STUDIES ON THE FAUNA OF CURAÇAO AND OTHER CARIBBEAN ISLANDS: No. 186

BIOLOGY OF THE GRAYSBY, EPINEPHELUS CRUENTATUS, OF THE CORAL REEF OF CURAÇAO

by

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I INTRODUCTION

1. General remarks

Groupers (family *Serranidae*) are important carnivorous fishes in tropical and subtropical areas. They are excellent food fishes and in many areas they form an important portion of the commercial and sport catch. According to Moe (1969), groupers were ranked second highest in pounds landed (8,446,443) of the food fishes in Florida in 1965.

However, little is known of their biology. Smith (1958, 1961, 1971) has studied the *Serranidae* to define the genera and species of the American groupers, and to trace the evolutionary trends in the Epinephelines. His studies give extensive, mainly taxonomic data on the American groupers. Another important contribution is the study by Moe (1969) on the biology of the Red grouper, *Epinephelus morio.* He studied several aspects of this species such as age structure, reproduction and growth. Also Thompson & Munro (1974) gave many data of several grouper species in Jamaica. However, they could not determine the age of these fishes. McErlean (1963) studied the biology of the Gag, *Mycteroperca microlepis.* He used otoliths for determining the age of this grouper species. Some general data on groupers are given by Bardach (1958a, 1958b), Longley & Hildebrand (1941), Randall & Brock (1960), and Clark (1965). Smith (1959, 1965, 1967) and Smith & Young (1966) made extensive studies on hermaphroditism and reproduction in several grouper species. Tagging experiments in groupers were done by RANDALL (1961, 1962), SPRINGER & MCERLEAN (1962), TOPP (1963), BEAUMARIAGE & WITTICH (1966) and MOE (1966, 1967). Food habits of groupers were studied by RANDALL (1965, 1967).

In Curaçao most grouper species on the coral reef at the southwest coast are very scarce probably because of heavy spear-fishing. However, two species are still abundant, namely the Coney, *Epinephelus fulvus* and the Graysby, *Epinephelus cruentatus*, both relatively small groupers with a maximum length (TL) of about 30 cm. Of these two species the Graysby was chosen for study object because of its great abundance in both the vertical and horizontal distribution on the coral reef and also because it was rather easy to collect by speargun.

In the above mentioned studies little attention has been paid to the distribution of groupers in relation to the habitat, in contrast with such aspects as reproduction, age and growth.

The present study deals with the following aspects of the Graysby: I. General aspects such as: description, relationship, geographic range, localities and description of the habitat. II. Vertical distribution in relation to the habitat. III. Determining of age. IV. Growth. V. Reproduction. VI. Feeding habits.

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2. NOMENCLATURE, RELATIONSHIP AND DESCRIPTION

For the nomenclature of *Epinephelus cruentatus* [= *Petrometopon cruentatum*] (Plates I–II) I refer to the paper of SMITH (1971) on the American groupers. SMITH has classified this species with the subgenus *Cephalopholis* and noted as: *Epinephelus* (*Cephalopholis*) *cruentatus* (Lacépède, 1802).

According to SMITH (1971) *Epinephelus cruentatus* and *E. panamensis*, formerly known with the genus name *Petrometopon*, are geminate forms, which have evolved as a result of the isolation caused by the emergence of the Middle American Isthmus. SMITH noted that they are well separated on the basis of color pattern, but structural differences are not very important.

Of the groupers at Curaçao the Graysby is most closely related to the Coney, *Epinephelus fulvus*. However, the color patterns of both are not very similar. Vertical distribution and also habitat are somewhat different. Coneys occur in more shallow water than Graysbys, the latter being more closely associated with the coral reef.

The Graysby (Plate I) is a small species of *Epinephelus* with a robust body, rounded preopercle, and large median canine teeth in the posterior row. Dorsal spines and rays IX, 14; anal spines and rays III, 8; pectoral rays 16. Gill rakers 18–21. Ground color varies from light gray or brown to olive green with numerous small reddish-brown spots. The nuance of the red color of the dots depends on the depth, at which the fish is caught. In general the deeper the place where the fish is caught, the lighter the red color of the dots. A clear white stripe is sometimes found from the tip of the lower jaw, continuing across the upper jaw and snout to near the origin of the dorsal fin. There are usually four pairs of spots along the base of the dorsal fin, the color of which can vary from white to dark. One specimen in an aquarium showed 4 pairs of white dots, which changed, however, into a black color when it was frightened.
For other features I refer to the description of SMITH (1971).

Some specimens may also show a banded pattern with vertical bars on the body and some bars on the head, running from the eye and the tip of the snout in the direction of the pectoral fin (Plate IIa). This pattern again becomes indistinct when the fish is frightened.

Juveniles are uniform grey-brown with dark spots on the head and especially on the lower part of the body (Plate IIb). They always have the above mentioned white stripe on the snout.

3. GEOGRAPHIC RANGE

Data in the literature on the distribution of *Epinephelus cruentatus* are from (Fig. 1):

Bermuda: (BÖHLKE & CHAPLIN, 1968); West Caicos (SMITH, 1971).

Bahamas: Little Bahama, Great Bahama, Cay Sal Banks, Hogsty Reef (BÖHLKE & CHAPLIN, 1968); Bimini (SMITH, 1959); Bimini, Exuma, Green Cay, New Providence, Rum Cay, Hawks Nest, Turks Island (SMITH, 1971); (TAYLOR & BRIGHT, 1973).

Florida: Tortugas (LONGLEY & HILDEBRAND, 1941); (RIVAS, 1949); (BRIGGS, 1958); (BÖHLKE & CHAPLIN, 1968); Key West, Alligator Reef Light, Triumph Reef, Miami, Cape Florida, Tortugas (SMITH, 1971); Florida Middle Ground (SMITH et al., 1975; SMITH, 1976); Central West Florida Shelf off Sarasota (SMITH, 1976); Alligator Reef (STARCK & DAVIS, 1966).

Gulf of Mexico: Northern part (BRIGGS, 1964); (BÖHLKE & CHAPLIN, 1968); Arcas Cay (SMITH, 1971); (TAYLOR & BRIGHT, 1973).

Texas: East Flower Garden, West Flower Garden (BRIGHT & REZAK, 1976); (RANDALL, 1968).

Cuba: Guantánamo Bay, Howana, Cienfuegos Bay, Corrientes Bay (SMITH, 1971); (DUARTE-BELLO & BUESA, 1973).

Glover Reef, Grand Cayman, Swan Island: (SMITH, 1971).

Jamaica: Rio Bueno, Discovery Bay, Port Antonio, Drunkenman Cay, off south Jamaica (CALDWELL, 1966); St. Anne's Bay (SMITH, 1971); Port Royal Reef, Morant Bank (MUNRO et al., 1973); Jamaica shelf, California Bank, Mackerel Bank, Pedro Bank, Morant Bank, Albatross Bank, Salmon Bank, Serranilla Bank, Alice Shoal, Nicaraguan Shelf (MUNRO, 1974).

Hispaniola: Port-au-Prince Bay (BEEBE & TEE, 1933); Port-au-Prince, Gulf of Gonave, Jeremie, Samaná Bay (SMITH, 1971).

Puerto Rico: (NICHOLS, 1930); Vieques (SMITH, 1971); La Parguera (NAGELKERKEN, pers. obs. 1973).

St. Thomas: (SMITH, 1971).

St. John: Cabritte Horn, Beehive Point (RANDALL, 1962); Lameshur Bay and Ramhead Bay (RANDALL, 1963); "Habitat Reef", "Sewer Reef" (COLLETTE & TALBOT, 1972); Lameshur Bay (SMITH & TYLER, 1972).

St. Croix: (SMITH, 1971); (NAGELKERKEN, pers. obs. 1975).

St. Martin: Cupe Coy Bay (NAGELKERKEN, in prep.).

St.-Barthélemy: Les Saintes (NAGELKERKEN, pers. obs. 1977).

Saba: Giles Quarter (NAGELKERKEN, in prep.).

St. Eustatius: Crooks Castle (NAGELKERKEN, in prep.).

St. Kitts, Buck Island, Dominica: (SMITH, 1971).

Isla de Aves: (BROWNELL & GUZMÁN, 1974).

Barbados, Grenada: (SMITH, 1971).

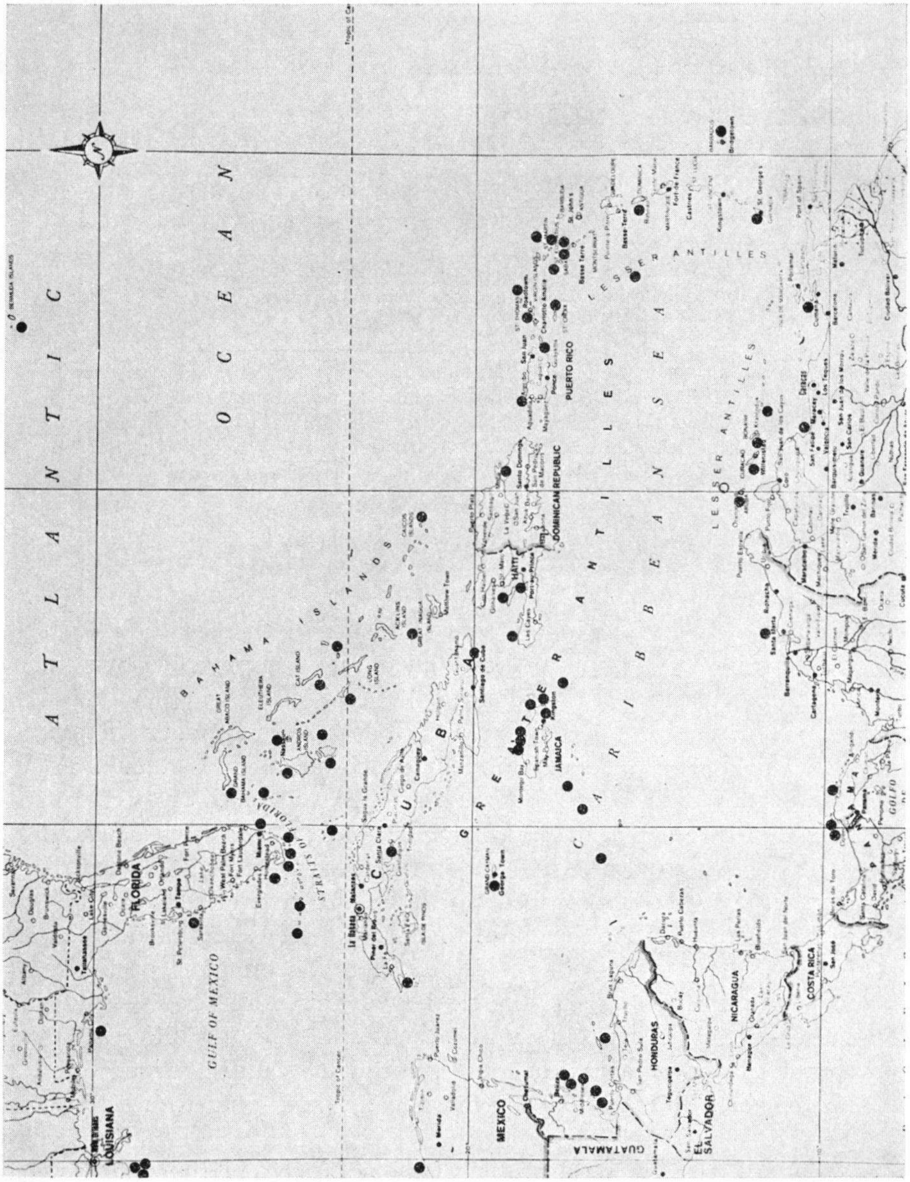

Fig. 1. Records of the distribution of the Graysby, *Epinephelus cruentatus* [= *Petrometopon cruentatum*].

Las Aves: (NAGELKERKEN, pers. obs. 1972).
Bonaire: (NAGELKERKEN, 1978).
Curaçao: (METZELAAR, 1919); (NAGELKERKEN, 1974, 1977, 1978).
Aruba: (NAGELKERKEN, in prep.).
México: Puerto Morelos (SMITH, 1971).
Belize: Columbus Cay, Spruce Cay, Channel Cay, Carrie Bow Cay (NAGELKERKEN, pers. obs. 1977).
Panamá: Toro Point, Colón, Porto Bello (MEEK & HILDEBRAND, 1925); Toro Point, Portobelo, Colón Reef (SMITH, 1971); San Blas Islands (NAGELKERKEN, pers. obs. 1977).
Colombia: Las Islas del Rosario y Punta de Betín (PALACIO, 1974).
Venezuela: Cubagua, Bahía de Charagato (CERVIGÓN, 1966); (MAGO, 1970); Puerto Cabello (SMITH, 1971).

In general groupers are found in Bermuda, the Bahamas and Florida, the Gulf of Mexico, the Antilles and the coasts of the Americas from North Carolina to Brazil (BÖHLKE & CHAPLIN, 1968; RANDALL, 1968; SMITH, 1971). Among the groupers the Graysby is especially abundant in areas with well-developed coral reefs such as those of Jamaica, Virgin Islands, Aves Islands, Bonaire, and Curaçao.

4. LOCALITIES AND HABITAT DESCRIPTION

Curaçao is located in the southern part of the Caribbean Sea (12°15'N, 69°00'W). Localities studied at Curaçao are shown in Fig. 2. Calculations of the percentage of coral cover and quantity of coral structure were performed in the following 9 stations: Fuikbaai, Jan Thielbaai, Piscaderabaai, Portomaribaai, Boca Grandi, Boca Pos Spañó, Boca Hulu, Westpuntbaai, Playa Kalki. Most of the fish counts were done at Boca Pos Spañó and Portomaribaai (Fig. 2).

At Curaçao coral reefs are found mainly from a depth of 1½ m to a depth of 36 m. As described by BAK (1975) there is a gradually sloping terrace from the shore to the drop-off (also called "blue-edge" by ROOS, 1964) at 7 to 12 m. Here a seaward slope begins varying from 45° to nearly vertical. Over this profile there is a definite series of coral communities each representing a different response to environmental factors such as light, sedimentation, water movement, substrate, bottom morphology and temperature (BAK, 1974).

Fig. 3 gives a general profile of the coral reef at the southwest coast of Curaçao. For the features of each zone I refer to BAK (1975).

Table 1 gives a survey of the percentage of cover in the habitat of

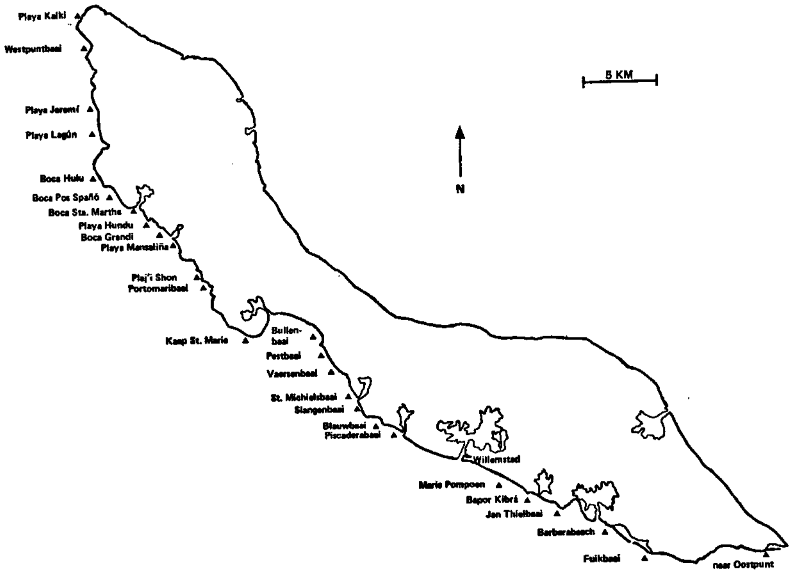

Fig. 2. Sketch-map of Curaçao, showing the localities.

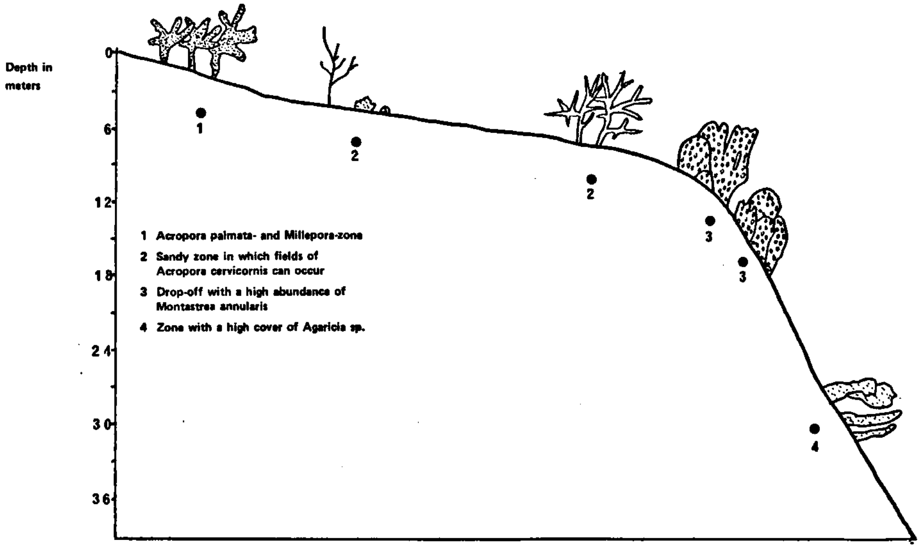

Fig. 3. General profile of the coral reef at the southwest coast of Curaçao.

TABLE 1.

Percentages of bottom cover per depth for the several types of cover in the habitat of the Graysby on the coral reef at Curaçao. Each figure is the mean percentage of the values of 9 different stations.

Type of cover	Percentages of cover per depth in meters													
	36	*33*	*30*	*27*	*24*	*21*	*18*	*15*	*12*	*9*	*7½*	*6*	*4½*	*3*
Bottom	57.6	42.9	39.1	32.7	31.1	17.8	18.9	15.6	15.0	22.9	27.9	46.4	61.1	63.3
Substratum	9.6	16.3	13.0	16.8	11.1	15.8	12.2	12.1	11.9	12.2	8.7	8.3	3.4	2.8
Sponges	3.1	4.8	3.8	2.2	2.8	1.6	1.1	1.6	0.7	0.6	0.4	—	—	—
Gorgonians	—	—	—	—	1.0	—	—	—	—	—	—	—	—	—
Acropora cervicornis	—	—	—	—	—	—	—	—	—	—	—	—	3.0	11.8
Agarica sp.	15.8	17.9	24.0	19.0	14.1	16.5	17.8	20.3	26.7	16.5	14.9	6.7	2.6	0.9
Colpophyllia sp.	—	—	—	0.2	0.6	0.9	1.4	0.7	1.6	0.6	1.0	0.6	—	1.1
Dendrogyra cylindrus	—	—	—	—	—	—	—	—	—	—	1.0	1.3	1.0	0.2
Dichocoenia sp.	1.0	0.3	0.4	0.3	0.7	0.2	0.4	0.1	0.1	0.7	0.3	0.4	0.1	0.9
Diploria clivosa	—	—	—	—	—	—	—	—	—	0.4	—	—	0.2	—
Diploria labyrinthiformis	—	—	—	—	—	—	—	—	—	0.7	0.2	—	1.0	0.3
Diploria strigosa	—	—	—	—	—	—	—	0.4	—	—	0.3	0.8	0.6	1.9
Eusmilia fastigiata	—	0.2	0.9	0.6	1.7	4.8	6.3	6.0	3.1	1.4	1.8	0.4	0.8	0.2
Favia fragum	—	—	—	—	0.1	—	—	—	—	0.1	—	—	0.1	—
Madracis sp.	—	0.3	—	—	—	—	2.2	0.6	3.1	2.6	6.6	5.8	7.3	5.2
Manicina areolata	—	—	—	0.6	2.0	3.7	4.8	3.8	5.0	1.1	4.1	0.8	0.7	—
Meandrina meandrites	1.9	2.2	2.9	3.5	5.9	5.0	4.2	2.7	2.4	0.9	1.4	0.8	1.4	0.6
Millepora sp.	—	—	—	—	—	0.1	0.6	—	0.4	0.7	0.7	0.6	0.8	0.7
Montastrea annularis	0.1	—	1.5	1.9	4.0	8.6	8.8	15.0	15.1	24.2	20.9	16.8	12.1	7.0
Montastrea cavernosa	2.8	1.7	1.9	5.1	4.2	1.9	2.6	4.0	1.9	3.1	2.7	3.9	1.2	1.1
Mussa angulosa	—	—	—	—	—	—	—	0.3	0.2	0.2	—	—	—	—
Mycetophyllia sp.	0.7	0.9	0.6	0.4	1.2	2.2	2.6	0.9	1.7	0.3	0.1	—	—	—
Porites astreoides	0.3	0.7	0.1	1.4	4.8	5.6	5.2	6.2	4.3	1.7	1.1	0.1	0.7	0.6
Porites porites	0.2	—	—	0.2	0.2	1.3	1.9	1.9	1.8	1.6	1.1	1.3	1.3	—
Scolymia sp.	—	0.1	0.1	—	0.1	—	—	—	—	—	—	—	—	—
Siderastrea siderea	6.0	9.5	9.0	10.8	7.2	6.9	2.3	4.4	2.7	7.1	3.4	4.7	1.6	1.4
Stephanocoenia michelinii	0.9	2.2	2.7	4.3	7.2	7.1	6.7	3.3	2.3	0.4	1.4	0.3	—	—

the Graysby at various depths. The figures are the mean of the data of 9 stations as mentioned in section 4 of this chapter. For the methods used I refer to chapter II.

The number of coral species (20) is highest at 9 m together with a relatively high coral cover of 65%. The coral species *Montastrea annularis* with a percentage of cover of 24% is especially abundant. At 36 m only 10 coral species are found with a relatively low coral cover of about 30%.

II VERTICAL DISTRIBUTION OF EPINEPHELUS CRUENTATUS ON THE CORAL REEF AT THE SOUTHWEST COAST OF CURAÇAO

1. INTRODUCTION

Knowledge about the distribution of groupers on the coral reef and their relationship with the habitat is rather scarce. BROCK (1954) in Hawaii used a visual census of coral reef fish along lines. ODUM & ODUM (1955) in Eniwetok made visual counts of groupers in 20 ft. quadrats. They also applied Rotenone, a fish poison, in order to obtain information about the hidden fish in the same quadrats. BARDACH (1959) also used the visual census method along lines with the help of SCUBA equipment. Counts were made in three different years. An estimate was made of nocturnal and crepuscular fish by Rotenone treatment of a smaller area on an adjacent, similar reef. RANDALL (1963) used Rotenone to get quantitative data on the fish population of coral reefs. POST (unpublished, 1972) studied the distribution of several species of fish on the coral reef of Curaçao by counting the numbers of fish in transects of 100 m wide from a depth of 1½ m to 36 m. SMITH & TYLER (1973) made a census of fish populations by means of visual counts in patches of habitat, small enough to be studied as complete units.

In the present study, the census method was chosen, because for determining the vertical distribution qualitative data are sufficient. Rotenone was only used in small areas (16 m^2) to study the number of hidden Graysbys and to estimate the distribution of juveniles, which live more permanently hidden in crevices in the corals.

