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Feeding Behavior of Some Carnivorous Fishes (Serranidae and Scorpaenidae) from Tuléar (Madagascar)

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Abstract

The feeding behavior of 8 species of sea basses (Serranidae) and 17 species of scorpionfish (Scorpaenidae) has been studied by quantitative analysis of their stomach contents. Most of the 459 specimens analysed were collected from the barrier reef of Tuléar (Madagascar). Examination of stomach contents revealed that in each species feeding behavior varies according to a nyctemeral rhythm, individual size of specimens, biotope and geographical area. Prey consumption by sea basses and scorpionfish on a reef tract is discussed in general terms.

Introduction

As pointed out by Randall (1963) and Bakus (1967) carnivorous fishes constitute the most important and diversified fish compartment of a coral reef. Sea basses (Serranidae) and scorpionfish (Scorpaenidae) display similar behavior and hunting techniques. They play a prominent role in the reef ecosystem through their great numbers and economical importance. More detailed investigations on their feeding ethology seemed of particular interest in order to determine their influence on trophic food webs of reefs.

There have been few studies on the feeding behavior of Serranidae and Scorpaenidae. Randall (1965) made a detailed study of one species of Serranidae, *Epinephelus striatus* (Bloch), in the Caribbean Sea. Information on the feeding ethology and behavior of a few species is also available from the general studies on the feeding of reef fishes from the Marshall Islands (Hiatt and Strasburg, 1960), the Virgin Islands (Randall, 1967), the Californian coasts (Hobson, 1968), Hawaï (Hobson, 1974), Madagascar (Merceron, 1969; Vivien, 1973), and from various other works which deal more with systematic aspects (Longley and Hildebrand, 1941; Wheeler and Ommanney, 1953; Randall, 1955). Starck and Davis (1966) made a great number of observations on the diurnal and nocturnal behavior of a few species in Florida, but provided no data on their feeding habits. Fishelson (1975) finally did discuss the feeding of *Pterois volitans* (Linnaeus), *Pterois radiata* (Cuvier and Valenciennes) and *Dendrochirus brachypterus* (Cuvier and Valenciennes) from the Red Sea, but studied more particularly the reproduction of the latter species.

Materials and Methods

Specimens were collected from the reef flats, both day and night, by poisoning with rotenone. Explosives were also used to collect fishes from 1.5 to 45 m deep on the reef slopes. Direct underwater observations were made at different periods, from the reef flat to the bottom of the deep coral flagstone at a depth of 60 m.

The dietary study includes 459 individuals from 8 species of Serranidae and 17 species of Scorpaenidae. The quantitative study of stomach contents was carried out according to the analysis method described by Vivien (1973). Several indices and coefficients were calculated to determine the feeding periods of the species and the relative importance of prey in their feeding.

The vacuity coefficient is the percentage of empty stomachs compared to the total number of stomachs examined. A diurnal vacuity coefficient (V_d) and a nocturnal one (V_n) are calculated to determine the feeding period.

Table 1. Results of quantitative analysis of stomach contents of Serranidae. Number of individuals examined, vacuity indices, average numbers and weights of prey per stomach are given

Species	Total no. of individuals	No. of individuals caught by		Vacuity indices		Average no. of prey caught by		Average weight of prey (g)	
		Day	Night	V_d	V_n	Day	Night	Day	Night
Cephalopholis argus	43	32	11	0.41	0.27	1.3	1.4	0.848	2.210
C. sonnerati	9	8	1	0.75	1.00	1.5	0	0.073	0
Epinephelus fario	12	8	4	0.25	0.00	1.7	7.0	0.990	2.790
E. fasciatus	12	11	1	0.09	0.00	2.0	1.0	0.870	1.290
E. fuscoguttatus	4	1	3	1.00	0.33	0	3.0	0	6.329
E. hexagonatus	10	8	2	0.25	0.00	0.8	1.0	0.330	0.070
E. macrospilos	8	6	2	0.33	0.00	1.5	1.0	1.960	0.108
E. merra	46	19	27	0.16	0.22	2.1	2.3	1.671	2.379

The occurrence index (f) is the ratio of the number of fishes containing a special kind of prey to the number of fishes with full stomachs.

The alimentary coefficient, Q, is computed by multiplying the numerical percentage (C_n) of each type of prey by its weight percentage (C_p). This coefficient is used to determine the importance order of prey types in the feeding.

Results

Feeding Behavior of Sea Basses

A food-habit study of sea basses (Serranidae) included 144 individuals from 8 species. Two other species, *Variola louti* (Forskål) and *Aethaloperca rogaa* (Forskål) have been included in the final discussion, but too few specimens were collected to include them in the general analysis.

General results from the stomach-contents analysis of 8 species of Serranidae are shown in Table 1. Since direct observations revealed a similarity in general behavior among the different species, all results for these species were combined. The averaged results are more truly representative than the results obtained separately for each species. In general, the diurnal vacuity index is higher than the nocturnal one (average V_d = 0.40; average V_n = 0.23). The average number and weight of prey per individual were more important at night than during the daytime. These data indicate that the Serranidae examined in this study feed both by day and night, but more actively at night.

Results of different authors vary according to geographical area and species considered. Randall and Brock (1960) assessed that the fishes collected in Tahiti were primarily diurnal, but could occasionally feed at night. However, they found a high percentage of full stomachs in fishes collected in the morning, which indicates that these species fed early in the morning or at dusk. Starck and Davis (1966) reported that most of the species they observed in Florida displayed similar behavior by day and night, with probably increased feeding activity during crepuscular periods. Randall (1967) came to the same conclusion about the Serranidae from the Caribbean Sea. Along the Californian coasts, Hobson (1968) also noticed that *Mycteroperca rosacea* (Streets) had a peak in feeding activity at dusk. On the other hand, he considered *Cephalopholis argus* (Block and Schneider) as diurnal in Hawaï, although suspecting additional nocturnal activity (Hobson, 1974). Collette and Talbot (1972) also reported all species of Serranidae which they observed in the Virgin Islands to be diurnal. However, these latter authors did not analyse stomach contents, and their conclusions were based on direct observations only.

