Place of Apogonid Fish in the Food Webs of a Malagasy Coral Reef

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Abstract—Twenty one species of Apogonidae were collected on the barrier reef at Tuléar (Madagascar). Most of them have a well defined ecological distribution across a reef transect. The feeding behaviors of the 11 most common species were qualitatively and quantitatively studied. Most cardinalfishes are nocturnal carnivores, feeding at night either on benthic organisms or on plankton. During the day, they rest sheltered under reef cover and capture available prey. Many differences appear between diurnal and nocturnal diets, which, in general, can be explained by the various rates of activity of the invertebrates, the distribution of food items among the biotopes and selectivity of the fishes. Finally, the trophic level of apogonid fishes in the reef food webs is discussed.

INTRODUCTION

The family Apogonidae (cardinalfishes) constitutes a permanent part of the ichthyofauna of Malagasy coral reefs. In spite of their small size, apogonid fishes hold a considerable place in the trophic structures of a coral reef tract because of their great number.

Little information about the feeding behavior of Apogonidae is available in the existing literature. Hiatt and Strasburg (1960) have studied the diets of ten cardinalfish species of the Marshall Islands, but the number of stomachs analyzed was too small for definitive results. They worked only by day and arrived at the conclusion that Apogonidae are diurnally active. They supposed nocturnal activity only for *Gymnapogon philippinus*. Stark and Davis (1966) described nocturnal habits in seven cardinalfish species at Alligator Reef (Florida). Six of these species catch benthic invertebrates, whereas only one, *Apogon conklini*, feeds on plankton. Randall (1967) analyzed the diet of *A. conklini* and *A. maculatus* and confirmed that they are planktophagous fishes. Hobson (1968) also observed, in the Gulf of California, an Apogonidae (*A. retrosella*) taking its prey at night among plankton in midwater. In a paper on the feeding behavior of fishes in Kona (Hawaii), Hobson (1974) described the nocturnal habits of three cardinalfishes and studied their diets. *Apogon erythrinus* feeds on benthic crustaceans while *A. menesmus* preys mostly on free-swimming crustaceans. The third species, *A. snyderi*, feeds on both planktonic and benthic crustaceans. A previous study was done at Tuléar on the feeding behavior of coral reef fishes (Vivien, 1973) in which 6 species of Apogonidae, collected on the inner reef flat, were analyzed. All were nocturnal predators feeding on plankton or on benthic invertebrates. A

Micronesica 11(2): 185-198. 1975 (December).

more complete study of the feeding relationships of cardinalfishes was undertaken to investigate in more detail their place in reef food webs.

MATERIALS AND METHODS

Twenty one species of Apogonidae (fig. 1) were represented in the 2,558 specimens collected on the Great Reef of Tuléar (Madagascar). Specimens were obtained by rotenone poisoning on the reef flat and by the use of explosives on the reef slopes during the day and at night. Underwater observations were made by scuba diving from the reef flat to the end of the outer deep coral flagstone at 60 m depth.

The feeding study includes the 11 most common cardinalfish species occuring on Tuléar reefs. Their feeding behaviors were studied by the quantitative analysis of 1,909 stomach contents, made according to a numerical and weight method previously described in Vivien (1973). Several indices and coefficients were calculated to indicate the relative importance of prey in stomach contents:

The vacuity coefficient is the ratio of the number of fish with empty stomachs to the total number of fish sampled. A diurnal vacuity coefficient (v_D) and a nocturnal one (v_N) were calculated in order to assess the extent of feeding activity during these two periods.

The occurence index (f) is the ratio of the number of fish containing each food item to the total number of fish with food in their stomachs. This index was also employed by Hobson (1974) to calculate his ranking index.

The food coefficient (Q) is computed by multiplying the numerical percentage of each food item (Cn) by its weight percentage (Cp). Food coefficients are used to rank the various prey by importance.

RESULTS AND DISCUSSION

Ecological Distribution of Apogonidae on Tuléar reef

In a schematic transect of the Great Reef of Tuléar, seven main biotopes can be distinguished as one moves from the sea towards the lagoon: outer reef slope (OS), outer reef flat (OF), boulder tract (BT), reef flat with coral alignments (CAF), reef flat with scattered coral growth (SGF), seagrass beds (GB) and inner reef slope (IS) (Clausade *et al.*, 1971).

