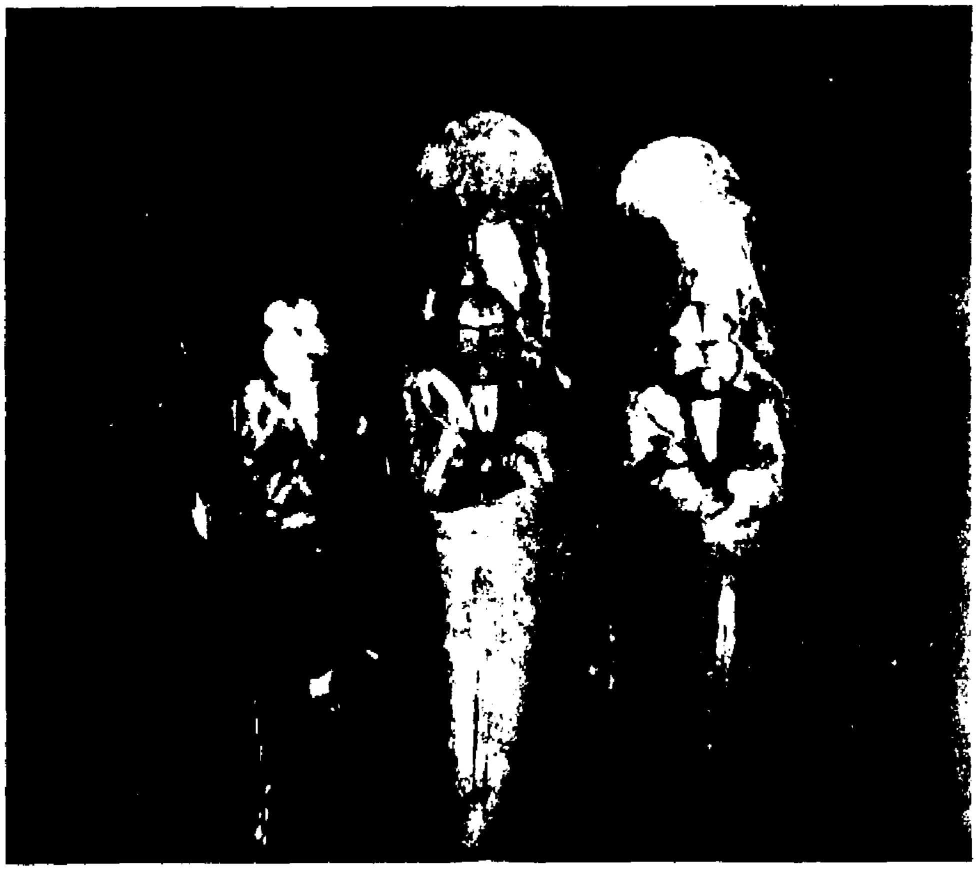


FIGURE 27

			"Optic lobes/Rest of brain"			
Species	N	Size Range	Mean	S.D.	S.E.	95% C.L.
Apogon maculatus	15	24.6 -71.4	0.486	0.022	0.006	0.486 ± 0.011
Apogon binotatus	15	20.7 -68.9	0.518	0.021	0.005	0.518 ± 0.010
Phaeoptyx conklini	15	20.7 -49.8	0.576	0.021	0.005	0.576 ± 0.010
Apogon townsendi	15	19.8 -40.5	0.573	0.023	0.006	0.573 ± 0.012
Phaeoptyx pigmentaria	6	25.4 -44.1	0.551	0.024	0.010	0.551 ± 0.019
Phaeoptyx xenus	6	25.5 -42.6	0.554	0.039	0.016	0.554 ± 0.031

Table 27. Relative size of the optic lobes of six apogonid species. N = number of specimens dissected. Size Range = the size range in mm Standard Length of the specimens dissected. "Optic lobes/Rest of brain" represents the length + width of the optic lobes divided by the sum of the lengths + widths of the cerebrum, cerebellum and medulla. S.D. = standard deviation. S.E. = standard error. 95% C.L. = the 95% confidence limits of the mean, computed as the mean ± 1.96 standard error.

III. Discussion

(A) Reproductive seasonality

The data given in Table 25 suggest that, loosely speaking, apogonids reproduce throughout the year in the Bahamas. Gaps in the data on occurrence of recruits and expanded mouths tend to reflect a low number of collections made for that month, or a low number of samples of that species. Thus in both January and March, when the collecting effort was greatest, over half of the species were represented by recruit-sized individuals or by individuals with expanded mouths, or both. And thus *Phaeoptyx conklini*, the most commonly collected of the species, is represented by recruits or expanded mouths or both for eight of the nine months during which collections were made; and *Apogon maculatus*, the next most commonly collected, is represented by such evidence in six of the nine months, and in a seventh by other evidence.

Therefore there is no indication of different, strictly defined breeding seasons among the various species that might reduce competition between them. There could, however, be different peaks in breeding activity that might serve this ecological function. Because of the many disparities in collection effort and sample size, no effort was made to estimate this possibility with the present data.

Data from the literature indicate that there are peaks, but that they tend to be shared by different species. Luckhurst and Luckhurst (1977) observed peaks in the occurrence of recruit-sized individuals ($<$ 20mm total length) of *A. lachneri*, *A. townsendi*, and *P. conklini* in visual censuses on coral reefs in Curaçao.

All three species showed one peak in recruit abundance in April-May and another in September. These are similar to the March-April and September-October peaks in larval apogonid abundance around Barbados reported by Powles (1975).

One final kind of observation, that emphasizes the lack of reproductive season differences among different apogonid species, was made by the author on two spearate occasions at Bimini. In July 1973, off Turtle Rocks, one or more individuals of each of three different species were observed orally brooding eggs in the same small cave at the same time. These species were: A. maculatus, A. townsendi, and P. conklini - the predominant cardinalfish species in that area at moderate depths (0-20m). A similar observation was made in July 1974, in the same general area.

In summary, there is evidence that many apogonid species reproduce throughout the year, and that periods of peak breeding are shared by different species. There is no evidence of any staggering of reproductive activity.

In connection with this discussion of apogonid reproduction, a brief account of the evidence of oral brooding among these species is of interest. The records of oral brooding in Table 25 (in preserved specimens, field observations, and literature) are the only ones recorded to date (to the author's knowledge) from apogonid species in the Bahamas. These records thus assign this habit to 7 of the 20 species known from the Bahamas: Apogon affinis, A. maculatus, A. mosavi, A. quadrisquamatus, A. townsendi, Astrapogon stellatus and Phaeoptyx conklini.

From my familiarity with specimens containing eggs in the mouth -

seen in the field or among preserved specimens - I can say that it is highly probable that the records of specimens with expanded buccal cavities (Table 25) represent oral brooding individuals that either swallowed or spat out the egg mass during capture. (This tabulation includes only specimens described in my notes as having the mouth "greatly expanded", and omits those noted as "moderately expanded" or "slightly expanded".) On this basis oral brooding can be attributed to 12 of the 16 species in "total collections", including 6 not among those mentioned above: *Apogon binotatus*, *A. lachneri*, *A. phenax*, *Astrapogon puncticulatus*, *Phaeoptyx pigmentaria*, and *P. xenus*.

Thus a total of 13 of the 16 species being examined in detail in the present study may be considered oral brooders. It is likely that the other 3 will also prove to have this habit. Indeed it would seem to be a family characteristic. A summary of the records of oral brooding for apogonids in the entire western Atlantic is given in Table 28. (A search of the literature was made, but some records may have been missed).

(B) Circadian activity patterns

1. *In situ* observations

Although the field data presented here are rather limited in scope, they do support three important generalizations about cardinalfish activity patterns.

a) The patterns are species-specific, as indicated by the similarity of Collette and Talbot's (1972) results to those given here.

b) Different species follow a sequence in time of changeover.

Species	Records of oral brooding
Apogon affinis	Vaillant, 1903; Smith et al., 1971; this dissertation
A. binotatus	Smith and Tyler, 1972; this dissertation
A. lachneri	this dissertation
A. maculatus	Longley and Hildebrand, 1941; Oppenheimer, 1970; Charney, 1976; this dissertation
A. mosavi	Dale, 1977; this dissertation
A. phenax	this dissertation
A. pseudomaculatus	Longley and Hildebrånd, 1940
A. quadrisquamatus	this dissertation
A. townsendi	Smith and Tyler, 1972; Dale, 1975; this dissertation
Astrapogon puncticulatus	Livingston, 1971; this dissertation
A. stellatus	Breder, 1948; Bohlke and Chaplin, 1968
Phaeoptyx conklini	Oppenheimer, 1970 (=Rubinoff, pers. comm.); Fraser, 1972; Charney, 1976; this dissertation
P. pigmentaria	Oppenheimer, 1970 (=Rubinoff, pers. comm.); Fraser, 1972; this dissertation
P. xenus	this dissertation

Table 28. Summary of records of oral brooding in western Atlantic apogonid species. Some of the records from "this dissertation" are based on indirect evidence, i.e., on the presence of a greatly expanded buccal cavity (in the manner characteristic of oral brooding individuals) in preserved specimens, as described in the text.

This also corroborates Collette and Talbot's findings for apogonids and the findings of these investigators and others (e.g. Domm and Domm, 1973) for other nocturnal as well as diurnal reef fishes.

c) Changeover behavior is mediated by light. Domm and Domm (1973) suggested that either light intensity, rate of change of light intensity, or a change in wavelength sets the phase of an endogenous rhythm which then controls the changeover pattern. Light-entrained endogenous rhythms in respiration have been shown for different cardinalfish species in the laboratory by Livingston (1971). In my opinion, however, these rhythms are not the cause of changeover behavior. They do not even parallel the changeover patterns in any apparent way, although there is presumably some adaptive synchrony between the multiple peaks in respiration rate and changing activity level requirements for a species over the course of a 24 hour day. An alternative view is offered in the following section.

1'. Differential phototaxis: an explanation for the proximate cause of changeover patterns

In my view light (probably simply light intensity) has a direct causative effect on the movement of apogonids and other reef species in and out of the reef during changeover, i.e. that changeover is basically a kind of phototactic response. This is certainly a more parsimonious explanation for control of changeover, and is more desirable for that reason alone. It is also supported by observations (by the author and others) that various kinds of changes in light level apart from the diel cycle tend to cause a kind of small-scale changeover response. Thus diurnal fishes tend to emerge slightly from the reef, and nocturnal fishes tend to stay closer to the reef, on clear moonlit nights. And thus diurnal fishes tend to hover closer to the reef, and nocturnal fishes tend to be more visible and active, on overcast days or in periods or areas of high turbidity. Even the momentary passing of a cloud across the sun on a clear day makes some fish respond in the predictable manner.

Collette and Talbot (1972) observed that the morning changeover itself was delayed for most species (including several apogonid species) during a notable increase in turbidity caused by a storm. They suggested that these species might therefore have exogenous clocks controlling their changeover. Again, I believe that some kind of simple phototaxis is a more parsimonious explanation for control of changeover, and the delay that Collette and Talbot observed could be understood just as well in these terms.

How would phototaxis promote changeover? It is not difficult to imagine in the case of nocturnal species such as cardinalfishes. A photophobic tendency would cause them to shun the rising light intensity at dawn by seeking the darker recesses of the reef. At dusk this motivation would be removed.

It is more difficult to imagine in the case of diurnal species. A photophilic tendency could be the basis of their emergence from shelter at dawn, but how could it promote their shelter-seeking at dusk, i.e., how could photophilia cause a species to seek a recess within the reef that is even darker than the reef surface?

I would suggest that the basic relationship of diurnal and nocturnal fishes to the reef environment differs in a fundamental way which makes the phototactic scenario plausible, even for diurnal species. Let us assume that the nocturnal reef species, in general, are basically adapted to life in the water column. In the absence of appreciable light to stimulate their photophobic tendencies, they may be found hovering or swimming over, around, or away from the reef. At dawn their photophobic tendency causes them to seek the darker confines of the reef, where they spend the daylight hours. At dusk, as the stimulus to their photophobia is reduced, they reoccupy their place in the water column. Interspecific differences in the degree of photophobia would bring about the sequential nature of changeover.

In the case of diurnal reef species, let us assume they are, in general, highly adapted to life on or in the reef. Without appreciable light to stimulate their photophilic tendencies they "rest" in close contact with the reef. At dawn their photophilia causes them to "emerge" from the reef. During the day they carry on their respective diurnal activities at a variable distance from the reef, and at dusk the stimulus to their photophilic tendency declines and they "settle" into the reef again. The changeover sequence would result from interspecific differences in photophilia.

Physiological cycles or rhythms, in respiration or locomotor activity, whether endogenous or exogenous, and whether linked to some aspect of the photic regime or not, could be expected to show some kind of synchrony with this phototactic cycle. They need not, however, have any direct causal relationship to the events of morning or evening changeover.

The assumptions regarding the fundamental differences between diurnal and nocturnal species are not without corroborative support.

In a discussion of reef fish community evolution, Smith and Tyler (1972: 142-144) distinguished three levels of specialization among reef species.

The first level - phylogenetically closest to the soft-rayed fishes, which are predominantly midwater forms - is the least specialized for reef dwelling. Smith and Tyler include, in this level, the pre-perciform genus Holocentrus, and certain generalized perciforms: the lutjanids, pomadasyids, apogonids, and generalized serranids. These groups also happen to be prominent among the nocturnally active reef fishes. The second level includes groups that are more specialized for reef dwelling such as damselfishes, groupers, wrasses, and parrotfishes. These groups are prominent among the diurnally active reef fishes. The third level includes the extremely specialized reef residents that do not undergo changeover.

Thus there tends to be a fundamental difference, in specialization for reef-dwelling, between nocturnal and diurnal species.

It should be noted that the photophobic and photophilic aspects of the differential phototaxis hypothesis, explaining the changeover of nocturnal and diurnal fishes, respectively, are not necessarily interdependent. Indeed the photophobic mechanism might reasonably be assumed to have a different physiological and evolutionary basis than the photophilic mechanism. Demonstration of the existence of one would neither prove nor require the existence of the other. They are, however, in each case plausible explanations of changeover and have simply been proposed in combination. In the author's view the photophobic mechanism is a slightly more satisfying explanation, but this may be due to a greater familiarity with cardinalfishes than with diurnal species.