Most of the Serranidae, particularly the species examined in this study, thus display similar feeding behavior by day and night. They are carnivorous fishes, generally lying in wait for their prey. On a reef, they can be found hidden among madreporarians or in crevices, with only their heads visible, or slowly swimming not far from the bottom. When disturbed in mid-water, they retreat into the numerous holes and crevices of the reef. From their hiding places, they passively wait for a prey to pass within their reach, suddenly dart upon it with a rapid lunge, and then return to their refuges. During the night, they generally emerge from their shelters and start hunting more actively.

Different kinds of dietary habits were differentiated according to the

Table 2. Results of analysis of stomach contents revealing different types of feeding diets among the Serranidae. +: present <0.001; -: absent

Species	Shrimps		Brachyurans		Galatheids		Stomatopods		Cephalopods		Fishes	
	Weight (g)	%	Weight (g)	%	Weight (g)	%	Weight (g)	%	Weight (g)	%	Weight (g)	%
Variola louti (Forskål, 1775)	-	-	-	-	-	-	-	-	-	-	47.715	100.0
Aethaloperca rogaa (Forskål, 1775)	-	-	-	-	-	-	-	-	-	-	7.663	100.0
Cephalopholis argus (Bloch and Schneider, 1801)	1.275	3.9	-	-	-	-	0.132	0.4	-	-	31.487	95.7
Epinephelus fuscoguttatus (Forskål, 1775)	-	-	0.739	5.8	-	-	-	-	-	-	11.920	94.2
E. hexagonatus (Bloch and Schneider, 1801)	-	-	0.090	4.4	-	-	0.439	21.5	-	-	1.515	74.1
E. merra (Bloch, 1793)	2.030	2.7	20.237	26.6	0.040	+	1.649	2.1	3.896	5.1	48.260	63.3
E. fasciatus (Forskål, 1775)	0.044	0.4	6.494	64.9	0.022	0.2	-	-	-	-	3.439	34.4
E. fario (Thunberg, 1793)	0.577	3.4	12.715	74.4	-	-	0.043	0.3	-	-	3.754	21.9
E. macrospilos (Blecker, 1855)	-	-	4.969	61.6	-	-	1.825	22.6	-	-	1.272	15.7
Cephalopholis sonnerati (Cuvier and Valenciennes, 1828)	-	-	0.040	27.0	0.107	72.3	-	-	-	-	0.001	0.7

Table 3. Results of quantitative analysis of stomach contents of Scorpaenidae. Number of individuals examined, vacuity indices, average numbers and weights of prey per stomach are given. -: no data

Species	Total no. of individuals	No. of individuals caught by		Vacuity indices		Average no. of prey caught by		Average weight of prey (g)	
		Day	Night	V_d	V_n	Day	Night	Day	Night
Dendrochirus brachypterus (Cuvier and Valenciennes, 1829)	3	2	1	0.00	0.00	3.0	11.0	0.080	0.425
Dendrochirus zebra (Cuvier and Valenciennes, 1829)	1	-	1	-	0.00	-	10.0	-	0.363
Dendroscorpaena cirrhosa (Thunberg, 1793)	9	9	-	0.44	-	1.0	-	0.268	-
Parascorpaena aurita (Rüppell, 1838)	18	11	7	0.18	0.00	1.5	3.4	0.101	0.161
Parascorpaena picta (Cuvier and Valenciennes, 1829)	13	12	1	0.58	0.00	1.8	3.0	0.329	0.012
Parascorpaenodes hirsutus Smith, 1957	8	7	1	0.57	1.00	1.0	0.0	0.001	0.000
Pteropterus antennata (Bloch, 1787)	1	1	-	0.00	-	4.0	-	0.155	-
Pteropterus mombassae Smith, 1957	2	2	-	0.00	-	3.5	-	0.314	-
Pteropterus radiata (Cuvier and Valenciennes, 1829	4	4	-	0.00	-	3.3	-	0.427	-
Pterois volitans (Linnaeus, 1758)	16	9	7	0.11	0.43	3.7	1.0	0.370	0.060
Scorpaenodes guamensis (Quoy and Gaimard, 1824)	25	11	14	0.09	0.07	1.4	2.2	0.022	0.160
Scorpaenodes parvipinnis (Garret, 1863)	5	5	-	0.40	-	1.0	-	0.207	-
Scorpaenodes varipinnis Smith, 1957	10	8	2	0.37	0.50	2.0	4.0	0.039	0.064
Scorpaenopsis gibbosa (Bloch and Schneider, 1801)	13	8	5	0.25	0.40	1.6	1.0	4.380	6.150
Sebastapistes kowiensis Smith, 1936	20	20	-	0.45	-	1.3	-	0.030	-
Sebastapistes nuchalis (Günther, 1874)	106	81	25	0.11	0.12	1.9	2.8	0.050	0.160
Sebastapistes oglinus Smith, 1947	61	42	19	0.41	0.26	1.6	2.8	0.060	0.074

Table 4. Results of analysis of stomach contents revealing different types of feeding diets among Scorpaenidae. +: present <0.001; -: absent