Cardinalfishes are not uniformly distributed on the reef tract and the number of species varies greatly from one biotope to another (Fig. 1). Biotopes completely emerged during low spring-tides shelter only a small number of cardinalfish species. Seagrass beds provide little cover for fishes, even during high tides, and only two species were collected in them. The boulder tract similarly gives little protection and is exposed to the strong effects of surge waves. Only two species can be found in this area. The outer reef flat, with flourishing corals and calcareous algae, offers more shelter than the two preceding biotopes, but it is

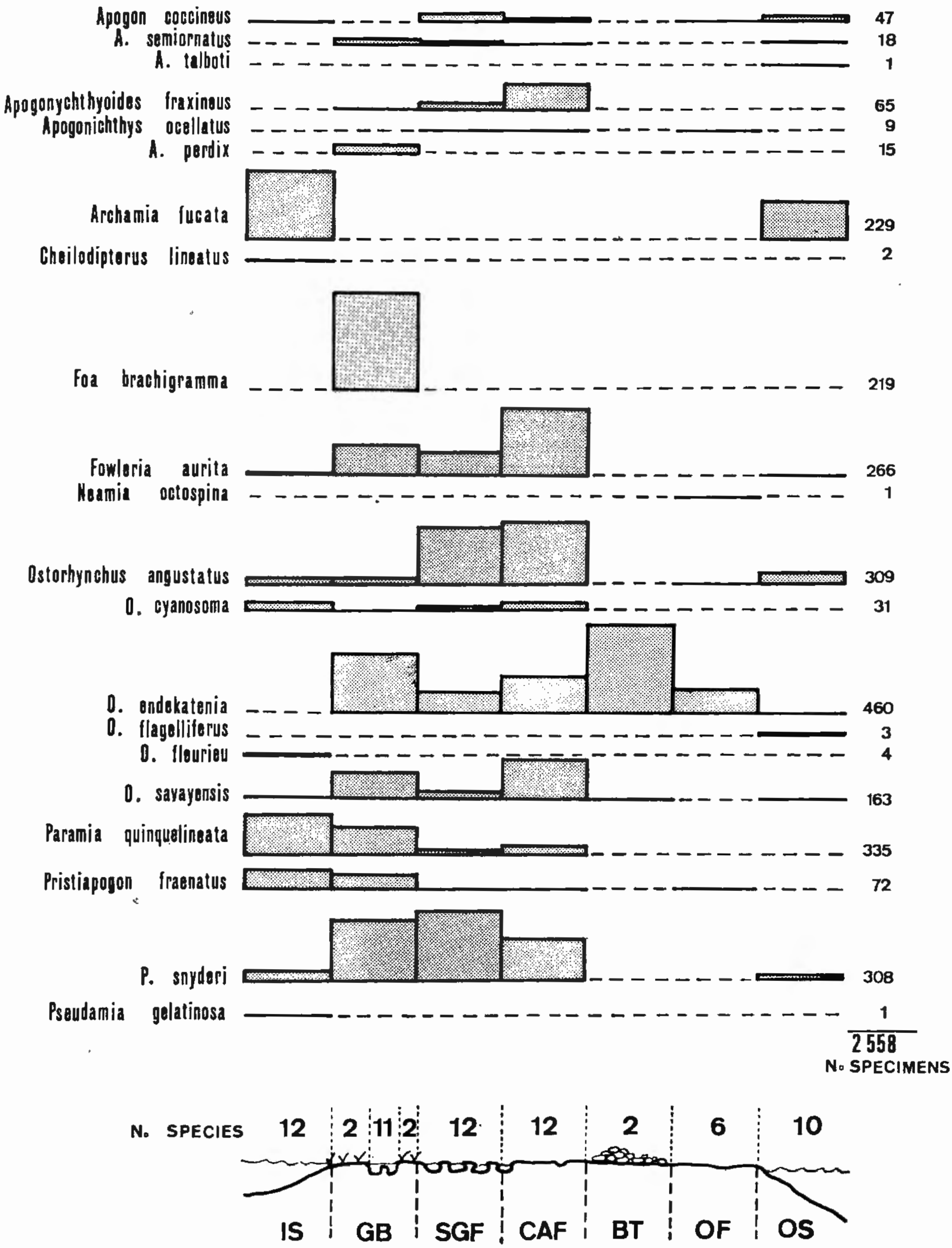

Fig. 1. Ecological distribution of Apogonidae on the Great Reef of Tuléar (Madagascar). Line thickness is proportional to the total number of specimens collected in all samples. IS=inner slope, GB=seagrass bed, SGT=reef flat with scattered coral growth, CAF=reef flat with coral alignments, BT=boulder tract, OF=outer reef flat, OS=outer reef slope.

strongly influenced by long sea-swell and by breaking waves during low tides. Of the six species sampled in the surge zone, only one (*Ostorhynchus endekataenia*) is numerically important.

In the biotopes where coral constructions are flourishing and where the water always remains relatively deep, more apogonid species are found. Ten species were collected on the outer reef slope, twelve on the inner reef flat (CAF+SGT) and twelve on the inner reef slope. Seagrass bed pools, where madreporarians often grow, contain many more species than the seagrass beds themselves. Twelve species of cardinalfish were recorded from pool samples.