2. VERTICAL DISTRIBUTION, 14 TRANSECTS FROM 3 –36 M

To study the vertical distribution of the Graysby on the reef, direct counts were made by two teams of divers in transects 40 m long and about 6 m wide. By experience it was found that a length of 40 m was the maximum distance to cover 14 depths during one SCUBA dive of about 45 minutes. During these dives the 14 transects were always situated at depths of 36, 33, 30, 27, 24, 21, 18, 15, 12, 9, 7½, 6, 4½ and 3 meters (Fig. 4). At the beginning of each dive a 40 m nylon line was laid parallel to the reef at a depth of 30 m to indicate the length of the transect.

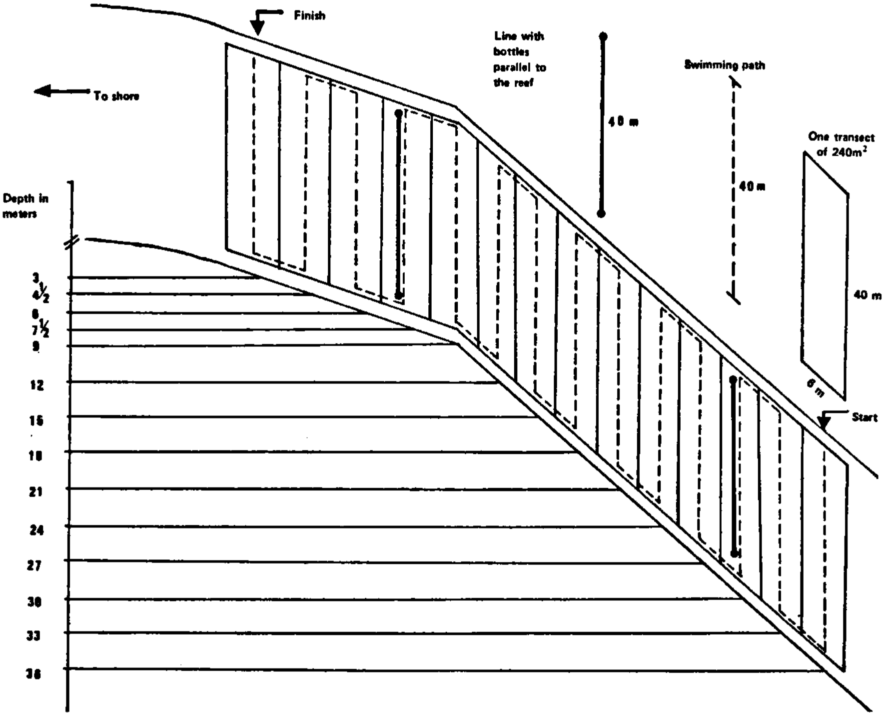

Fig. 4. Survey of the 14 transects on the reef, where the counts were performed. The dotted line indicates the swimming path.

Both ends of the line were marked with white plastic bottles, floating about 1½ m above the nylon line.

In Fig. 4 the dotted line shows the swimming path of the counters with the start at a depth of 36 m and the finish at a depth of 3 m. Fishes at depths of 12, 9, 7½, 6, 4½ and 3 m were counted when the line and bottles were laid down at a depth of 7½ m for good identification of the length of the transect. The width of the transects (6 m) appeared to be more or less the distance between the various depths mentioned and this distance was always estimated visually during the counts.

Due to steepness of the slope of the reef from 36 m to 9 m, the transects with a width of 6 m were adjacent to each other in that depth range. Above 9 m (the drop-off zone) the slope becomes flatter, so that the reef transects between 9 and 6 m and 6 and 3 m were no longer adjacent. Therefore intermediate areas at a depth of 7½ m and 4½ m were counted in order to prevent gaps in the counting.

Data were collected at 9 different stations, but most data are from the stations Pos Spañó and Portomaribaai.

The maximum depth was limited to 36 m, as this depth is the maximum security limit for diving with SCUBA.

During the counts all Graysbys were not only counted, but also roughly divided into size classes e.g. extra small, small, medium, large and extra large. Moreover notes were made about color, cleaning symbiosis, grouping.

During night lamps were used instead of white plastic bottles to indicate both ends of the line. The divers also used lamps.

Counts were made throughout the whole year at different times during the day.

To increase objectivity counts were always made by 2 divers, who, swimming side by side, counted simultaneously. In this study I used two counting teams: team A–B, and later team B–C. Team A–B made 18 counting dives (each dive includes 14 transects), and team B–C made 29 counting dives. The data of both teams were studied statistically in order to control the accuracy of the counts.

The mean number of Graysbys counted by divers A, B and C are presented in Table 2. Also the mean number per transect and the cumulative proportional frequency is given. The results of the 3

TABLE 2

Mean number of Graysbys counted by divers A, B and C, mean number of fish per transect, and the calculated cumulative proportional frequency.

Depth in meters	Mean number of counted fish			Mean number per transect n = 94	Calculated cumulative proportional frequency		
	n = 18	n = 47	n = 29				
	A	B	C		A	B	C
3	0.6	0.9	0.6	0.7	3.1	3.6	2.9
4½	0.7	1.3	0.9	1.1	6.9	9.2	7.8
6	1.2	1.8	1.2	1.6	13.8	17.1	13.9
7½	1.8	2.6	2.0	2.5	23.8	30.0	24.2
9	2.3	3.0	2.7	2.8	36.6	42.7	38.3
12	1.8	2.2	1.7	2.0	46.6	52.2	47.0
15	1.8	1.9	1.7	1.8	56.6	60.1	55.7
18	1.1	1.6	1.7	1.5	62.8	66.7	64.4
21	1.3	1.5	1.2	1.3	70.0	72.9	70.6
24	0.9	1.0	0.9	0.9	75.0	76.9	75.4
27	0.8	1.3	1.3	1.2	79.7	82.3	82.0
30	1.6	1.6	1.1	1.4	88.4	88.9	87.7
33	1.0	1.1	1.1	1.1	94.1	93.7	93.2
36	1.1	1.5	1.3	1.4	100.0	100.0	100.0
Total	*17.8*	*23.9*	*19.4*				

counters were tested statistically with the aid of Kendall's rank-correlation test. The data demonstrate considerable differences in numbers counted by the divers, with diver B scoring consistently highest. However, the distribution as shown in the cumulative proportional frequencies shown in Table 2, appears to be similar. In view of the differences between the divers the mean of the results of the three counters is subsequently used as shown in the fifth column of Table 2.

In Fig. 5 the mean number of fish per 40 m transect, counted by the three divers, is plotted against the depths studied. It shows that most Graysbys are found at depths of 7½ to 9 m. At depths of more than 9 m the number of Graysbys decreases gradually with a suggestion of a second lower maximum at a depth of 30 m.

The distribution was further studied by the use of Rotenone techniques, as a control on the numbers counted and to collect juveniles

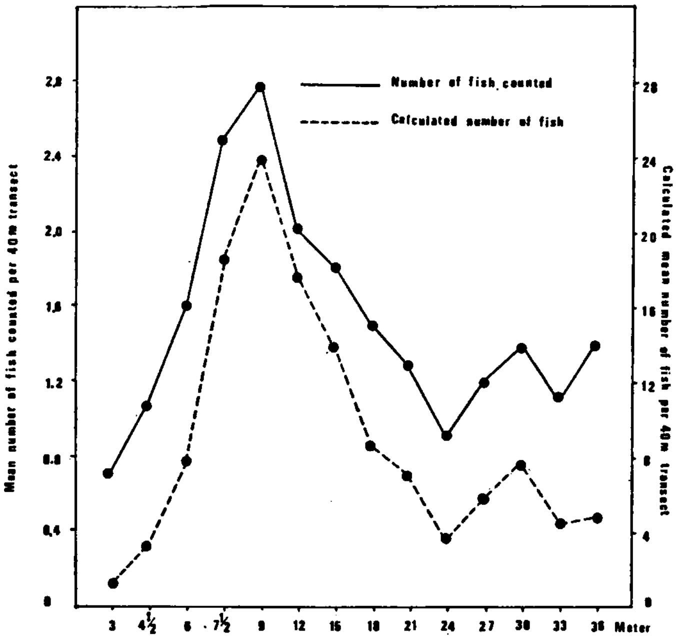

Fig. 5. Mean number of fish counted per 40 m transect, plotted against depth. The dotted line gives the calculated distribution of the absolute numbers of Graysbys over the depth-range.

for studying their distribution. Catches were made at 33 stations at different depths. In all cases, representative sampling areas of 4 × 4 m were chosen since, according to SCHEER (1967), catches in such areas give a reliable impression of the type of coral field as a whole. Every sampling area was marked by 4 iron pins connected by a nylon line. Graysbys, escaping, were counted and their size estimated. At depths greater than 12 m only few inventories were made, because at depths of 12 to 24 m it was very difficult to find partly isolated patches of coral reef and at depths greater than 24 m collecting was difficult as a result of decompression problems.

Table 3 shows the number of adult fish collected (including the fish observed escaping), the mean number of adult fish per station and the number of stations as well as the number of juveniles and their mean number per station. Only for the depths of 6, 7½, 9 and 12 m,

TABLE 3

Numbers of fish collected with Rotenone at different depths (fish observed to escape are included). The mean number of fish per station of 16 m² is given for the depths of 12, 9, 7½ and 6 meters.

DEPTH in meters	Number of fishes collected (except juveniles)						mean number of fishes per station	number of Rotenone-stations	number of juveniles	mean number of juveniles per station
	extra small	small	medium	large	extra large	total				
3						0		1	0	
4½			1			1		2	1	
6		3	6	1		10	2.5	4	22	5.5
7½	3	5	9	2	1	20	2.9	7	30	4.3
9	10	17	18	2	1	48	4.0	12	24	2.0
12		4	3	1	2	10	2.5	4	6	1.5
15		1	1	1		3		1	0	
18								0		
21			2			2		1	0	
24	1	3	1			5		1	0	
27								0		
30	1		1			2		1	0	
33								0		
36			1	1		2		2	0	

for which sufficient observations were present, the mean number was calculated per 16 m^2 areas.

It is evident that Graysbys are found mostly at a depth of 9 m. Juveniles were only found from 12 up to 3 m, with the greatest number at 6 m. At depths of more than 12 m no juveniles were found.

Table 4 gives, for 4 depths the mean numbers of fish counted per 40 m transect, and the calculated mean number of fish per 40 m transect, using the Rotenone-method, which should represent the number of fish actually present in a transect.

At first sight the counting technique by visual census seems highly inefficient, because the data suggest that, i.e., for the depth of 9 m only 5% of the fish present were observed by the divers. As for vertical distribution, it may be concluded that both techniques compare favorably.

For the calculation of the fish actually present, only the data of the well-sampled depth of 9 m (12 stations) were used and integrated into the numbers of the fish counted at the different depths.

The method applied to compute absolute density could lead to overestimation of the numbers of fish. With the census method the whole 240 m^2 area was counted. Sampling with Rotenone in the 16 m^2 areas was done only at places where the cover of *Montastrea annularis* and *Agaricia* species was very high. (These being the most important corals in relation to the distribution of *E. cruentatus*, see section 3 of this chapter). In areas with a sandy bottom no inventories were made, because hardly any adults or juveniles were found there, when collecting. Therefore, to calculate the number of fish

TABLE 4

Mean numbers of fish counted per 40 m transect and calculated mean number of fish per 40 m transect, given for four depths.

DEPTH in meters	Mean number of fish counted per 40 m transect (240 m^2)	Calculated mean number of fish per transect (240 m^2) from Rotenone-method.
6	1.6	37.5
7½	2.5	36.0
9	2.8	60.0
12	2.0	37.5

actually present, a correction factor had to be introduced to account for the % cover, e.g.:

$$C = \frac{\text{area covered by } \textit{M. annularis} \text{ and } \textit{Agaricia} \text{ spp. in transect}}{\text{total area of transect}}$$

The formula is then: $n = \frac{T}{R} \cdot \bar{x} \cdot C$,

n = number of fish present, T = transect area (240 m^2), R = Rotenone area (16 m^2), $\bar{x}$ = mean number of fish collected per 16 m^2 area and C = correction factor.

On the basis of this formula the number of fish actually present at a depth of 9 m in a transect of 240 m^2 would then be approximately 24 fish instead of 60. The counting efficiency of the divers, though still low, would increase to about 12%.

As observations on absolute abundance, using the Rotenone-method, are insufficient in other depth strata, the numbers were calculated by using the ratio "actually present" on "counted" at the 9 m stratum without applying the correction factor. This ratio is

TABLE 5

Mean number of counted fish per transect and per depth as compared with the calculated number of fish per transect and per depth (for formula see text).

DEPTH in meters	Mean number of counted fish per transect (± 240 m^2)	Calculated number of fish per transect	Efficiency of counting in %
3	0.7	1.2	58.3
4½	1.1	3.4	32.4
6	1.6	7.5	21.3
7½	2.5	18.4	13.6
9	2.8	24.0	11.7
12	2.0	17.6	11.4
15	1.8	13.7	13.1
18	1.5	8.6	17.4
21	1.3	7.0	18.6
24	0.9	3.4	26.5
27	1.2	5.5	21.8
30	1.4	7.5	18.7
33	1.1	4.3	25.6
36	1.4	4.8	29.2

60/2.8 = 21.4 (Table 4). The numbers in each stratum were computed according to: $n_x = P_x \cdot 21.4 \cdot C_x$, in which n_x = number of fish actually present at a depth of x meter, P_x = mean number counted at that depth per 240 m², C_x = correction factor for cover at depth x.

Following this procedure, mean numbers of counted fish, numbers of fish actually present at the different depths and efficiency of counting in percentages are given in Table 5. It appears that at depths of 7½, 9, 12 and 15 m the actual population is about 8 times greater than shown by the results of the counts. At depths of 3, 4½, 24, 33 and 36 m the counting efficiency is taken to be higher, probably due to the lower rate of cover. The now-corrected distribution of the Graysby over the depth range is shown in Fig. 5 (dotted line).

The difference in numbers of fish from each method is probably caused by the numerous fishes smaller than 12 cm, which tend to hide much more in the corals than the larger, and are, therefore, not observed during the counts. It appears that the Graysbys are living more within the corals than outside, which is corroborated from many field observations of holes and crevices in the corals. These results agree also with those found by STARCK & DAVIS (1966) and GALZIN (1977).

3. VERTICAL DISTRIBUTION IN RELATION TO THE PERCENTAGE OF CORAL COVER AND QUANTITY OF CORAL

RANDALL (1963) suggests that the structure and composition of the reef itself is of great importance for maintaining a population of fishes. The higher and more complex the structure and the more hiding places it provides, the greater will be the number of fishes that will live in it. TALBOT (1964) found a very distinct relationship between quantity of fish and percentage of bottom cover by living coral. TYLER (1971) noted that several fish showed preference for some species of corals. LUCKHURST (1972, unpublished) found a positive correlation between several species of coral fish and the percentage of cover of *Porites porites*. NAGELKERKEN (1974) observed a striking preference of a number of fish species for either *Millepora*- or *Acropora palmata*-fields. SMITH & TYLER (1975) studied the development of fish communities associated with *Montastrea* dome reefs.

A high percentage of coral cover does not necessarily mean an enlargement of the habitat as suggested by TALBOT (1964), because that depends on the structure of the coral species. For instance a field of *Madracis mirabilis* can have a high percentage of cover, but a very small quantity of coral structure in comparison with a field of *Montastrea annularis* (an abundant coral species in the habitat of *E. cruentatus*) with the same percentage of cover. The Graysby preferentially dwells between and under corals. The higher the coral the more places to dwell for the Graysbys. Therefore, in this study, the correlation between the number of fish and the percentage of coral cover is studied, as well as the correlation between the number of fish and the height, respectively the quantity of the corals. Because a high quantity, derived from the height of the corals, means many hiding places, this is a measure for availability of shelter for the Graysbys.

Following the method of LOYA (1972) and PORTER (1972) measurements were made of the percentage of bottom cover as living coral, dead coral, sponges. In each of the 14 transects a measuring rope of 10 meter, divided into centimeter marks, was laid parallel to the reef and the number of centimeters, covering each species of coral or any other kind of bottom cover, was determined.

The height of the coral structure was measured along the same 10 meter rope. At each half meter of the rope an iron measuring rod, divided into decimeter marks, was pushed to the bottom and the height of the structure was read on the rod and noted. Using these figures the area of this profile was calculated in square meters. Using as a third dimension the width of the transects (6 m), a calculation could be made yielding cubic meters of quantity of structure (i.e. quantity of shelter) available for the Graysbys. The measurements of quantity of structure were made at 9 stations along the southwest coast of Curaçao (Fig. 2).

In Fig. 6 the calculated number of fish per 40 m transect, the mean quantity of structure and the percentage of total bottom cover are plotted against depth. It appears that fish abundance is most closely associated with the quantity of the coral structure ($r = 0.8799$,

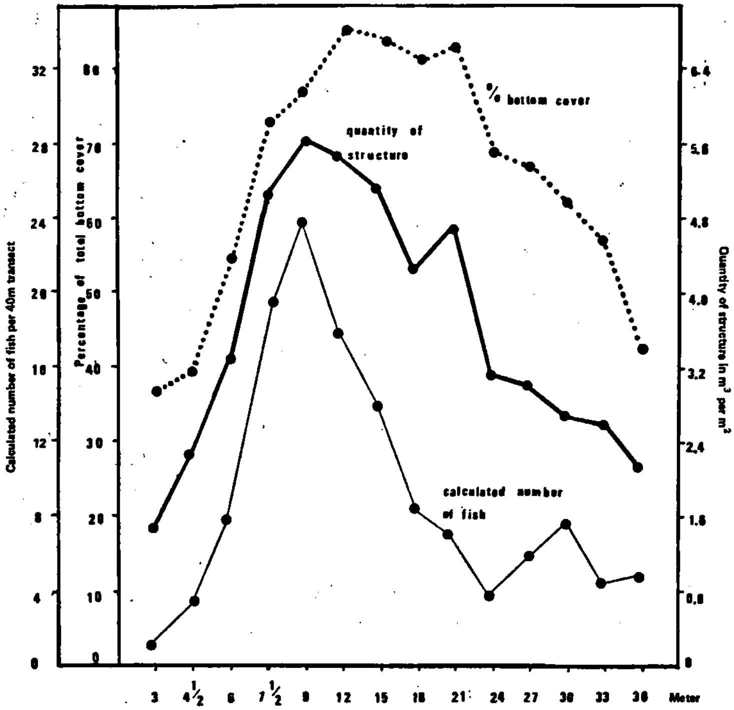

Fig. 6. Vertical distribution of the calculated number of Graysbys, the percentage of total bottom cover and the quantity of structure.

$p < 0.01$ for the relation fish – quantity of structure, and $r = 0.6411$, $p < 0.01$ for the relation fish – percent of bottom cover), although the number of fish is positively correlated with both parameters.

Now *Montastrea annularis* and *Agaricia* spp. because of their growth form contribute strongly to the quantity of coral structure present and provide possible hiding places for the Graysbys. Therefore, in Fig. 7 the calculated number of Graysbys and the mean percentage of bottom cover of *M. annularis* and *Agaricia* are plotted against the different depths. A very strong correlation was found ($r = 0.94$, $p < 0.01$, $n = 14$). The earlier mentioned secondary maximum of the number of fish at a depth of 30 m, appears to be associated with a peak in the percentage of bottom cover of these coral species. At this depth the higher percentage of cover is es-

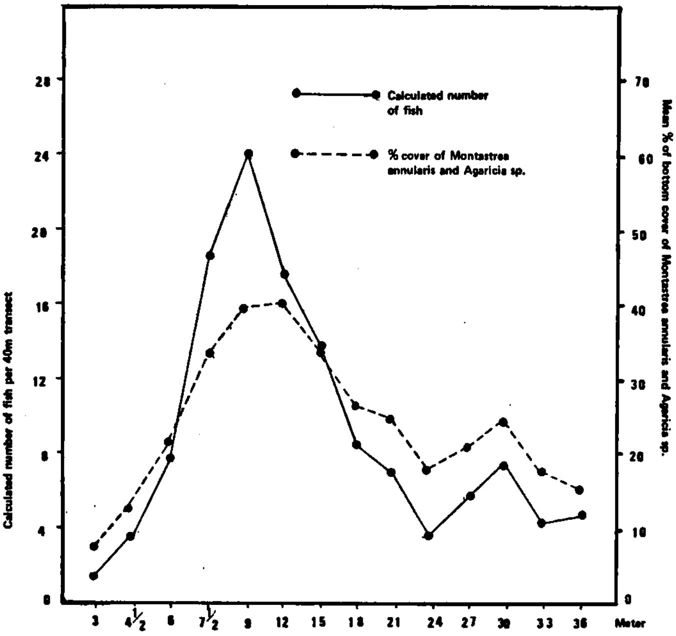

Fig. 7. Vertical distribution of *Epinephelus cruentatus* and that of the corals *Montastrea annularis* and *Agaricia* spp. for 9 stations.

pecially caused by *Agaricia* spp. (1% bottom cover of *M. annularis* and 24% bottom cover of *Agaricia* respectively).

It would seem, therefore, that the distribution of the Graysby is largely determined by the quantity of coral structure present, more than by the percentage cover. In addition, however, *M. annularis* and *Agaricia* may have an important influence upon the vertical distribution of *E. cruentatus* by their growth form, which supplies hiding possibilities e.g. holes, overhangs, crevices.

An additional point might be that by their appearance both species of coral offer the Graysby camouflage. Both coral species form by their pattern of calices a good background for the pattern of dots of *E. cruentatus*. However, probably the strong association between *E. cruentatus* and the two species of coral is not so much the result of camouflage against both coral species as is their structure, which results in many hiding places.

4. VERTICAL DISTRIBUTION IN RELATION TO LENGTH AND SEX

During the counts along the transects, the fish observed were roughly classified according to size groups. These classes do not include juveniles, because most of them, hidden in the crevices of the corals, were not observed. During dives many Graysbys of different sizes were first classified, then shot and measured on the beach. In this way it was possible to test the validity of estimated size of the counted fish.

Table 6 shows the actual length-range of the size classes, as verified by measurements.

In Fig. 8 the numbers of the different size classes are plotted against depth, to study the vertical distribution of the size classes on the reef. It appears that "extra small" fish are found especially around a depth of 7½ m and occur only very rarely at greater depths. This size class does not include juveniles, which, however, were also only found (with the aid of Rotenone) around a depth of 6 m (Table 3). The distribution of size class "small" resembles the vertical distribution of the total population, with a maximum around a depth of 7½ or 9 m and a smaller peak at a depth of 27 or 30 m. The size class "medium" is quite numerous at a depth of 9 m with a second maximum at a depth of 36 m. During occasional visits to depths of more than 36 m Graysbys were found to be scarce. At the depth of 36 m the coral cover and other bottom cover is sparse. However, a relatively high number of Graysbys was counted here. It is possible that some of these fish are searching for food and coming from their

TABLE 6

Calculated total lengths of the different size classes of the counted fishes, derived from data of the collected fishes.