Species	Polychaetes		Isopods		Amphipods		Shrimps	
	Weight (g)	%	Weight (g)	%	Weight (g)	%	Weight (g)	%
Scorpaenopsis gibbosa	-	-	-	-	-	-	-	-
Dendroscorpaena cirrhosa	-	-	-	-	-	-	0.068	6.3
Pterois volitans	-	-	0.019	0.1	-	-	0.529	16.6
Sebastapistes nuchalis	0.197	2.6	0.110	1.5	0.349	4.6	0.866	11.5
Parascorpaena aurita	0.258	12.8	0.037	1.8	0.136	6.7	0.270	13.4
Sebastapistes kowiensis	-	-	-	-	-	-	0.105	40.1
Pteropterus mombassae	-	-	-	-	-	-	0.043	6.8
Dendrochirus zebra	-	-	-	-	0.003	0.8	0.062	17.4
Parascorpaena picta	-	-	-	-	0.009	0.5	0.081	4.9
Pteropterus radiata	-	-	-	-	-	-	0.085	5.0
Dendrochirus brachypterus	0.011	2.1	0.032	6.0	-	-	0.150	28.1
Sebastapistes oglinus	0.250	9.1	0.093	3.4	0.157	5.7	1.460	53.2
Pteropterus antennata	-	-	-	-	-	-	0.101	65.2
Scorpaenodes varipinnis	-	-	-	-	0.001	0.5	0.129	66.5
Scorpaenodes guamensis	0.380	16.7	-	-	0.003	0.2	1.576	69.5
Scorpaenodes parvipinnis	-	-	-	-	0.013	6.3	0.194	93.7
Parascorpaenodes hirsutus	0.002	66.6	-	-	0.001	33.3	-	-

types of ingested prey and their relative proportions (Table 2). Two species, *Variola louti* and *Aethaloperca rogaa*, appear to be strictly piscivorous. In Tuléar, Merceron (1969) and in the Marshall Islands Hiatt and Strasburg (1960), also noticed the strictly piscivorous feeding habit of *V. louti*. The other Serranidae examined in the present study ingest both crustaceans and fishes, but the respective proportions of these prey vary greatly between species. Species with piscivorous tendencies (60 to 95% fishes in their diet) can be distinguished from species feeding primarily on crustaceans (60 to 95% crustaceans).

Among the Serranidae belonging to the first category, the diets of 2 species, *Epinephelus fuscoguttatus* (Forskål) and *Cephalopholis argus* consist of over 90% fishes. In addition to fishes, *C. argus* also catches shrimps. In the Gilbert Islands, Randall (1955) reported the same feeding characteristics for this species but did not give the respective proportions of fishes and shrimps. In the Marshall Islands, one-third of the specimens of *C. argus* collected by Hiatt and Strasburg (1960) contained shrimps in their stomachs, the others contained mainly fishes. Specimens from Hawaï examined by Hobson (1974) only contained fishes. In Tuléar, Merceron (1969) found nearly the same proportions of shrimps). and fishes for this species as we did (numerical percentages: shrimps = 14%, fishes = 85%) and so did Randall and Brock (1960) in Tahiti (fishes = 77.5%, crustaceans = 22%, the major part of the latter consisting of shrimps).

In *Epinephelus fuscoguttatus*, brachyurans are ingested in addition to fishes, corroborating the results of Hiatt and Strasburg (1960). Randall and Brock (1960) and Merceron (1969) reported as many brachyurans as fishes in the diet of this species.

The two other species with piscivorous tendencies, *Epinephelus hexagonatus* (Bloch and Schneider) and *E. merra* (Bloch), catch fewer fishes than *E. fuscoguttatus* and *Cephalopholis argus* (only 63 to 74% of their diet consist of fishes). In Tuléar, *E. hexagonatus* also catches stomatopods and brachyurans. Hiatt and Strasburg (1960) found 3 specimens of this species containing fishes and one containing polychaetes. *E. merra* is one of the most frequent species on the Indo-Pacific reefs. In Tuléar, it feeds mainly on fishes (63%), brachyurans (27%) and also catches stomatopods (5%) and some other crustaceans. Merceron (1969) found equal numerical percentages of brachyurans and fishes in the diet of this species, and his observation was confirmed by Hiatt and Strasburg (1960). For *E. merra* in Tahiti, Randall and Brock (1960) observed a higher consumption of crustaceans and above all brachyurans (68%) during the period March to May, while from December to March more fishes were consumed due to the appearance of a great number of juveniles during this time.

The 4 following species belong to the second category: *Epinephelus fasciatus* (Forskål), *E. fario* (Thunberg), *E. macrospilos* (Bleeker) and *Cephalopholis sonnerati* (Cuvier and Valenciennes) feed primarily on crustaceans. The total proportions of crustaceans in the diet vary from 65% for *E. fasciatus* to 99% for *C. sonnerati*. Brachyurans form the dominant prey (61 to 74%) for the 3 *Epinephelus* species,

Brachyurans		Galatheids		Stomatopods		Gastropods		Cephalopods		Fishes	
Weight (g)	%	Weight (g)	%	Weight (g)	%	Weight (g)	%	Weight (g)	%	Weight (g)	%
-	-	-	-	-	-	-	-	-	-	46.768	100.0
-	-	-	-	-	-	-	-	0.174	16.2	0.863	77.5
1.305	41.0	0.027	0.8	-	-	0.005	+	-	-	1.298	40.8
4.200	55.9	-	-	0.033	0.4	-	-	-	-	1.758	23.4
1.080	53.5	0.032	1.6	-	-	0.022	1.1	-	-	0.182	9.0
0.157	59.9	-	-	-	-	-	-	-	-	-	-
0.586	93.2	-	-	-	-	-	-	-	-	-	-
0.292	81.9	-	-	-	-	-	-	-	-	-	-
1.549	94.0	-	-	-	-	0.009	0.5	-	-	-	-
1.623	95.0	-	-	-	-	-	-	-	-	-	-
0.224	41.9	0.117	21.9	-	-	-	-	-	-	-	-
0.763	27.8	0.008	+	-	-	-	-	-	-	0.015	0.6
-	-	0.054	34.8	-	-	-	-	-	-	-	-
0.063	32.5	-	-	-	-	-	-	-	-	0.001	0.5
0.271	11.9	0.039	1.7	-	-	-	-	-	-	-	-
-	-	-	-	-	-	-	-	-	-	-	-
-	-	-	-	-	-	-	-	-	-	-	-

whereas galatheids constitute the principal prey for *C. sonnerati*. The secondary prey for all 4 species consists of fishes (0.7 to 34%), stomatopods and shrimps.