A final important argument in favor of either the photophobic or photophilic mechanism is that it is falsifiable as a general explanation of the proximate causation of changeover (of nocturnal or diurnal fishes, respectively) by the demonstration of a species that undergoes changeover, in an otherwise typical manner, at a time when no change in light intensity is occurring **(see Popper, 1968, on the importance of falsifiability.**

The ecological significance of changeover behavior, a most crucial consideration, will be dealt with in a final section of this chapter, after the discussion of laboratory observations and brain measurements.

2. Laboratory investigation

It should be pointed out that the experimental tank environment is a poor analog of the real coral reef environment. In fact, although the observed behavioral changes have been described as "changeover", the space limitations of the tanks virtually prevent any real spatial changeover. Thus, for example, the majority of the Apogon maculatus individuals remain outside of the shelter areas even at midday, and the rest emerge at night. This is not, however, evidence that the normal diurnal behavior is prevented, since in situ observations reveal that A. maculatus is normally found during the day in relatively well lit areas within the reef, near but not necessarily inside more protected or more enclosed spaces. It is, rather, the nocturnal behavior - movement away from the reef completely - that is prevented in the tank.

Thus the present data do not really represent changeover per se, but rather the phototatic responses which, it is argued here, are the basis of changeover behavior.

In this context, the species in Figure 24 could be assigned to three categories: moderately photophobic (A. maculatus), intermediate (A. binotatus), and highly photophobic (Phaeoptyx conklini). Among the other species, studied in smaller numbers, A. townsendi would be in the moderately photophobic category, while P. pigmentaria and P. xenus would be in the highly photophobic category.

Certain genus-specific tendencies are apparent in these data. The Apogon species are intermediate to moderate in photophobia, while the Phaeoptyx species are highly photophobic. The apparent extreme photophobia of P. xenus may be related to its sponge-dwelling habit. This association gives it, in its natural habitat, the darkest and most sheltered hiding place of all these species. It would be interesting to determine the changeover schedule of Astrapogon stellatus, whose inquiline habit is even more extreme.

The trends in the present results more or less parallel the trends in field data for these species. Smith and Tyler (1972) include data for the same six apogonid species. The Apogon species tended, in their study, to undergo changeover together in the morning and in the evening, while P. conklini and P. pigmentaria had a later evening changeover time, shortly after that of the Apogon species (these authors do not include morning changeover information for P. conklini or P. pigmentaria). P. xenus evidently returned to its diurnal habitat earliest in the morning and left it latest in the evening. Collette and Talbot (1972) include data for four of the six species, which is roughly consistent with the findings of Smith and Tyler.

Dale (1975) found that *A. maculatus* and *A. townsendi* differed only slightly in evening changeover, and not at all in morning changeover, which is again consistent with the laboratory results.

Chave (MS) showed specific differences in light tolerance in the laboratory among several apogonid species of Hawaii. (One species, *Apogonichthys waikiki*, behaved in a manner somewhat like that of *P. xenus* in the present study. It retreated into tight corners or holes within the experimental tank for the duration of her experiments). These differences were more or less paralleled by the results of field measurements of the light intensities in which they were located in their diurnal habitats. Chave concluded that light intensity was a critical factor controlling their diurnal location.

3. Brain morphology

Without further investigation it is difficult to say whether the correlation between relative optic lobe size and photophobic behavior observed among *Apogon maculatus*, *A. binotatus*, and *P. conklini* is based on some direct or indirect relationship between these two factors, or is merely fortuitous. In the context of the idea that changeover is an essentially phototactic phenomenon, such an anatomical correlation would perhaps not be surprising, since changeover behavior may be a very fundamental aspect of the biology of these fishes. Furthermore, the optic lobes are exceedingly prominent in these species, forming the predominant component of what is evidently a rather large brain. Apogonids had the highest "encephalization index" (a measure of relative brain size) among 35 teleostean families from Hawaii in a recent study (Bauchot et al., 1977).

Correlations between brain anatomy and other aspects of behavior or ecology are well known among fishes. Most widely studied are correlations with feeding habits (see Kapoor et al., 1975, and their bibliography; Gupta and Shrivastava, 1972, also cite many pertinent references). Fishes that rely for food selection on abundant taste buds in the skin, lips, or sensory barbels may have enlarged lobes, termed facial lobes, in the region of the medulla that receives the facial nerve fibers. Fishes relying on oro-pharyngeal taste buds, which are supplied by the glossopharyngeal and vagus nerves, may have enlarged vagal lobes on the medulla. Fishes feeding primarily by sight, in which category apogonids would presumably be placed, tend to have prominent optic lobes.

Blind cave or phreatic fishes tend, as might be expected, to have extremely reduced optic lobes (e.g. Ercolini and Berti, 1975).

A relationship between cerebellum size and habitat has also been shown (Karamian, 1949), and a tendency toward increased cerebellum size in catastomid fishes has been correlated with life in faster water (Miller and Evans, 1965).

A correlation between optic lobe size and activity cycles, such as that suggested in the present findings, has not previously been reported in the literature.

4. Phototactic habitat partitioning: a possible space-sharing mechanism.

At this point a general discussion of the significance of changeover patterns is in order. Why do apogonids and other reef fishes undergo nocturnal-diurnal changeover in a gradual, sequential manner? What is the ecological significance of the interspecific differences in time of changeover? Helfman (1978) has discussed several hypotheses in this regard.

Hobson (1972) found evidence in Hawaii that fishes seek shelter (at dusk) in order of decreasing vulnerability to predation, as roughly indicated by increasing body size. Elsewhere this seems to hold for within-species differences in body size but not for between-species differences.

Domm and Domm (1973) have suggested a second possibility: that sequential shelter-seeking at dusk reduces a kind of "confusion" that would aid predators, and also reduces interspecific aggression involved in competition for shelter sites. However, there are considerations arguing against this view (Helfman, 1978). An orderly sequence also occurs in the morning, when confusion might be more advantageous to the prey species. As far as reduction of interspecific aggression is concerned, it is often <u>intraspecific</u> aggressive competition that is most prominent.

A third explanation is that the orderly sequence results from a kind of temporal resource subdivision which reduces competition for predator avoidance (Helfman, 1978). In this view the changeover time of a given species represents a compromise between the need to maximize the time spent feeding or carrying out some other activity, and the need to avoid crepuscular predators. This third explanation still does not establish how the orderly, sequential nature of changeover that is so striking to the observer is conducive to predator avoidance at either dawn or dusk.

A fourth hypothesis will be offered here as an explanation for changeover time differences among cardinalfishes, which may have wider applicability: phototactic habitat partitioning. In the case of cardinalfishes and other nocturnal species, this mechanism would work as follows. As light levels begin to rise in the morning, the most photophobic species would return first to the reef, eventually occupying the deepest and darkest spaces. Then less photophobic species would return and seek shelter in intermediate spaces, and finally the least photophobic species would return and occupy the remaining, well-lit spaces. In this way a passive partitioning of space on the reef would be effected. In the case of diurnal species one could imagine that at dusk the less photophilic species would settle into the deeper recesses of the reef and the more photophilic species would occupy the shallower spaces that are reasonably well-lit further into the evening and remain slightly illuminated on moonlit nights. Again, there is a passive partitioning of space on the reef.

The advantages of this explanation, which argue in its favor, may be summarized as follows:

a) It is a simpler explanation than those previously proposed, being entirely based on a simple phototactic response. The operation of more complex behavioral factors is implied in the other hypotheses. Thus it is favored by the parsimony principle as applied to animal behavior.

If the argument advanced earlier, in favor of differential phototaxis as a proximate cause of changeover differences, is accepted, then habitat partitioning is a logical view of the underlying ecological significance of changeover.

b) Since space is widely believed to be the limiting factor for

for most reef fish species, this mechanism would provide a fundamental means of coexistence among these species. Any explanation whose ecological significance is framed in terms of resources other than space is therefore less satisfying.

The overall diurnal-nocturnal transition is itself a basic space-sharing mechanism (Smith and Tyler, 1972), allowing the two large groups of species to share the protection offered by the reef structure. Habitat partitioning is, in a sense, an extension or elaboration of that mechanism.

c) The hypothesis is falsifiable on two different levels. First of all, it would lose a certain basic support if differential phototaxis, proposed earlier as the proximate cause of changeover, were falsified in the manner previously described. Secondly, it would be falsified by the demonstration of related species that are not space-limited but that clearly differ in phototactic response and changeover time.

d) The evolutionary basis of the changeover differences behind the partitioning is no more difficult to envision than that of other competition-restricting niche differences that have been suggested, such as food or habitat preferences. One could imagine that allopatric populations of an ancestral species acquired slight differences in phototaxis in response to slightly different photic environments. After breakdown of the geographic barrier, these differences would enhance the coexistence of the two forms by promoting habitat partitioning.

A somewhat rash speculation in this context would be that the evolution of interspecific differences in adult body size may be linked in some way to differences in phototaxis, and hence in changeover time. Hobson (1972) found evidence, mentioned earlier, of a body size sequence during coral reef changeover. In addition, there is a widespread tendency among marine and freshwater fishes for within-species or between-species differences in body size to be related to light preferences (including nocturnal vs. diurnal habits) or to other apparent preferences (e.g. depth, water turbulence) that may in fact represent light preferences.

Perhaps allometric differences (ontogenetic or phylogenetic) in some morphological factor (eye or brain anatomy?) are at the basis of these preferences. The size-light preference relationship is generally one in which larger forms are associated with darker conditions, and this would be logical if the relationship has a morphological basis, since larger fish can have, e.g., larger eyes and optic lobes, containing more sensory cells and neurons.

In conclusion, it would seem that light is a very fundamental factor in reef fish ecology. This is most certainly true for cardinalfishes. It may be viewed, for example, as the very basis of their feeding habits, in the sense that their phototactic tendencies put them (spatially and temporally) where a certain food supply is available. Adaptations for exploiting this particular food supply could be viewed as, in a sense, subordinate to the nocturnal habit adaptation.

Perhaps photic factors, either in terms of light intensity or wave-length, are also involved in the selection, by larval reef fishes, of habitat or depth at the time of recruitment. Such factors could well be among the most important competition-restricting mechanisms of coral reef fishes.

I believe that the diel cycle of light is a very prominent factor promoting reef fish diversity. It provides a heterogeneity in the temporal dimension that species have exploited in their avoidance of interspecific competition. This is probably true of animals in general. Such a fundamental ecological role of the light-dark cycle is perhaps not surprising in view of its existence as part of the physical environment of the planet since before life evolved.

CHAPTER FIVE: Trophic Factors

I. METHODS

(A) Feeding habtis

1. Stomach content analysis

a) Selection of specimens

The feeding habits of several of the more abundant cardinalfish species were investigated by means of stomach content analysis. Because of an awareness of certain difficulties in interpreting interspecific feeding habit differences, fish samples were chosen for this study which met the following criteria:

(i) On the assumption that most of the feeding activity of the species concerned is nocturnal, and in the absence of night collections, only morning collections were analyzed. Food organisms taken at night would be more readily identifiable in fish collected in the forenoon. Moreover, omission of afternoon samples minimized the complication of including diurnally taken food organisms, which might differ in some fundamental way.

(ii) Collections from only a few different, related habitat types were selected to reduce the possible complication of having unequal samples from habitats in which prey availability differed widely.

(iii) Collections were chosen which included at least five specimens each (all over 20mm SL) of at least two different species, so that within-collection comparisons could be made. On this basis six different collections were selected. Within each collection all 20mm+ apogonid specimens were dissected, up to a maximum of 20 specimens for a given species.

b) Volumetric estimation of different food items: a new method

Specimens were opened by cutting into the visceral cavity at its anterior, dorsal, and posterior margins on the right side of the body. Stomachs were removed by cutting through the esophagus and pylorus. (Preliminary dissections had indicated that virtually no identifiable food items were to be found further on in the digestive tract).

The percent fullness of the stomach was visually estimated to the nearest 10%. Both the relative thinness of the stomach wall and the volume of its contents, considered in relation to the size of the specimen, allowed this rather subjective estimate to be reasonably consistent. This was shown by the fact that reestimates of fullness, without knowledge of the first estimates, usually differed from the first estimates by no more than 10%, and only rarely by more than 20%.

Identification of food items ranged in precision from "unidentified animal material" to species. The percent volume of each category (of whatever precision) of the total contents of a given stomach, was visually estimated to the nearest 10%, or to the nearest 1 or 2% for categories judged to comprise 5% or less.

Multiplying this value by the percent fullness of that particular stomach gave a value representing the "fraction-of-full-stomach" for that food category, for that specimen. Thus if stomatopod larvae constituted an estimated 50% of the contents of a stomach judged to be 30% full, stomatopod larvae had a "fraction-of-full-stomach" value of 15%.

The reason for calculating this somewhat artificial figure was that it seemed more reasonable in certain respects to add such figures together for a group of specimens of a given species to estimate the importance of food categories than to add together either actual weight or volume units, or simple percentages of stomach contents.

The reasons for this are as follows:

(i) Unless only specimens from a narrow size range are used in a stomach content study (often possible, no doubt, but not so in the present case), adding estimates made in grams or cubic centimeters may unreasonably overemphasize those items found in larger specimens. Thus, hypothetically, a 60mm fish might have a full stomach containing only mysid shrimps, and a 30mm fish might have a full stomach containing only stomatopods. The stomatopods from the smaller fish would amount to only about 1/10 the volume or weight of the mysids from the larger fish (based on the approximate length-weight relationship of the typical apogonid species, and assuming that the proportionate size of the stomach is similar in large and small fish). Thus if only weights or volumes are added in pooling the food data for a given fish species, the mysids in the larger fish would add ten times more to the mysid category than the stomatopods from the smaller fish would add to the stomatopod category. This gives the results an undesirable bias. It is surely more reasonable to give a stomach-full of mysids and a stomach-full of stomatopods equal importance, regardless of the size of fish from which they came. If there is some reason to consider the feeding habits of smaller fish far less important, it makes more sense to simply omit them from the study. If their feeding habits are believed to be fundamentally different, then they should be studied separately for that very reason, since the meaning of pooled results in such a case would be rather ambiguous.