SIZE CLASSES	Calculated total length (cm) of the counted fishes	Number of fish
Extra small	12	4
Small	12–15.9	16
Medium	16–20.9	33
Large	21–24.9	20
Extra large	24.9	16

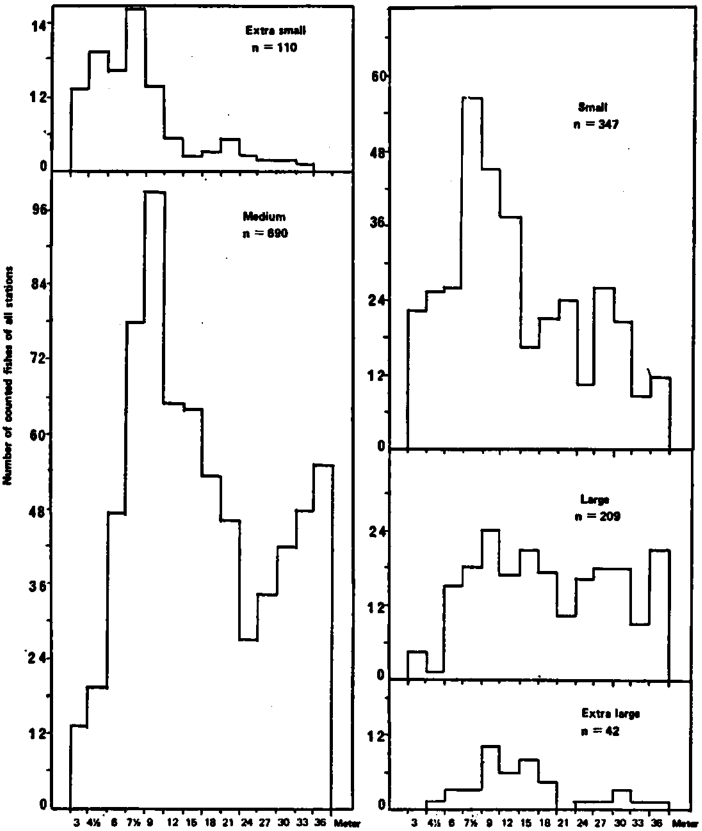

Fig. 8. Vertical distribution of the numbers of fish of the 5 size classes on the reef.

near-by "home" at a depth of around 30 m with much more coral cover. When they are frightened, they flee mostly upward to hide in the coral cover at a depth of about 30 m. Size class "large" shows a more even distribution on the reef, whereas the relatively rare "extra large" fish are found to be distributed similarly to size class "medium".

To compare the distribution of females and males on the reef, data of the collected fish were put into one of the 5 size classes. A difficulty was that only the "medium", "large" and "extra large" fish could be collected a-selectively. Capture of "small" fish was more difficult. Of the "extra small" only a few were sampled, because they were too difficult to spear. Furthermore, collections were made to a depth of 36 m, but because of problems of decompression, the time spent collecting at that depth and adjacent depths was relatively short. In view of the limitations set by the material, the size data of the fish collected were only used for a comparison of the distribution of males and females in the depth range. During histological studies of the gonads it was found that most mature females are 14 to 25 cm long (TL), representing principally the size classes "medium" and "large". Mature males are 19 cm long and longer but most of them are between 22 and 30 cm, representing principally the size classes "large" and "extra large". In Fig. 9 the distribution

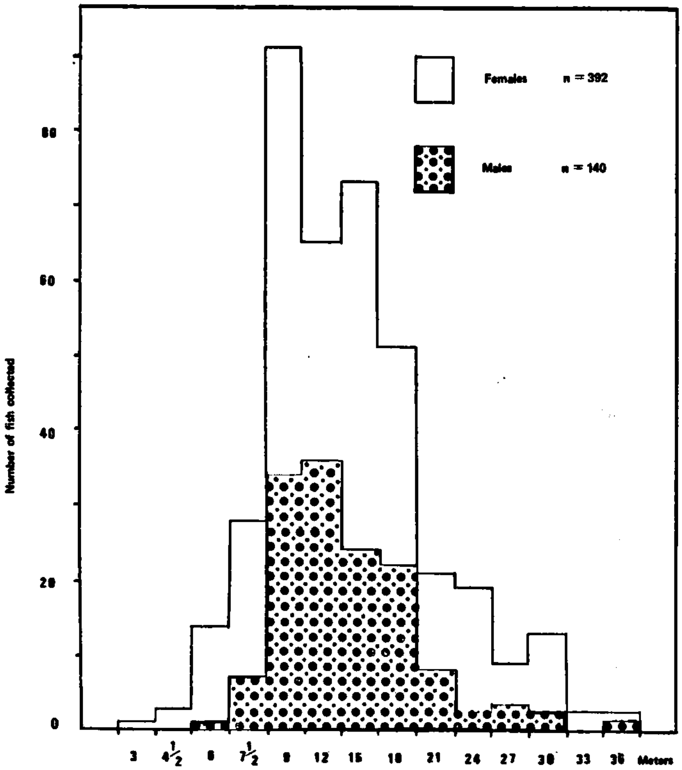

Fig. 9. Distribution of females and males of the fish collected.

of females and males of the collected fishes is given, representing especially the "medium", "large" and "extra large" classes. As shown, the distribution of females and males of these three classes on the reef is very similar. So it is likely then that the distribution of the "medium" and "large" size-fishes especially, as shown in Fig. 8, applies to females as well as males.

5. VERTICAL DISTRIBUTION DURING THE SEASONS

To study the vertical distribution of *E. cruentatus* during the seasons fish counts were made at different depths at the stations Pos Spañó and Portomaribaai during six periods of the year: at Pos Spañó in February, June and October, at Portomaribaai in May, August and December. The counts were performed in the same way as described earlier. On each occasion 5 counts were made.

In Table 7 the percentage of counted fish is plotted against 2 different depth strata for each period. It appears that in the course of the year a vertical movement occurs, with the fish staying deep in October-November and shallower in May-June. This change in the vertical distribution of the population during the different periods coincides with the change in the gonads and with the spawning season. In the beginning of May the development of the eggs begins. The spawning process occurs especially in August and September, when post-spawning females are found. Probably the movement of the Graysbys to the "drop-off" zone is related with the mating of these fish.

TABLE 7

Percentages of fish counted in two different depth strata during 6 periods of the year.

DEPTH-ZONES	October n = 199	December n = 233	February n = 244	May n = 215	June n = 212	August n = 299
Sandy and drop-off zone (3–14 m)	44	40	55	61	62	52
Slope-zone (15–36 m)	56	60	45	39	38	48

During the fish counts several Graysbys were found sometimes close together, forming couples (also found by Collette, 1972) or groups of three, occasionally groups of four or five individuals. Smith (1972) found the same sort of spawning aggregations for Nassau groupers. It is certain that not all of these couples are mating couples, because some of them consisted of two "small" size fishes or "small" and "extra small" size fishes, and these classes do not include males. Also no significant differences in numbers of couples during the year were found. In December couples were found especially in the upper "slope" zone, but also in the lower "slope" and "drop-off" zone. In May and June most couples were found in the "drop-off" zone and in August in the upper "slope" and "drop-off" zone. So a movement in the population to shallower waters during the spawning season is indicated.

6. Vertical distribution during a day

To study the distribution of the Graysbys on the reef during a day (24 hours), census were made by two divers at the stations Portomaribaai and Pos Spañó 6 times a day. These series of census were made at Portomaribaai 3 times: in May, August and December, and at Pos Spañó also 3 times: in February, June and October.

In Fig. 10 the numbers of fish per 40 m transect are plotted against depth for 6 different times of day, testing only for relative abundance, because chances for the various observations over the day showed no differences, except for the number of fish counted at midnight.

It can be concluded that there is no change in distribution and numbers of fish during a day. In the night most Graysbys are living hidden in the corals as observed during night dives and as shown in Fig. 10.

It is worth mentioning that fish-counting at night is arbitrary. There are fish which react to light by fleeing into the corals, which influences the counting results. Starck & Davis (1966) found for most nocturnal species that they are either immobilized by light or move slowly in a confused way. Smith (1972) found that most of the fish that were quiescent at night seemed not to be disturbed when the light was played on them for a considerable period of time. Many

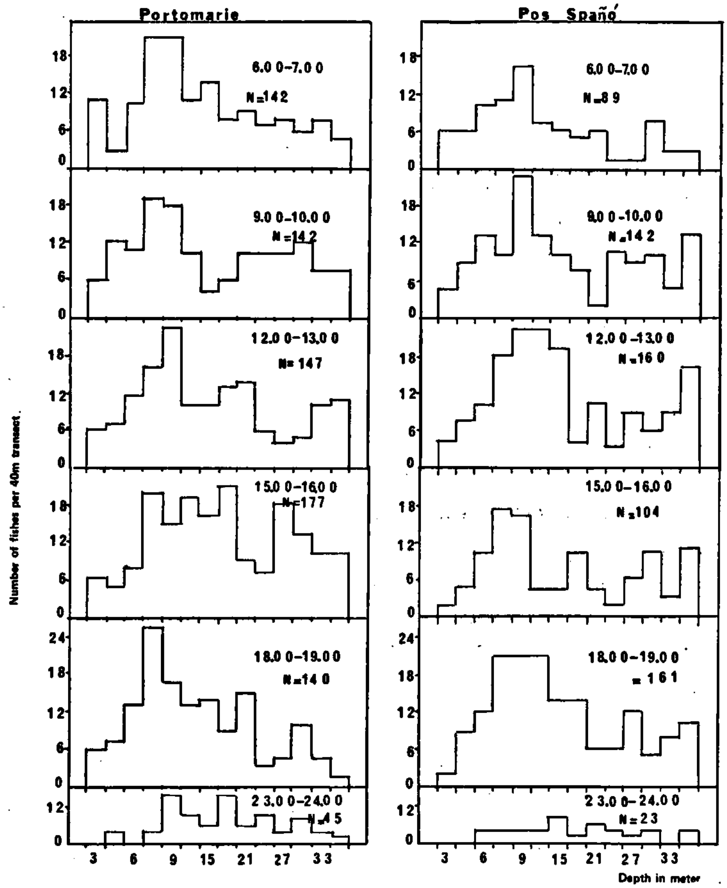

Fig. 10. Vertical distribution of *Epinephelus cruentatus* at 6 different times a day for the stations Portomari and Pos Spañó.

of the species that were active at night appeared to "freeze" when the light was aimed at them. The reaction of the Graysby in my stations to light was about the same, sometimes they stayed immobilized, sometimes they moved slowly away. They appeared more or less lethargic. COLLETTE & TALBOT (1972) found active specimens of *E. cruentatus* late at night. HOBSON (1965, 1968), STARCK & DAVIS (1966) and RANDALL (1967) observed the same, with peaks of feeding activity around sunrise and sunset.

In Curaçao the Graysbys appear to be diurnal. They move during the night deeper into caves and crevices of the reef. They are not active at night, nor do they show substantial feeding activities, because no fresh stomach contents were found in fishes collected at 24.00 hours. Only in one case at 23.00 h, in a stomach of a male (24.9 cm TL), collected at a depth of 18 m, a fresh crab of 1.9 grammes was found (*Portunus* sp.) (Chapter VI).

7. VERTICAL DISTRIBUTION IN RELATION TO *Chromis multilineata*

From the results of the food studies (Chapter VI), it appeared that *E. cruentatus* feeds especially on the Brown Chromis, *Chromis multilineata*. During field observations this *Chromis* species was found to abound on the reef and seemed to show about the same distribution as *E. cruentatus*. Therefore counts were also made of this species at the same depths and at several stations.

Fig. 11 shows the vertical distribution of the calculated number of

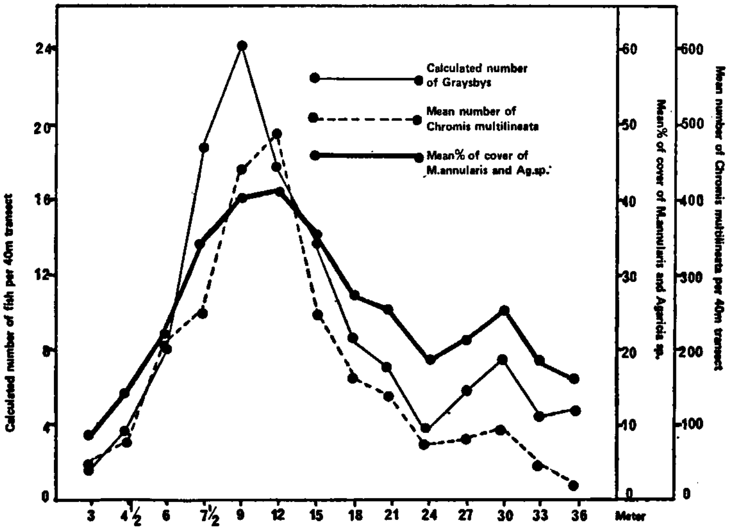

Fig. 11. Vertical distribution of *Epinephelus cruentatus* and *Chromis multilineata*, and that of the percentage of cover of the corals *Montastrea annularis* and *Agaricia* spp.

Graysbys, the vertical distribution of the counted *Chromis* and the percentage of cover of *M. annularis* and *Agaricia* spp. A strong association can be observed between the mean number of *Chromis* and the percentage cover of *Montastrea annularis* and *Agaricia*. Just like *E. cruentatus*, *Chromis multilineata* is diurnal. They are plankton-feeders and during the day they are found in great aggregations above the corals (Plate IIIa). At night they hide in the corals, especially in *M. annularis* and *Agaricia* spp. These data are in accordance with those of TALBOT (1964), who found a very clear relationship between numbers of *Chromis* and percentage and type of bottom cover.

The day and night movement of the *Chromis* specimens is about the same as found for *E. cruentatus*. Also MYRBERG, BRAHY & EMERY (1967) found during daytime that they frequented the area

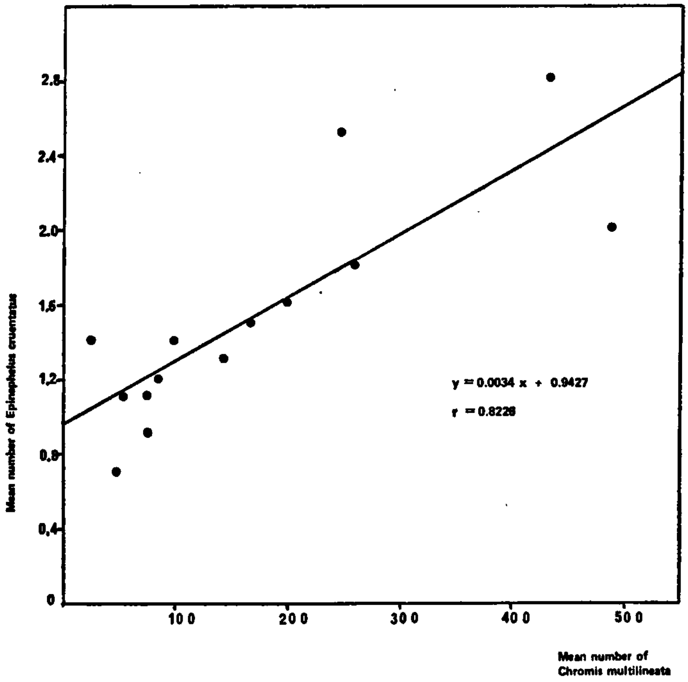

Fig. 12. Relationship between the mean number of *Epinephelus cruentatus* and the mean number of *Chromis multilineata*.

above coral heads. COLLETTE & TALBOT (1972) observed the same during the day. At night they noted that the aggregations of *C. multilineata* descended to the reef and the individuals retreated into holes. They observed that during this change-over they were more easily scared down to the reef by larger fish. This was also found by HOBSON (1973).

In Curaçao the change-over of *C. multilineata* at sunset and sunrise coincides with the high feeding activity of *E. cruentatus* during these times as appeared from the food study (Chapter VI).

It seems possible that the almost identical vertical distribution of *E. cruentatus* and *C. multilineata* as shown in Fig. 11 is coincidental, both distributions being determined by the percentage of coral cover and coral quantity. This is corroborated by the high correlation coefficients found for the relation between counted *Chromis* and percentage of cover ($r = 0.9117$), and counted *E. cruentatus* and percentage of cover ($r = 0.8758$), together with the lower correlation coefficient between the abundance of *Chromis* and *E. cruentatus* ($r = 0.8226$), shown in Fig. 12.

III AGE DETERMINATION

1. INTRODUCTION

Since the end of last century, determinations of the age of fishes have been made with the aid of scales, otoliths, opercular bones, vertebrae, fin rays etc. Scales and otoliths of many fishes consist of alternating concentric layers of opaque and translucent zones. HOFFBAUER (1898) used scales for the first time and REIBISCH (1899) otoliths for age reading.

In temperate regions these zones can be found more often and more distinct than on the otoliths of fish of the tropical and sub-tropical regions. For most species the formation of these two zones is an annual or seasonal phenomenon and it can be used then for age determination (GRAHAM, 1929; HICKLING, 1933; BROWN, 1946; MOLANDER, 1947; MENON, 1953; GAMBELL & MESSTORFF, 1964). DAHL (1967) found in eels that they can produce annually 2 growth rings in their otoliths. MORIARTY (1975) discovered that otoliths of eels may even show 3 growth zones per year.

For determination of age of groupers generally scales were not used, because these are small embedded structures with no visible annular marks and are inadequate for age determination as noted by MOE (1969) for the Red grouper. He used otoliths, because they were rather flat and displayed readily discernible growth checks. MCERLEAN (1963) used otoliths for determining the age of the grouper *Mycteroperca microlepis*, the Gag. BORTONE (1971) did the same for another species of the Serranidae: *Diplectrum formosum*, the Sand perch. ROEDE (1972) could not distinguish regular zone formation in otoliths of Labrid fishes in Curaçao. MUNRO (1974), working with various species of fish, including groupers, found that, with the exception of *Mycteroperca venenosa*, the otoliths appeared usually translucent or showed numerous light and dark bands, but he was not able to interpret the data. With *Epinephelus cruentatus* he could not obtain indications of age and growth from either scales or otoliths.

In Curaçao a pattern of opaque and translucent zones, as found for the Red grouper and the Gag, was also found in the otoliths of the Graysbys. Scales and bones were not used, because it was very difficult to distinguish any growth checks. I studied the otoliths to see if the following conditions, established by VAN OOSTEN (1929), had been met:

1. Growth of the otolith must be proportional to the overall growth of the fish.
2. The number of marks must increase with the size of the fish.
3. Growth check marks must be formed at the same time of the year.
4. Calculations of fish size classes based on the marks, should agree with observed size classes.

2. MATERIAL AND METHODS

a. *Collection of otoliths*

Each fish has three pairs of otoliths i.e. the sagitta, lapillus and asteriscus. Sagittae are the largest of the three and are commonly used to determine age, because they show most clearly the alternating concentric layers of translucent and opaque material.

Posterior to the orbits of a fish a vertical cut was made with a hacksaw from dorsal to ventral and then the anterior part of the head was bent downwards. A horizontal cut then was made through the cranium to the first dorsal spine. The upper part of the head was taken away and the brains removed. With the aid of tweezers the otoliths were taken out of the cranium. After cleaning, the otoliths were preserved in small numbered tubes with glycerine.

b. *Otolith description*

Otoliths of the Graysby are similar to those of *Mycteroperca microlepis* (McErlean, 1963), *Epinephelus morio* (Moe, 1969) and *Diplectrum formosum* (Bortone, 1971), three other members of the family Serranidae.

For description, the methods of McErlean (1963) and Moe (1969) were used. However, as landmarks for measurements two structural elements were chosen i.e. the anterior distal zone and the kernel point, a small central translucent zone (Fig. 13). The kernel point in large juveniles and adults is surrounded by a wide opaque zone, the core. The core is surrounded by alternating narrow translucent and broad opaque zones. A translucent zone plus the opaque zone immediately around it are together defined as a "growth ring" or "annulus", because in the smallest juveniles with a size of 2.5 cm, the translucent zone is the first zone formed around the core followed by a zone, which becomes gradually more opaque. The beginning of the second ring is translucent and sharply separated from the former opaque zone.

False rings are incomplete rings on the otoliths and these are mostly found close to a normal ring. They have never been found in juveniles. These false rings are probably caused by changes in growth rate before and after the time of normal ring formation and due to e.g. climatic factors, scarcity of food, physical injury, abnormal sexual development (Rounsefell & Everhart, 1953; Moe, 1969; Coble, 1970).

c. *Measurements*

Total length of the fish was measured to the nearest millimeter from the tip of the snout to the tip of the caudal fin. Sex was determined from the gonads. From the 792 specimens, available for this study, 630 pairs of otoliths could be read on growth rings. 162 pairs of otoliths could not be used for age analysis, because they were either damaged or fully opaque.

The otoliths were examined in glycerine in a black-painted glass dish. Readings for check marks were made with reflected light under a binocular dissecting microscope. Whenever possible, readings

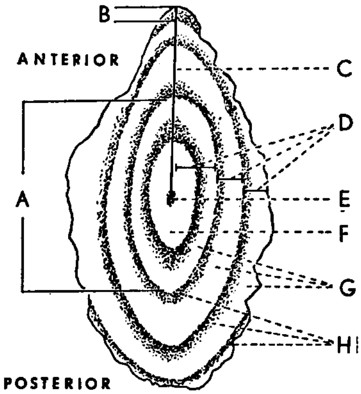

Fig. 13. Diagram of a right otolith of *Epinephelus cruentatus*, showing check marks and criteria used for aging of the species. A: first ring. B: marginal increment. C: radius. D: first, second and third ring. E: kernel point. F: core. G: opaque zones. H: translucent zones.

and measurements were performed on both otoliths, and the average of both measurements taken as the final value.

The following measurements were made with the help of an ocular micrometer (Fig. 13):

A. *Otolith radius* (radial measurement): the shortest distance from the kernel point to the anterior distal edge of the otolith at a magnification of 12 × (1 ocular micrometer unit = ca 0.08 mm). This was done with 627 pairs of otoliths.

B. *Width of the growth ring*: measurements were made along a line from the kernel point to the outer anterior edge of each presumed ring. This was done with 150 pairs of otoliths, chosen on the basis of clarity of rings, enabling comparison with body length. Otoliths of fishes of age groups 5 and older were not used in relation to body length, because the first 5 to 7 growth rings of the fishes of 5 years and older tend to become more indistinct, which makes the measurements of ring width unreliable. The measurements were made at the same magnification as under A.

C. *Marginal increment width*: the distance from the last opaque ring to the otolith margin, measured along the above mentioned line. The marginal increment width consists of a translucent zone, which can be followed by a zone becoming gradually opaque. Thus the width of the marginal increment can never be zero. Measurements of the width of the marginal increment smaller than 2 micrometer units were not possible, because they could not be distinguished with certainty. Measurements were made at a magnification of 50 × (1 ocular micrometer unit = ca 0.02 mm). This was done with 627 pairs of otoliths.

D. *Condition factor*: the condition factor, calculated from the formula $K = \frac{W}{L^3}$, was used to investigate seasonal differences in the length - weight relationship. For the calculation the fish computer of Ritchie, C.A. Oklahoma city, Okla. 73114, U.S.A. was used.

RESULTS

a. *Proportional growth of the otolith*

In Fig. 14 the mean otolith radius is plotted against total length for 627 Graysbys. The relationship is probably curvilinear, but it can be approximated by two straight lines. Therefore, to show proportionality between otolith radius and total length two regression lines were fitted, one of a set of 9 size classes of juveniles (up to 11 cm) and one of a set of 21 size classes of the older fishes (from 11 cm onwards). The regression line for the juveniles can be expressed by the equation:

$$y = 3.03\,x + 0.62$$

The regression line for the older fishes can be expressed by the equation:

$$y = 1.76\,x + 13.24$$

The calculated correlation coefficients ($r = 0.998$ and $r = 0.998$) indicate a high proportionality between otolith radius and total length. Therefore, the relationship between fish size and otolith radius can be used in studying ring formation in relation to size.

The difference in growth rate of the otoliths of fishes smaller than 11 cm and those larger than 11 cm is difficult to explain. The often suggested explanation of non-isometric growth, in which initially the head would increase faster than the body, could not be confirmed.