Some species are restricted to a single biotope, while other species exist across the whole reef tract (Fig. 1). *Foa brachygramma* and *Apogonichthys perdix* are characteristic species of seagrass beds. The other species found in "seagrass beds" live in fact in pools. *Archamia fucata* occurs on reef slopes and was never collected nor observed on the reef flat. Perhaps this species needs considerable water depth or cannot endure strong variations of temperature. *Ostorhynchus fleurieu* and *Cheilodipterus lineatus* were only found on the inner reef slope in areas of coral growth. *O. flagelliferus*, collected between 15 and 30 meters deep, seems representative of the outer reef slope. *Apogonichthys fraxineus, O. cyanosoma* and *Paramia quinquelineata* were only sampled behind the boulder tract and probably require relatively calm areas. *Apogon coccineus, A. semiornatus, Fowleria aurita, Ostorhynchus angustatus, O. endekataenia, O. savayensis, Pristiapogon fraenatus* and *P. snyderi* are found in varying abundance in several biotopes. *O. endekataenia*, the only apogonid species found on the boulder tract and the most abundant one on the outer reef flat, appears to be the species most resistant to surge action. *Apogon talboti, Neamia octospina* and *Pseudamia gelatinosa* were represented by only one specimen each in our samples and so their distributions remain unclear.

Analysis of Feeding Behavior

The results of the quantitative analysis of the stomach contents of the 11 most abundant cardinalfish species are summarized in Table 1.

Nocturnal vacuity coefficients are, for the most part, smaller than the diurnal ones. The mean values are $v_N = 0.09$ and $v_D = 0.36$, indicating the nocturnal feeding activity of Apogonidae. *Paramia quinquelineata* is the only species with a smaller v_D than v_N, suggesting that this species feeds more by day than by night.

The average numbers of prey caught during the night are higher than during the day. The average weights of prey per stomach are also generally higher by night than by day, but this varies according to the species. The ratio of nighttime to daytime prey weight varies from 1.2 in *Fowleria aurita* up to 14.8 in *Apogonichthyoides fraxineus*. The two species of *Pristiapogon* show little nocturnal/diurnal difference in prey weight, but their very low nocturnal vacuity coefficients indicate that they are nocturnally active feeders. The average weight of prey ingested by

Table 1. General results of the food analysis of 11 cardinalfish. Numbers of individuals collected, vacuity coefficients, average number of prey per stomach and average weight per stomach are given by day and by night.

	Total No.	Number of individuals (Day)	Number of individuals (Night)	v_D	v_N	No. prey/stomach (Day)	No. prey/stomach (Night)	weight/stomach(mg) (Day)	weight/stomach(mg) (Night)
Archamia fucta	141	141		0.36		6		38	
Apogonichtyoides fraxineus	58	25	33	0.16	0.06	20	160	14	208
Foa brachygramma	108	96	12	0.28	0.08	3	23	28	67
Fowleria aurita	210	119	91	0.41	0.07	2	3	42	51
Ostorhynchus angustatus	279	207	72	0.05	0.19	5	13	33	85
O. cyanosoma	20	10	10	0.60	0.10	2	23	5	10
O. endekataenia	478	275	203	0.34	0.03	3	10	56	140
O. savayensis	99	71	28	0.19	0.03	18	111	34	124
Paramia quinquelineata	146	136	10	0.21	0.33	2	2	98	11
Pristiapogon fraenatus	55	51	4	0.49	0.00	2	5	65	58
P. snyderi	315	186	129	0.47	0.08	3	5	64	55
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Paramia quinquelineata during the day is higher than during the night. This species shows a tendency for diurnal activity, but it would be necessary to study a greater number of specimens collected by night to confirm these results. *Archamia fucata* was collected only during the day, but its diurnal vacuity coefficient ($v_D = 0.36$) indicates a high proportion of empty stomachs during the day and it is probable that *A. fucata* is nocturnally active.

Some cardinalfishes, e.g. *Apogonichthyoides fraxineus, Ostorhynchus cyanosoma* and *O. savayensis,* feed entirely on plankton. During the day they ingest organisms which are always planktonic such as calanoïd copepods, planktonic larvae of polychaetes and crustaceans, and planktonic shrimps. During the night they catch invertebrates which emerge out of the reef tract or out of the sand, and which spend a free-swimming phase during the night such as some polychaetes (Phyllodocidae, Nereidae in heteronereid phase), ostracods, some amphipods and shrimps, and cephalochordates. Other apogonid species are strictly benthic feeders. *Fowleria aurita* and *Pristiapogon fraenatus* seize prey which move about on the bottom or swim near it. Several species (*Archamia fucata, Ostorhynchus angustatus, O. endekataenia, Paramia quinquelineata* and *Pristiapogon snyderi*) eat both types of prey, but although they catch occasional planktonic organisms, they primarily feed on benthic invertebrates. *Foa brachygramma,* living on seagrass beds, catches invertebrates swimming around seagrass leaves or creeping on them.