(ii) Adding simple percentages of stomach contents without considering relative fullness is misleading in a different way. In this case, for example, one isopod comprising the entire stomach contents of a 1/10-full stomach contributes ten times more to the isopod category than a similarly-sized amphipod, comprising 1/10 of the stomach contents of a full stomach, contributes to the amphipod category. Surely this overemphasizes isopods. Using the method devised for the present study, described above, the isopod and the amphipod in this example would contribute equally to their respective categories in the pooled results. Equal importance is given to the eating of a "tenth-of-stomach-filling" isopod and the eating of a "tenth-of-stomach-filling" amphipod, (even though the amphipod-eater had a lot more of other things to eat or, alternatively, the isopod eater regurgitated 90% of its stomach contents during capture).

The need for avoiding these pitfalls is not as apparent (and perhaps not really as important) in studies of the feeding habits of a single species, or even in purely descriptive studies of several species. In the present study, however, the primary objective is to establish the degree of similarity or dissimilarity of the feeding habits of different species. In order to do this with any confidence, all such sources of misleading results must be avoided. To the author's knowledge, the method here described for doing so has not been previously proposed.

c) Description and comparison of apogonid feeding habits.

Following the procedures described in a) and b) above, stomachs were removed from 286 specimens of ten different species. Six of the species were represented by enough specimens with non-empty stomachs to allow at least a tentative description of their feeding habits. For each species subtotals of "fraction-of-full-stomach" values for each food category were converted to percentages of the totals of values for all food categories and the results were tabulated.

Phaeoptyx conklini and _Apogon maculatus_ constituted more than half the specimens dissected. Their representation together in sizable numbers in four of the collections permitted a somewhat more detailed comparative study.

For this purpose calculations were made of the degree of food overlap between the two species, using the overlap measure of Morisita (1959), as modified by Horn (1966), and as used for comparing feeding habits of fishes by Zaret and Rand (1971):

$$\hat{C}\lambda = \frac{2 \sum_{i=1}^{S} X_i Y_i}{\sum_{i=1}^{S} X_i^2 + \sum_{i=1}^{S} Y_i^2}$$

where S is the total number of food categories, and X_i and Y_i are the proportions of total diet of species X and Y, respectively, represented by food category i. $\hat{C}\lambda$ varies from 0, when two species samples have no food categories in common, to 1, when the samples are identical in proportional food category composition.

Food category tabulations of the kind mentioned earlier do not, by themselves, permit any reliable quantitative comparisons. Converting them into pie diagrams, as is often done, only creates an illusion of greater comparability. The $\hat{C}\lambda$ statistic provides a tool for truly quantitative comparisons.

d) Miscellaneous remarks on stomach content analysis

As pointed out by Randall (1967:669), stomach content studies of carnivorous fishes taken with rotenone may be unreliable because such fishes may feed on organisms that succumbed to the poison first, but which are not ordinarily fed on. Apogonids, however, are among the small fishes that succumb almost immediately, and their stomach contents are therefore not influenced in this way to any significant extent. (They may in turn be taken by larger predators, such as groupers, during the poisoning. This was frequently observed by the author during application of the fish anesthetic quinaldine, which does not cloud the water in the way rotenone does).

Fishes reported on in the present study were all taken in relatively shallow water, so there was no particular problem from swim bladder expansion having caused regurgitation. Although not included in the present data, many specimens taken from deeper water (especially *Apogon lachneri*) were also dissected. It was frequently observed in such cases that the stomach was large and thin-walled but empty and dorso-ventrally flattened, evidently as a result of swim bladder expansion. Such individuals had presumably regurgitated the contents of relatively full stomachs, for if their stomachs had been empty they would be thick-walled and contracted. Any study of the food habits of apogonids collected in deep water would have to contend with this problem.

2. Field and aquarium observations

An effort was made to gain additional information on feeding among the various species by observing them in the field and in aquaria. *In situ* observations were made on several occasions at night and during the day. To aid in the diurnal observation of possible prey organisms, a special mask apparatus was constructed, with a rotating polarizing filter (Figure 28). Emery (1968) used a large, hand-held sheet of polaroid plastic, rotating it to the correct plane of polarization, to facilitate the detection of small transparent plankton. The mask apparatus devised for the present study allowed use of the hands for other purposes while making such observations.

Various cardinalfish species were kept on different occasions in outdoor aquaria at the Lerner Lab in Bimini, and in a marine aquarium at the American Museum. A few casual observations of

Figure 28. Face mask with polarizing filter attachment, for facilitation of in situ viewing of transparent planktonic organisms. The polarizing disc consits of a sheet of plastic polarizing material bonded between two thin sheets of clear, rigid plastic. It is attached at the tightening bolt of the metal mask frame. A short piece of thin metal rod is bent at one end in a tight circle around this bolt and at the other end is bent in another tight circle so that it may be riveted to the disc. For use, the disc is rotated until the plane of polarization is achieved that best reveals the transparent organisms. It was found, in trying discs of high transmission material (approx. 40%) and lower transmission material (approx. 30%) that the high transmission material was preferable, because of an apparent trade-off between polarizing enhancement and darkening of the visual field.

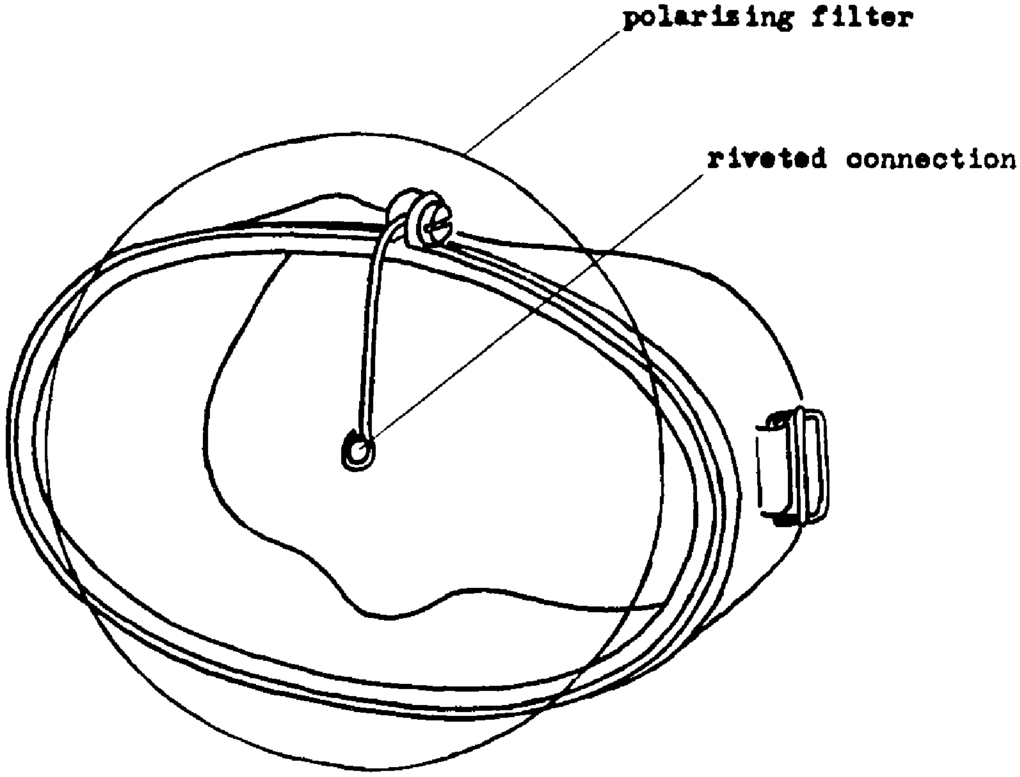


FIGURE 28

feeding behavior were made on these occasions.

(B) Scanning electron microscopy of teeth

Before describing the details of the selection, preparation, and examination of material carried out in this study, the rationale for a scanning electron microscope (SEM) study of cardinalfish teeth will be explained.

1. Rationale

Adaptations which would allow trophic specialization by various related species would be important factors allowing the coexistence of those species. Studies of African cichlids have revealed modifications of the teeth that are clearly related to feeding specializations. Within the single genus _Haplochromis_, there is a complex array of dentitional types corresponding to an equally complex array of feeding specializations including piscivory, insectivory, lepidophagy, algal scraping, mollusc eating, and generalized feeding (Greenwood, 1973, 1974).

It was apparent at the outset of the present study that such variety in tooth morphology or feeding habits was not likely to be found among western Atlantic apogonids. In fact there is probably less overall divergence in dentition and feeding types in the entire family Apogonidae than in _Haplochromis_. Nevertheless, there was an initial assumption, in the present study, that the kind of scrutiny enabled by the SEM might reveal much smaller differences that would help define more finely partitioned trophic niches.

An initial survey of the dentition of the various species, by examination under a dissecting microscope, had failed to reveal much divergence from a typical pattern, beyond those instances already recognized and used by taxonomists. These taxonomic characters include the enlarged canines of Apogon affinis, the lateral extension of the premaxillary tooth patches in A. robinsi, and the slightly enlarged teeth of Phaeoptyx pigmentaria. Even if these relatively minor tooth characteristics could be shown to be related to feeding specializations, the majority of species would remain unaccounted for in this regard.

With this background, a scanning electron microscope survey seemed appropriated and suitable for detecting subtle differences in the teeth.

The scanning electron microscope affords the viewer a depth of focus 300-500 times greater than optical light microscopy (Black, 1970) and provides clear, high contrast black and white photos of highly three-dimensional surfaces. Its use is described in detail by Hearle et al.(1972) and biological applications are reviewed by Hollenberg and Erickson (1973). Its effectiveness for studying fish teeth has been shown quite recently by Liem (1972), Reif (1973), Preuschoft et al.(1974), Lanzing and Higginbotham (1976), and Shellis and Berkovitz (1976).

2. Selection, preparation, and examination

The study was arbitrarily limited to the jaw teeth, i.e., those on the premaxillary and dentary. Superficially, at least, there seemed to be more interspecific variation in these teeth than among those of the other tooth-bearing bones.

Specimens were selected for the study that met the following criteria:

a) approximately 40 mm SL. Comparison would be facilitated if no great size differences were involved. The specimens selected ranged from 37.5 to 40.5 mm SL.

b) undamaged, and not apparently aberrant among others of the same species

c) collected from "region 2" of the Bahamas. Although there was no evidence of geographic variation in any morphological features of apogonids in the Bahamas, it was reasoned that any such effect, if present, would be minimized if all specimens were taken from one general region of the Bahamas. The specimens selected came from Bimini, Ragged Island, Little Ragged Island, Rose Island, Little San Salvador, Cat Island, and the Berry Islands, all in "region 2" (see Figure 12).

Since there was virtually no information in the literature regarding the preparation of fish jaws for the SEM, a certain amount of trial and error was involved in finding a suitable technique. The most delicate aspect involved removing the soft tissue from the vicinity of the teeth. It was discovered that the use of very brief heating or brief treatment with trypsin facilitated this removal, but in any excess tended to loosen the connection of the teeth.

The following procedure, presumably suitable for preparing the jaws of any small fish specimen for the SEM, was eventually adopted:

a) Dissect and remove upper and lower jaws from one side of specimen.

b) Carefully separate dentary from articular and premaxilla from maxilla.

c) Under a dissecting microscope, pick and brush away as much as possible of the skin, muscle, connective tissue, and oral mucosa from the dentary and premaxilla, especially near the teeth.

d) Place in a small test tube and boil in distilled water for ten seconds over an alcohol lamp. Cool by immersing test tube in cold water.

e) Carefully brush tooth patches for thirty seconds with a saturated trypsin solution (in buffer), using a small, stiff-bristled artists' brush.

f) Rinse in distilled water.

g) Place in 100% isopropyl alcohol in a small beaker, place beaker in an ultrasonic bath, and clean for sixty seconds.

h) Allow bones to dry in air, place in acetone in a small beaker, and clean again with ultrasound for sixty seconds.

i) Allow to air dry and attach to a numbered aluminum SEM specimen stub with conductive paint.

j) Coat specimen with gold.

This final coating step, and the subsequent operation of the SEM for viewing and photography, were carried out by the author at the SEM facility in the Biology Department at City College of the City University of New York, during the first portion of this study. The SEM at this facility is a Kent-Cambridge, Model S-4. Photographs were taken with Polaroid black and white 4 x 5 film, positive-negative, type 55, using a Polaroid Land 4 x 5 camera back. A data sheet was prepared so that all settings used in obtaining a given photograph could be recorded, including magnification, Z , θxy, fine magnification, voltage, filament current, focusing magnification, right, middle and final condenser, black level, signal, working distance, magnification factor, line and frame running settings for record raster, and contrast and brightness settings for camera. This facilitated reproducing the settings with which good results were obtained.

The study was completed at the SEM facility of the American Museum, where coating, operation of the SEM, and photography were carried out by a technician. This SEM is also a Kent-Cambridge, Model S-4, and the same type of film and camera were used.

II. RESULTS

(A) Feeding Habits

1. Stomach content analysis

Table 29 summarizes the important data on locality, etc. for the six collections from which specimens were taken for the food habit study.

a) Description of food habits of six species

Tables 30-35 give food habit summaries for the six cardinalfish species represented by ten or more specimens in these six collections. Several points regarding these summaries should be noted.

Widely different taxonomic levels are used as food categories. This is commonly done in such studies (e.g. Randall, 1967) and is required by the variable identifiability of food items due to differences in degree of digestion, and other factors.

The category designated "shrimp and shrimp larvae" includes, for the most part, unidentified decopod shrimps (suborder Natantia), probably mostly carideans and caridean larvae, but not those identifiable (by their unique snapping chelipeds, which are large, thick-shelled, and slow to digest) as alpheids, which are listed separately since they form a substantial food category for some cardinalfish species. "Shrimps" identifiable as mysids (Mysidacea) and euphausids (Euphausidacea) are listed as such.

Although fish eggs were prominent in a number of stomachs, there was evidence that in some cases these may have represented oral broods swallowed at the time of capture. An egg mass, spat out by the brooder during poisoning, might be eaten by another fish;

Field Number	Locality	Date	Time	Habitat	Depth (feet)
S64-80	San Salvador, reef in Graham's Harbor	17-XI-64	0945-1145	top of bank, coral stack	to 12
S65-41	Acklin's Island, nr. Salina Point	3-IV-65	0900-1030	outer shelf, patch reef	2-15
S66-3	Little San Salvador, West Bay	4-III-66	0830-1000	outer shelf, patch reef	to 10
S66-26	Little Inagua, off Southwest point	18-III-66	0715-0900	outer shelf, patch reef	to 25
S68-1	New Providence, off Clifton Pier	8-I-68	0900-0945	outer shelf, coral stack	38
GD73-2	Bimini, off Turtle Rocks	31-VII-73	1035-1220	outer shelf, patch reef	28

Table 29. Collections from which specimens were taken for stomach content analysis.