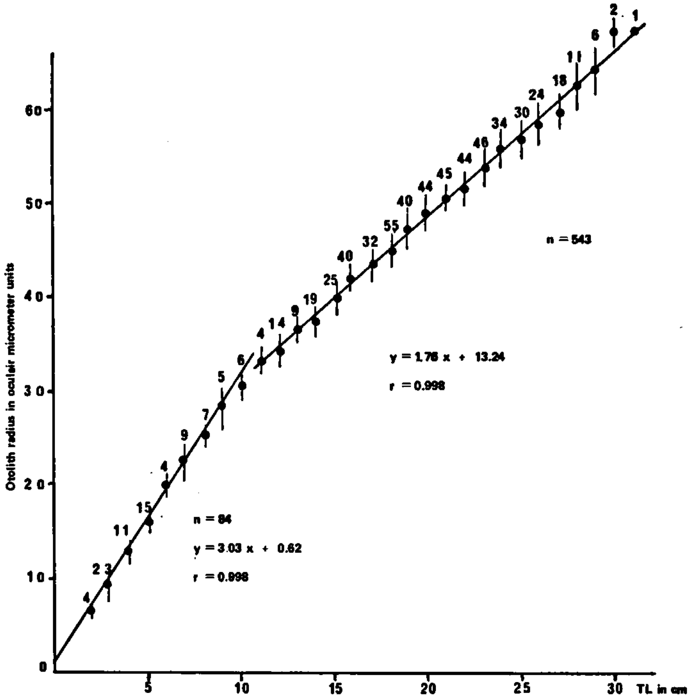

Fig. 14. Relationship between mean otolith radius and total length (TL) for 627 Graysbys. Number of fish in each class is indicated. The standard deviation is indicated by a vertical line.

b. *Number of rings in relation to total length*

To use otoliths for determining the age, the number of rings must increase with the size of the fish.

In Fig. 15 the total length of 634 Graysbys is plotted against the number of rings. The regression line is described by the equation:

$$y = 1.04\,x - 2.848$$

The calculated coefficient of correlation is very high ($r = 0.999$), which means that the increase in number of rings is proportional to the increase in total length.

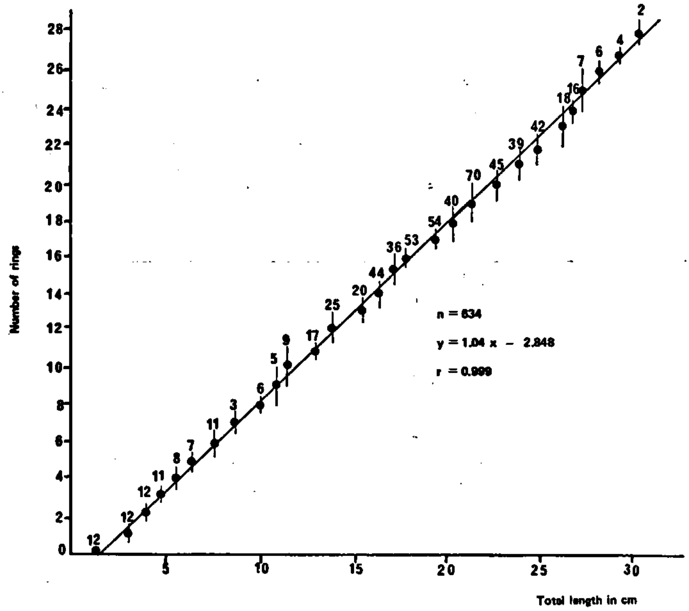

Fig. 15. Relationship of total length to number of rings for 634 Graysbys. The figure listed by each mean indicates the number of fish contributing to the mean. For each mean the standard deviation is given.

c. *Ring formation with time*

In Curaçao small juveniles of *Epinephelus cruentatus* are found in the second half of September and to a lesser extent during October. During these months the juveniles have a length varying from 2.4 to 2.8 cm. Therefore, 1 September is taken as the nominal birthdate of this species. Mating takes place mainly in August and September. MITO et al. (1967) found for larvae of the grouper *Epinephelus akaara* 35 days after hatching a total length of 2.45 cm. If the growth of Graysby larvae is comparable with that found in *E. akaara*, then larvae of Graysbys in the second half of September are from eggs spawned in the first half of August.

From September to September of the next year, juveniles were collected each month with Rotenone and the formation of new rings in the otoliths was recorded.

TABLE 8

Increase of the number of growth rings of 74 juvenile Graysbys during their first year. Mean total length + standard deviation, mean number of rings + standard deviation, range of the number of rings and the number of juveniles are given.

MONTHS	Mean total length + standard deviation	Mean number of rings + standard deviation	Range of the number of rings	Number of fish
September	2.5 ± 0.1	0.0	–	10
October	3.2 ± 0.5	1.4 ± 1.3	0–4	8
November	3.5 ± 0.9	1.9 ± 1.1	1–4	12
December	5.2 ± 1.7	2.3 ± 0.9	1–3	8
January	4.5 ± 0.9	3.0 ± 1.1	2–5	11
February	5.2 ± 1.5	3.7 ± 1.8	1–6	7
March	5.8 ± 2.3	4.5 ± 2.1	3–6	2
April	6.8 ± 0.9	5.1 ± 0.8	4–6	9
May	7.9 ± 0.5	6.2 ± 0.5	6–7	5
June	9.2	7.0	–	1
July	—	—	–	—
August	8.7	7.0	–	1

Table 8 gives for each month the mean total length, the mean number of rings + standard deviation, the range and the number of juvenile fishes. It appears that the formation of the first ring is finished for most fishes in October. Then the juvenile has one translucent and one opaque zone around the core. The second ring is finished in November and December. In January the third ring is found, in February the fourth (Plate III b), in March and April the fifth and in May the sixth. The formation of ring 7 is completed in September, when they are 1 year old. So during the first year about 7 growth rings are formed.

In the first column of Fig. 16 the percentage frequency distributions of the width of the marginal zone in the otolith are shown (width of the zone outside the last opaque ring) for all fishes with more than 7 rings, during all months of the year. The measurements are given in micrometer units. In September the zone is small, but the distribution shows a shift to higher values with a maximum in November-December. In January an abrupt shift to low values is found. In this month a bimodality can be observed in the distribu-

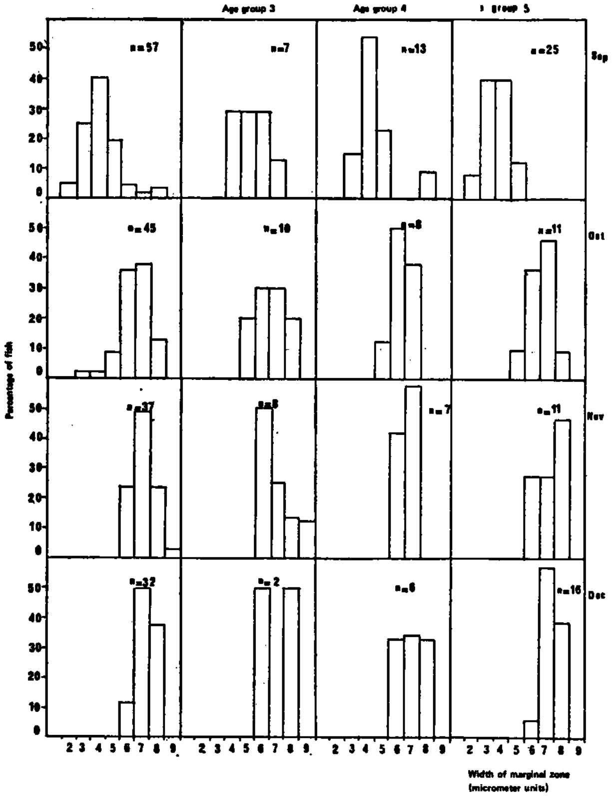

Fig. 16. Percentage frequency distributions of the width of the marginal zone in the otoliths of fishes with more than 7 rings (first column) and of age groups 3, 4 and 5 during all months of the year.

tions. This might indicate that the formation of a new translucent zone does not start at the same time in all fish. After January values increase again with a maximum in March-April. Partly in May, but mostly in June, another abrupt shift to lower increments can be found. In these months again a bimodality is suggested; i.e. in May only a few specimens, forming a new zone and most of the fishes not finished with the last ring, and in June most fishes, forming a new zone and only a few, which are "late". After that the increment increases again with a maximum in August.

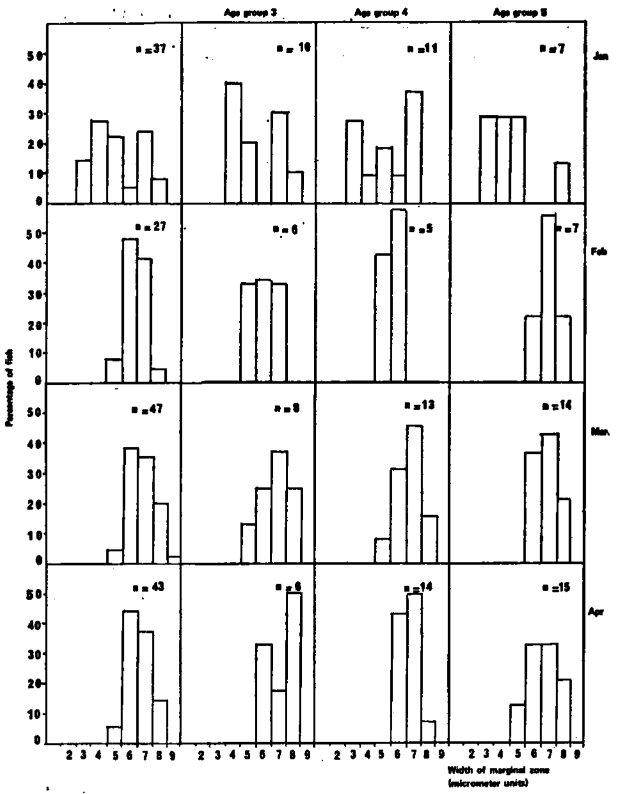

Fig. 16a. Percentage frequency distributions as in Fig. 16.

These results show clear fluctuations in the widths of the marginal zones during the season with maxima in November-December, March-April and August, and minima in January, June and September. This could signify that each year, in the months January, June and September, a new translucent zone is formed (which becomes, however, later more opaque). In the months following these three periods an opaque zone is laid down. It is not quite clear whether all fish with over 7 rings in the otolith take part in the marginal zone formation in January, June and September. In these months small and large marginal zones appear, which might indicate a not quite synchronized formation of a new zone or, alternatively, that part of the population skips the formation of a marginal zone. In the

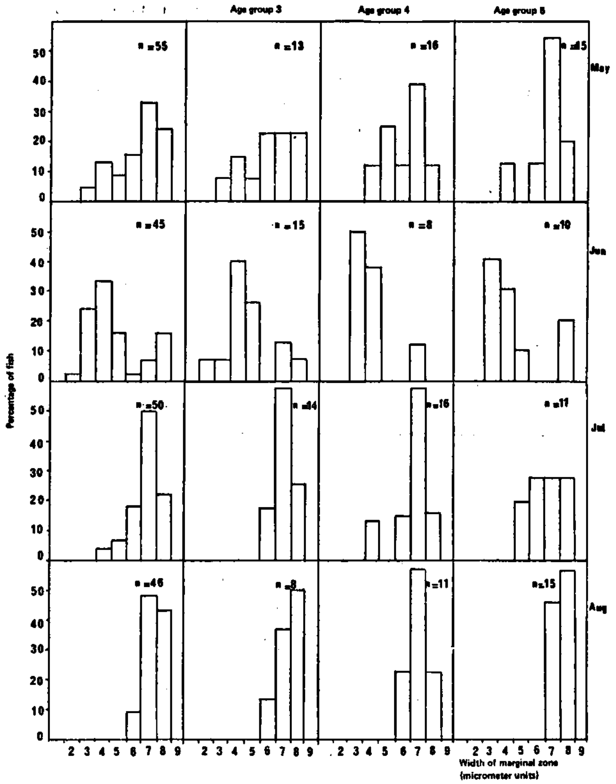

Fig. 16b. Percentage frequency distributions as in Fig. 16.

latter case the age of the fish would be overestimated by assuming the formation of 3 growth rings annually. However, as our data show unambiguously the presence of three periods of growth-zone formation annually in the fish over 1 year old and the second possibility is difficult to interpret in the ageing practice, the first possibility has been adopted.

In Fig. 16 the percentage frequency distributions of the width of the marginal zone in the otoliths are also given for presumably 3, 4 and 5 year-old fish, because they were sufficiently abundant to provide a complete record of the change of marginal increment width with time. More or less the same pattern is found for the three separate age groups as found for all fishes (except juveniles) together.

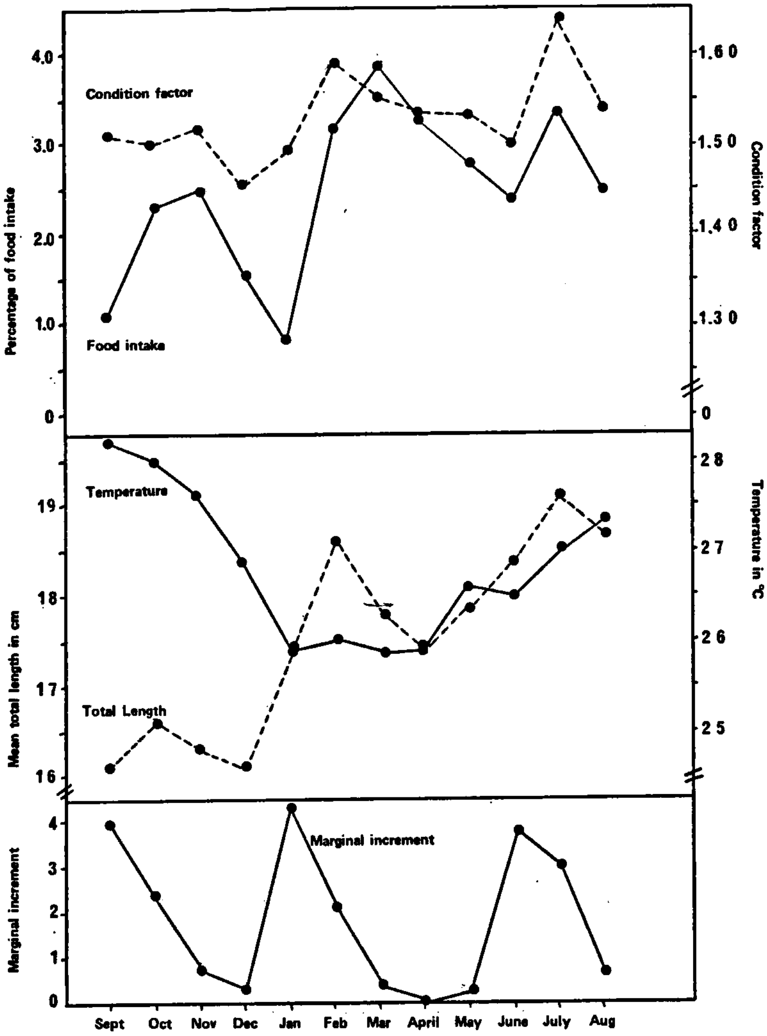

Fig. 17. Marginal increments during the different months, compared with water temperature, total length (mean of age groups 2, 3, 4 and 5), percentage of food intake (quantity of food in stomach, taken as a percentage of total body weight) and condition factor.

Again, especially in January and June, a bimodality in the width of the marginal zones is present.

In the lower part of Fig. 17 the marginal increment (the increase in width of the new ring) is plotted against the month. The most rapid increase of the marginal zone occurs in January (4.3 ocular micrometer units), in June (3.8 ocular micrometer units) and in September (4.0 ocular micrometer units), when translucent zones are formed. In the months following the three mentioned months, the growth of the otoliths is slower and then opaque zones are formed.

d. *Back-calculation of length on the basis of ring-formation*

Calculations of fish size based on the annual rings should agree with observed sizes. Calculated lenghts were determined by a modified proportional method described by TESCH (1968) using the equation:

$$L_n = \frac{S_n (L - C)}{S} + C$$

For the otoliths of the Graysby, accepting 7 growth rings in the first and 3 in subsequent years, it means: L_n = calculated total length; L = total length of fish at time the otolith sample was obtained; S_n = radius to the outer anterior edge of ring 7 for age 1, or ring 10 for age 2, or ring 13 for age 3, or ring 16 for age 4, or ring 19 for age 5 along a line from the kernel point to the anterior distal point of the otolith; S = total otolith radius along the same mentioned line.

The observed lengths were taken from fishes collected in September (1973, 1974, 1975), that is in the month during which they have hatched and form a new ring. For the calculated lengths, only those fishes collected in September were used, which had otoliths suitable for measurements of the width of the several growth rings.

A correction factor (C), the x-axis intercept for the regression line of otolith radius and total length was used in an attempt to compensate for the change in otolith symmetry. The correction factor for juveniles (Fig. 14) is — 2.1 mm, the factor for other fish (Fig. 14) is — 75.2 mm.

Table 9 shows the observed length (taken from fishes collected in

TABLE 9

Comparison of observed and calculated total length (in cm) for age groups 0 through 5 at time of ring formation in September.

AGE GROUP	Observed T.L.	n	Calculated T.L.	n
0	2.5	15	2.5	15
1	8.2	2	8.0	9
2	11.2	1	11.2	26
3	15.2	7	14.8	38
4	17.7	13	17.6	24
5	20.8	25	20.7	2

September, at birthdate and also at time of ring formation), and calculated lengths of age groups 0 through 5. The back-calculated length (L_n) was determined with the aid of 114 pairs of otoliths. It is shown that body lengths, calculated from prior annuli, agree very well with empirical body lengths of the same "age" group, in which the age was determined by the number of rings.

Table 10 shows the calculated and observed lengths from measurements of the rings of 74 pairs of otoliths of juveniles. Calculated and observed lengths agree rather well. It should be added that for lack of sufficient numbers of juveniles the mean observed lengths are derived from fishes, collected not only at the time of a new ring formation, but also during the whole period of ring formation. Therefore the observed lengths are somewhat larger than the calculated

TABLE 10

Comparison of observed and calculated total length in cm for ring groups 0 through 7 of the juveniles of *Epinephelus cruentatus*

NUMBER OF RINGS	Number of fish	Observed TL	Calculated TL
0	12	2.6	2.6
1	12	3.0	2.7
2	12	3.7	3.3
3	11	4.5	3.9
4	8	5.1	4.7
5	7	6.4	5.9
6	9	7.6	7.2
7	3	8.6	8.1

lengths for most ring groups, since collections do not coincide with the precise time of ring formation. The systematic deviation, however, indicates the valability of the results.

e. *Conclusions*

The four criteria by VAN OOSTEN (1929) have been satisfied by the data of *Epinephelus cruentatus*, because:

A. proportionality was found between otolith radius and total length.

B. the increase in number of rings is proportional to the increase in total length, with a high correlation coefficient ($r = 0.999$).

C. growth rings were formed for *E. cruentatus* (except juveniles) at the same time of the year, namely one starting in September, one in January and one in June. Juveniles form 7 rings a year.

D. there was close agreement between observed and calculated lengths.

It is concluded therefore, that the age of *E. cruentatus* caught at the coral reef of Curaçao can be tentatively determined with the help of the analysis of otolith rings. The possibility, however, that not all fish form 3 rings annually, as mentioned under section 3 of this chapter, cannot be completely excluded.

4. DISCUSSION

Readings of otoliths of *Epinephelus cruentatus* of Curaçao demonstrate that these otoliths can be used for determining the age. This species shows three well defined periods in the course of the year, in which growth rings are laid down, each ring consisting of a narrow translucent zone and a broad opaque zone. The translucent zones are mainly formed in September, January and June, and the opaque zones in the periods following these months (these translucent zones are first broad, but become later for the greater part opaque, so that only a rather small translucent zone remains). Juveniles form 7 growth rings a year.

Further support for the validity of using these otoliths for establishing age, is found in the close agreement in a comparison between my studied age groups and Peterson's method. Fig. 18 shows a

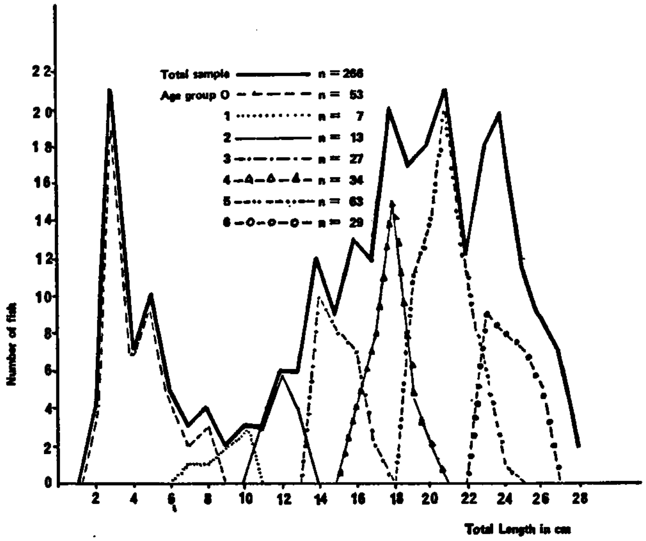

Fig. 18. Length-frequency distributions of total samples and of age groups 0 through 6 during the season September-December.

polymodal length – frequency distribution for fishes up to 28 cm and during three seasons, namely September – December, January – May and June – August. In the same Fig. 18 length – frequency distributions of the different age groups for the three seasons are given for comparison. It appears that the consecutive age groups closely coincide with the consecutive modes in the length-frequency distributions.

Otoliths of fishes consist mainly of calcium carbonate. Irie (1955, 1957, 1960) demonstrated that otoliths grow by formation of microcrystal grains of $CaCO_3$ on the otolith surface. In periods of rapid growth of the otoliths the microcrystals of $CaCO_3$ are formed quickly and only little protein is laid down between them. In this way the translucent zones are formed. In periods of slow growth of the otoliths, the crystals are formed slowly and much protein is laid down between them, thus leading to the opaque zones. In the Graysby it is probable that the translucent and opaque zones are formed in a comparable way.