Feeding Behavior of Scorpionfish

The feeding study included 315 individuals from 17 of the 22 species of Scorpaenidae present on the reefs of Tuléar. General results of the feeding study (Table 3) reveal appreciable similarity among the species studied. The occurrence of ingested prey was the same by day and night (average V_d = 0.25, average V_n = 0.25). However, the average number and weight of prey per individual were higher at night than during the daytime, suggesting increased feeding activity of this species at night. Hidden near the corals or in holes during the daytime, unseen thanks to their shape, color and stillness, scorpionfish generally escape notice whilst waiting for prey to pass within their reach. Since they occupy reef cavities during the daytime they also feed on the invertebrates (cryptofauna) which live there. Scorpionfish emerge from hiding at dusk and hunt during the night, generally not far from their daytime shelters. They are frequently visible, motionless on the bottom, in open areas. Their hunting technique appears to be the same by both day and night, but at night they probably use other means than vision for location of prey.

Different kinds of diet could be established among the Scorpaenidae according to the types of prey preferred and their relative proportions in the diet (Table 4).

Only one species out of the 17 studied, *Scorpaenopsis gibbosa* (Bloch and Schneider), feeds exclusively upon fishes, both day and night. Hiatt and Strasburg (1960) also recognized *S. gibbosa* from the Marshall Islands as a piscivorous species. *Dendroscorpaena cirrhosa* (Thunberg) essentially catches fishes, although it is not entirely piscivorous (78% of the total weight ingested); it also ingests cephalopods (16%) and shrimps (6%). Two species, *Pterois volitans* (Linnaeus) and *Sebastapistes nuchalis* (Günther), regularly feed on fishes and crustaceans. *P. volitans* consumes fishes and brachyurans in equal amonts (40%), whereas *S. nuchalis* catches more brachyurans (56%) than fishes (23%). Merceron (1969) only found crustaceans in the few specimens of *P. volitans* he examined, and Hiatt and Strasburg (1960) reported one shrimp in the single specimen they collected.

The other Scorpaenidae studied in this work mainly feed on crustaceans: 7 species principally catch brachyurans, whereas 5 species consume predominantly shrimps and one (*Parascorpaenodes hirsutus*) consumes mainly polychaetes (66%). Brachyurans are the dominant prey of *Dendrochirus brachypterus* (Cuvier and Valenciennes) (42% of total weight ingested), *Parascorpaena aurita* (Rüppell) (54%), *Sebastapistes kowiensis* Smith (60%), *D. zebra* (Cuvier and Valenciennes) (82%), *Pteropterus mombassae* Smith (93%), *Parascorpaena picta* (Cuvier and Valenciennes) (94%) and *Pteropterus radiata* (Cuvier and Valenciennes) (95%). For this last species, Hiatt and Strasburg (1960) reported a

diet based only on crustaceans and dominated by brachyurans (Xanthidae) at percentages as high as 50%. Merceron (1969) also observed a dominance of brachyurans in the diets of *D. brachypterus* and *Parascorpaena aurita*.

The following species ingest mainly shrimps (Caridea and above all Alpheidae): *Sebastapistes oglinus* Smith (53%), *Pteropterus antennata* (Bloch) (65%), *Scorpaenodes varipinnis* Smith (67%), *Scorpaenodes guamensis* (Quoy and Gaimard) (69%) and *Scorpaenodes parvipinnis* (Garrett) (94%). The secondary prey of all these species consists of other crustaceans, generally brachyurans and sometimes galatheids and amphipods.

Discussion

Ecological Distribution

Serranidae and Scorpaenidae were collected from all the biotopes investigated on the barrier reef of Tuléar, from the bottom of the lagoon and various parts of the reef flat to the various levels of the outer reef slope. Certain species live essentially in one or two definite biotopes, whereas others are present in almost all biotopes (the so-called ubiquitous species).

Most of the Serranidae studied in the present work are encountered in all the environments. *Cephalopholis argus, Epinephelus fario, E. hexagonatus, E. macrospilos* and *E. merra* are the most important ubiquitous species; nevertheless, juveniles are numerically dominant on the inner reef flat, whereas adults live mainly on the slopes and especially the outer reef slope. *C. sonnerati* frequently occurs in the "spurs and grooves zone" between 10 and 20 m, whereas *E. fasciatus* is one of the most abundant serranids on the deep coral flagstone between 20 and 45 m.

For scorpionfish, the main ubiquitous species include *Dendroscorpaena cirrhosa, Parascorpaena aurita, Scorpaenodes parvipinnis, Pteropterus antennata* and *Pterois volitans*. The two latter species are more frequent on the slopes, especially the inner reef slope. Two species, *Dendrochirus brachypterus* and *Sebastapistes oglinus*, live essentially in the seagrass beds located at the inner part of the reef flat. *Sebastapistes kowiensis* and *Scorpaenodes guamensis* are dominant on the inner reef flat with coral growth, whereas *Parascorpaena picta, Scorpaenopsis gibbosa* and *Sebastapistes nuchalis* are mainly encountered on the boulder tract.

In addition to ubiquitous species, *Parascorpaenodes hirsutus, Pteropterus mombassae, Pteropterus radiata* and *Scorpaenodes parvipinnis* are also found on the outer reef slope, which appears to be the most favorable habitat for these two families since all the Serranidae species and 12 of the 17 Scorpaenidae species studied were found there.

Variations in Feeding Behavior

The diet of any species may vary according to various factors: collection period, size, biotope and geographical area.

Two species of sea basses (*Cephalopholis argus* and *Epinephelus merra*) were collected in sufficient numbers for study of possible nyctemeral variations in feeding. The diet of *C. argus* (Fig. 1A) remains constant whatever activity period is considered; both day and night, fishes constitute its principal prey, followed in vastly reduced percentages by shrimps. On the other hand, the diet of *E. merra* varies slightly with feeding period (Fig. 1B). The high alimentary coefficient and occurrence index obtained for the fishes in its diet indicate that these constitute its principal prey during the daytime; brachyurans are caught regularly, but in small quantities. At night, however, brachyurans are the dominant prey, with a high occurrence index and alimentary coefficient. Fishes are then ingested in smaller quantities and less frequently. *E. merra* thus feeds primarily on fishes during the day and on brachyurans during the night.