In fish species catching mainly benthic prey, the nocturnal increase of prey

Table 2. Quantitative analysis of the diet of *Ostorhynchus endekataenia*. Weights are given in grams. The food coefficient (Q=Cn×CP) reflects the importance of prey in the diet. Np=number of prey, n=number of fish with the prey in their stomach, N=number of fish with full stomach, f=occurence index (—n/N), Pp=weight of prey, Cn=numerical percentage, Cp=weight percentage, Q=food coefficient.

Total number of specimens=478 { DAY 275 empty = 95 v_D=0.34; NIGHT =203 empty = 7 v_N=0.03 }

	Np		n		f		Cn		Pp		Cp		Q	
	D	N	D	N	D	N	D	N	D	N	D	N	D	N
Polychaetes	55	276	51	148	0.28	0.75	9.1	14.6	1.696	19.097	16.7	69.5	151.9	1014.7
Ostracods	3	10	1	4	0.005	0.02	0.5	0.5	0.006	0.007	0.05	0.03	0.03	0.02
Copepods	71	—	6	—	0.03	—	11.7	—	0.006	—	0.05	—	0.6	—
Cumacea	—	14	—	12	—	0.06	—	0.7	—	0.005	—	0.01	—	0.01
Isopods	153	273	52	85	0.28	0.43	25.3	14.5	2.857	0.899	28.2	3.3	713.5	47.9
Amphipods	138	929	51	115	0.28	0.58	22.8	49.2	0.504	1.699	5.0	6.2	114.0	305.0
Shrimps	47	197	37	79	0.20	0.40	7.8	10.4	1.228	1.700	12.1	6.2	94.4	64.5
Brachyuran larvae	35	56	9	25	0.05	0.12	5.8	3.0	0.127	0.154	1.3	0.6	7.5	1.8
Brachyurans	52	49	47	37	0.26	0.18	8.6	2.6	2.448	2.118	24.1	7.7	207.3	20.0
Galatheidae	—	9	—	7	—	0.03	—	0.4	—	0.174	—	0.6	—	0.2
Paguridae	1	1	1	1	0.005	0.005	0.2	0.05	0.073	0.475	0.7	1.7	0.1	0.08
Stomatopods	4	5	3	4	0.02	0.02	0.6	0.3	0.528	0.019	5.2	0.06	3.1	0.02
Crustacean fragments	25	14	25	14	0.13	0.07	4.1	0.7	0.315	0.224	3.1	0.8	12.7	0.6
Insects	2	17	2	7	0.01	0.03	0.3	0.9	0.029	0.010	0.3	0.05	0.03	0.03
Insect larvae	—	10	—	4	—	0.01	—	0.5	—	0.004	—	0.01	—	+
Polyplacophores	—	1	—	1	—	0.005	—	0.05	—	0.003	—	0.01	—	+
Opistobranchia	—	5	—	5	—	0.02	—	0.3	—	0.307	—	1.1	—	0.3
Gastropods	15	21	15	17	0.08	0.08	2.5	1.1	0.257	0.403	2.5	1.5	6.3	1.7
Cephalochordates	—	2	—	2	—	0.01	—	0.1	—	0.002	—	0.005	—	+
Fishes	4	6	4	6	0.02	0.02	0.6	0.3	0.063	0.168	0.6	0.6	0.4	0.2
	603	1893							10.137	27.468				

Average number of prey/stomach { DAY =3.3; NIGH = 9.6 }

Average weight of prey/stomach { DAY =0.056 g; NIGHT =0.140 g } number always remain low. In species feeding on planktonic organisms, the ingested prey number is higher and shows a strong increase at night.

The detailed study of the diet of *Ostorhynchus endekataenia,* summarized in Table 2, is an example of the diurnal-nocturnal variations of the food of Apogonidae. The principal prey ingested by this cardinalfish differ from day to night. During the day, *O. endekataenia* eats principally isopods (Q=713) and brachyurans (Q=207). The secondary prey (20<Q<200) are polychaetes, amphipods and shrimps. During the night, polychaetes are the main food item with a very high food coefficient (Q=1,014), followed by amphipods which are considerably less important (Q=305). The secondary prey (shrimps, isopods and brachyurans) are