Several suggestions have been offered about the cause of annulus

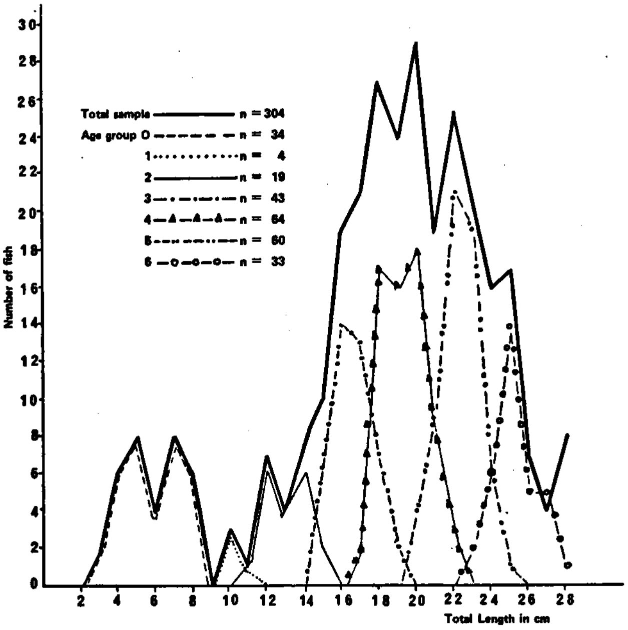

Fig. 18a. Length-frequency distributions of total samples and of age groups 0 through 6 during the season January-May.

formation. GRAHAM (1929) and HICKLING (1930) suggested that they reflect metabolic changes, hyaline (translucent) material being formed, when anabolism is low, and opaque material, when it is high. These metabolic changes would result from interactions between special phenomena during one year of the life cycle, e.g. spawning and migration, and environmental factors such as food and temperature. CHEVEY (1933), using scales, argues that seasonal fluctuations in the quantity of food and small annual variations in the water temperature at the time of annulus formation can cause a new annulus, a difference of 4 to 5°C, being sufficient. MENON (1953) suggests that an inherent physiological rhythm, associated with spawning and decrease in food intake during gonad maturation, might play an effective part in the periodic formation of the annual growth checks in the skeletal parts of the fish. IRIE (1960) has shown experimentally that the calcification rate of the otolith is strongly positively

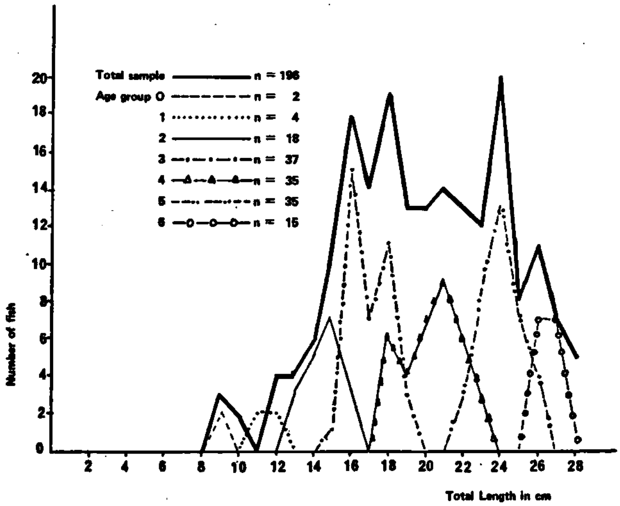

Fig. 18b. Length-frequency distributions of total samples and of age groups 0 through 6 during the season June-August.

correlated with water temperature and the amount of food available. Moe (1969) found for the Red grouper that the formation of annuli is associated with time of spawning, increasing photoperiod and rising bottom temperatures. He suggests that spawning and associated physiological processes are the cause of annulus formation, because the fluctuations in bottom water temperature are only 5° to 6°C (see, however, Chevey, 1933). Vooren (1972) found in early spring at two stations at different depths in the Bay of Plenty (New Zealand) no differences in bottom temperature, but differences in available food. He suggests that these differences may account for the variation in otolith growth in spring between both stations.

At Curaçao the annual variation in temperature is much less and therefore it is difficult to find a possible connection between ring formation and temperature fluctuations. Ring formation in September coincides with the highest temperature of the year (Fig. 17). Thereafter temperature drops to a minimum in January when another ring is formed. Ring formation in June coincides with a rise in temperature that begins in April.

A more convincing coincidence was found between food intake and condition factor on the one side and ring formation on the other hand. During the formation of the translucent zones in September, January and June the values for food intake and condition factor are low. In the periods following these three months, when the opaque zones are formed, the values for food intake and condition factor are relatively high. Probably the translucent zones are formed in periods of low anabolism (September, January and June), as appears from the low values of the food intake (Fig. 17) and as suggested by GRAHAM (1929) and HICKLING (1930). The opaque zones should then be formed in the periods following these three months, when the anabolism is higher as appears from the high values of the food intake (Fig. 17).

IV GROWTH

1. INTRODUCTION

Data on growth of groupers are scarce. BARDACH & MENZEL (1957) studied the growth of some groupers during field and laboratory observations in Bermuda. RANDALL (1962) gives notes on growth of several groupers, derived from tagging experiments in the Virgin Islands. MCERLEAN (1963) studied the age and growth of the Gag, *Mycteroperca microlepis*, determining age by otolith readings. MOE (1969) gives extensive data on the growth of the Red grouper, *Epinephelus morio* of the West Coast of Florida. BEAUMARIAGE (1969) gives some indications of growth for groupers in Florida obtained from tagging experiments. THOMPSON & MUNRO (1974) made estimates of age and growth for groupers based upon analyses of length-frequency distributions. In a later study (1978) they calculated relative and absolute growth rates for Serranidae.

During this study growth in length and weight was studied in relation to the age. Also a note is given on the mortality of this species.

2. MATERIAL AND METHODS

For this study on growth 640 Graysbys were used, which could be aged with the aid of otoliths, accepting 7 growth checks in the first, and 3 in subsequent years. Total length (TL) was measured in millimeters. Body weights were measured to the nearest gram. For the length-weight relationship 738 specimens and for the relationship between total and standard length 267 specimens were used. The following symbols are applied: TL = total length, L_t = length at age t, L_{t+1} = length at age t + 1, K = a constant, determining the rate of change in length increment, L_∞ = asymptotic length, e = base of the natural logaritm, t_0 = theoretical origin of the growth curve. Catch curve = a graph of the logarithm of numbers of fish taken at successive ages (RICKER, 1958).

3. RESULTS

a. *Seasonal growth*

In Fig. 19 the mean monthly lengths of age groups 0 to 9 years are given for all Graysbys (n = 640) whose age could be determined. Because the first juveniles appear in September, this month is used as the first. The graph suggests that growth for age groups 2, 3, 4 and 5 took place mainly in February and to a lesser extent in

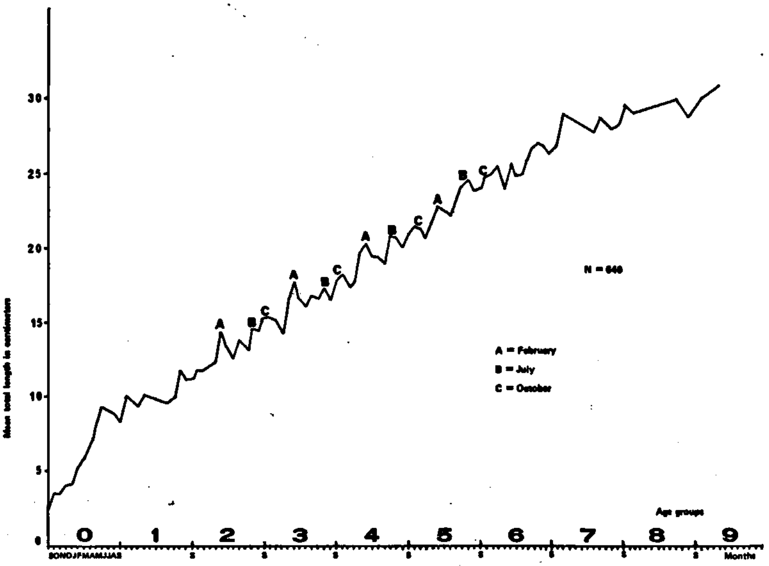

Fig. 19. Monthly mean lengths of age groups 0 to 9.

July and October. These three possible growth peaks follow ring formation in January, June and September and they coincide with high values of food intake and condition factor in February, June and October. However, the lower values of the mean lengths in the periods following these three months are difficult to understand, because it is not likely that fishes shrink after periods of rapid growth.

b. *Annual growth*

In Fig. 20 the mean lengths (averaged over the whole year) are plotted against the different age groups. The individual total length varies from 2.4 to 30.7 cm. The annual growth rate decreases gradually from about 5.2 cm in juveniles to about 2 cm after the 6th year.

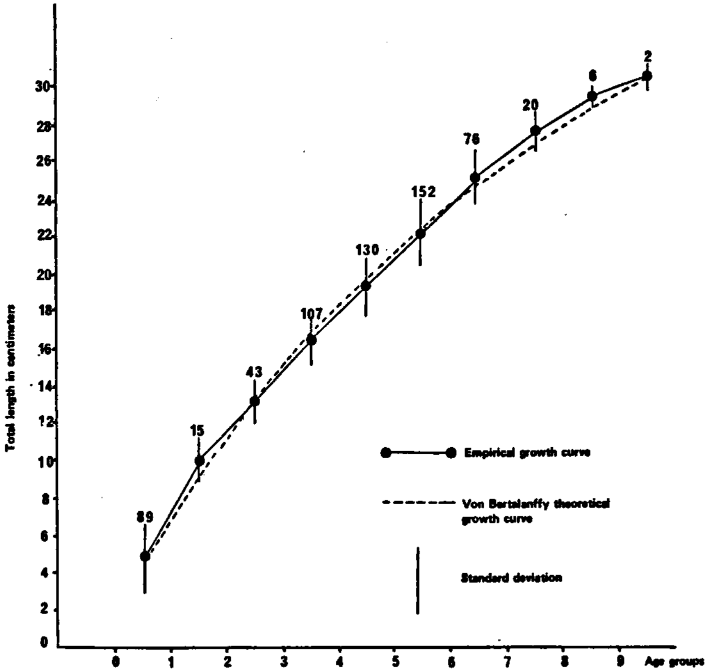

Fig. 20. Growth curve derived from mean total length with standard deviation, compared with the Von Bertalanffy theoretical growth curve. Numbers of fish contributing to the mean are given. Mean length averaged over the whole year.

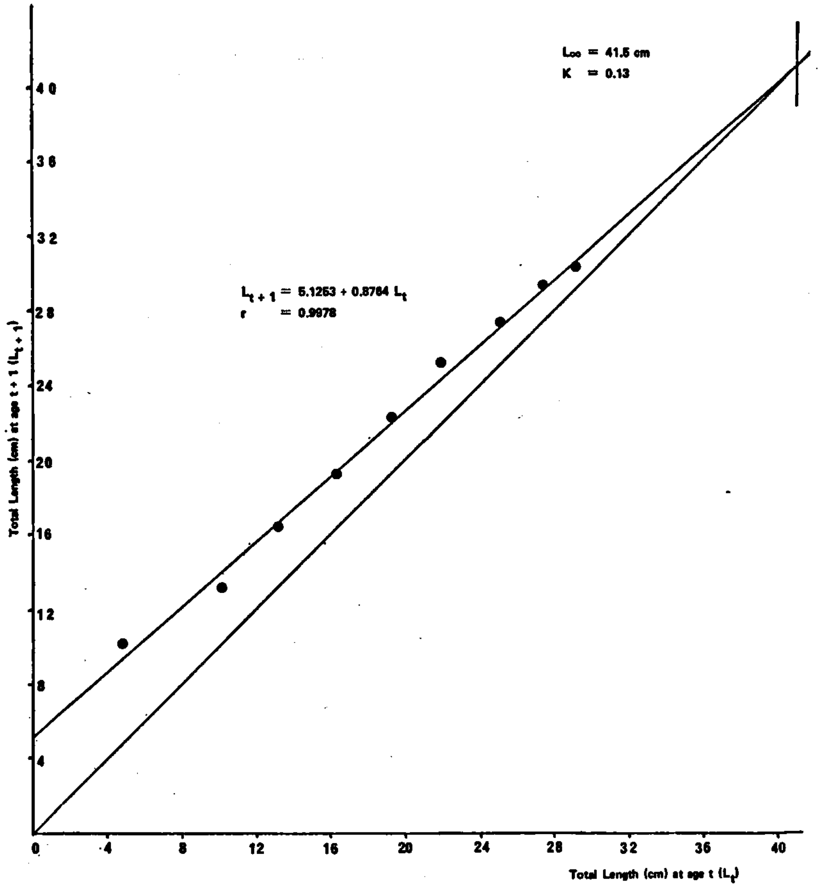

Fig. 21. Ford-Walford growth transformation of the empirical growth curve.

Fig. 21 shows the Ford-Walford graphic growth transformation, as described by GULLAND (1965), of the absolute growth curve derived from the empirical total lengths of each age group. L_t (length at age t) along the x-axis is plotted against L_{t+1} (length at age t + 1). A line is drawn at 45° through the zero point. From these two lines and also from the regression formula two constants could be obtained, namely $K = 0.13$ (the slope of the fitted Walford-line) and the asymptotic length $L_\infty = 41.5$ cm. The difference between asymptotic length (41.5 cm) and measured maximum length (30.7 cm) is difficult to interpret, but it could be due to insufficient data on fishes of 8 and 9 years old combined with a less perfect reading of the otoliths of these old fishes, resulting in no reliable mean lengths for these age groups. THOMPSON & MUNRO (1978) mentioned a maximum length of 33 cm for *E. cruentatus* and 37.5 cm for *E. fulvus*, a closely related grouper. They estimated the asymptotic length in the region of 33–35 cm TL for *E. cruentatus*. So it is possible that in Curaçao some larger specimens also occur, however, they have not been collected.

In Fig. 20 also the Von Bertalanffy growth equation was fitted to the data of *E. cruentatus* by means of the Ford-Walford regression. This equation is:

$$L_t = L_\infty (1 - e^{-K(t - t_0)}),$$

where L_t = length at age t, L_∞ = asymptotic length, K and t_0 are growth constants.

The estimate of t_0 is the mean of the estimates of age groups 0 to 6: $t_0 = -0.94$; the range within the age groups is between -0.78 and -1.14.

The Von Bertalanffy growth equation for the Graysby in Curaçao is:

$L_t = 41.5 (1 - e^{-0.13 (t+0.94)})$ and fits the data well.

c. *Growth of females and males*

In Fig. 22 the mean lengths of females and males are given for the different age groups. The length of the males is always greater than that of the females of the same age group.

Computing the growth-constants with help of a Ford-Walford growth transformation, $K = 0.1282$ and $L_\infty = 41.8$ cm for females and $K = 0.1299$ with $L_\infty = 40.6$ cm for males.

d. *Annual increase in body weight*

Fig. 23 shows a plot of increase in body weight against age through the year. All age groups are similar in growth pattern showing remarkable peaks in February and July and a third, but small peak

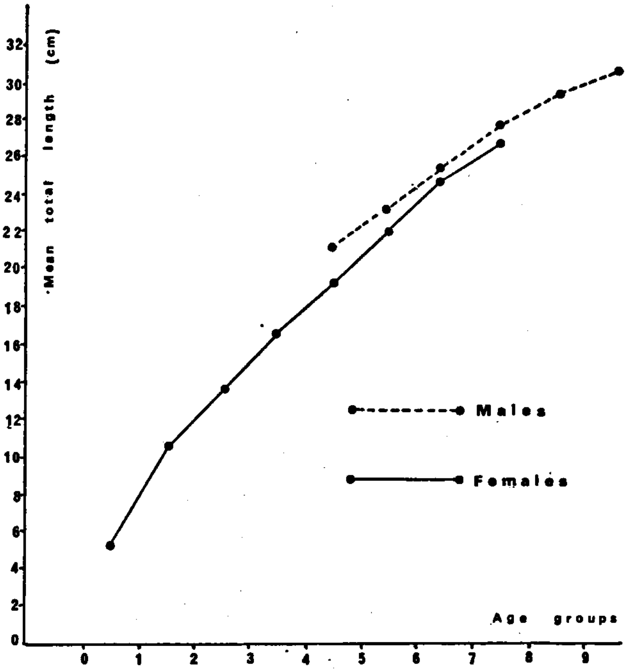

Fig. 22. Empirical growth curves of males and females derived from the mean total lengths of each age group.

in October. These three peaks coincide with maxima found in the same periods for food intake and condition factor.

e. *Relationship total length – standard length*

Total lengths and standard lengths of 267 Graysbys were used for the analysis of the relationship between total and standard length. For the calculations the mean total and standard lengths of each 10 mm length-group were used. Fig. 24 shows that the relationship between total and standard length is linear. The relationship is expressed by $y = 1.2091\ x + 0.2326$.

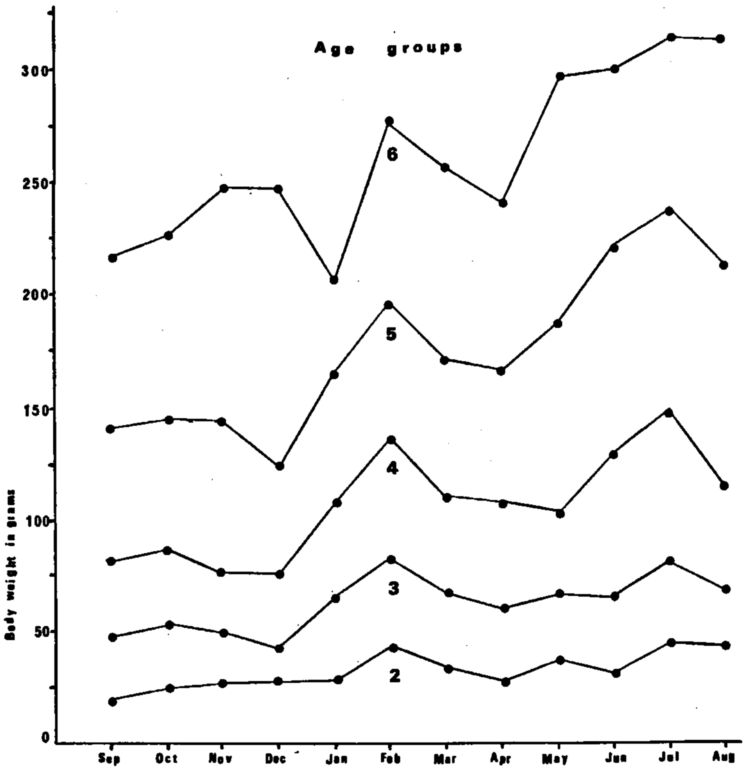

Fig. 23. Monthly mean weights of age groups 2 to 6.

f. *Length – weight relationship*

Total lengths and total body weights of 738 Graysbys were used for the analysis of the relationship between length and weight. For the calculations the mean lengths and mean weights of each 20 mm length-group were used.

In Fig. 25 the mean length of each 20 mm group is plotted against the mean weight. At the same time the regression line is plotted for the weight against Log_{10} length. A high linear correlation was found between both: $r = 0.9998$. This means that an equation of the type $W = a L^{b}$ fits the data well (W = weight, L = length, a and b are constants).

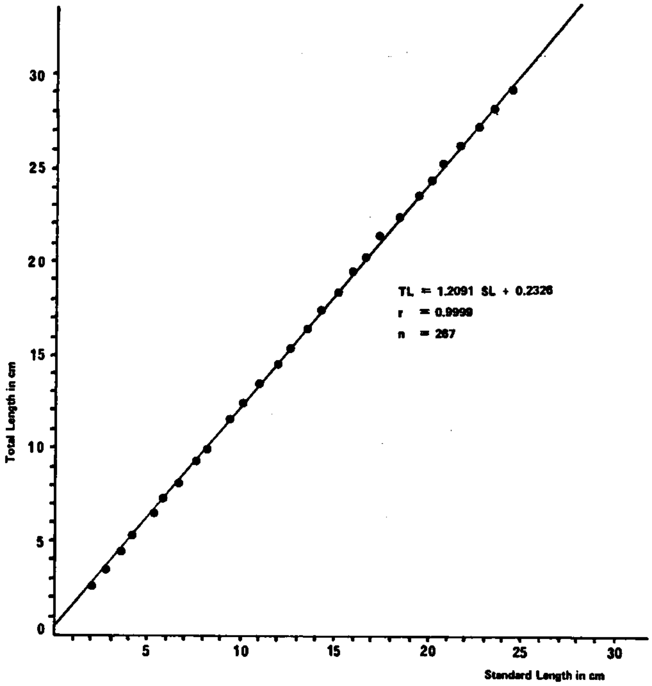

Fig. 24. Relationship between standard length and total length.

The equation found is $W = 0.0121 \times TL^{3.0821}$, which indicates that the weight of the Graysby probably is a function of the cube of the length.

g. *Mortality*

Catch curves, as described by RICKER (1958) can be used to estimate mortality rates. When plotting log numbers per age group on age, as shown in Fig. 26, the observation should fall on a straight line, provided a constant mortality over the total age range and a constant recruitment. The catch curve shown in Fig. 26 deviates strongly from this picture, which might either be due to a low recruitment in recent years, or a mortality increasing with age, or both. More likely, however, our catches gave a poor representation

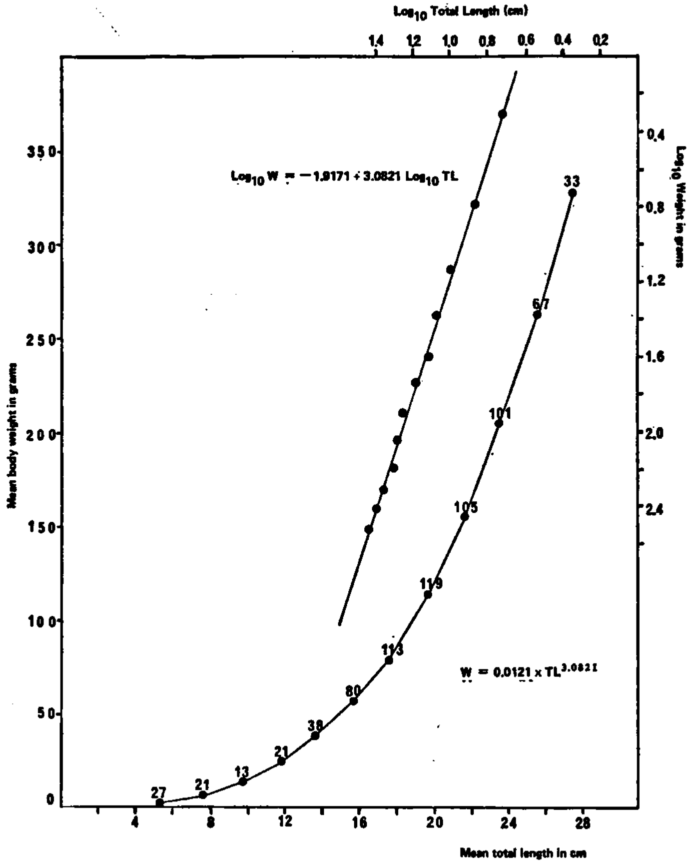

Fig. 25. Relationship of length to weight for 738 Graysbys. Each dot represents the mean weight of each 20 mm length group. Regression line for weight against Log $_{10}$ Total length.

of the population, underestimating the younger fish, due to their tendency to hide more in the reef and to a lower availability to the speargun. Scarcity of the old fish could be caused by overfishing, especially by trap-fishing, working selectively by taking mainly large specimens (see chapter V, discussion). The very old animals could also be underestimated, because they possibly live deeper than 36 m, where we did not operate. This suggestion is supported by the

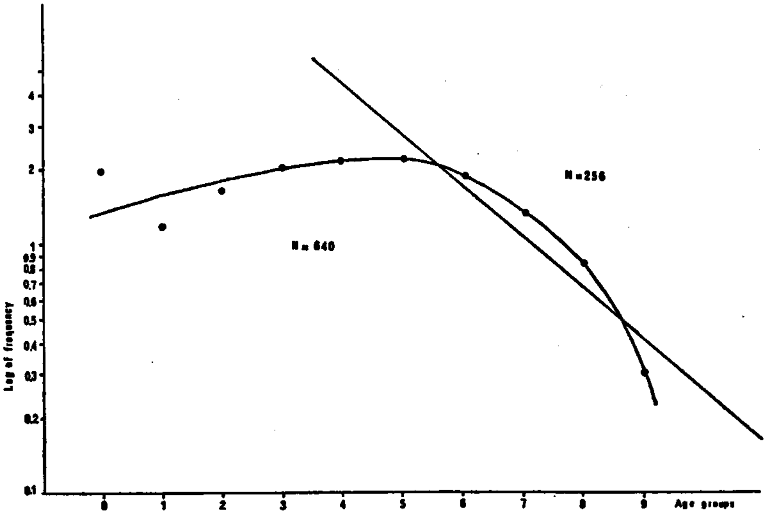

Fig. 26. Catch curve for all 640 aged Graysbys. Regression line is calculated for fishes of 5 years and older ($n = 256$).

fact, that the larger (and older) animals tend to live deeper. Alternatively, it could be that our age determination for the older fishes is far from perfect. Under these circumstances it seems inadvisable to try to compute mortality rates for the Graysby.