Food	Percentage
Fish and fish fragments	30.0
Crustacean fragments	27.8
Shrimp and shrimp larvae	11.4
Stomatopods	8.5
Larval stomatopods	5.3
Paguroid larvae	5.1
Megalopa	4.1
Unidentified animal material	2.1
Isopods: including 1 juvenile gnathid	1.4
Alpheids	1.3
Polychaetes	1.0
Brachyuran crabs	0.7
Mysids	0.5
Ostracods	0.4
Copepods: Calanoid: including Pleurogramma ? Cyclopoid: including corycaeids	0.3
Nebaliaceans	0.2

Table 30. Food habits of Phaeoptyx conklini. Based on 86 specimens; 20.1-48.0 mm SL; 31 empty; from 6 collections: S64-80, S65-41, S66-3, S66-26, S68-1, and GD73-2. The percentage given is based on a volumetric estimation technique described in the text.

Food	Percentage
Shrimp and shrimp larvae	30.3
Stomatopods	17.6
Alpheids	15.0
Crustacean fragments	15.0
Fish and fish fragments	12.5
Unidentified animal material	3.4
Brachyuran crabs	2.5
Paguroid crabs	0.9
Megalopa	0.9
Mysids	0.8
Amphipods	0.6
Euphausids	0.3
Polychaetes	0.2

Table 31. Food habits of Apogon maculatus. Based on 82 specimens; 20.1-62.9 mm SL; 17 empty; from 5 collections: S65-41, S66-3, S66-26, S68-1, and GD73-2. The percentage given is based on a volumetric estimation technique described in the text.

Food	Percentage
Crustacean fragments	31.8
Copepods: Calanoid Cyclopoid: including *Farranula gracilis* Wilson Harpactacoid	17.3
Shrimp and shrimp larvae	14.0
Fish and fish fragments	13.1
Alpheids	11.7
Crab larvae: including brachyuran	5.1
Unidentified animal material	2.8
Fish scales	1.2
Amphipods	1.1
Polychaetes	1.0
Mysids	0.8
Ostracods	0.2

Table 32. Food habits of *Apogon townsendi*. Based on 54 specimens; 26.5-37.4 mm SL; 15 empty; from 6 collections: S64-80, S66-3, S66-26, S68-1, and GD73-2. The percentage given is based on a volumetric estimation technique described in the text.

Food	Percentage
Crustacean fragments	54.7
Shrimp and shrimp larvae	13.9
Fish and fish fragments	10.0
Unidentified animal material	4.9
Mysids	4.4
Copepods: Calanoid: including *Pleurogramma* ? Cyclopoid: including corycaeids	3.8
Brachyuran crabs, larvae	3.0
Ostracods	1.9
Paguroid larvae	1.3
Cumaceans	1.1
Isopods: including juvenile gnathid, probably *Paragnathia* sp.	1.0

Table 33. Food habits of *Apogon binotatus*. Based on 25 specimens; 22.7-71.4 mm SL; 11 empty; from 5 collections: S64-80, S66-3, S66-26, S68-1, and GD73-2. The percentage given is based on a volumetric estimation technique described in the text.

Food	Percentage
Crustacean fragments	37.0
Fish and fish fragments	20.1
Mysids	18.2
Amphipods	13.0
Euphausids	5.2
Unidentified animal material	5.2
Shrimp and shrimp larvae	1.3

Table 34. Food habits of Phaeoptyx pigmentaria. Based on 21 specimens; 22.6-37.9 mm SL; 4 empty; from 5 collections: S64-80, S65-41, S66-26, S68-1, and GD73-2. The percentage given is based on a volumetric estimation technique described in the text.

Food	Percentage
Fish and fish fragments	52.3
Stomatopods	24.7
Shrimp and shrimp larvae	13.6
Crustacean fragments	8.1
Cumaceans	1.0
Ostracods	0.5

Table 35. Food habits of Apogon affinis. Based on 10 specimens; 27.3-52.7 mm SL; 1 empty; from 2 collections: S66-3, and S66-26. The percentage given is based on a volumetric estimation technique described in the text.

or the brooder itself might swallow the egg mass. One Apogon townsendi specimen, for example, had a large mass of eggs in the stomach (and nothing else), but also a few (identical) eggs in the mouth and an expanded buccal cavity. Deletion of fish eggs from the data in cases where brood swallowing was suspected led to eliminating most cases of fish eggs in stomachs. Among the remaining cases some identifications (as fish eggs rather than crustacean eggs) were doubtful. Therefore all fish egg data were arbitrarily deleted.

The "crustacean fragments" category includes (in a few cases) partially digested whole crustaceans, and (in most cases) variously fragmented crustaceans which could not be more precisely identified. In some cases a mass of fragments may have included non-crustacean material, but since the only recognizable fragments were crustacean, the whole mass was identified as such. Perhaps if specimens had been injected with formalin shortly after capture, in addition to being simply immersed in formalin, stomach contents would have been slightly less digested. This procedure would certainly be essential for larger fish species, but is probably less critical for apogonid-sized fishes.

Unfortunately, "crustacean fragments", a rather imprecise category, forms a very large part of the stomach contents data for some species. In many cases a fairly reliable estimate of the identity of such fragments on some lower taxonomic level could have been made. However, in the author's view, unidentified specimens were far less undesirable than misidentifications, and therefore a conservative approach was maintained in this regard throughout the study. With a greater degree of consultation with specialists or a greater use of reference specimens (both done in a few cases), greater taxonomic precision would have been possible. For this study, however, most identifications were made by the author using various published references (Brattegard, 1969, 1970; Davis, 1955; Day, 1973; Gosner, 1971; Gurney, 1942; Jespersen et al., 1939; Manning, 1961; Newell and Newell, 1967; Owre and Foyo, 1967; Renaud, 1956; Trégouboff and Rose, 1957a, 1957b).

b) Quantitative comparison of the food habits of *Phaeoptyx conklini* and *Apogon maculatus*.

The food categories for *P. conklini* and *A. maculatus*, in the four collections in which they were represented together in sizable numbers, are shown in Table 36. This tabulation deletes (from Table 30 and 31 data) the "crustacean fragments" and "unidentified animal material" categories, considered too non-descript to be of comparative value, and also the stomach contents of the specimens of these species in the other two collections.

Based on this pooled data (Table 36) the $\hat{C}\lambda$ value for these two species is 0.635. This value indicates a substantial amount of overlap in the diets of these two species. Interpretation of this result is, however, difficult for several reasons. Most simply, it may be presumed that identifications of food items at lower taxonomic levels would considerably reduce this overlap. Some degree of difficulty in this regard seems unavoidable.

A "pooling artifact" may also be involved. Pooling may tend to average out real differences that exist in single collections, and thus magnify the overlap. Conversely, pooling could result in a misleadingly low $\hat{C}\lambda$ if the two species had similar diets in one collection and other diets (again similar in the two species) in

Percentage in *P. conklini*	Food	Percentage in *A. maculatus*
0.3	Nebaliaceans	0
0.5	Ostracods	0
2.1	Isopods	0
14.4	Shrimp and shrimp larvae	38.5
7.5	Paguroid larvae	0
5.1	Megalopa	1.2
1.0	Brachyuran crab	3.2
44.5	Fish and fish fragments	15.9
1.5	Polychaetes	0.2
12.6	Stomatopods	22.4
0.7	Mysids	1.1
1.9	Alpheids	15.3
7.8	Larval stomatopods	0
0	Amphipods	0.7
0	Euphausids	0.4
0	Paguroid crabs	1.1

Calculated overlap:

$\hat{C}\lambda = 0.635$

Table 36. Food habit data for *Phaeoptyx conklini* and *Apogon maculatus* from 4 collections: S65-41, S66-3, S66-26, and GD73-2. The percentage given is based on a volumetric estimation technique described in the text. The $\hat{C}\lambda$ value given, calculated from the data in the table, is a measure of food overlap.

other collections, but were not similarly represented (in numbers of specimens) in the different collections. Pooling such data would make the diets appear different. This second problem would be minimized by maximizing the sample size.

A new analytic approach, proposed in this dissertation, which makes use of the $\hat{C}\lambda$ statistic, may provide a way of studying food overlap which avoids some of these difficulties. It is described in the following section.

c) Interspecific-intracollection-overlap vs. intraspecific-intercollection-overlap: a proposed analytical approach.

If the food habits of _P. conklini_ and _A. maculatus_ are compared in each of the four collections, much lower $\hat{C}\lambda$ values are obtained: 0.454, 0.426, 0.416, and 0.484, or an average of 0.445. Thus it would seem that the higher value for the pooled data resulted from a pooling artifact. Alternatively, the lowered $\hat{C}\lambda$ value may simply reflect random differences due to small sample size. This may be checked by calculating $\hat{C}\lambda$ for each possible within-species, between-collection comparison, and obtaining an average. Thus the data for _P. conklini_ from collection 1 are compared with that from collection 2, then with that from collection 3, and so forth, until all the following comparisons are made:

for _P. conklini_: 1 vs 2, 1 vs 3, 1 vs 4, 2 vs 3, 2 vs 4, 3 vs 4

for _A. maculatus_: 1 vs 2, 1 vs 3, 1 vs 4, 2 vs 3, 2 vs 4, 3 vs 4.

When $\hat{C}\lambda$ is calculated for each of these 12 data pairs, an average value of 0.556 is obtained.

Thus the average interspecific-intracollection $\hat{C}\lambda$ value is 0.445, as compared with an average intraspecific-intercollection $\hat{C}\lambda$

value of 0.556. This could be interpreted as evidence that species identity is more of a determinant of diet for these two species than collection identity (i.e. than local factors such as availability of prey). Put in a different way, it is evidence that the "food preferences" of the two species are at least slightly distinct.

This is not a trivial conclusion. In the case of a pair of species whose diets are very opportunistic, but appear to be similar in a given habitat, it provides an unambiguous approach to testing the possibility that their feeding preferences are, in fact, essentially identical. Such a possibility would not be unreasonable among many pairs of reef fish species, including apogonids such as P. conklini and A. maculatus.

To be truly quantitative this approach must, of course, be given a statistical framework.

The question of whether or not a similarity or difference in diet, however it is shown, is an indication of competition or lack of competition, is a separate subject fraught with its own interpretational difficulties, which will be described in the DISCUSSION section.

2. Field and aquarium observations

During the excursions made at dusk from the Hydrolab habitat, that were described earlier (in the Temporal Factors chapter), a few isolated observations were made regarding the nighttime foraging areas of the species which were diurnal residnets of the study reef. These observations, and some related information from the literature, are described (under (B) Circadian activity patterns,

1. In situ observation) in the RESULTS section of that chapter.

Livingston (1971) reported that both of these species occasionally feed during the day, and numerous attempts were made to observe diurnal feeding by these or other species. The polarizing filter-mask (with the higher transmission polarizing material) was helpful in revealing various planktonic organisms in the vacinity of the reef, particularly during use of the device at Bimini, off Turtle Rocks. Here it was helpful in viewing mysids and also a particularly transparent larvacean tunicate (Oikopleura sp.?). Feeding on plankton by certain reef fishes (including Eupomacentrus and Coryphopterus species) was observed on these occasions, but no feeding by cardinalfish was observed. On another occasion, in shallow water off New Providence, diurnal feeding by Apogon maculatus on unidentified crustaceans was observed.

Feeding behavior by cardinalfishes in the outdoor aquaria at the Lerner Marine Laboratory was observed during the changeover experiments carried out in August, 1974. As described in that section of this dissertation, tank populations were fed at night, whenever possible, on freshly caught live plankton. All of the different species kept in the tanks at that time seemed to feed voraciously and non-selectively on the variety of organisms contained in the food they were presented with, which included crustaceans, polychaetes, larval fishes and other zooplankton. On a few occasions they were also fed, much less successfully, with freeze-dried brine shrimp. My impression was that the non-motile nature of that food was the reason for the low frequency of feeding on it.

Observations of feeding by A. maculatus were also made when individuals of that species were kept in an "Instant Ocean" marine aquarium in the Ichthyology Department at the American Museum. They were purchased through the marine aquarium trade and kept for experiments on their optomotor behavior (Dale, MS). They were fed, on different occasions, live brine shrimp, guppies, and chunks of frozen shrimp. Again live, moving prey was voraciously eaten, while the fish had to be "coaxed" into taking the shrimp chunks. The latter food was only taken while it was sinking to the bottom of the tank. If not taken by the fish before it reached bottom it was picked up and dropped again from the top.

Two observations regarding their feeding on guppies are noteworthy. First, on more than one occasion _A. maculatus_ individuals fed on guppies nearly two thirds as long as themselves. In such cases the guppy was swallowed head first and it took as long as fifteen minutes or so before the tail of the guppy fully disappeared into the mouth. Secondly, despite this rather voracious predatory capability, the general impression of the act of predation on fish was one of considerable awkwardness. Despite the distressed and ineffective escape attempts of the prey (there were no hiding places in the tank) it often took several awkward approaches and snaps of the jaws before successful predation was achieved by the cardinalfish. Apparently _A. maculatus_ is not a swift and sure piscivore.

(B) Scanning electron microscopy of teeth

At least one good photograph of the premaxillary teeth, and one of the dentary teeth, were obtained for each of 12 different species, at magnifications ranging from 65x to 260x (Figures 29-40).

Figure 29. Scanning electron photomicrographs of the jaw teeth of *Apogon affinis*. (A) Premaxillary teeth, ventral aspect, x 130. (B) Dentary teeth, dorsolateral aspect, x 65.

FIGURE 29 (A)

FIGURE 29 (B)

Figure 30. Scanning electron photomicrographs of the jaw teeth of _Apogon binotatus_. (A) Premaxillary teeth, ventral aspect, x 130. (B) Dentary teeth, dorsolateral aspect, x 260.

FIGURE 30 (A)

FIGURE 30 (B)

Figure 31. Scanning electron photomicrographs of the jaw teeth of _Apogon lachneri_. (A) Premaxillary teeth, ventral aspect, x 130. (B) Dentary teeth, dorsolateral aspect, x 260.