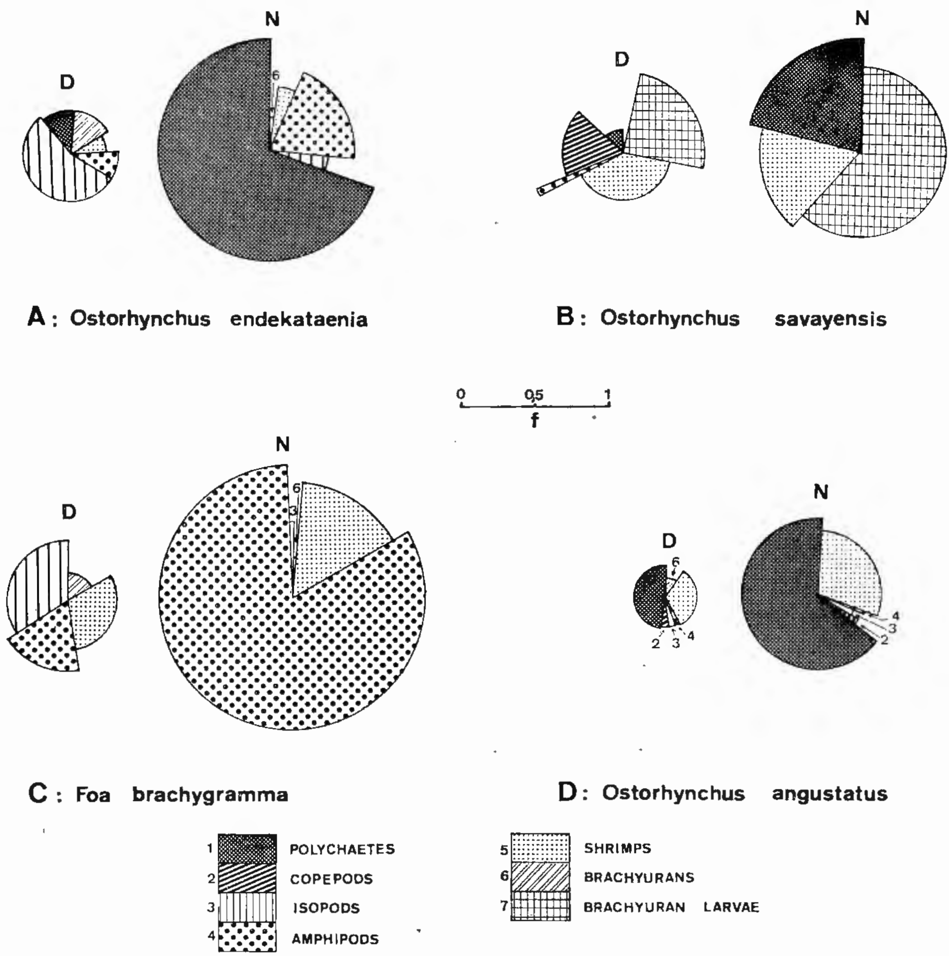

Fig. 2. Graphic representation of the diet of four Apogonidae, A=*Ostorhynchus endekataenia*, B=*O. savayensis*, C=*Foa brachygramma*, D=*O. angustatus*, showing the differences between diurnal (D) and nocturnal (N) diets. Angles are proportional to the food coefficient Q and radii to the occurence index f.

of little importance (20<Q<64). The main food items eaten by *O. endekataenia* are benthic invertebrates, but this species also ingests some planktonic organisms: calanoïd copepods and brachyuran larvae by day, and ostracods, cumacea and cephalochordates by night.

The vacuity coefficient in *O. endekataenia* is low at night and high by day ($v_N = 0.03$, $v_D = 0.34$) and the average number and weight of prey per stomach are higher by night than by day. It can also be observed that food coefficients and occurence indices of principal prey are higher by night than by day. This implies either an increase of prey number in the environment during the night or their more active and selective capture by the predator. The graphic presentation of the diet of *O. endekataenia* (Fig. 2A) shows these diurnal-nocturnal differences of feeding, which are also noteworthy in *O. savayensis* (Fig. 2B) and *Foa brachygramma* (Fig. 2C) diets. At night, *O. savayensis* ingests preferentially the polychaetes which become planktonic in addition to free-swimming shrimps and shrimp larvae and actively hunts brachyuran larvae instead of merely taking those swimming around its shelter as it does during the day. In seagrass beds, *Foa brachygramma* consumes mainly isopods by day and amphipods by night. *O. angustatus* (Fig. 2D) shows little difference in daytime and nighttime diets, although quantitative differences still exist: diurnal occurence indices of prey are very low