4. DISCUSSION

Length growth of the Graysbys seems to occur especially in January – February and to a lesser extent during July and October.

The empirical growth data are shown to fit the theoretical growth model of Von Bertalanffy.

From a Ford-Walford plot two growth-constants could be derived: $K = 0.13$ and $L_\infty = 41.5$ cm.

The growth equation of Von Bertalanffy for *Epinephelus cruentatus* in Curaçao is: $L_t = 41.5\ (1 - e^{-0.13\ (t\ +\ 0.94)})$. The slope of the line in the growth curve shows that during age 0 the annual growth rate is higher than at the older ages (about 5 cm per year in juveniles and about 3 cm per year in older animals). After the 6th year a decrease in growth rate can be found to about 2 cm per year. MOE (1969) observed a mean increase in growth of 4.7 cm per year for the age group 1 to 8 of the Red grouper. The maximum age of the Red grouper is 24 years with a length (SL) of 70.2 cm in contrast to the Graysby with a maximum age of probably 9 years. MOE found a change in growth rate in the Red grouper at the age females start reproductive activities. For the Graysbys, in which females reach sexual maturity at an age of 3 years, no change in growth rate at this age was found.

The pattern of growth of females and males is the same. Only the mean lengths of males and females of 4, 5, 6 and 7 years old are different. The mean length of the males is always larger than that of the females. The greatest difference is found in age group 4 and then it decreases with the older ages. Also during and shortly after the transition of females into males the growth rate in males increases strongly. For all the respective ages the growth rate for females and males is very similar with K = 0.13.

A strong increase in body weight was found in February and July, and a small peak in October. These three peaks in growth in body weight coincide with maxima of food intake and condition factor in the same mentioned months, and follow the beginning of the formation of new growth rings in the preceding months. Although in the chapter on determination of age during these three mentioned months some temperature fluctuations could be observed, it is nevertheless questionable how far such small differences in temperature can be an inducing factor for increase in weight, food intake, condition factor and annulus formation as suggested by earlier mentioned literature data.

The strong increase in weight during July coincides partly with the development of the gonads, especially with the vitellogenesis during this time, and is mainly found in age groups 4 and older, e.g. mostly among mature fishes.

The total length – standard length relationship is expressed by the equation:

$$y = 1.2091\, x + 0.2326$$ and is highly linear.

The length – weight relationship found for the Graysbys is:

$$W = 0.0121 \times TL^{3.0821}.$$

As shown the weight of the Graysby is closely proportional to the cube of the length.

V REPRODUCTION

1. INTRODUCTION

Most of the marine serranid fishes are hermaphroditic. Some are synchronously hermaphroditic: the gonad is divided into male and female parts and both parts are active simultaneously (VAN OORDT, 1929; LONGLEY & HILDEBRAND, 1941; D'ANCONA, 1950; GINSBURG, 1952; SMITH, 1959). Others are proterogynous hermaphroditic: the entire gonad transforms with increasing age from an ovary into a testis. The latter was found by LAVENDA (1949) for the Atlantic sea bass, *Centropristes striatus.* He observed more males in the larger size classes and explained this phenomenon on the ground of proterogynous hermaphroditism. He was able to confirm this by histological studies. SMITH (1959, 1965) observed this type of gonad in some serranid fishes from Bermuda, including *Epinephelus cruentatus.* He found that most members of the subfamily *Epinephelinae* (groupers) are proterogynous on the basis of the following evidence: "1. No males were found in the smallest size groups. 2. Males appeared among medium size fish and the proportion increased among the larger size classes until the largest size groups were exclusively males. 3. Regressive oocytes were found in the testes of functional males."

Proterogynous hermaphroditism was also found by MOE (1969) for the Red grouper, *Epinephelus morio.* He also studied spawning time and sex-ratio of this species. A comparable study was done on many groupers of Jamaica, including Graysbys, by THOMPSON & MUNRO (1974).

In this study gonads were analysed histologically to get sufficient information on spawning season, sex-ratio, sexual development, sexual transition and related problems in *Epinephelus cruentatus*.

2. MATERIAL AND METHODS

a. *Collecting*

Fishes were collected by speargun at different depths during the years 1973–1975.

After collecting, gonads were removed and preserved in 10% formalin. Some gonads were placed in Bouin's fixative. Because it appeared later that for the requirements of this study both fixatives were equally good, in later fixations only formalin was used.

b. *Sectioning*

In the laboratory the gonads were embedded in paraffin, sectioned at 7 μ and stained with Harris' haematoxylin and eosine for better distinction of the different parts of the cells. The rest of the paraffin blocks were retained for additional data on important gonads.

c. *Measurements*

Total length (TL) of each specimen was measured from the tip of the snout to the tip of the caudal fin with an accuracy up to ± 1 mm. The weight of each specimen was determined with the aid of a beam balance with an accuracy up to ± 1 gram. Specimens smaller than 50 mm were weighed with an analytical balance to the nearest mg.

The gonads were first dried with Kleenex tissue and then weighed with an analytical balance to the nearest mg. The width of the gonads was measured with the aid of vernier callipers to the nearest 0.1 mm.

Measurements were made of the diameter of oocytes at the different stages of oogenesis with the aid of an ocular micrometer at 12 x. The longest axis of a cell was taken since the oocytes were not always spherical.

d. *Fecundity*

For fecundity determination, 12 ripe gonads were used. First they were dried with Kleenex tissue and then weighed on an analytical balance. From each gonad three small samples of each 3 mg were taken with tweezers and each sample was weighed to the nearest mg. The eggs in each sample were then counted separately with the aid of a binocular dissecting microscope. The diameter of 26 eggs was measured with the aid of an ocular micrometer at 50 x. One ocular micrometer unit at 50 x is equal to 0.0196 mm.

3. Results

a. *General remarks on gonadal structure*

The structure of the gonads of *Epinephelus cruentatus* conforms to that described by Smith (1965) for the Coney, *Epinephelus fulvus*.

The gonads are hollow sacs, lying below and behind the posterior part of the air bladder (Fig. 27) and connected to it by mesenteries. The weight of ripe gonads relative tot the total weight of the Graysbys is small. Smith (1965) found for *E. fulvus* a weight of the gonads of less than 5% of the total body weight. For Graysbys the weight of the ripe gonads ranges from 1.8 to 5.6 percent of the total body weight with a mean of 3.2%.

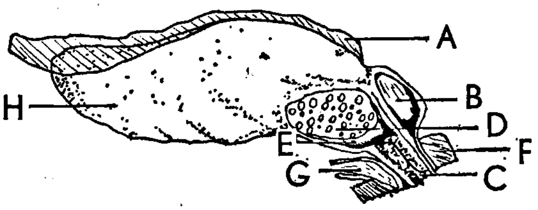

Fig. 27. Gonad structure in the Graysby (after Smith, 1965). A: supporting mesentery B: urinary bladder. C: oviductal plug and egg canal. D: germinal tissue. E: lumen of the ovary. F: body wall. G: rectum. H: muscular tunica surrounding gonad.

Both lobes, mostly unequal in size, join posteriorly and descend with a common oviduct to the genital aperture immediately behind the anus. The lumen of the gonad is lined with a germinal epithelium, which forms the surface layer of a series of longitudinal, slightly oblique, folds or lamellae. The central part of each lamella is composed of loose connective tissue and blood vessels. There are no lamellae in the ventral portion of the lumen. SMITH (1965) suggests that this probably allows distension of the ripe gonad without damage to the germinal epithelium.

b. *Oogenesis*

To come to a classification of gonad development classes for further study on the sexual development, it was necessary to study oogenesis and spermatogenesis. Therefore, oocytes were grouped into stages according to the system defined for members of the perciform genus *Tilapia* by KRAFT & PETERS (1963). This system was also used by SMITH (1965) and MOE (1969) for groupers.

For a detailed description of the oogenesis I refer to KRAFT & PETERS (1963).

Only a short description of the oogenesis and diameters of oocytes of *E. cruentatus* are given:

Primary stage: oogonia of this stage range from 3 to 15 μ in diameter. The nucleus is large in proportion to the cell (Plate IVa).

Stage 1: oocytes are small and range from 10 to 40 μ in diameter. Nucleus is smaller in proportion to the cell than in the primary stage (Plate IVb).

Stage 2: oocytes are large and range from 30 to 70 μ in diameter. They have very dark cytoplasm and many peripheral nucleoli in the nucleus. As the oocytes expand beyond 50 μ they begin to lose affinity to haematoxylin and become more clear (Plate Va).

Stage 3: oocytes range from 40 to 125 μ in diameter, yolk vesicles and yolk globules are present (Plate Vb).

Stage 4: in this stage a rapid growth of the oocytes begins. Oocytes range from 100 to 400 μ in diameter. There are yolk vesicles and yolk globules and a thick zona radiata (Plate VIa).

Stage 5: these oocytes were only sporadically found (Plate VIb).

Apparently the final maturation process takes place very quickly immediately before spawning, probably in a few hours. SMITH (1966) noted that in groupers the final stages of egg development take place immediately before ovulation or perhaps even after ovulation as, for instance, found for *E. fulvus*, closely related to *E. cruentatus*. Also SPRECHER (1938) noted a rapid ripening of eggs in certain centrarchids.

In the gonads of 3 specimens of the Graysby, stage 4 oocytes did not develop into stage 5, but the oocytes of stage 4 were degenerating without showing evidence of spawning (empty follicles, vacuolated cells). This was also found by YAMAMOTO (1956) and REINBOTH (1962).

After spawning many oocytes of stage 4 are retained in the gonad and degenerate. From the remnants of yolk globules and yolk vesicles the atretic bodies are formed. For a description of the formation of these bodies I refer to MOE (1969).

c. *Spermatogenesis*

A description of the spermatogenesis is given by KRAFT & PETERS (1963). The same description was also used by MOE (1969) for the Red grouper. No measurements were performed for the different stages of the spermatogenesis, because it was very difficult to determine the exact measurements of the different cells.

Maturity classes in the males were defined according to relative abundance of certain stages of spermatogenesis.

d. *Gonad development classes*

With the aid of the data of the oogenesis and spermatogenesis it was possible to classify the gonads in gonad development classes for further study on the sexual development of the gonads during the year.

HJORT (1910), SCHAEFFER & ORANGE (1956), BOWERS & HOLLIDAY (1961), POLDER (1961), SMITH (1965), SMITH & YOUNG (1966) and MOE (1969) have designated maturity stages of teleost gonads.

In this study the same system is used. Atretic bodies were used to distinguish immature and mature inactive classes of the females.

Atretic bodies could be distinguished easily by their typical brownish color when stained with haematoxylin – eosine (Plate IVb).

For the Graysby the following description of the classes is used:

Immature ovary: diameter of the ovary is small, mean diameter of one lobe is 2.1 mm. There is no evidence of prior spawning and no atretic bodies can be found. Oocytes in stages 1 and 2 are present in the center of the lamellae. Oogonia are found more at the periphery of these lamellae (Plate IVa).

Mature inactive ovary: diameter of the ovary is larger, mean diameter of one lobe is 3.5 mm. Oocytes in stages 1, 2 and 3 are present, but oocytes in stage 2 are dominating in the ovary. Oogonia and oocytes in stage 1 are also often present, but much less than in the immature ovary. Atretic bodies are often found (Plate Va).

Mature ovary: diameter of the ovary is large, diameter of one lobe is 9.3 mm. There is an active vitellogenesis. Oocytes in stage 1, 2, 3 and 4 are present, but oocytes in stage 3 are dominating the ovary in the beginning of this stage (Plate VIIa) and later the oocytes in stage 4 are dominating the ovary (Plate VIIb) until spawning takes place. Atretic bodies are more difficult to find than in the mature inactive class, because of the strongly expanding oocytes. This stage occurs principally from May through August.

Post-spawning ovary: empty follicles and vacuolated cells are present. Stage 3 and stage 4 oocytes are degenerating. Diameter of the ovary is reduced to a smaller size, mean diameter of one lobe is 4.8 mm. Well developed lamellae cannot be distinguished. Found from July through October (Plate VIIIa).

Transitionals: remains of stage 2, 3 and 4 oocytes. Atretic bodies are often present. In the germinal epithelium seminiferous crypts are proliferating (Plate VIIIb). This sexual transition mostly takes place in females immediately after spawning. The percentage of transitionals found during July through October was 14.4%, taken as a percentage of all mature and post-spawning females found during these months. MOE (1969) found a rate of transition of about 15% per year for age groups 5 to 10 for the Red grouper. Sexual transition was also observed before spawning during the vitellogenesis, but to a lesser extent i.e. 10.4% and taken as a percentage of all mature inactive females found in March and April.

Mature inactive testis: crypts are fully developed. In the testis early stages of spermatogenesis are dominating. Some crypts contain mature sperm, but most crypts contain primary spermatocytes. Many atretic bodies are found in this stage (Plate IXa). This class was found from November to April.

Ripening mature testis: this class was only found during March through July. Many primary and secondary spermatocytes are present, also spermatids and spermatozoa. The spermatozoa begin to aggregate in the central part of the crypts (Plate IXb).

Ripe testis: common from July to October. Most crypts are expanded and filled with tailed sperm. The earlier stages are very scarce (Plate Xa).

Post-spawning testis: many crypts of spermatogonia and connective tissue can be found. There is very little sperm. This stage occurs during October and November. Plate Xb shows a gonad of a male,

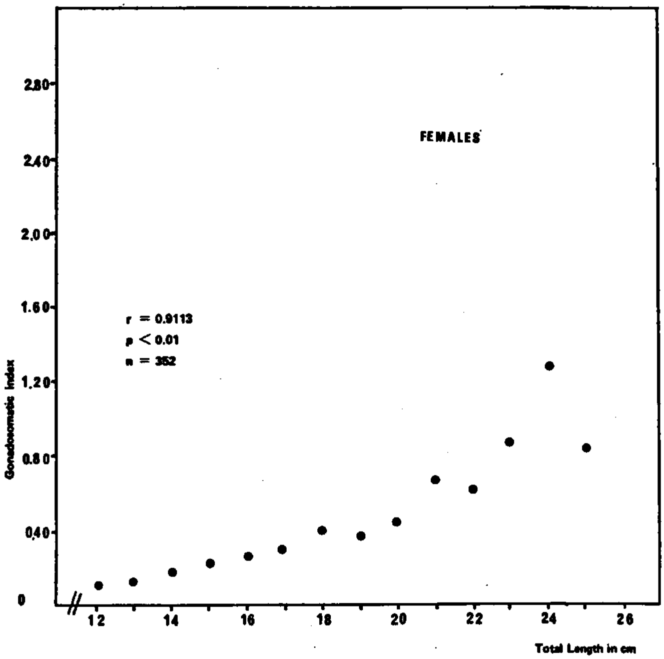

Fig. 28. Relation between gonadosomatic index and total length for females.

who has spawned partly, as discussed in the section "discussion" of this chapter.

e. *Maturation in relation to length*

For a preliminary assessment of the course of the development of the gonads and the sexual activity during the year, the gonadosomatic index (the weight of the gonad as a percentage of the total body weight), was used, according to TONG (1972).

Fig. 28 shows the relation between length and gonadosomatic index for females. A significant correlation was found between both ($p < 0.01$). So gonadosomatic index in females is dependent on length. This was not found for males, as shown in Fig. 29.

In Fig. 30 the gonadosomatic index of the females is plotted against length for 6 different seasons, January–February, March–April, May–June, July–August, September–October and November–December.

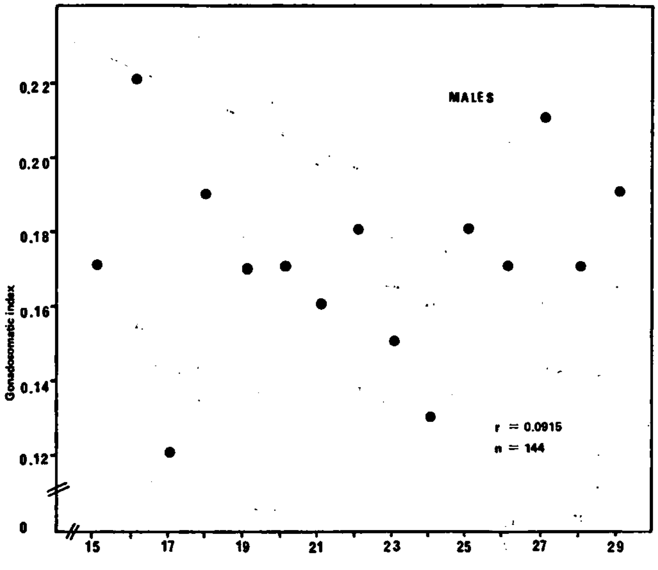

Fig. 29. Relation between gonadosomatic index and total length for males.

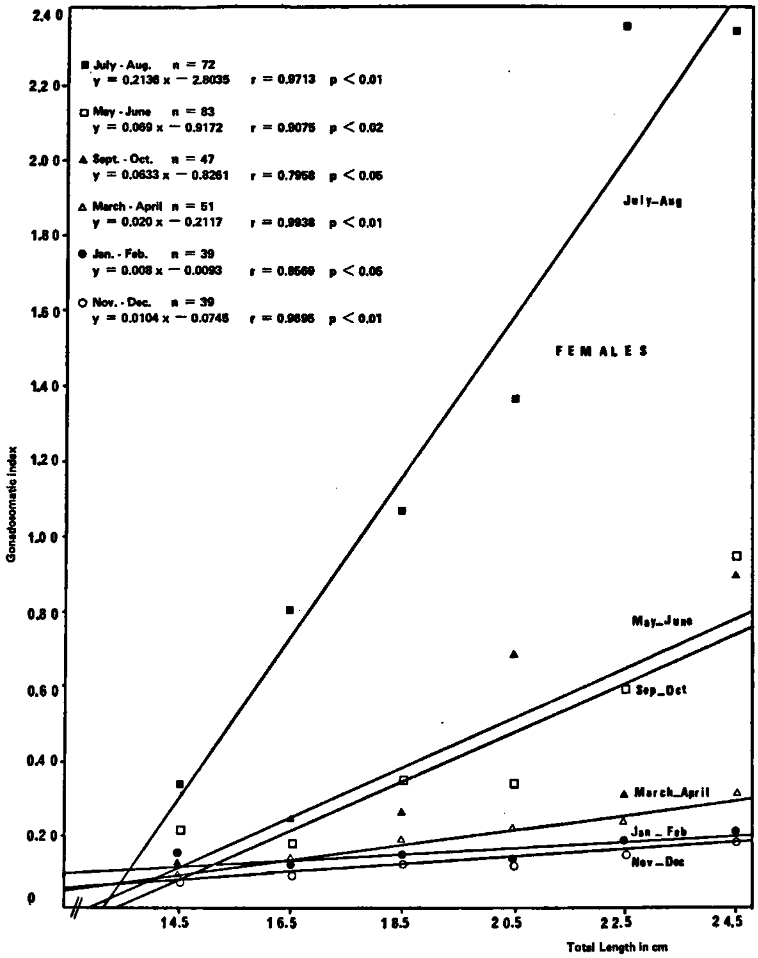

Fig. 30. Relationship between gonadosomatic index and total length for females during 6 different seasons.

To increase the number of observations per group, the fish (n = 331) was put into 2 – centimeter length-classes. For each period the linear regression line was calculated. It is shown that

a. for each period a significant correlation between both parameters was found, that means that for each length group the gonadosomatic index is dependent on length,

TABLE 11

Observed maturity stages and sex-ratio of 670 specimens by 2 cm size-groups (TL).

TL IN CM	Females					Transitionals	Males					Sex-ratio ♀ : ♂
	Immature	Mature inactive	Mature	Post-spawning	Total		Mature inactive	Ripening mature	Ripe	Post-spawning	Total	
9.5–11.4	12				12							
11.5–13.4	31				31							
13.5–15.4	39	5	4	5	53	1						
15.5–17.4	38	23	19	8	88	4						
17.5–19.4	19	56	20	15	110	3	3		2		5	24 : 1
19.5–21.4	2	49	26	10	87	10	9	3	3		15	6 : 1
21.5–23.4		34	22	7	63	6	7	10	9	6	32	2 : 1
23.5–25.4		14	20	6	40	1	11	14	11	4	40	1 : 1
25.5–27.4		5	6	1	12	1	1	14	12	5	32	1 : 3
27.5–29.4			1		1		3	10	5	2	20	1 : 20
29 5–31.4			1		1				2		2	
Total	141	186	119	52	498	26	34	51	44	17	146	

b. for all length groups the gonadosomatic index was found to vary according to season in approximately the same way,

c. in May–June an increase in gonadosomatic index can be observed. In July–August this index is for all length classes very high. In September–October the gonadosomatic index is found to decrease,

d. in the larger size groups the seasonal variation in gonadosomatic index was found to be highest.

For the males no significant correlations were found between length and gonadosomatic index, with the exception of the 24–25 cm length-class.

In Table 11 the observed maturity stages of 670 Graysbys are given by 2 cm size-groups, collected during 1973, 1974 and 1975.

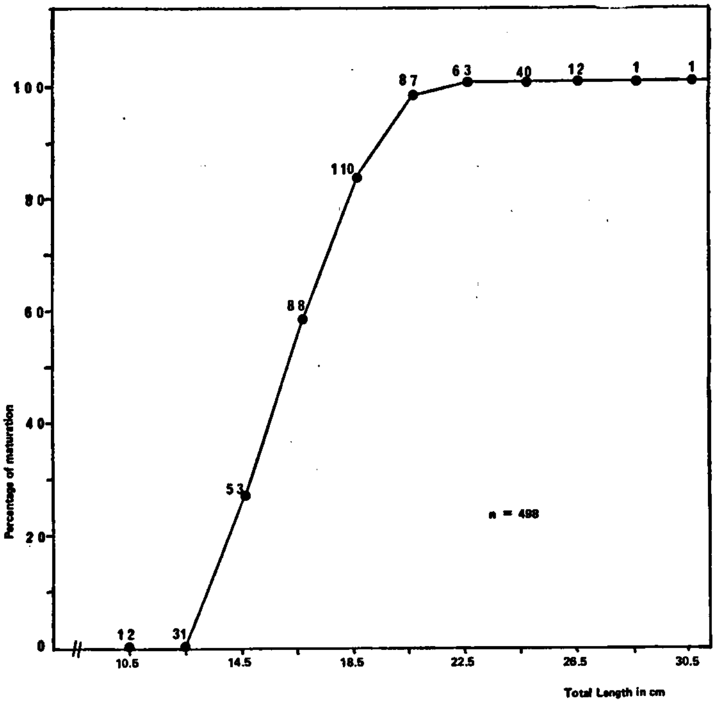

Fig. 31. Percentage of mature females, given as a percentage of all females of each 2 cm length-class.

In Fig. 31 the percentages of mature females are given for each 2 cm length-group. As shown, maturation begins at a length of ± 14 cm TL. At a length of ± 16 cm more than 50% of the females are mature and when they reach a length of ± 21 cm all females are mature. Mature females can be found up till a length of about 31 cm.