In the Serranidae, as in all fishes, the juvenile diet differs slightly from that of adults. As an example, the diets of 2 size-classes of *Epinephelus merra* were considered. Class I contained the smallest individuals collected (60 to 90 mm) and Class II the largest (100 to 240 mm). A difference in the respective proportions of ingested prey between the two classes was apparent. Individuals from Class I contained essentially brachyurans (63% in weight) and relatively few fishes (35%). Individuals from Class II had ingested few brachyurans (only 22%) but a large quantity of fishes (68%). They also contained cephalopods (8%), which did not emerge as prey among the smaller individuals. *E. merra*, therefore, strongly tends to become piscivorous with increasing size. According to direct observations in the natural environment and relevant data in the literature, this phenomenon seems common among the Serranidae.

The diet of a species may also vary according to the biotope in which it lives. This has already been demonstrated for the Holocentridae by Vivien and

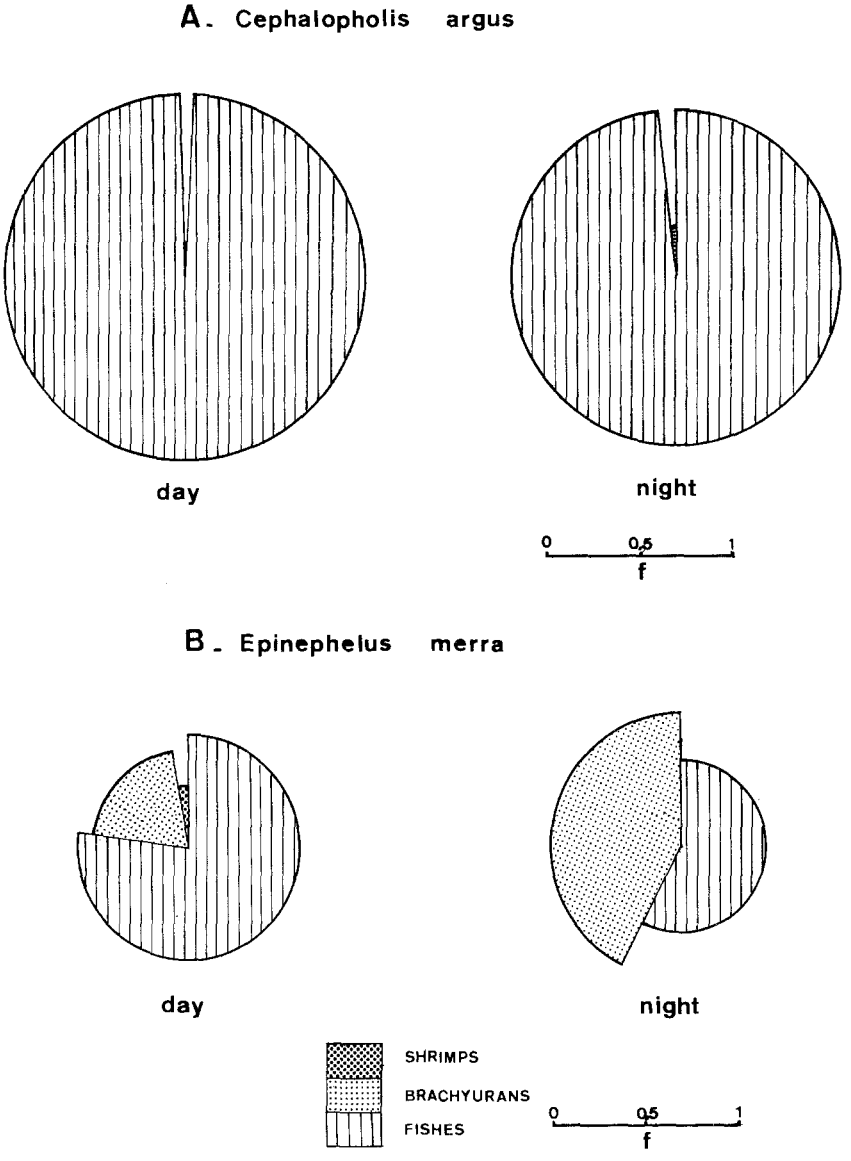

Fig. 1. Diurnal and nocturnal diets of two serranid fishes. Radii are proportional to the occurrence index of prey, *f*, and angles to their food coefficient, *Q*

Peyrot-Clausade (1974) and for the Apogonidae by Vivien (1975). However such variations could not be observed in *Cephalopholis argus*, whose diet was the same regardless of original biotope. For *Epinephelus merra*, its diet remains constant in most biotopes except in seagrass beds, in which biotope *E. merra* consumes many more brachyurans than fishes; this can be explained by the particular abundance of brachyurans in seagrass beds, especially at night.

The dietary habits of *Epinephelus merra* have also been studied by us in three different islands of the Indian Ocean: Madagascar, La Réunion and Mauritius. In these 3 different geographic areas, the diet of *E. merra* remained generally the same, and the nyctemeral variations observed in Tuléar were also noticeable in La Réunion and Mauritius. In all 3 islands, *E. merra* feeds mainly on fishes by day and on brachyurans by night. However, this species appears to have a slightly different feeding ethology in other parts of the world (see Hiatt and Strasburg, 1960, Marshall Islands; Randall and Brock, 1960, Tahiti).