FIGURE 31 (A)

FIGURE 31 (B)

Figure 32. Scanning electron photomicrographs of the jaw teeth of *Apogon maculatus*. (A) Premaxillary teeth, ventral aspect, x 130. (B) Dentary teeth, dorsolateral aspect, x 260.

FIGURE 32 (A)

FIGURE 32 (B)

Figure 33. Scanning electron photomicrographs of the jaw teeth of *Apogon phenax*. (A) Premaxillary teeth, ventrolateral aspect, x 130. (B) Dentary teeth, dorsolateral aspect, x 250.

FIGURE 33 (A)

FIGURE 33 (B)

Figure 34. Scanning electron photomicrographs of the jaw teeth of *Apogon planifrons*. (A) Premaxillary teeth, ventral aspect, x 130. (B) Dentary teeth, dorsolateral aspect, x 260.

FIGURE 34 (A)

FIGURE 34 (B)

Figure 35. Scanning electron photomicrographs of the jaw teeth of *Apogon quadrisquamatus*. (A) Premaxillary teeth, ventral aspect, x 130. (B) Dentary teeth, lateral aspect, x 260.

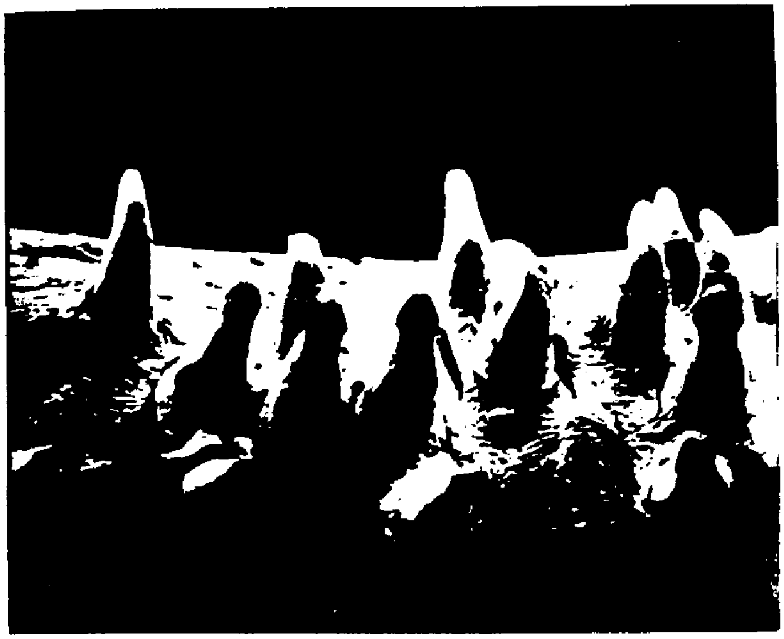


FIGURE 35 (A)

FIGURE 35 (B)

Figure 36. Scanning electron photomicrographs of the jaw teeth of <u>Apogon robinsi</u>. (A) Premaxillary teeth, ventral aspect, x 130. (B) Dentary teeth, lateral aspect, x 250.

FIGURE 36 (A)

FIGURE 36 (B)

Figure 37. Scanning electron photomicrographs of the jaw teeth of *Apogon townsendi*. (A) Premaxillary teeth, ventral aspect, x 130. (B) Dentary teeth, dorsolateral aspect, x 260.

FIGURE 37 (A)

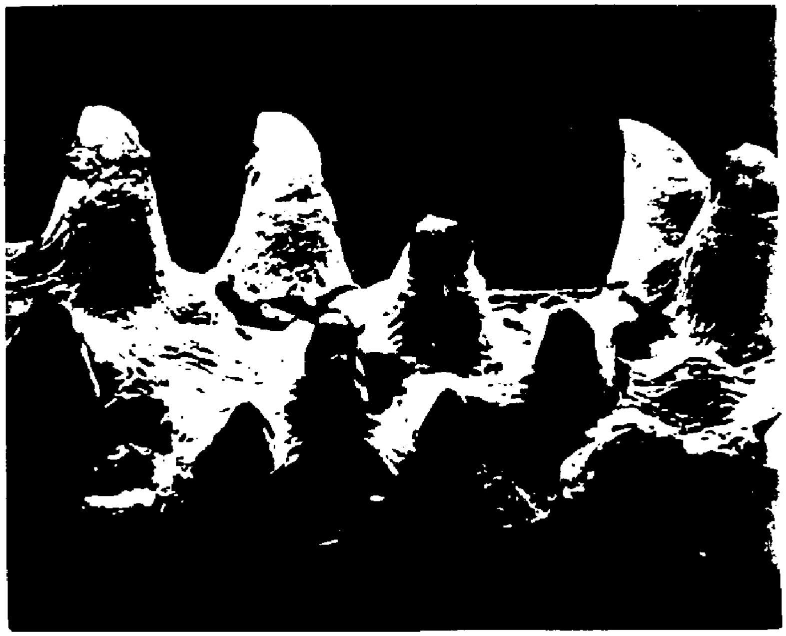


FIGURE 37 (B)

Figure 38. Scanning electron photomicrographs of the jaw teeth of _Phaeoptyx conklini_. (A) Premaxillary teeth, ventral aspect, x 130. (B) Dentary teeth, dorsolateral aspect, x 250.

FIGURE 38 (A)

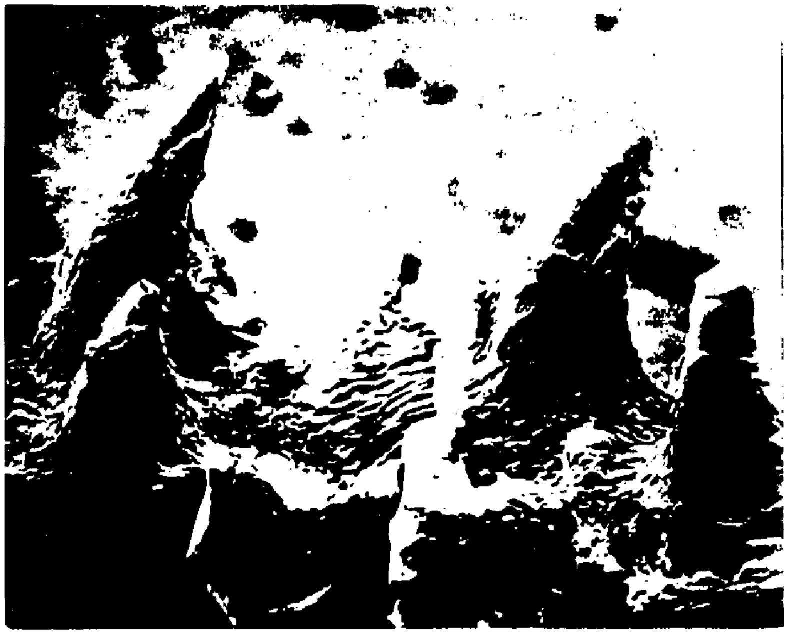


FIGURE 38 (B)

Figure 39. Scanning electron photomicrographs of the jaw teeth of *Phaeoptyx pigmentaria*. (A) Premaxillary teeth, ventral aspect, x 130. (B) Dentary teeth, dorsolateral aspect, x 260.

FIGURE 39 (A)

FIGURE 39 (B)

Figure 40. Scanning electron photomicrographs of the jaw teeth of Phaeoptyx xenus. (A) Premaxillary teeth, ventrolateral aspect, x 130. (B) Dentary teeth, lateral aspect, x 250.

FIGURE 40 (A)

FIGURE 40 (B)

Photographs of the premaxilla are ventral or ventro-lateral views, centered at a point in the anterior third of that bone (but never at the anterior end), and the dentary is photographed in dorsal, dorso-medial, or dorso-lateral views at a point about 1/3 to 2/5 of the distance from the anterior to the posterior end of the tooth-bearing edge of the bone.

This SEM study provided no special revelation about the comparative morphology of the teeth that could be related to the feeding habits of these fishes. The enlarged canines of _A. affinis_ (Figure 29) and the slightly enlarged teeth of _P. pigmentaria_ (Figure 39), are quite evident under a dissecting microscope, as mentioned earlier (and even with the naked eye in the case of _A. affinis_). These specializations may have some demonstrable trophic significance. In the food habits data of _A. affinis_ (Table 35) there were more "fish and fish fragments" (52.3%) than for any other species studied. The enlarged canines may indeed give this species a special piscivorous capability. The food habits of _P. pigmentaria_ (Table 34) also include a large proportion of "fish and fish fragments" (20.1%) but the food habits of _P. conklini_, which does not have enlarged teeth, included even more (30.0%) in that category.

There are several other structural features of the teeth revealed in the SEM study, and visible in Figures 29-40, that are noteworthy even though they have no presently demonstrable comparative ecological significance. These include the curious shovel-shaped tips of the teeth of most species, and the manner of tooth attachment and replacement. Description of these features will not be undertaken here.

III. DISCUSSION:

(A) Feeding habits

1. Stomach content analysis

a) Description of food habits of six species

The food habits indicated for six cardinalfish species in Tables 30-35 serve as qualitative indications of the diets of these species. For three of the species: *A. binotatus, P. pigmentaria*, and *A. affinis*, the data are based on too few specimens to be considered more than very tentative indications.

Three of the food items encountered should be commented on:

i) Copepods were present in the diets of *A. townsendi* (17.3%), *A. binotatus* (3.8%), and *P. conklini* (0.3%). Corycaeids (order Calanoida) were represented among these copepods in all three of these species, especially *A. townsendi*, where one corycaeid species: *Farranula gracilis* Wilson, was especially common (8 stomachs). The presence of this species and of other corycaeids is noteworthy because of their very small size. *F. gracilis* is less than 1mm in length (see Owre and Foyo 1967:119). It seems surprising that fish with mouths and teeth capable of capturing fishes not too much smaller than themselves and swallowing them whole, should also capture tiny transparent organisms smaller than the head of a pin. A possible explanation is that such organisms are the prey of some larger, soft-bodied organism, which is eaten by the cardinalfish and digested quickly, releasing the contents of its own digestive tract into the fish stomach.

ii) Juvenile gnathid isopods (Suborder Flabellifera) were present in two stomachs: one in an A. binotatus specimen, one in a P. conklini specimen. Such forms are known to be fish ectoparasites (Barnes, 1974:570) and the possibility that occasional ectoparasite feeding (i.e.,"cleaning") is included in the feeding habits of these species is suggested. Far more evidence, however, would be required to substantiate this suggestion.

iii) Ten ctenoid fish scales (1-2½mm in diameter) were present in one A. townsendi stomach. No other fish parts (or other food items) were present. Further evidence would be required, however, to suggest that lepidophagy is part of the feeding habits of this species.

b) Quantitative comparison of the food habits of Phaeoptyx conklini and Apogon maculatus.

The overlap indicated by the pooled data for these two species, $\hat{C}\lambda = 0.635$, is within the range that Zaret and Rand (1971) specify as indicative of significant overlap (0.60 - 1.00). As pointed out earlier, however, imprecise taxonomic identifications and pooling artifacts may greatly affect the calculated overlap.

Randall (1967) included these same two species in his study of West Indian reef fish food habits. To compare his results with the present findings, food overlap was calculated in the same way with his data, after eliminating the "unidentified crustaceans" category from his data (see Table 37). The calculated value of $\hat{C}\lambda$ is a very low 0.045 if "shrimp larvae - alpheids" is considered distinct from "shrimp and shrimp larvae - carideans", as in Table 37. On the

Percentage in <u>P. conklini</u>	Food	Percentage in <u>A. maculatus</u>
29.5	*Shrimp larvae - alpheids	0
23.0	Amphipods	0.7
12.2	Crab larvae	0
8.9	Tunicates	0
7.2	Polychaetes	4.2
7.2	Copepods	10.4
6.5	Isopods	1.3
3.3	Tanaids	0
2.2	Fish eggs	0
0	*Shrimps and shrimp larvae - carideans	56.1
0	Crabs	27.1

Calculated overlap: $\hat{C}\lambda = 0.045$

*If "Shrimp larvae - alpheids" and "Shrimps and shrimp larvae - carideans" are considered equivalent:

$$\hat{C}\lambda = 0.616$$

Table 37. Food overlap in <u>Phaeoptyx conklini</u> and <u>Apogon maculatus</u>, based on data of Randall (1967). Percentages are that author's "Volume (%)" figures, adjusted after deletion of "unidentified crustaceans" category.

chance that these two categories were not entirely distinct, but shared some shrimp varieties in common (alpheids *are* carideans) then these categories might be treated as a single comparable "shrimp" category. When this is done, a much higher $\hat{C}\lambda$ value, 0.615, is obtained for Randall's data. This clearly illustrates the effect of data categorization on calculated overlap. It also renders comparison with the present findings rather difficult.

A detailed comparison of these findings with feeding studies on other apogonid species, from other geographic areas (e.g. Hiatt and Strasburg, 1960; Hobson, 1974; Vivien, 1975) will not be undertaken here. A more or less similar variety of prey organisms was shown for apogonids in these studies. In nearly all cases crustaceans predominate.

To return to the subject of food overlap as measured by the $\hat{C}\lambda$ statistic, let us ignore the various reasons for questioning the calculated value (0.635) for the pooled data, and assume it has some validity. What does this fairly high degree of overlap say about competition for food in these two species? According to the interpretation of many published ecological studies, similarity of diet in fishes or other animals is an indication of competition.

In my view the opposite interpretation makes more sense. Hynes (1970:376) makes this point, with reference to fresh water fishes: "...Kawanabe (1959) argues, surely correctly, that change of diet caused by the presence of another species indicated competition for food, not similarity of diet. Indeed, one can probably go further and argue that similarity, or near identity, of diet between two species in the same habitat indicates that, however else they may be competing, they are not competing for food." It would seem that there is some confusion about the meaning of interspecific competition.

Perhaps the confusion comes from describing situations as competitive which only satisfy part of the kind of definition of competition exemplified by that of Weatherly (1963): "Competition is the demand, typically at the same time, of more than one organism for the same resource of the environment in excess of immediate supply." It is the last part of the definition - "in excess of immediate supply" - that is not always satisfied.

Zaret and Rand (1971) showed that high overlap values occurred among the diets of certain tropical stream fishes during times of abundant food supply, when competition would be low, and low overlap values occurred at a time of food scarcity. This is in keeping with Hynes' (1970) view of competition quoted above.