In Fig. 32 the percentage of females for each length group is given in proportion to the males. It appears that females are found exclusively till a length of ± 17 cm. The first males occur at a length of ± 18 cm. After that the percentage of males increases and consequently the percentage of females decreases. At a length of ± 24 cm the percentage of each is about the same. In length-group 29.5–31.4 cm a somewhat high percentage of 33% females was found, however,

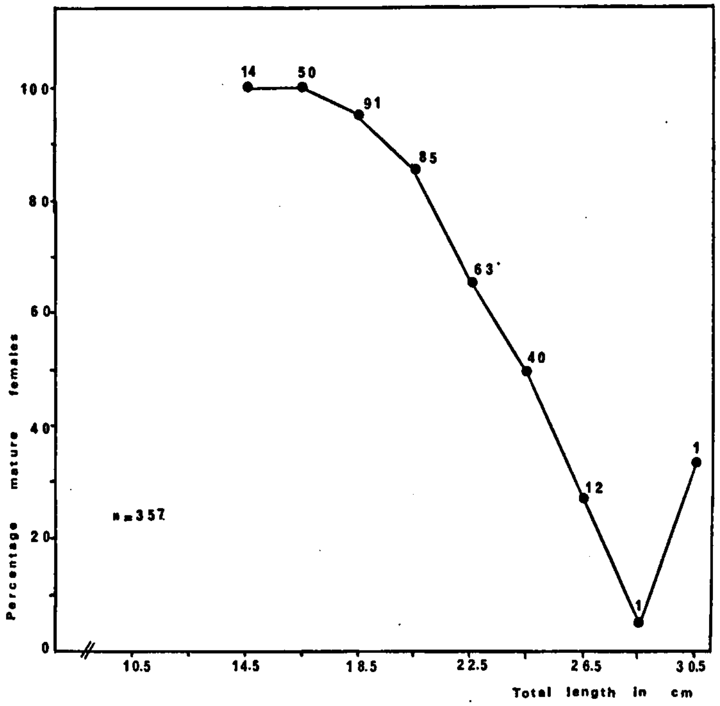

Fig. 32. Percentage of mature females in proportion to males of each 2 cm length-group.

derived from only 3 specimens, so that not too great value can be attributed to this percentage.

In Table 11 it is shown that most transitionals are found between a length of about 14 and 26 cm. However, transition occurs especially between 20 and 23 cm. In this length-range the highest transition rate of 10% was found (given as a percentage of all mature females of mentioned length-range). The percentage of males in this length-range is 24%. In the range smaller than 20 cm a transition rate of 4% was found and only 3% males. In fishes larger than 23 cm a transition rate of 4% could be observed and 64% males. So it is clear that there is a coincidence of a high transition rate and a strong increase in the percentage of males in the length classes from 20 up to 23 cm.

f. *Maturation in relation to age*

In Fig. 33 in each sexual development class the percentage of fish is plotted against the age groups. For each age group the percentage of fish is given as a percentage of all females, males and transitionals (n = 616), which could be aged with the aid of otoliths as described in the chapter on determination of age. In age group 0 and 1 only immature females were found. In age group 2 most females are immature (83%), but also some mature specimens were found (17%). At age 3 the proportion of immature and mature females is about 1 : 1. At this age also the first transitionals were found. In age group 4 a relatively high percentage of transitionals was found (8%) and the first males occur (7%). In age group 5 immature females have disappeared. In the higher age groups there is a strong increase in ripe males. The highest percentages of post-spawning females and transitionals are observed in age group 4 and 5, 10% and 9% for females, and 8% and 7% for transitionals respectively. Most transitionals were found directly after the spawning season, when in several females the post-spawning gonads showed symptoms of transition. The change-over is in accordance with the earlier mentioned data. Most males of the first male development class were found in age group 5 (9%) and 6 (11%). This points to age groups 4 and 5, in which most transitionals were found.

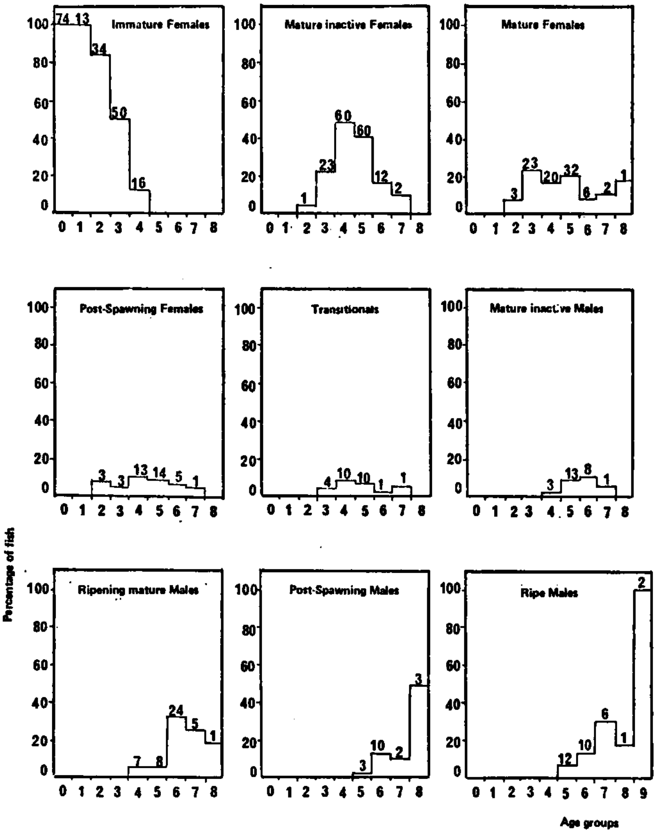

Fig. 33. Percentage of fish, given as a percentage of the total number of fish in each age group, for 9 different gonad development classes. The figure listed above each percentage column indicates the number of fish.

g. *Maturation in the course of the year*

The annual weight changes in the gonads, shown in a preceding section, will be further analysed with the aid of the gonad development classes.

In Fig. 34 the 9 development classes are plotted against season. The percentage of fishes are given for each month as a percentage of all fishes collected during one special month. The data are derived from the gonads of 668 specimens collected during the years 1973,

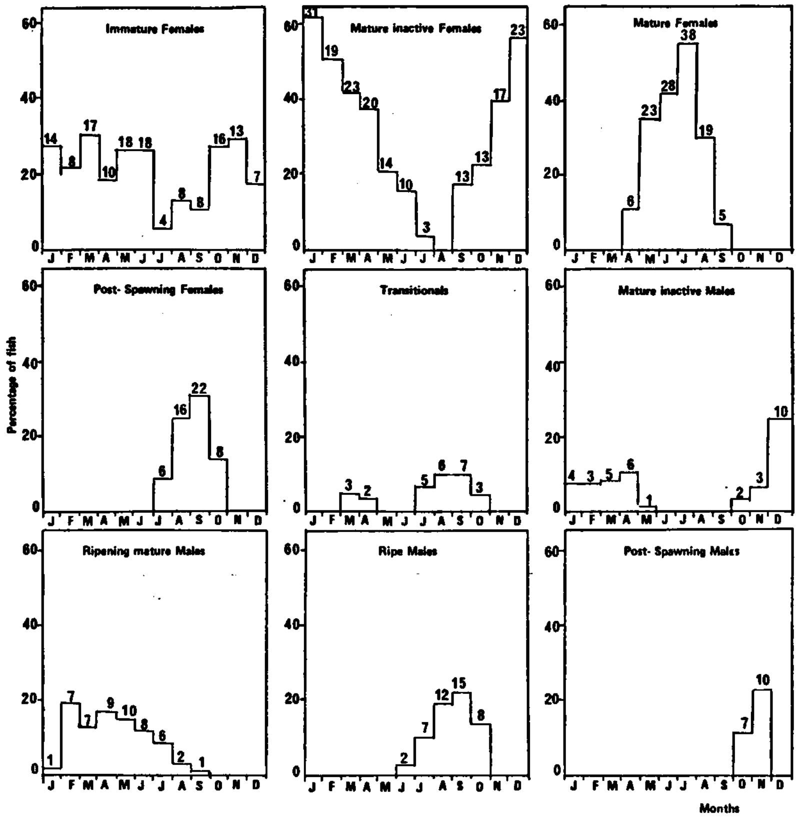

Fig. 34. Percentage of fish for each maturity stage, given as a percentage of all fish collected during each month. The figure listed above each percentage column indicates the number of fish.

1974 and 1975. Immature females are present in more or less constant numbers throughout the year. In July–September a decrease can be observed, possibly due to development into class 2. The numbers of mature inactive females decrease from January to August and increase from August to January. In August no mature inactive females are found. These data can be interpreted with the aid of the data of the mature females. When the number of mature inactive females decreases, there is an increase of mature females due to the change from one class into the other.

Especially in May maturation begins. The greatest numbers of mature females are found in July and only a few in September. Post-spawning females espacially occur in August and September. So spawning takes place during these months. However, there are already females spawning in July, and the latest spawning females are found in October.

Transitionals are found in smaller numbers in March and April before the spawning season and in greater numbers in July, August and September. Transitionals are also found in October. The transitionals of July through October were, with the exception of three specimens in July, all fishes with a clearly post-spawning state of the gonad (degenerating stage 4 oocytes, vacuolated cells). So after spawning some females (14.4%) change into males (see this chapter under section: gonad development classes, transitionals).

The occurrence in three mature females in July of several crypts with spermatids between oocytes of stage 4, shows that formation of spermatogonia and crypts of spermatocytes probably begins in some fishes already during the maturation of eggs. During June to September no mature inactive males were found, because of the development of these classes into ripening mature and ripe classes. Post-spawning males, with gonads with only little retained sperm, were found only during October and November. During July, August and September males were found with gonads with signs of spawning: in some parts of the gonad empty crypts could be found and also a local thickening of the muscular tunica, indicating a local contraction of this muscular layer (Plate Xb). However, the gonads were still full of sperm. Probably the males spawn several times during the spawning season, serving more than one female (see discussion).

h. *Sex-ratio*

The sex-ratio is given in the last column of Table 11. The mean total length in cm + S.D. (standard deviation), the number and percentages of females and males for each age group, and sex-ratio are given in Table 12.

A sex-ratio of 1 : 1 was found for lengths of 23.5–25.4 cm. For the age groups this sex-ratio can be found in age groups 5 and 6. At

TABLE 12

Distribution of females and males in each age group. Mean total length + standard deviation (S.D.), N (number of fish), % of females and males and sex-ratio is given for each age group.

AGE	Females			Males			Sex-Ratio
GROUPS	Mean TL in cm + S.D.	N	%	Mean TL in cm + S.D.	N	%	♀ : ♂
0	4.8 ± 1.9	89	100				
1	10.0 ± 1.1	13	100				
2	13.1 ± 1.2	41	100				
3	16.3 ± 1.3	99	100				
4	19.0 ± 1.5	109	92	20.9 ± 1.1	10	8	12 : 1
5	21.9 ± 1.6	106	75	23.0 ± 1.5	36	25	3 : 1
6	24.6 ± 1.2	23	31	25.4 ± 1.4	52	69	1 : 2
7	26.8 ± 0.8	5	26	27.5 ± 1.1	14	74	1 : 3
8	29.8	1	17	29.1 ± 0.3	5	83	1 : 5

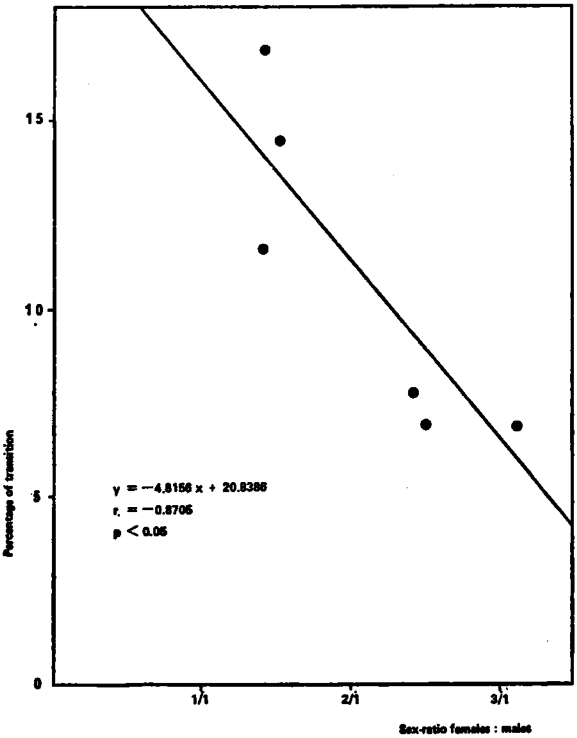

Fig. 35. Relationship between percentage of transition and sex-ratio.

TABLE 13

Number of females, males and transitionals, sex-ratio, rate of transition and mean total length + S.D. (standard deviation) for males are given for 5 sufficiently collected stations and for all stations together (n = 26).

STATIONS	Females (mature)	Males	Transitionals	Sex-Ratio ♀ : ♂	% Transition	Mean TL in cm + S.D. for males
All Stations	357	146	26	2.5 : 1	6.8	
Portomaribaai	165	54	12	3.0 : 1	6.8	24.4 ± 2.3
Playa Hundu	12	5	1	2.4 : 1	7.7	24.6 ± 2.4
Westpuntbaai	12	8	2	1.5 : 1	14.3	26.7 ± 2.7
Boca Grandi	23	16	3	1.4 : 1	11.5	25.1 ± 1.5
Playa Mansaliña	10	7	2	1.4 : 1	16.7	26.7 ± 2.4

higher ages the percentages of males are many times higher than those of the females.

To study the influence of the number of males on the transition rate, the number of females, males and transitionals, sex-ratio, rate of transition and the mean total length + S.D. are given for 5 stations in Table 13.

In Fig. 35 the rate of transition is plotted against the sex-ratio, as given in Table 13, showing a significant correlation ($p < 0.05$).

i. *Fecundity*

Fecundity was calculated by the formula:

$$E_g = \frac{E_s}{W_s} \times W_g$$

E_g = number of eggs in the gonad, E_s = mean number of eggs of the three samples, W_s = mean weight of the three samples, W_g = weight of the gonad.

Table 14 shows the estimated number of eggs of 12 ripe gonads. The mean number of eggs for these 12 gonads is 298, 343 eggs. THOMSON & MUNRO (1978) found for *E. cruentatus* an estimated number of 262, 604 eggs.

TABLE 14

Fecundity estimates for 12 ripe gonads of females of *Epinephelus cruentatus* during 1973.

DATE	Body weight in gram	TL (cm)	Age	Gonad weight in gram	Number of ripe eggs
6 June	229	23.7	5	4.6	235,613
6 June	280	25.5	6	5.2	133,351
6 June	313	26.5	6	5.9	194,104
15 June	452	29.8	8	13.8	559,136
7 July	231	24.0	5	4.4	142,410
15 July	143	21.0	4	3.5	86,204
15 July	267	24.9	5	15.7	615,387
21 July	191	24.0	5	5.6	154,861
21 July	285	26.4	6	8.9	291,646
13 August	238	23.8	5	12.8	446,061
13 August	222	24.0	5	9.4	320,729
13 August	246	24.4	5	11.0	400,610

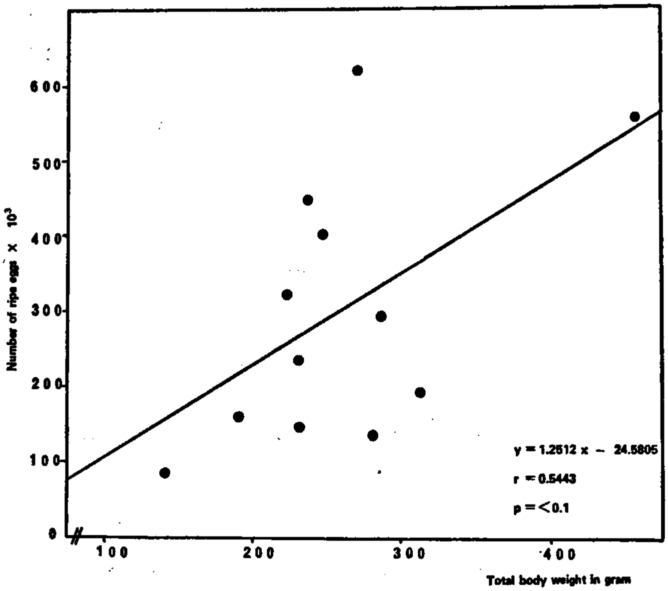

Fig. 36. Relationship between number of ripe eggs in the gonads and total body weight.

The mean egg diameter was 0.53 mm with a range of 0.47 to 0.59 mm.

Fig. 36 shows the relation between body weight and number of eggs, but no significant correlation was found ($p < 0.1$), probably owing to insufficient data.

4. DISCUSSION

a. *Spawning season*

It was found that *Epinephelus cruentatus* of the coral reef at the southwest coast of Curaçao has a spawning season from May to October. Maturation starts in May and spawning mainly occurs in August and September.

MUNRO et al. (1973) found a maximum of ripe Graysbys on the Port Royal reefs (Jamaica) in March during 1969 to 1971. In Curaçao most ripe Graysbys were found in July. In Jamaica the water temperature ranges from ± 26.5 to about 29.5°C. MUNRO suggests a relation between water temperature and spawning activity in such a way that when the temperature falls to 28°C, spawning is initiated and when the minimum temperature is attained in March, spawning reaches a maximum. This is not in agreement with our data of Curaçao, where a temperature rise coincides with an increase of spawning activity. Apparently the temperature is only one of the possible environmental factors, which influences the spawning process.

b. *Length and age of the spawning partners*

Spawning of females of the Graysbys occurs usually between a length of 16 cm and 25 cm TL and at an age of 4 and 5 years, but they can reach maturity at as early an age as 2 years, and at a length of 14 cm TL. Also a mature female was found of 8 years old and with a length of 29.8 cm.

Males are found mainly in age group 6 and to a lesser extent in age groups 5 and 7. The youngest males found were 4 years old.

c. *Transitionals and sex-ratio*

A broad overlap of the length distributions of the sexes was observed in the Graysbys. This suggests that there is no close correlation of age or size with sexual transition. MOE (1969) found for the Red grouper a broad overlap in age and size of most specimens in transition i.e. from 5 to 11 years and from 450 to 650 mm SL.

Transitionals were found in the age groups 3, 4, 5, 6 and 7, and with lengths varying from 15 to 27 cm. However, most transitionals (10%) occurred in age groups 4 and 5 at a corresponding length between 20 and 23 cm. The percentage of males in this length-range is 24%. In the length-group of 23.5–25.4 cm a transition rate of 4% was found and 50% males. In agreement with a high transition rate of 10% in the length-group 20–23 cm, a strong increase in the percentage of males is observed. In the length-group 23.5–25.4 cm 40 females were collected and only 1 transitional. This means a transition rate of only 2.5%. However, in length-group 27–31 cm almost no females were found, so that most females of the 23.5–25.4 cm length-class change into males and the low transition rate probably is caused by insufficient sampling. Alternatively the transition rate of 2.5% in the length-group 23.5–25.4 cm could be correct and the low number of females in the length-group greater than 27 cm is then caused by a high mortality rate of females.

A close correlation was found between transition and spawning state of the gonad for transitionals found during the spawning season.

Transition occurs mainly during September, but also during July, August and October, immediately after spawning. Most of the transitionals collected during this period showed histological symptoms of spawning (degenerating oocytes 4 and vacuolated cells) and beginning stages of the spermatogenesis (spermatogonia, crypts of primary and secondary spermatocyts).

During March and April only 5 transitionals were found. In their gonads spermatogonia and spermatocyts 1 and 2 were present. Also oocytes 1 and 2, and atretic bodies were found. This could mean that a small percentage of females transforms before the spawning season into males, participating as male in the coming spawning season. Three transitional specimens found in July did not show signs of spawning. Most of the stage 4 oocytes were degenerating. Possibly spawning could not take place in default of sufficient males, which resulted in degeneration of the ripe eggs. Factors inducing transition in *Serranidae* are largely unknown. FISHELSON (1970) regulated protogynous sex reversal in *Anthias squamipinnis* (fam. *Anthiidae*) by the presence or absence of a male fish. LIEM (1963) and HARRINGTON (1967) demonstrated that such environmental conditions as temperature, crowding, and starvation can strongly influence the sex-ratio, sexual succession and the development of primary male gonochorists in clones of homozygous hermaphrodites. Possibly in the Graysbys one or more of these factors affect the transition rate, or other factors such as the number of males as shown in Table 13. For all collected mature females and males a sex-ratio was found of 2.5 : 1 with a transition rate of 6.8%.

In general it is shown that a strong dominance of females coincides with a relatively low transition rate and vice versa, and that in the stations with few males also a relatively low mean length of the males is found.

Along the whole southwest coast of Curaçao, hook and line, trap, and spear are the predominant features of Caribbean reef fisheries. Especially trap-fishery and spear-fishery work selectively by taking mainly large specimens, most of which are males. Along the whole coast the Antillian fish-trap is used, but the station Portomaribaai is in particular heavily exploited by this type of fishery. Here one mile of reef is daily fished by about 14 fish-traps at a depth between 6 and 9 m. In the other stations trap-fishery is more incidental and less intensive. In all probability it can be concluded that trap-fishery has a great influence upon the sex-ratio of the Graysbys. A sample of Graysbys out of these traps at Portomaribaai showed a length range from 20.0 to 28.4 cm TL with a mean of 23.6 cm. MUNRO (1974) found that groupers are not prone to entering traps at sizes less than 20 cm. RANDALL (1961) found for three tagged Graysbys at recovery a range from 27.0 to 29.5 cm with a mean of 27.8 cm.

Because most transitionals are found in the length-classes 19.5 to 23.4 cm they have also a great chance to be caught by trap-fishing, in this way influencing the transition rate as shown by the low rate in the heavily exploited station Portomaribaai. In the stations Westpuntbaai, Boca Grandi and Playa Mansaliña, where trap-fishing is incidental, a relatively high transition rate was found. The total lengths of the males of these 3 stations is much greater than that found in Portomaribaai and Playa Hundu. The sex-ratio in the 3 stations also approaches 1 : 1. In station Playa Hundu no data are on hand of trap-fishery, but also there it is shown that a sex-ratio with relatively many females coincides with a low transition rate and a low mean total length of the males.

MUNRO (1974) found a female: male sex-ratio of 0.72 : 1 and 0.85 : 1 respectively for mature *Epinephelus striatus* (Nassau grouper) and *Mycteroperca venenosa* (Yellowfin grouper) taken from relatively unexploited oceanic banks. On the intensively exploited Port Royal reefs the sex-ratio of *Epinephelus guttatus* (Red Hind) and *E. cruentatus* was 5.6 : 1 and 6.0 : 1 respectively. In an area with high fishing intensity the largest, mostly male individuals, were relatively less abundant. MUNRO states that according to FISHELSON (1970) this should induce earlier transformation in an area such as Port Royal, but this is not reflected in the Port Royal catches. The smallest recognizable male of *E. guttatus* at Port Royal was 26 cm TL whereas on oceanic banks the smallest male was 27 cm TL. He suggests that according to MOE (1969) sustained high fishing pressure probably decreases the rate of transition, thereby increasing the reproductive potential of the population by increasing the number of females. The ratio of females to males found by BARDACH (1958) was about 1 : 1 for large Nassau groupers on the Bermuda banks, which were in the initial stages of exploitation and the sex-ratio was about 2 : 1 for large Red groupers of the Florida West Coast, a heavily exploited place.