Nyctemeral variations in the feeding habits of the Scorpaenidae differ interspecifically and are influenced by the original biotope. Certain species, such as *Sebastapistes nuchalis*, select the same diet both day and night; brachyurans constitute the primary prey of this species, followed by fishes. On the other hand, *Dentrochirus brachypterus* feeds mainly on brachyurans at night and shrimps dur-

Table 5. Consumption of various prey types by the Serranidae and the Scorpaenidae related to a nyctemeral rhythm. Data presented as average weights in grams for one individual from each family. -: no data

	Isopods	Amphi-pods	Shrimps	Brachy-urans	Gala-theids	Stomato-pods	Gastro-pods	Cepha-lopods	Poly-chaetes	Fishes
Serranidae										
Day	-	-	0.051	0.266	0.001	0.040	-	0.004	-	0.726
Night	0.001	-	0.017	0.695	0.001	0.042	-	0.009	0.007	1.125
Scorpaenidae										
Day	0.001	0.002	0.017	0.055	0.001	0.001	0.0001	0.001	0.001	0.014
Night	0.001	0.006	0.044	0.042	0.003	-	0.0003	-	0.015	0.026

ing the day; while the main prey of *Scorpaenodes guamensis* consists of brachyurans during the day and shrimps at night.

As already noted for seabasses, the diet of scorpionfishes also varies with individual size. Specimens of *Sebastapistes nuchalis* were also separated into two groups. Class I contained individuals of <50 mm (20 to 50 mm) standard length (SL) and Class II specimens >50 mm (50 to 90 mm) SL. The average weight of prey per individual is 6 times greater in Class II than in Class I, and the respective quantities of ingested prey types vary a great deal. Class I specimens ingest many small brachyurans (49%) and shrimps (28%); small crustaceans are fairly important (amphipods 11%, isopods 4%), while fishes represent only 6% of the total prey weight. Class II specimens catch more large brachyurans (57%) and many more fishes (34%). Other crustaceans barely represent 7% of the prey caught. This suggests that for this species too, the piscivorous tendency increases with size and that feeding of adults is more restricted, fishes and brachyurans then representing over 90% of ingested prey. An increase in the piscivorous habit among adults can also be observed in *Dendroscorpaena cirrhosa* and *Pterois volitans*.

Prey Consumption Related to a Nyctemeral Rhythm

In calculating the total prey consumption by the Serranidae and the Scorpaenidae examined herein, strictly piscivorous fishes have not been included, since insufficient numbers were collected. Moreover, most of the individuals examined had not attained maximal size. As the piscivorous habit increases among adults, it is therefore obvious that on the reef fish-consumption by these 2 families is in fact superior to that found for the other species examined in this study.

The Scorpaenidae consume primarily crustaceans (75%), consisting mainly of brachyurans (42%), followed by shrimps (26%) and fishes (18%); the other prey representing only 7% of the total weight ingested. The Serranidae ingest principally fishes (61%); brachyurans represent 31% and other crustaceans barely 5% of the total prey. The other prey (polychaetes and cephalopods) represent only 3% of the total weight ingested.

However, the various types of prey are not consumed consistently. The average weights of each prey type per individual, by day and night, were calculated for both families (Table 5). The results are presented as percentages in Fig. 2. Scorpionfish display increased consumption of shrimps, polychaetes and fishes at night. Brachyuran consumption is slightly less important at night than during the day. This can be explained by more selective hunting of prey at night. Since the scorpionfish themselves hide in the reef crevices during the day, they are able to catch the most active crustaceans among the cryptofauna, and thus a part of the brachyurans which they ingest by day also belong to the cryptofauna, the other part consisting of diurnal species.

Among the Serranidae, brachyuran consumption is more important at night than during the day, although fishes constitute the principal prey during both periods. Being larger than scorpionfish, seabasses shelter during the day in larger caves and cannot therefore reach invertebrates hidden in smaller crevices. At night, however, whilst actively pursuing prey on the reef, they can also catch brachyurans which have emerged from shelter. An increased consumption of cephalopods during nocturnal feeding

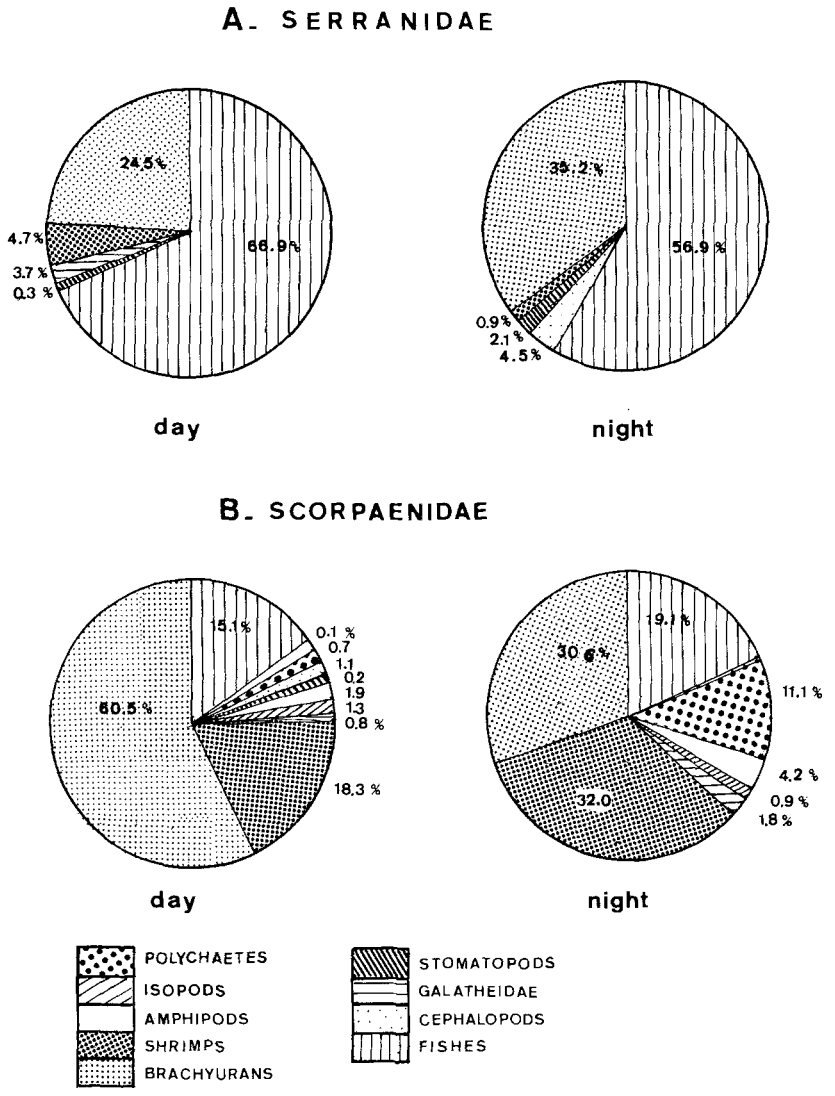

Fig. 2. Diurnal and nocturnal consumption of various kinds of prey by Serranidae and Scorpaenidae. Angles are proportional to weight percentages of prey

is noticeable, also due to the appearance of these animals at night.