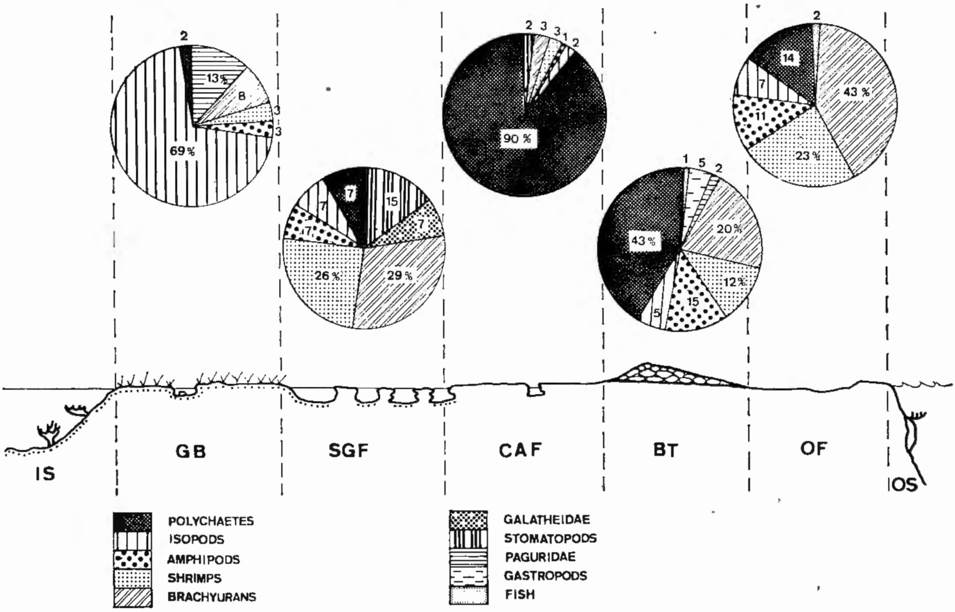

Fig. 3. Variations of the diet of *Ostorhynchus endekataenia* according to the biotope. In each biotope and for each food item, average weight per fish was calculated and converted to weight percentage. Sector sizes are proportional to weight percentages, each circle representing 100% of the total average weight.

and the quantity of prey ingested at night is three times as great as during the day.

The general diet of *Ostorhynchus endekataenia* (day and night combined) was studied in the five areas in which it was collected. For this study only the weight of ingested items was taken into consideration (Fig. 3). Considerable variations in the diet of *O. endekataenia* from area to area are indicated. Isopods constitute 69% of prey in seagrass beds, while very few of them are eaten in other biotopes. Brachyurans (29%) and shrimps (26%) are dominant on the reef flat with scattered coral growth. There is some consumption of stomatopods in this area (15%) but not at all in others. On the reef flat with coral alignments, polychaetes make up about 90% of the total weight of prey. They comprise 43% on the boulder tract, followed by the brachyurans (20%). On the outer reef flat, brachyurans are most important (43%) and shrimps (23%) and polychaetes (14%) are also eaten in considerable proportions.

Pristiapogon snyderi also ingests many isopods in seagrass beds (68%), but catches more shrimps (49%) than brachyurans (18%) on the reef flat with scattered

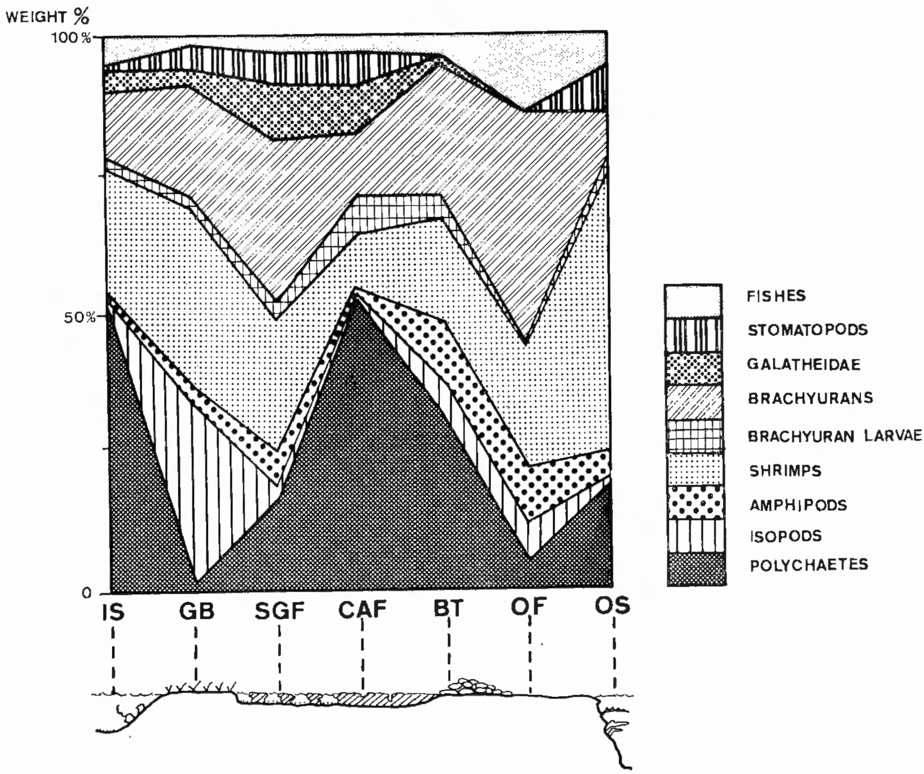

Fig. 4. Food consumption of 11 Apogonidae in the various biotopes of the Great Reef of Tuléar. The average weights of ingested prey are expressed as weight percentages. In each biotope 100% correspond to the total food ingested by all the cardinalfish collected.