Considering the widely accepted view that food is not, in general, limiting to coral reef fishes, some appreciable degree of overlap would not be unexpected among related species. Evidently such overlap does exist between _P_. _conklini_ and _A_. _maculatus_, but is not complete, as indicated by the "interspecific-intracollection-overlap vs. intraspecific-intercollection-overlap" approach.

2. Field and aquarium observations

The field and aquarium observations of feeding by cardinalfishes were quite limited. They do, however, support certain generalizations. It would seem that cardinalfishes are opportunistic, generalized carnivores. They seem to attempt to feed on almost anything - within a rather wide size range - that moves. They are probably primarily visual predators, although the importance of the cephalic sensory canals and sensory buds cannot be discounted. (Ida and Moyer, 1974, showed these to be well developed in various Pacific apogonid species.) Finally, they seem to be rather awkward predators. Perhaps this is amply compensated for in their natural foraging habitat by exceptional visual capability at night.

(B) Scanning electron microscopy of teeth

In hindsight, the essentially negative results of this painstaking study are not surprising. One would not expect extremely subtle specializations in the teeth of rather generalized feeders, for whom space rather than food is probably the limiting factor.

And yet there are hints that tooth morphology may have some very basic ecological and evolutionary significance for these species. Fraser and Robins (1970) described and illustrated slight differences in the size of the dentary teeth between the eastern Atlantic populations (Gulf of Guinea) and western Atlantic populations of both A. affinis and P. pigmentaria. In each species the teeth are slightly smaller in eastern Atlantic specimens. Although these authors ascribed no special significance to these differences, a speculation will be offered here. Only three apogonid species are known from the Gulf of Guinea: these two species and Apogon imberbis. In the western Atlantic, of course, there is a diverse collection of cardinalfishes (twenty species known from the Bahamas, for example). Perhaps the greater tooth size of western

Atlantic specimens of A. affinis and P. pigmentaria represents character displacement resulting from greater interspecific trophic competition in this more diverse fauna!

CHAPTER SIX: Taxonomic Factors

The diversity of Bahamian apogonids, especially that of the *Apogon* speices and the coexistence of related species that promotes it - central problems of the present study - are made manifest by the prevailing taxonomy. It is therefore essential to consider the extent, if any, to which that taxonomy might improperly bias the perception of these problems.

Since the assignment of rank to any supraspecific taxon is essentially arbitrary, the diversity of *Apogon* could be an artifact of a "lumping" tendency in the taxonomy, or simply of poor knowledge of the group. Even prior to the present study, neither explanation seemed satisfactory in this case, since the taxonomy had been quite recently and rigorously defined (Böhlke and Randall, 1968; Fraser and Robins, 1970; Fraser, 1972).

In the course of the present study, a new apogonid species (*Apogon mosavi*) was discovered (Dale, 1977). This species possesses at least one of the characters diagnostic for *Phaeoptyx*, but is closer to *Apogon* in most other characters, and was placed in the latter genus. The intermediacy of this new species suggested that *Apogon* and *Phaeoptyx* might be very closely related, and indeed that the validity of Fraser and Robins' (1970) removal of the three *Phaeoptyx* species from *Apogon* should perhaps be reappraised.

Three characters separating *Phaeoptyx* and *Apogon* are mentioned in both the abstract of the original generic description (Fraser and Robins, 1970:302) and in the remarks on the genus *Phaeoptyx* in Fraser's (1972:25) study of apogonid osteology, which are the only two sections in these works specifically listing characters separating the two genera.

The first of these characters, as stated in the diagnosis, is: "fleshy posteroventral portion of free preopercular margin well developed, extending well posterior to a line along the vertical margin of the preopercle", a condition which is not distinct from that in Apogon leptocaulus (Gilbert, 1972:422).

The second, "caudal skeleton with 3 hypurals", is present also in A. mosavi and A. quadrisquamatus. Large numbers of both these species were X-rayed in conjuction with the description of A. mosavi (Dale, 1977). Although some variability was present, 94% of A. mosavi and 68% of A. quadrisquamatus examined had three hypural elements rather than five separate hypurals as in other Apogon species.

The third, "basisphenoid present, reduced, or absent", indicates an advanced trend. It is not by itself diagnostic, however, since it does not distinguish Phaeoptyx conklini, which may have a complete basisphenoid (Fraser, 1972:25), from Apogon.

Another diagnostic character, "coloration brown, the pattern composed of obvious melanophores over the entire surface of the body", does not (in alcohol, at least) distinguish some exceptionally pigmented specimens of A. quadrisquamatus from Phaeoptyx (pers. obs.). A fifth diagnostic character, "scales on body ctenoid", is present in all Apogon subgenera except Apogon (Paroncheilus) (Fraser, 1972:20).

The value of the last remaining diagnostic character, "inner pelvic ray connected along its entire length by a membrane to the abdomen", may be questioned for two reasons. First, an examination of this character in Phaeoptyx and Apogon indicates that a qualitative difference is impossible to define. Instead there seems to be a continuum of connectedness, with some Apogon species having only a short connection, other Apogon species (including A. mosavi, A. leptocaulus, and A. lachneri) having a connection of intermediate length, and Phaeoptyx having the longest connection.

Second, the west Atlantic genus Astrapogon, although it may not be closely related on other grounds, is not distinguished from Phaeoptyx by this character or by three other of the remaining five characters in the Phaeoptyx diagnosis. It has an inner pelvic ray to body connection comparable, in its length along the inner pelvic ray, to Phaeoptyx (pers. obs.), has three hypurals and lacks the basisphenoid (Fraser, 1972:13,14), and has a coloration not distinct from that specified in the Phaeoptyx diagnosis (pers. obs.).

This taxonomic reappraisal suggested initially to the author that the three species in Phaeoptyx should be referred back to Apogon, since the Phaeoptyx diagnosis, as originally stated, did not now include any single character, derived or otherwise, rigorously limited to the Phaeoptyx species. Certain nerve patterns (T. H. Fraser, pers. comm.) or behavioral and ecological factors (Livingston, 1971) may provide such a character, but a sufficient number of Apogon species has not as yet been studied in either case.

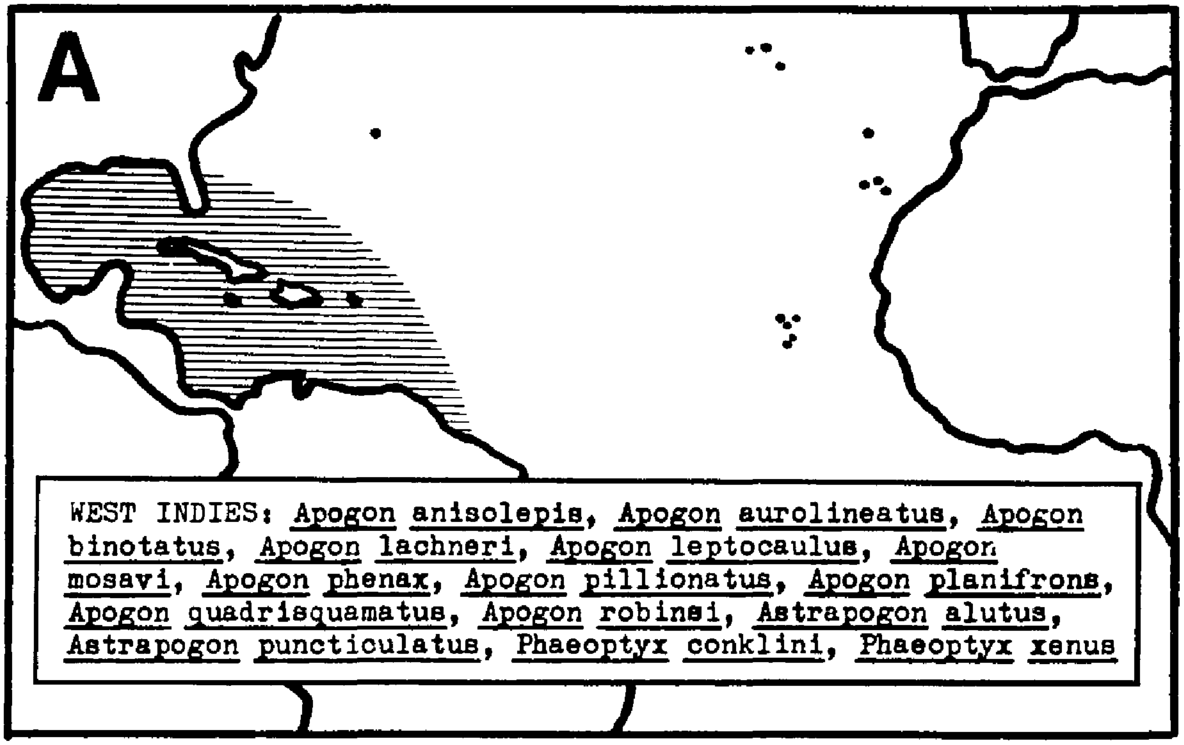
There are other reasons, however, for retaining the present taxonomy. Phaeoptyx can be readily distinguished by the diagnostic characters in combination, and there is no evidence that it is not monophyletic. Although all supraspecific taxa should ideally be defined by synapomorphies for a truly phylogenetic classification, selective insistance on such a definition in the existing taxonomy ignores the complexity of percoid systematics. A more prudent approach would be to look further for synapomorphic characters in Phaeoptyx. Perhaps the preopercular flap is a synapomorphy, and its presence in A. leptocaulus could be shown, by parsimony, to represent a convergence.

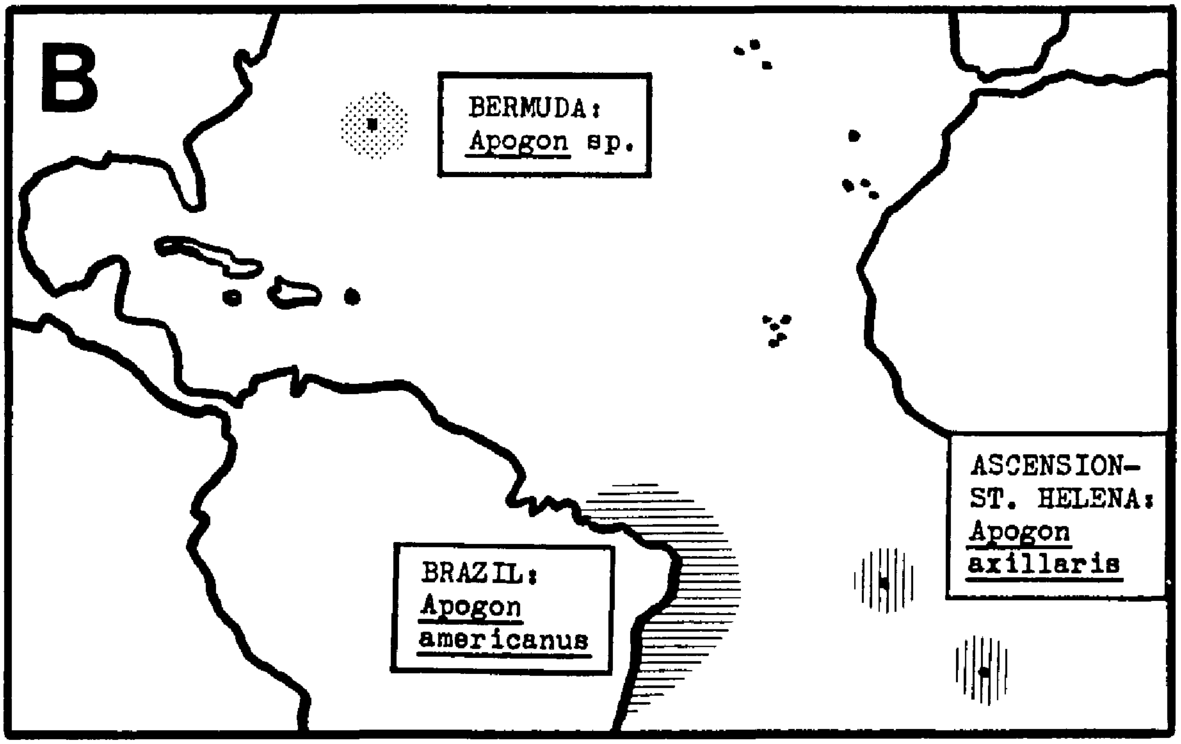
These taxonomic observations tend to stress the relatedness of the western Atlantic apogonid taxa. The possibility that they might, in fact, form a monophyletic group (sensu Hennig, 1966) led to an effort to clarify their phylogenetic relationships and biogeographic history.

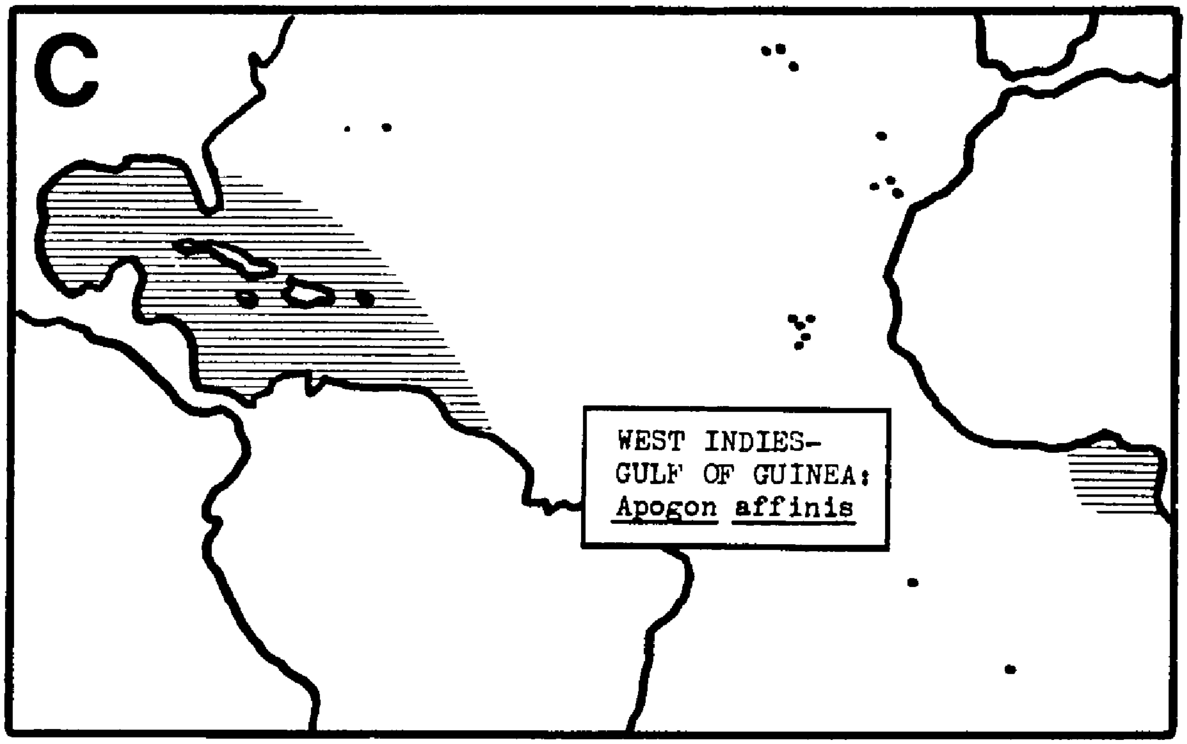
A cladistic analysis of the five western Atlantic supraspecific taxa (Phaeoptyx, Astrapogon, and three Apogon subgenera: Apogon, Zapogon, and Paroncheilus), based on data in Fraser (1972) was inconclusive. Ultimately, a numerical cladistic analysis was performed on the entire subfamily Apogoninae (Dale, in preparation).