Prey Consumption Related to the Biotope

Prey consumption by Serranidae and Scorpaenidae varies not only temporally but also spatially. Fish species-composition varies among biotopes, and ubiquitous species sometimes adjust their diet to the food available. Prey consumption in these families thus differs according to the biotope.

The average consumption of various prey by Serranidae (Table 6) and Scorpaenidae (Table 7) has been calculated for the various biotopes encountered along a section across the barrier reef of Tuléar. The results show that for the Serranidae (Fig. 3), fishes constitute the principal prey in all biotopes, except seagrass beds. This can be explained by the exceptional abundance of brachyurans in this latter environment, above all at night, and by the fact that fishes are more numerous in biotopes with luxuriant growth than in seagrass beds. Brachyurans and stomatopods were also caught in large quantities on the outer reef flat. This environment has indeed an important carcinological fauna (Peyrot-Clausade, in press), whereas the ichthyofauna is slightly diminished. The results obtained for the outer reef slope for the Serranidae correspond to the dietary requirement of juvenile individuals, who feed mainly on brachyurans. The serranids collected were indeed generally smaller than 30 cm SL. However, adults are very numerous on the

Table 6. Consumption of various prey types by the Serranidae according to biotope. Data presented as average weight in grams

Prey	Biotope				
	Seagrass beds	Inner reef flat	Boulder tract	Outer reef flat	Outer reef slope
Polychaetes	0.011	-	-	-	-
Isopods	0.0006	-	-	-	-
Shrimps	0.032	0.061	-	-	0.002
Brachyurans	0.935	0.285	0.142	0.285	0.262
Galatheids	0.002	0.001	-	-	0.012
Pagurids	0.001	+	-	-	-
Stomatopods	0.052	0.0005	0.062	0.247	0.012
Cephalopods	0.029	0.062	-	-	-
Fishes	0.262	1.449	1.380	0.889	0.330
Total	1.324	1.858	1.584	1.421	0.618

Table 7. Consumption of various prey types by the Scorpaenidae according to biotope. Data presented as average weight in grams

Prey	Biotope					
	Inner reef slope	Seagrass beds	Inner reef flat	Boulder tract	Outer reef flat	Outer reef slope
Polychaetes	-	0.001	0.009	0.006	0.007	+
Isopods	-	0.003	-	0.001	-	-
Amphipods	-	0.003	+	0.005	0.002	0.001
Shrimps	0.031	0.032	0.050	0.010	0.020	0.031
Brachyurans	-	0.044	0.013	0.053	0.056	0.142
Galatheids	0.001	0.003	0.002	-	-	-
Cephalopods	-	-	-	-	-	0.011
Fishes	-	0.024	0.004	0.009	-	0.042
Total	0.032	0.110	0.078	0.084	0.085	0.227

outer reef slope, and reach large sizes, and it is therefore likely that fish consumption by the Serranidae is much more important than indicated by our study, and that it can amount to 70 to 80% of total prey caught.

For the Scorpaenidae (Fig. 4), crustaceans constitute the dominant prey in all biotopes examined. However, the various types of crustaceans are not caught in equivalent quantities in all environments. Shrimp consumption (Alphaeidae, Caridae) is more important in the inner part of the reef (inner reef slope, seagrass beds and inner reef flat) than in the seaward part. Brachyurans are consumed in fairly important quantity in seagrass beds (40%), but above all on the boulder tract (63%), the outer reef flat (66%) and the outer reef slope (63%). In these biotopes, Peyrot-Clausade (in press) recorded a very high proportion of brachyurans among the cryptofauna.

Bardach (1958) in the Bermudas and Springer and McErlean (1962) in Florida tagged different fish species, and found that serranid fishes strongly tended to remain in the initial place of tagging at least for several months. Thus, individuals of *Epinephelus guttatus* and *E. striatus* have been observed to remain in the same place for about 10 months (Bardach, 1958). It is probable that scorpionfish are also sedentary, although no tagging experiment was made. During direct observations on several crepuscular occasions in Tuléar, the same individuals were seen to come back in the morning to the shelter they had left the previous evening.

The species studied do not have a well defined resting period in feeding, contrary to some other fishes (e.g. Labridae). The vacuity index, important whatever period is considered, shows that prey catching is intermittent.

In general, the Serranidae, most of them displaying a piscivorous tendency, are at a higher trophic level than the Scorpaenidae, which feed mainly on crustaceans.