coral growth. On the reef flat with coral alignments, polychaetes represent only 46% of the food weight and brachyurans 25%. There is also a high consumption of shrimps on the reef slopes (80% on the inner reef slope and 90% on the outer reef slope). Modifications do indeed appear in the diet of fishes according to the biotope. However, comparison of the diets of *Ostorhynchus endekataenia* and *Pristiapogon snyderi* show some differences in the relative proportions of different prey items in fishes taken from the same biotopes, suggesting that the fishes make a selection among the available prey.

The combined diets of all eleven abundant species are presented in Fig. 4, showing the relative importance of various prey organisms in each biotope. The reef slopes were omitted because only diurnal samples have been taken in these areas. On the reef flat relationships can be noted between the consumption of prey by cardinalfishes and the relative abundance of invertebrates *in situ.*

POLYCHAETES: The polychaete consumption, very low in seagrass beds (2%), increases on the reef flat with scattered coral growth (16%) and reaches its highest level on the reef flat with coral alignments (54%). Still important on the boulder tract (31%), it falls abruptly on the outer reef flat. This is quite parallel to the distribution of the cryptofaunal polychaetes (Clausade, 1970), except for the outer reef flat where, although the polychaete biomass is important, their consumption by Apogonidae stays rather low. The increase of polychaete consumption observed on the reef flat with coral alignments is related to the highest biomass of polychaetes *in situ.* Clausade (1970) found 15.9 g/dm^3 of polychaetes on the reef flat with coral alignments, 5.1 g/dm^3 on the reef flat with scattered coral growth and only 0.6 g/dm^3 on seagrass beds. Polychaetes ingested by Apogonidae belong for the most part to the cryptofauna and are caught primarily during the night when they emerge from reef holes. This phenomenon was previously described by Vivien and Peyrot-Clausade (1974).

ISOPODS: Isopod consumption is greatest in seagrass beds. In this biotope, they represent 32% of the food weight. Two isopod species, *Cirolana natalensis* and *Paracilicea mossambicus,* are very numerous in seagrass beds (Roman, 1970). They are diurnally active and are eaten by apogonids during the day. At night they take shelter near the lower part of seagrasses or are hidden in the upper sand layer (Roman, personal communication), and few of them are eaten by apogonids at night. On the inner reef flat very few isopods are captured (1 to 3% of prey weight), which is related to the low number of species and individuals indicated by Roman (1970) in these biotopes. This author has found a population of isopods on the boulder tract and on the outer reef flat where the presence of much algae provides shelter to this invertebrate. A slight increase in isopod consumption (6 to 7%) was observed in these aras.

AMPHIPODS: Amphipods are regularly ingested in the various biotopes but in none of them are they especially important (1 to 12%). In seagrass beds they are primarily caught at night (Fig. 2C) when the sand species, emerging from the sediment, join the amphipods living permanently around seagrass leaves (Ledoyer, 1973). The small increase in their capture on the reef flat with scattered coral growth is related to the nocturnal emergence of sandy species; their abundance is therefore related to the abundance of sandy areas. The increase in their consumption recorded on the boulder tract and on the outer reef flat corresponds to a high biomass of cryptofaunal amphipods (Ledoyer, 1972).

SHRIMPS: Shrimps are more regularly eaten on the reef flat than are polychaetes. Shrimps live in sand, reef holes, clusters of algae and around seagrass leaves, and, according to the species, are diurnally or nocturnally active. They are very important in seagrass beds (Ledoyer, 1969) and are consumed in great quantity in this biotope (32% of the food weight). Although some species only appear at night, the shrimp population of seagrass beds does not vary very much during 24 hours (Ledoyer, 1969) and their diurnal consumption by apogonids is high. In the other biotopes, there is often a small increase in their capture during the night, when they emerge from sand and reef cavities.

BRACHYURANS: According to the biotope, brachyurans caught by Apogonidae live either in soft bottoms or in reef holes. In seagrass beds, brachyurans ingested (20%) are primarily portunid crabs, which are eaten at night when they rise from the sediment. During the day, brachyuran species which move about on sand or on seagrass leaves are also caught, but in smaller quantity. On the reef flat with scattered coral growth, brachyuran consumption is quite high (29%) and crabs are caught equally by day and by night. Brachyurans are abundant in the cryptic habitats of the reef flat with scattered coral growth (Peyrot-Clausade, in press) and in soft bottom environments (Thomassin, 1974). On the reef flat with coral alignments, a decrease of brachyuran abundance occurs and they are less important in the diet of cardinalfish, especially since polychaetes are very important in this biotope and preferentially eaten. Brachyuran consumption increases on the boulder tract (24%) and is the most important prey on the outer reef flat, where they represent 41% of the food weight. This can be explained by the strong increase in brachyuran biomass (Peyrot-Clausade, in press) in the cavities of the outer reef flat.