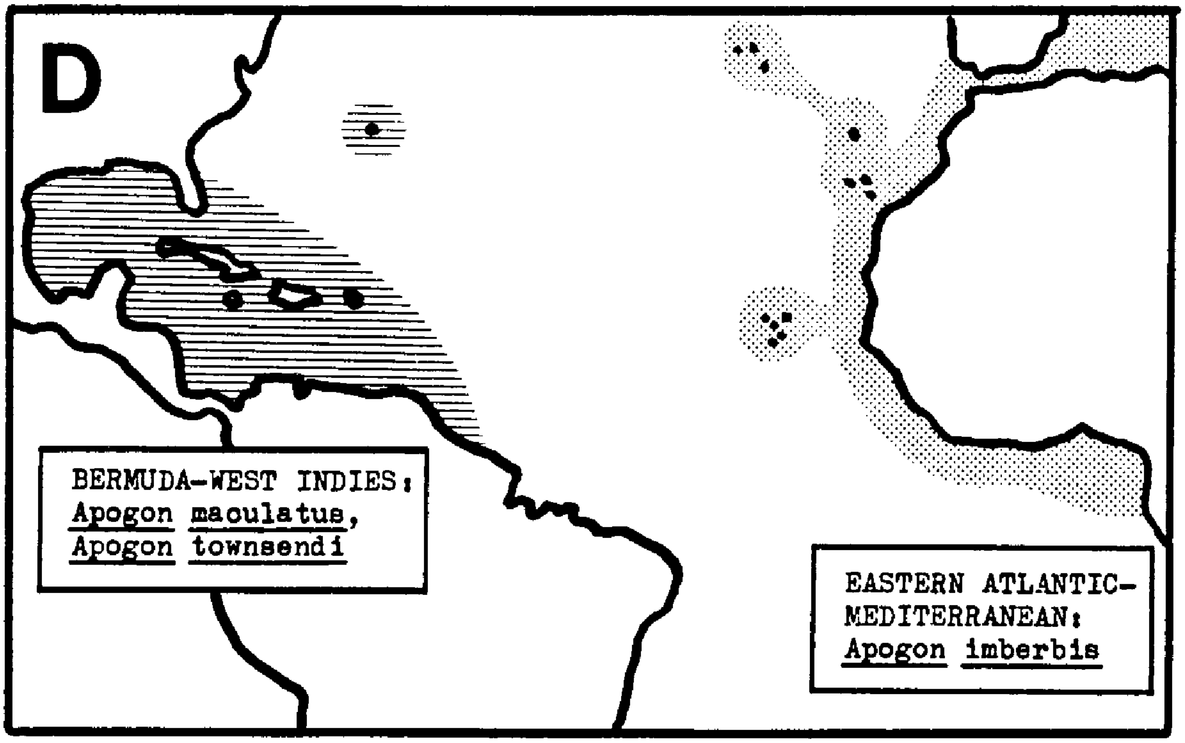
An attempt to understand the historical biogeography of western Atlantic cardinalfishes led to the compilation of the records of all Atlantic apogonid species (of the subfamily Apogoninae, to which all inshore species belong). No real progress has yet been made in solving the biogeographic problems, but the compilation of Atlantic apogonid distribution is summarized and presented in Figure 41. The "West Indies" category (including adjacent continental shorelines) is based on records in Starck (1968), Böhlke and Chaplin (1968), Gilbert (1972), and Dale (1977). The "Bermuda" records are based on recent collecting there and supersede previous (some apparently erroneous) records (W. F. Smith-Vaniz, pers. comm.). The "Brazil" records are based on Gilbert (1977), the "Gulf of Guinea" records on Fraser and Robins

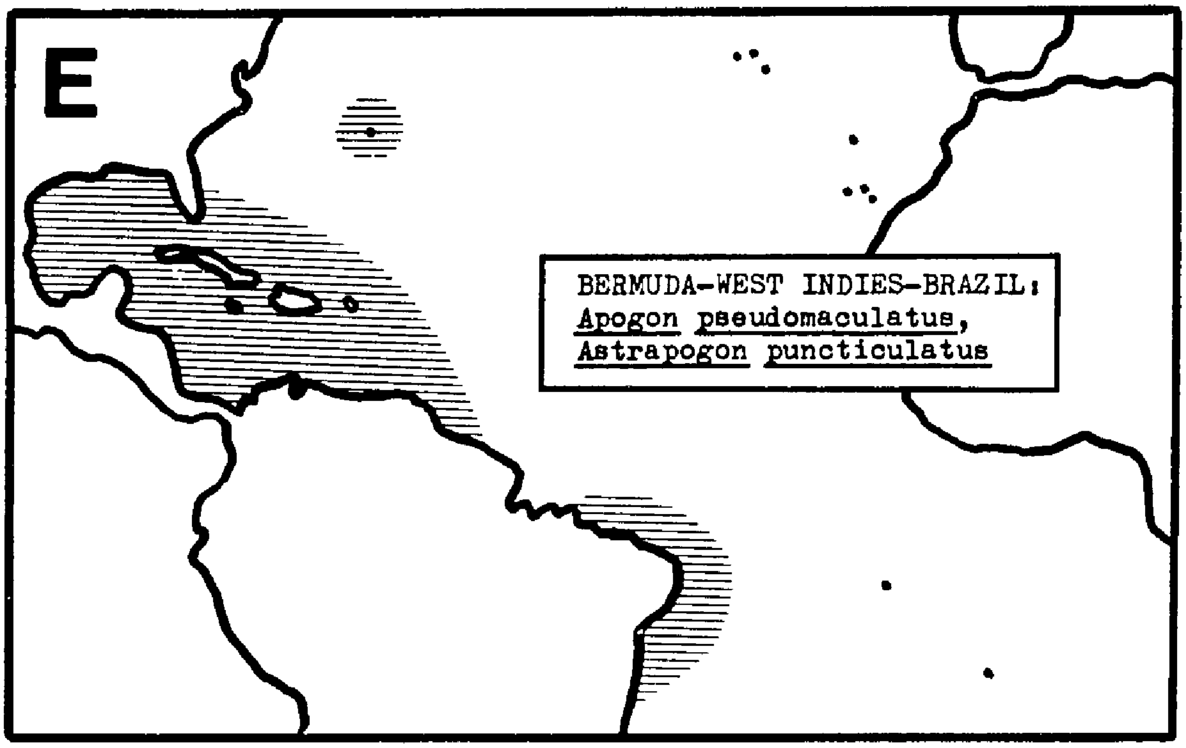
Figure 41. Summary of the distribution of shallow water cardinalfish species in the Atlantic. Nine different distributional categories are shown on six maps (A-F).


A
WEST INDIES: Apogon anisolepis, Apogon aurolineatus, Apogon binotatus, Apogon lachneri, Apogon leptocaulus, Apogon mosavi, Apogon phenax, Apogon pillionatus, Apogon planifrons, Apogon quadrisquamatus, Apogon robinsi, Astrapogon alutus, Astrapogon puncticulatus, Phaeoptyx conklini, Phaeoptyx xenus


B
BERMUDA: Apogon sp.
BRAZIL: Apogon americanus
ASCENSION-ST. HELENA: Apogon axillaris

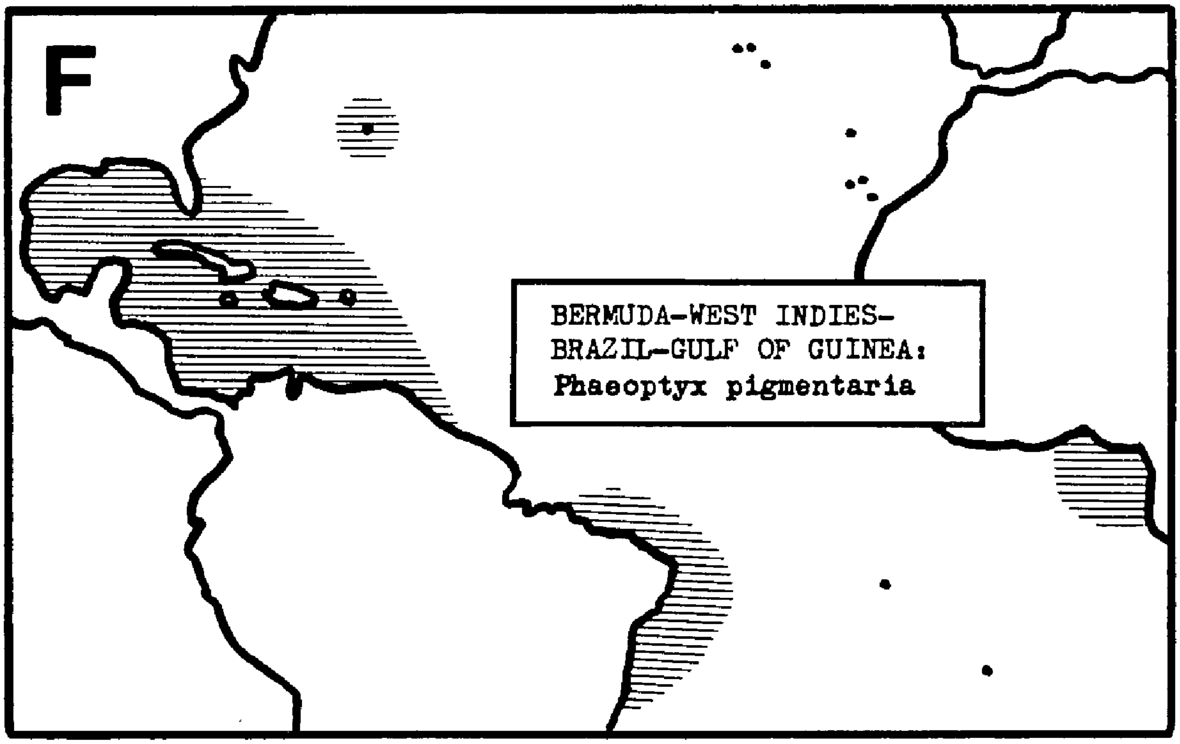

C
WEST INDIES-
GULF OF GUINEA:
Apogon affinis


D
BERMUDA-WEST INDIES:
Apogon maculatus,
Apogon townsendi
EASTERN ATLANTIC-
MEDITERRANEAN:
Apogon imberbis



E

BERMUDA-WEST INDIES-BRAZIL: *Apogon pseudomaculatus*, *Astrapogon puncticulatus*



F

BERMUDA-WEST INDIES-BRAZIL-GULF OF GUINEA: **Phaeoptyx pigmentaria**

(1970), the "Ascension-St. Helena" records on Cadenat and Marchal (1963), and the "Eastern Atlantic-Mediterranean" records on Fowler (1936), Cadenat (1950), Garnaud (1962), Fraser and Robins (1970), Lalami (1971), and Collignon and Aloncle (1973).

CHAPTER SEVEN: Summary and Conclusions

SUMMARY

Cardinalfishes are a very prominent component of coral reef fish communities in the Bahamas and elsewhere. Clarification of the basis of their diversity and their avoidance of competitive exclusion, and, by extension, clarification of these matters in the entire reef fish community, were central objectives of this dissertation research. Information was sought by studying an extensive series of rotenone collections of Bahamian reef fishes and by means of field and laboratory observations. The approaches used fall into several categories.

1. Typologic Factors

A study of species abundance patterns indicated that Bahamian cardinalfishes fit a lognormal curve i.e., an overlapping, multidimensional niche hypothesis.

A study of abundance-frequency patterns among all the species in Bahamian reef fish communities emphasized the prominence, perhaps even the predominance, of cardinalfishes in these terms.

Investigation of species association patterns, using 2 x 2 contingency tables, revealed that nine species pairs showed a positive and two a negative association.

Interest in species diversity patterns led to the derivation of a new statistic, the omission effect index, which estimates the contribution of a taxon or other unit to the Shannon-Weaver species diversity index of a community. The two most important Bahamian apogonid genera were found, using this statistic, to have prominent though opposite effects on calculated species diversity: Apogon makes a "positive contribution" and Phaeoptyx makes a "negative contribution".

A study of the relationship of apogonid species richness vs. community species richness determined that apogonid species comprise about 8–10% of the total species in communities of various total richness.

Investigation of body size patterns included the calculation of length-weight relationships, and of "coefficients of stoutness" for 14 species. Estimates of "adult length" and "adult weight" were also made, and a negative correlation was discovered between adult length and stoutness at a given size. A name was suggested for this relationship: allometromorphism, and its possible evolutionary significance was discussed.

Comparison of adult body size data with the abundance and frequency data and with the species association results provided evidence that body size differences may play a role in interspecific competition avoidance.

In the course of examining specimens, a frequent ectoparasitic infestation of Apogon townsendi was noted, and two undescribed parasitic copepods were discovered.

2. Topographic factors

An investigation of the geographic distribution of different apogonid species within the Bahamas indicated that most, perhaps all, of the twenty species known from the Bahamas are found throughout that area, with the possible exception of A. pseudomaculatus.