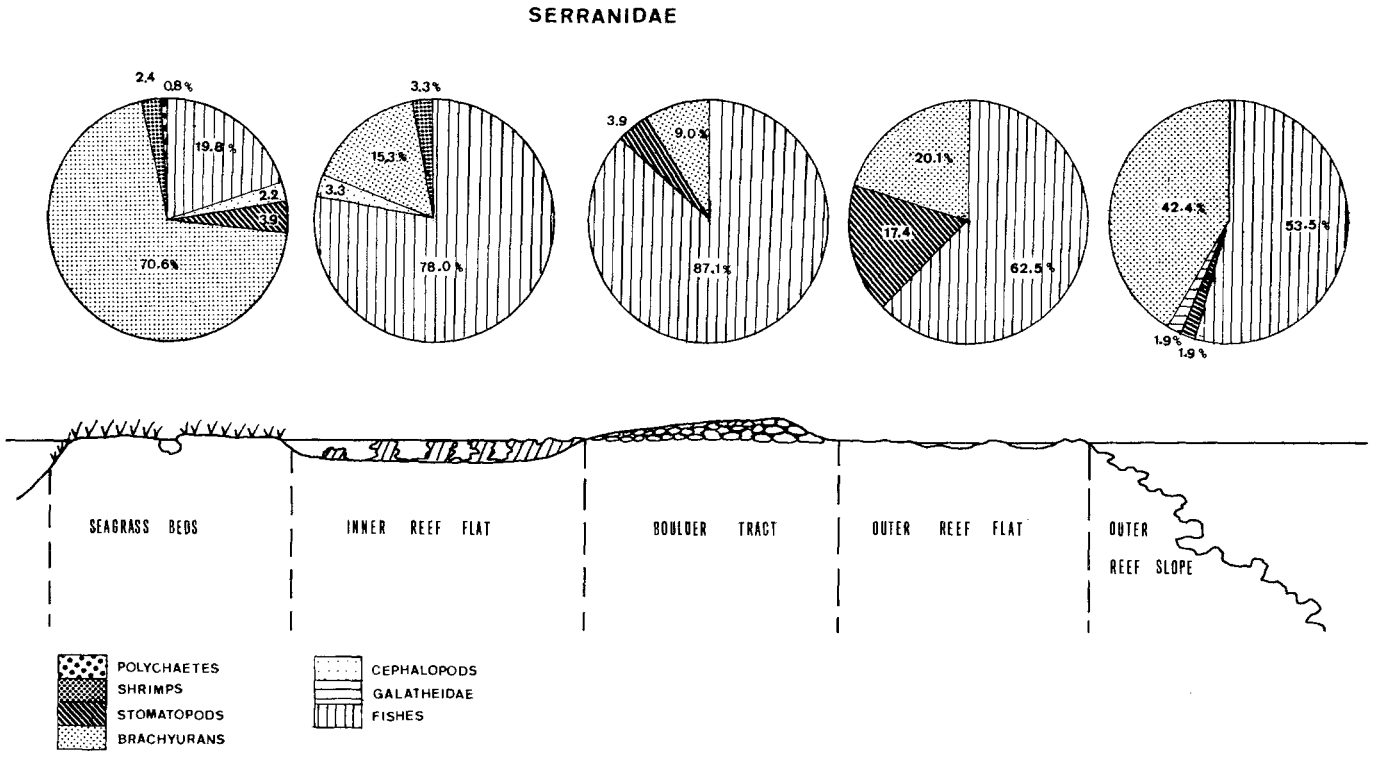

Fig. 3. Prey consumption by Serranidae according to biotope. Angles are proportional to weight percentages of prey

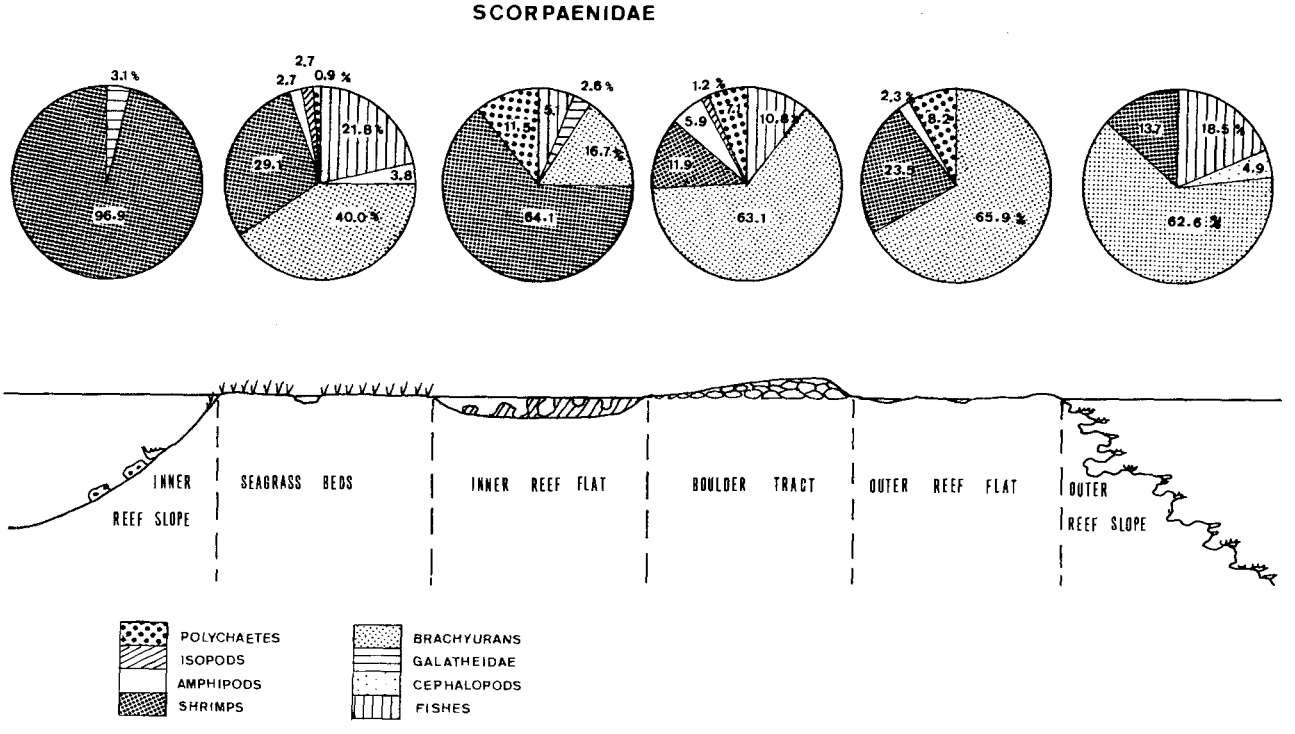

Fig. 4. Prey consumption by Scorpaenidae according to biotope. Angles are proportional to weight percentages of prey

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