Brachyuran larvae are eaten by Apogonidae feeding in midwater. Their consumption is highest in pools on the reef flat with coral alignments.

GALATHEIDAE: Galatheidae are eaten primarily on the inner reef flat (SGF= 10% and CAF=9%), where they are most numerous (Peyrot-Clausade, in press). They belong for the most part to the cryptofauna and are caught by apogonids at night.

STOMATOPODS: Stomatopods are not usually preyed upon by Apogonidae. The small consumption of these invertebrates on seagrass beds and on the reef flat with scattered coral growth seems to be related with the importance of some species in the sediment of these areas (Thomassin, 1974).

FISH: Only small quantities of fish are ingested in all the biotopes. Fish represent an important group of prey only for one cardinalfish species, *Paramia quinquelineata*. They are caught by day as well as by night.

Table 3. Total food consumption of Apogonidae. For each prey category, food weights found for all the cardinalfish are summarized and divided by the number of fish to give the average weight of food per fish. Percentages of food consumption were calculated from the average weights.

Prey	Average Weight in mg	Percentage
Polychaetes	25	32
Isopods	4	5
Amphipods	3	4
Shrimps	19	24
Brachyuran larvae	2	3
Brachyurans	14	18
Galatheidae	4	5
Stomatopods	3	4
Fishes	4	5

Polychaetes, shrimps and brachyurans are the most important prey of apogonids comprising 74% of the total food weight (Table 3). Polychaetes represent 32% of the food ingested and crustaceans make up 64% of cardinalfish diets. Among them, shrimps dominate (24%), followed by brachyurans (18%). The great importance of crustaceans in reef-fish diets was previously noticed by Randall (1967) in the West Indies.

CONCLUSIONS

The Apogonidae present a well-defined ecological distribution on the reef tract. Several factors (e.g., tides, waves and currents, extent of coral construction, behavior and feeding specialization of fish), acting together, influence this distribution. The total species number in the various biotopes is related to the behavior and requirements of the individual species. Like many other nocturnal fishes, apogonids need to be protected during the day and take shelter under coral ledges or in dark reef holes. This necessity of diurnal shelter concentrates most of the species in biotopes where coral constructions are important. Tidal fluctuation also influences apogonid distribution. Very few species live in seagrass beds and on the boulder tract because these environments are exposed during low spring tides and present only sparse cover. Waves and currents also affect the distribution of fish species. In spite of the presence of favorable shelter, many species cannot stay on the outer reef flat which corresponds to the surge zone most of the time. The feeding specialization of fish can also be a factor of species distribution. For example, the plankton feeders *Apogonichthyoides fraxineus, Ostorhynchus cyanosoma* and *O. savayensis* are more numerous on the reef flat with coral alignments than in other areas. They were collected in relatively deep reef pools occuring in this biotope, where the available plankton biomass was greater than on the reef flat itself. *Foa brachygramma* and *Apogonichthys perdix*, confined to seagrass beds, mainly feed on the isopods, amphipods and shrimps which are very numerous in these areas. But many other cardinalfish (*O. endekataenia, O. angustatus, Fowleria aurita, Pristiapogon snyderi*), which are ubiquitous species, adapt their diets to the food possibilities of the various biotopes.

The results of quantitative analysis of stomach contents corroborate the observations and conclusions of other authors (Stark and Davis, 1966; Randall, 1967; Hobson, 1968 and 1974) and those previously carried out in Tuléar (Vivien, 1973): Apogonidae are primarily nocturnal carnivores, spending the daytime with a low activity level. Day/night variations of fish diet are closely related to the activity level of the fish and to the differences of availability of prey during day and night. For the most part, the nocturnal/diurnal variations in the kinds of prey eaten reflects the temporal variation of prey availability, although the neglect of available nocturnal brachyurans in favor of polychaetes by *O. endekataenia* suggests selective feeding by the fish. We have also noticed that the prey consumption by Apogonidae is generally related to the biomass of prey organisms in each biotope. The diet of cardinalfish varies, then, according to several factors acting simultaneously: selectivity of the fish, relative abundance of prey in an area and availability rates of these prey during the day and the night.

The family Apogonidae play a part in the transit of energy from lower to higher trophic levels. Their importance lies in their great number and the speed of their turn-over. Cardinalfish feed almost exclusively on invertebrates and are themselves eaten in the coral reef by large piscivorous fish such as Serranidae, Aulostomidae and Scorpaenidae.

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