Based on relative abundance and frequency at different ranges of depth of capture, a certain depth association was shown for each species, ranging from a fairly clear preference for shallower water by Phaeoptyx conklini and Astrapogon puncticulatus, and for deeper water by Apogon affinis, A. lachneri, A. phenax, and P. xenus, to less pronounced tendencies among other species.

Based on relative abundance and frequency in collections from different broad habitat categories, the most notable apparent "preferences" are by Astrapogon puncticulatus for the shoreline category, by Apogon affinis and A. lachneri for the dropoff category, by A. binotatus for the top of bank category, and by A. townsendi for the outer shelf category. Other species showed less pronounced tendencies.

Among various microhabitat associations observed, facultative association with the long spine sea urchin Diadema antillarum, recorded for the first time for three additional cardinalfish species, is the most widespread, and tends to emphasize a lack of strictly defined and distinct microhabitats among most of the common species.

Consideration of the lack of a clearly circumscribed spatial niche for most apogonid species led to proposal of a model of reef fish coexistence for explaining such instances. It is offered as an alternative to the "reef fish lottery" model, which does not (it is argued) provide a means of escaping competitive exclusion. In the proposed "money-in-the-bank" model (and financial analogy) two or more species ("investors") can continually coexist in some habitats ("stock market") because of excess larva production ("interest") in other habitats ("savings banks") in which they occur alone. Various features of this model are described and examples among cardinalfishes from the present results are suggested.

3. Temporal Factors

Tabulation, according to month, of several kinds of evidence of reproduction, including evidence of oral brooding and occurrence of recruit-sized individuals, indicated that apogonids tend to reproduce throughout the year, and do not avoid competition by a staggering of breeding season. Direct or indirect evidence of the oral brooding habit was obtained in the present study for 12 different species, including three for which this habit had not previously been reported.

In situ observations of cardinalfish changeover patterns supported previous reports of the species-specific and sequential nature of this behavior, and of its mediation in some way by light. A new hypothesis is offered to explain the proximate cause of this behavior: differential phototaxis. Arguments in terms of its conformity to various observations, its greater parsimony, and its falsifiability are offered in favor of this hypothesis.

Laboratory observation of cardinalfish changeover behavior corroborated the view of its species-specific, sequential, and light-mediated nature.

Brain dissections indicated a kind of brain morphology-behavior correlation previously unreported in the literature. Slight differences in relative optic lobe size were shown to be positively correlated with photophobic tendency among the three species for which the laboratory changeover data were most reliable.

In addition to the differential phototaxis hypothesis, which addresses the "how" of changeover behavior, a new explanation is proposed for the "why" of this behavior, i.e., for its ecological significance. This hypothesis, termed phototactic habitat partitioning, states that changeover is a space-sharing mechanism in which differences in photophobia or photophilia result in a passive partitioning of shelter space on the reef. It is argued that this explanation is parsimonious, is framed in terms of the resource that is widely considered limiting for most reef fishes (i.e., shelter space), is falsifiable, and has a plausible evolutionary basis.

4. Trophic factors

Stomach content analyses were performed utilizing a new volumetric estimation method. In this technique the fraction of a stomach's contents that a given food item represents is multiplied by the fullness fraction of that stomach, giving a "fraction-of-full-stomach" value for that item. Adding and comparing such values to determine a species' food habits avoids certain misleading characteristics of other methods. Food habits determined by this method were tabulated for six species. Crustaceans dominated the food habits of all except *A. affinis*, in which fish constituted more than half the diet.

Food overlap between two of the six species, *A. maculatus* and *P. conklini*, was studied with the $\hat{C}\lambda$ statistic. Although the calculated overlap between these species is high, it is argued that possible pooling artifacts render such results unreliable. An analytic approach is suggested for testing the possibility that the food habits of two such species are essentially identical. This approach, termed "interspecific-intracollection-overlap vs. intraspecific-intercollection-overlap", is intended to specify whether species identity or collection identity is more of a determinant of diet.

The pitfalls of relating food overlap to competition are discussed.

A few field and aquarium observations of feeding were made. Most notably they supported a view that cardinalfishes are voracious, opportunistic, generalized carnivores, whose somewhat awkward predatory behavior is offset by superior visual capability.

The rationale for a comparative study of the teeth using the scanning electron microscope is explained, and the methods for selecting and preparing material for that study are described. Photographs of the premaxillary and dentary teeth of twelve species did not reveal any special modifications which could be shown to be related to feeding differences. The enlarged teeth of _A. affinis_ and _P. pigmentaria_, which do not require the SEM for demonstration, may be associated with piscivory by these species.

5. Taxonomic Factors

The discovery of a new apogonid species led to an examination of the characters separating _Phaeoptyx_ from _Apogon_ and _Astrapogon_, which tended to stress the relatedness of these genera. This, in turn, led to systematic and biogeographic investigations. These are not described, but a summary of Atlantic apogonid distribution is presented, without comment.

CONCLUSIONS

The diversity of apogonids, especially _Apogon_ species, in the Bahamas and in the coral reef environments throughout the world, was described at length in the _Introduction_. Various findings of the present study contribute to an understanding of this diversity.

Investigation of abundance-frequency patterns, of "diversity contribution" among the different reef fish taxa, and of species richness patterns, confirmed the view that cardinalfishes are a central component of high diversity reef fish communities in the Bahamas. A brief geographic analysis indicated that most, if not all, of the various species are indeed sympatric within the Bahamas. Evidence was also discussed which suggested that Bahamian cardinalfish specioseness, and that of Apogon in particular, is not merely a taxonomic artifact.

Curiously enough (since not by design) the first calculated "results" presented - the finding that Bahamian cardinalfish species abundance patterns fit a lognormal curve, i.e. an overlapping, multidimensional niche hypothesis - provide a kind of first approximation or indication of the most general concluson of this study: that Bahamian cardinalfish species coexist within a complex array of competitive relationships. These relationships include several important competition-avoiding mechanisms for which evidence was provided by subsequent aspects of the study.

To begin with, there is evidence that adult body size differences are greater among species that tend to be found together than among species which tend to be found apart. This could have a role in reducing interspecific competition for either food or space. "Allometromorphism" might be an evolutionary mechanism promoting such body size differences.

Depth and broad habitat "preferences" account for some spatial separation among species, while microhabitat specializations are probably of great importance for only a few species. The money-in-the-bank model may help explain cases of coexistence without any apparent spatial resource partitioning.

Among possible temporal factors, reproductive seasonality is apparently <u>not</u> an important competition-avoiding mechanism. On the other hand, differences in changeover time, which may be promoted by a simple differential phototaxis, seem to represent a very fundamental habitat-partitioning mechansim.

Investigations of food habits and of the comparative morphology of the teeth indicate that trophic niche partitioning does <u>not</u> provide a critical competition-avoiding mechanism for most species.

Even if slightly different food habits could be established for different apogonid species, and correlated with dentitional or other anatomical factors related to feeding, these factors may still be subordinate to more fundamental differences. I do not believe a given species is somehow "programmed" to consume a given combination of prey organisms, or somehow seeks out the prey that its dental equipment is best suited for.

Instead I believe that apogonids and perhaps many other reef species, are essentially opportunistic feeders that eat what they are "presented" with as a result of being where they are. Being where they are may be a result, over the diel cycle, of factors such as phototactic response. Over their entire juvenile and adult life span (assuming that they remain more or less sedentary after recruitment), it is a result of the depth and/or habitat factors that promoted their settling from planktonic larval existence.

Table 38 summarizes all of the factors of probable and possible importance in the reduction of competition among the sixteen apogonid species in this study. The species are arranged in order of decreasing estimated adult body size. Differences in this dimension, shown in Chapter 2 to be of apparent ecological significance among these species, represent the simplest kind of specializations that allow resource sharing. "Adult weight" is used in Table 38 as the estimate of adult body size, and the reader should recall that a two-fold difference in body weight seems to be sufficient, according to MacArthur (1972), to allow coexistence of otherwise similar animal species. In the following remarks each of the sixteen apogonid species is discussed in terms of the ecological factors which may separate it from other species of roughly similar size.

Apogon robinsi is nearly three times larger in "adult weight" than the second largest species, A. binotatus, and may lack the latter species' ability to associate with the long spine sea urchin Diadema antillarum. (Its distinctive dentition may also give it some special feeding capability.)

A. binotatus is not much larger than the next three smaller species, but differs from them in other ways: it differs from A. maculatus in photophobic tendency; from A. planifrons (possibly) in the ability to associate with Diadema, and from A. phenax in depth and habitat preference, as well as in the Diadema association.

A. maculatus differs from each of the two smaller species (of roughly similar size) in Diadema association, and from A. phenax in

Table 38. Interspecific differences in various factors that may be related to reduction of competition among sixteen cardinalfish species in the Bahamas. "Adult weight" data are from Table 16. Depth and habitat preference data are from Figures 13, 14, 15, and 16; a dash indicates no pronounced indication. Microhabitat and photophobic tendency data are from Chapters 3 and 4, respectively; dashes indicate no data; all Diadema associations are facultative. Teeth specializations are tentatively included, even though their importance was argued against earlier (in Chapter 6).

Species	"Adult weight" (grams)	Depth Preference	Habitat Preference	Microhabitat	Photophobic Tendency	Teeth Specialization
Apogon robinsi	21.78	shallow	-	-	-	extending out on premaxilla
Apogon binotatus	7.80	shallow-intermediate	top of bank	*Diadema*	intermediate	-
Apogon maculatus	7.55	shallow-intermediate	absent at dropoff	*Diadema*	low	-
Apogon planifrons	6.72	-	-	-	-	-
Apogon phenax	5.44	deep	dropoff	-	-	-
Apogon affinis	3.08	deep	dropoff	-	-	canine jaw teeth
Phaeoptyx conklini	2.32	shallow	least common at dropoff	*Diadema*	high	-
Apogon quadrisquamatus	2.23	-	-	sea anemones	-	-
Astrapogon puncticulatus	2.17	shallow	shoreline	empty tests	-	-

Table 38. (continued)

Species	"Adult weight" (grams)	Depth Preference	Habitat Preference	Microhabitat	Photophobic Tendency	Teeth Specialization
Apogon lachneri	1.85	deep	dropoff	-	-	-
Phaeoptyx pigmentaria	1.74	-	-	*Diadema*	high?	enlarged jaw teeth
Phaeoptyx xenus	1.54	deep	most common at dropoff	sponge-dweller	high?	-
Apogon townsendi	1.48	intermediate	outer shelf	*Diadema*	low?	-
Apogon mosavi	0.91	deep	-	-	-	-
Astrapogon stellatus	intermediate?	-	-	*Strombus gigas*	-	-
Apogon leptocaulus	large?	deep?	-	-	-	extending out on premaxilla

Table 38. (continued)

depth and habitat preference.

Although no clear trends in depth or habitat preference by A. planifrons were apparent in the present study, Böhlke and Chaplin (1968) describe it as a shallow water species, and thus it may differ most from A. phenax in this respect.

A. phenax differs from the next smaller species, A. affinis, in lacking enlarged canine jaw teeth, and consequently may differ in feeding capability from the latter species.

A. affinis differs from the various smaller (but not much smaller) species in various ways. Its preference for deep water and the dropoff habitat differs from the depth and habitat preferences of Phaeoptyx conklini, Astrapogon puncticulatus, and Apogon townsendi. It may lack the ability of P. conklini, P. pigmentaria, and A. townsendi to associate with Diadema, and its enlarged canine jaw teeth may give it some distinct feeding capability. Finally, it also lacks the microhabitat specializations of A. quadrisquamatus, Astrapogon puncticulatus and P. xenus.

P. conklini differs from each of the smaller species, except P. pigmentaria, in either depth and habitat preference, microhabitat, or photophobic tendency. It is apparently quite similar, ecologically, to P. pigmentaria, but may differ in its feeding habits in some way related to its lacking the enlarged teeth of the latter species.

A. quadrisquamatus has the habit, unique among these 16 species (but shared by the rarer A. aurolineatus), of associating with the sea anemones Bartholomea annulata and Condylactis gigantea.

Astrapogon puncticulatus differs from the smaller species in depth, habitat or microhabitat.

Apogon lachneri differs from the three smaller (but not much smaller) species either in depth, habitat, or microhabitat preference.

P. pigmentaria differs from P. xenus in lacking the latter species' sponge-dwelling habit, from A. townsendi in photophobic tendency, and from both of these species and A. mosavi in its jaw dentition and, possibly, in its consequent feeding capability.

P. xenus is the only obligate sponge dweller among these sixteen species (A. quadrisquamatus may carry out that habit facultatively), and also tends to differ in depth, habitat, and photophobic tendency from the most similarly sized species, A. townsendi.

A. townsendi differs in depth preference from the smallest species, A. mosavi and perhaps also in the Diadema association habit.

The remaining two species, Astrapogon stellatus and Apogon leptocaulus were not represented by enough specimens for any adult body size estimate to be possible. Based on Böhlke and Chaplin's (1968) remarks, Astrapogon stellatus is probably an intermediate-sized cardinalfish as an adult. Its curious habit as an inquiline in the mantle cavity of Strombus gigas gives it a unique microhabitat.

Apogon leptocaulus is similar in morphology, including dentition, to A. robinsi, and may also be a very large species (see the discussion of allometromorphism in Chapter 2). It evidently differs markedly from A. robinsi in depth preference.

Thus for each of the sixteen species there is evidence of some factor or combination of factors associated with it which may be significant in its ecological separation from the other species. Is any general pattern discernible?

In a recent paper on mosaic phenomena in natural communities, Robert Whittaker and Simon Levin (1976) concluded that: "Ecologists have sought a theory or master plan of evolution permitting interpretation of communities through a limited number of strongly linked and widely significant relationships. Such a theory is naturally desired by ecologists as scientists; but the reasoning of this paper suggests that there may be no master plan except, perhaps, the evolution of such a diversity of relationships as to frustrate that desire."

This view may be correct for other biotic communities, but I believe it is too pessimistic to apply to studies of coral reef fish communities. Indeed I think there is mounting evidence that the space-sharing hypothesis of Smith and Tyler (1972) represents a durable basic explanation of diversity and coexistence in these communities. Most, if not all, of the mechanisms suggested in the present study as being important for competition avoidance among cardinalfishes have their ultimate significance in terms of this fundamental unifying principle.

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