In the Windward Islands of the Netherlands Antilles (St. Martin, Saba, St. Eustatius) trap-fishery is relatively low and the abundance of large specimens of the species *Epinephelus fulvus*, closely related to the Graysby (rare in the Windward Islands), is remarkable in comparison with the Leeward Islands (Aruba, Bonaire, Curaçao). In the Windward Islands females and males of *E. fulvus* approach much more a sex-ratio of 1 : 1 than found in the Leeward Islands, where the sex-ratio probably is the same as found for the Graysby (NAGELKERKEN, in prep.). The observed sex-ratio for mature Graysbys of 2.5 : 1 not always means a lack of sufficient mature males, because I found indications that *E. cruentatus* males can spawn several times during a season.

For the females of the Graysby it was shown that the weight of the gonads is only high during a short period in July and August. YAMAMOTO & YOSHIOKA (1964) suggest that high ovary weight values over a long period, followed by a gradual decline, are typical of teleosts, which spawn more than once in a season. So for the Graysby females it is likely that they spawn only once a year. This is corroborated by histological data. When spawning symptoms were observed histologically by the presence of empty follicles and vacuolated cells, the remaining oocytes 4 in the gonad were never intact, but always degenerating.

For the males it was shown that the weight of the gonads is high during a long period from March through September with a gradual decline. Therefore for the males I believe that they spawn several times during one season, because:

1. the sex-ratio found for the mature females and males is 2.5 : 1. This means that, if the males should mate with only one female during one season, there would be a lack of males. Histological studies show that almost all females spawn, because only 3 (out of 52) females were found without signs of spawning and with degenerating oocytes 4.

2. post-spawning males with almost empty gonads were only found in October and November, whereas the spawning process occurs in August and September. Histological studies demonstrate that many ripe males, collected in July through October, show signs of spawning as empty crypts in some parts of the gonad attended by a relatively thick muscular tunica on that place, indicating a local contraction of the tunica (Plate Xb). However, the other parts of the gonad were still full of spermatozoa. This should mean that the males do not mate once, but several times a season and in this way can serve several females.

VI FEEDING AND FOOD

1. INTRODUCTION

Groupers are carnivorous, feeding mainly on fishes and crustaceans. The food of groupers has been studied by RANDALL (1965, 1967). MOE (1969) reported on the feeding of *Epinephelus morio*, the Red grouper, in the Gulf of Mexico. MUNRO (1974) studied the feeding of *Epinephelus guttatus*, *E. striatus* and *E. mystacinus*.

Little is known on the feeding habits of the Graysby. RANDALL (1967) gives some notes on the food composition consisting of 66.2% fish, 17.3% shrimps, 8.9% stomatopods, 3.8% crabs and 3.8% gastropods. He suggested feeding during the whole 24 hours period for this species, with a peak at sunrise and sunset. PARRISH & ZIMMERMANN (1977) found in stomachs of *E. cruentatus* brachyuran crabs, caridean shrimps, a few other small invertebrates and possibly fish remains.

In this study the food composition (quantitative and qualitative) of juvenile and adult Graysbys is discussed as well as the daily feeding pattern.

2. MATERIAL AND METHODS

797 Graysbys were examined for stomach contents. Larger specimens were collected with the aid of a speargun, juveniles, however, with Rotenone. Most groupers often regurgitate when shot. In this

case we always tried to recover the regurgitated stomach content. This was not always successful, because groupers, when shot, try to flee into holes or caves. Therefore data on food could not be used to quantify food intake. Of the specimens examined 284 (35.6%) were found with stomach contents (239 adults and 45 juveniles). Immediately after collecting, the stomach contents were weighed and put in 10% formalin and determined in the laboratory.

To study feeding times of the Graysby only those specimens (n = 407) were used of which collecting time was known. For the other 390 specimens the collecting time was not recorded and therefore they were not included in the data for the study of the feeding times. Because juveniles (n = 89) were collected with Rotenone, no stomach contents were lost, which resulted in a higher percentage of filled stomachs (50.6%) as compared with the adults (33.8%).

3. RESULTS

a. *Food composition of the Graysbys*

Table 15 gives a survey of the composition of the food of Graysbys of one year and older. In 179 out of 239 filled stomachs (75%) the main part was fish, whereas the remaining stomachs (25%) contained especially Crustacea (18%) and indistinguishable material (7%). The fishes and fish-remains of 113 stomachs could not be determined, because they were unrecognizable due to digestion processes.

The most common food fish for the Graysby is the Brown Chromis, *Chromis multilineata*. It was found in ± 55% of the cases for which determination was possible. Of the Crustacea the shrimps are especially important food for the Graysbys: ± 60%. In only one case a bunch of compressed small spines of a sea-urchin was found. The question arises here, whether this specimen had taken an urchin as food, or whether it had fed on a fish with this urchin in its stomach. *Halichoeres* sp., food fishes of the Graysby, are known to feed on Echinoids.

Of the 45 stomachs studied of juveniles, most contained shrimps i.e. 80%. Fish was found in only 13.3% of the studied stomachs. In juveniles it was not possible to determine the species of the prey. In

TABLE 15

Frequency of occurrence of different food items in 239 stomachs of Graysbys from one year and older.

FOOD ITEMS	Number of filled stomachs	FOOD ITEMS	Number of filled stomachs
Fishes			
Chromis multilineata	36	Stomatopod Crustacea	
Centropyge argi	7	*Gonodactylus curacaoensis*	4
Apogon sp.	7	*Pseudosquilla ciliata*	1
Eupomacentrus partitus	3		
Chromis cyanea	2	Decapod Crustacea	
Mulloidichthys martinicus	2	*Brachycarpus biunguiculatus*	8
Apogon maculatus	1		
Aulostomus maculatus	1	*Barbouria* sp.	1
Eupomacentrus planifrons	1	Indet. sp.	1
Eupomacentrus sp.	1		
Halichoeres sp.	1	Brachyura Crustacea	
Myripristis jacobus	1	*Portunus* sp.	2
Priacanthus cruentatus	1	*Pilumnus* sp.	1
Synodus synodus	1		
Ophichthydae	1	Unidentified shrimp rest	17
Unidentified fish	113	Unidentified other Crust. rest	9
Echinoids	1	Indet. rest	15

only one case a shrimp could be determined as *Thor* sp., fam. Hippolytidae.

Most stomachs usually contained only one food item, but there were exceptions. One Graysby with a length of 17 cm had 4 *Chromis* specimens in its stomach in about the same state of digestion, suggesting that the prey was devoured almost simultaneously. A few other Graysbys had combinations of *Chromis multilineata* with *Eupomacentrus* sp. (a Damselfish) or with *Priacanthus cruentatus* (Glasseye snapper) or with shrimps in their stomachs. Also a few stomachs with only shrimps were found. Another combination found was *C. multilineata* with shrimps and fish-remains. The latter indicates feeding during different times.

Also in juveniles mostly one food item in a stomach was found. Only in 6 (out of 45) juveniles, was more than one prey (all shrimps) observed.

TABLE 16

Frequency of occurrence of different food items found in 284 filled stomachs, and given for the different length-classes. In the lower part of the Table are percentages of fish and Crustacea in the stomachs of Graysbys of different length-classes.

FOOD ITEMS	Length-classes in cm														
	0–2	3–4	5–6	7–8	9–10	11–12	13–14	15–16	17–18	19–20	21–22	23–24	25–26	27–28	29–30
Fishes															
Chromis multilineata	—	—	—	—	—	—	1	1	7	5	9	6	3	1	2
Centropyge argi	—	—	—	—	—	—	1	1	1	—	1	2	1	—	—
Apogon sp.	—	—	—	—	—	—	5	—	2	—	1	—	1	—	—
Eupomacentrus partitus	—	—	—	—	—	—	—	—	—	1	—	—	1	—	—
Chromis cyanea	—	—	—	—	—	—	—	—	—	—	—	1	1	—	—
Mulloidichthys martinicus	—	—	—	—	—	—	—	—	—	—	—	1	1	—	—
Aulostomus maculatus	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—
Eupomacentrus sp.	—	—	—	—	—	—	—	—	—	—	1	1	—	—	—
Halichoeres sp.	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—
Myripristis jacobus	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—
Priacanthus cruentatus	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—
Synodus synodus	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
Ophichthydae	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—
Unidentified fish	1	3		3	2	3	5	11	14	24	15	18	12	5	2
Crustacea															
Shrimps	2	21	8	7	3	2	1	4	4	9	3	2	—	—	—
Stomatopods	—	—	—	—	—	—	—	—	1	1	—	1	1	—	—
Brachyura	—	—	—	—	1	—	—	1	1	—	—	—	1	1	—
Unidentified Crustacea	—	—	—	—	—	2	—	1	1	1	1	1	—	—	—
Indet. Rest.	—	1	2	—	1	—	—	2	2	2	1	4	1	2	1
Total number of filled stomachs examined	3	25	10	10	7	7	13	23	34	43	33	37	23	10	6
Percentage of fish	33	12		30	29	43	92	65	74	70	85	78	87	70	83
Percentage of Crustacea	67	84	80	70	57	57	8	26	21	26	12	11	9	10	

b. *Food composition in relation to length*

In Table 16 the frequency of occurrence of different food items is given, fround in 284 filled stomachs of the Graysbys. It appears that juveniles of the length classes up to 9 cm feed almost exclusively on shrimps. The number of Crustacea in the food decreases in the larger length-classes. In length-class 13–14 cm *Chromis multilineata* is found for the first time as prey. In length-class 17–18 cm the percentage of *Chromis* is 21% and in length-class 21–22 cm 27%. *Centropyge argi* (Cherubfish) shows about the same distribution over the length classes. *Apogon* species, small fishes, living hidden during the day under small overhangs of corals or other substratum, are strongly represented in length-class 13–14 cm. They can therefore be caught more easily by the smaller Graysbys than by the larger ones. All other fish species were found only in stomachs of Graysbys of the length-classes 15–16 cm and larger. In the lower part of Table 16 are percentages of fish and crustaceans for the different length classes. Juveniles are feeding mostly on crustaceans (around 80%). In the larger length classes this percentage decreases to about 50% in classes 9–12 cm, about 20% in classes 13–20 cm with a minimum of ± 10% in the classes 21–30 cm.

c. *Relation between length predator and weight of prey*

For a study on the relation predator – prey no data about length of prey were on hand. Therefore the data of the weight of the stomach contents were used. For a good calculation of the mean weight of the prey for the different size classes only fresh stomach contents were used.

Fig. 37 shows a double logarithmic plot of the mean weight of fishes and crustaceans separately in the stomachs, and the lengths of the Graysbys. The two lines have been eye-fitted to the points. It appears that the relation between mean weight of prey and length of predator is highly significant for groups of prey ($p < 0.01$). Although in general the weight of the prey increases with the length of the predator, the crustacean food appears to be much lighter than fish food at least at lengths of over 12 cm.

In Fig. 38 the mean weight of the stomach contents is plotted a-

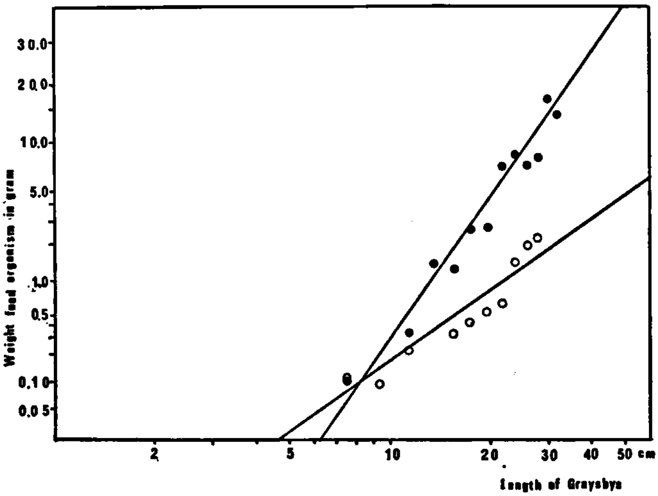

Fig. 37. Double logarithmic plot of mean weight of the length of fishes (●) and crustaceans (o) in the stomachs against length of Graysbys. The two lines have been eye-fitted to the points.

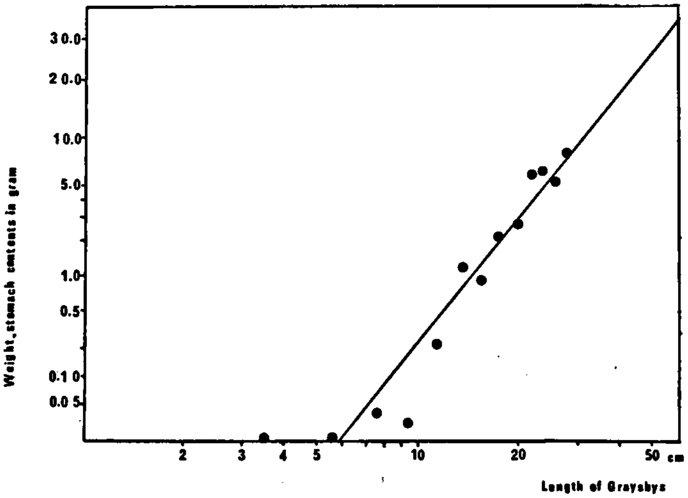

Fig. 38. Double logarithmic plot of total mean weight of the stomach contents and length of Graysbys. The straight line represents the calculated functional relationship: $\overline{w} = 0.00567 \times TL^{3.5917}$.

gainst different size classes. Following DAAN (1973) in taking the form: $\overline{w} = a\,L^{b}$ to describe the relationship, with $\overline{w}$ signifying mean weight of the stomach contents, L length of the Graysbys, a and b constants, the equation found is:

$$\overline{w} = 0.00567 \times TL^{3.5917},$$

which indicates the weight of the stomach contents to be a function of about the third power of the length. A high degree of correlation was found between $\overline{w}$ and L (r = 0.9078).

d. *Dial variation in feeding*

In Fig. 39 the mean weights of the stomach contents (given as a percentage of body weight) are plotted against the different times of day and night, separately for fish and crustacean preys. It appears that, as far as fish is concerned, the fullest stomachs are found at 06.30 and 17.00 hours, so at sunrise and at sunset. At 06.00 the

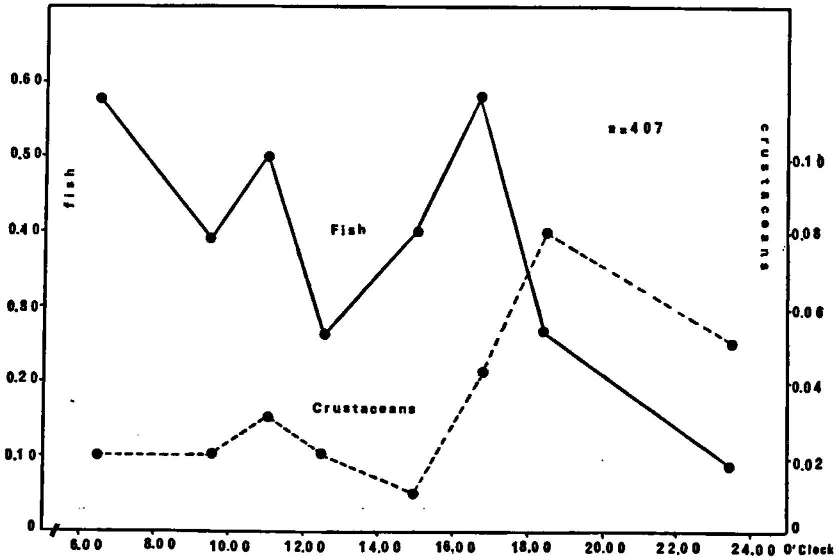

Fig. 39. Percentage of fish and crustaceans as stomach contents during different times of day and night. The percentages are given as percentages of the total body weight.

percentage of fish in the stomachs is 0.58%, decreasing to a minimum of 0.26% around noon. A second maximum of 0.58% occurs at 17.00, followed by a minimum of 0.09% at about 24.00 hours. In the morning and during the day feeding on crustaceans appears to be very low. Mainly around sunset a strong increase can be observed in the feeding on crustaceans, which coincides with a strong decrease in the feeding on fish.

e. *Seasonal variation in feeding*

In Fig. 40 the food intake (stomach content), given as a percentage of the total body weight, and the condition factor are plotted against the different months. A significant correlation between each was found ($p < 0.01$). In general food intake is high between February and August and lower in the rest of the year. In addition, minima in food intake can be observed in January and September and possibly in June, and maxima in food intake in October-November, February-March and July.

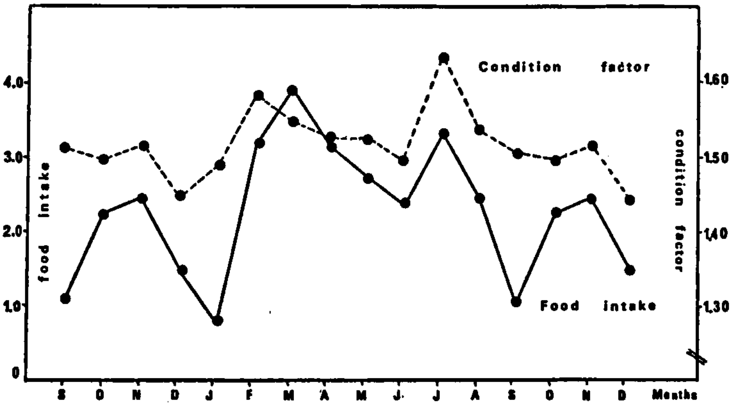

Fig. 40. Food intake (stomach content), given as a percentage of the total body weight, and the condition factor in the course of the year.

4. DISCUSSION

Epinephelus cruentatus feeds mainly on fish (75%) and to a lesser extent on crustaceans (18%). Juveniles, however, specialize more on shrimps (80%) than on fish. Probably the difference in food can be explained by the mode of living. Adult Graysbys are living in and around the corals. They can hide also in the shelter of corals, probably waiting for passing fish. Juveniles, however, always live in and under the corals in close attachment with them. In this way it is easier to catch crustaceans, which are mostly also living on and between the corals. In addition, crustaceans are smaller, slower and more easy to catch.

Epinephelus adscensionis (the Rock Hind), a closely related grouper species, keeps feeding on Crustacea throughout its whole life, which can be explained from its way of life: staying in close contact with the bottom, so in a good position for feeding on crustaceans.

The weight of the prey (fish and crustaceans) increases with the size of the predator, although fish-prey are consistently heavier than crustaceans.

The equation describing the relation between mean weight of stomach contents and size class of the Graysby was found to be $\overline{w} = 0.00567 \times TL^{3.5917}$, indicating that the weight of the stomach contents is a function of about the third power of the length.

Graysbys show a preference for *Chromis multilineata* (± 55%), a food species very common in the area of the Graysbys (see Chapter II on vertical distribution, where a significant correlation was found between the distribution of both species).

In *E. cruentatus* feeding rates on this species are higher at sunrise and sunset, which may be related to the behaviour of *Chromis*. In day time *Chromis* is living above the coral, feeding on plankton. At sunset they come closer to the corals looking for shelter during the night. At sunrise they come out of the corals again to move into the water above the coral reef. Therefore, at sunset and sunrise *Chromis* is entering and leaving the coral structures, active and within reach of the Graysbys. If true, it is, however, remarkable that in the night, when both species are in the corals, the Graysbys do not feed on *Chromis* specimens. Both species are probably inactive during the night. RANDALL & BROCK (1960) found in 11 species of groupers that the majority had full stomachs in the morning. STARCK & DAVIS (1965) found in the grouper *Mycteroperca rosacea* peaks of feeding activity around sunrise and sunset. RANDALL (1967) suggested for the Graysby in his study on the food habits of Caribbean reef fishes, a diurnal/nocturnal feeding habit, but with a peak at sunrise and sunset.

Feeding on crustaceans takes place mainly at and after sunset, when feeding on fish decreases and when the Graysbys move more into the corals. At sunset crustaceans are leaving the crevices in the corals, in which they stay during day-time, thus becoming more available to preying Graysbys. During the night no full stomachs were found and fresh stomach contents were absent, so feeding during the night seems to be low.

A significant correlation was found between food intake and condition factor during the year ($p < 0.01$). Food intake varies considerably during the year and is in general high between February and August and lower in the rest of the year. In addition, minima in food intake can be observed in January, September, and possibly in June. These minima coincide with the timing of formation of translucent zones in the otoliths as discussed in chapters III and IV. The maxima in food intake in October-November, February-March and July coincide with the formation of the opaque zones and body growth in the same periods. The slight increase in food intake in June also coincides with gonad development.

SUMMARY

Epinephelus (*Cephalopholis*) *cruentatus* (Lacépède, 1802) [*Petrometopon cruentatum*], the Graysby, is one of the most common groupers on the coral reef at the southwest coast of Curaçao. They are very abundant at a depth from 7½ to 9 m. A second, lower maximum in their vertical distribution is found at a depth of 30 m. Juveniles are found mainly at a depth of about 6 m in crevices of the coral species *Montastrea annularis*. The calculated number of fish actually present appeared to be 24 specimens in a transect of 240 m^2 at a depth of 9 m.

Measurements were made of the percentage of bottom cover and of the quantity of coral structure. A strong correlation was found between both. For the studied coral reef in Curaçao a high percentage of bottom cover means at the same time a high quantity of structure and thus of hiding places for the Graysbys. A strong correlation ($p < 0.01$) could be observed between the mean number of *E. cruentatus* and the mean percentage of bottom cover of the coral species *M. annularis* and *Agaricia* spp. These coral species have an important influence upon the vertical distribution of *E. cruentatus* by their growth form, which supplies hiding possibilities e.g. holes, overhangs, crevices. There is a suggestion of a movement in the population to shallower waters during the spawning season.

In Curaçao the Graysbys appear to be diurnal. During the night they move deeper into caves and crevices of the reef. The most important food fish of the Graysby, *Chromis multilineata*, shows the same vertical distribution as its predator and seems also to be strongly determined by the percentage of cover of *M. annularis* and *Agaricia*.

Otolith readings of *E. cruentatus* demonstrate that each year 3 growth rings are formed, the formation of which starts in September, January and June. Juveniles, however, form 7 growth rings a year. The translucent zones in the adults are formed in September, January and June, when food intake, condition factor and body growth is low. In the periods following these three months, the opaque zones are formed and this formation coincides with maxima in food intake, condition factor and body growth. Possibly a change in temperature is a factor in initiating a new growth ring.

Growth in length and weight of the Graysbys occurs especially in February and to a lesser extent during July and October.

The growth equation of Von Bertalanffy for *E. cruentatus* in Curaçao is:

$$L_t = 41.5\,(1 - e^{-0.13\,(t\,+\,0.94)}).$$

The total length–standard length relationship is expressed by the equation: $y = 1.2091\,x + 0.2326$ and appears to be linear. The length–weight relationship found for the Graysbys is: $W = 0.0121 \times TL^{3.0821}$, and is closely proportional to the cube of the length.

The spawning season occurs from May to October. Mating takes place especially in August and September. Mature females are found mainly between 16 and 25 cm TL, at an age of 4 and 5 years, mature males between 21.5 and 27.4 cm TL in age group 6 and to a lesser extent in age groups 5 and 7, transitionals between 19.5 and 23.4 cm in age groups 4 and 5. For the transitionals in the length-range of 19.5–23.4 cm a transition rate of 10% was found. This relatively high rate is linked with a high increase of numbers of males in this length-range. Transition occurs usually in September, and to a lesser extent during July, August and October, immediately after spawning. A sex-ratio of 2.5 : 1 was observed for mature females and males. A significant correlation ($p < 0.01$) exists between transition rate and sex-ratio. In general a strong dominance of females coincides with a relatively low transition rate and vice versa.

Females spawn only once a season, whereas males spawn more frequently and can mate with more than one female.

E. cruentatus feeds mainly on fish (75%) and to a lesser extent on crustaceans (18%). Juveniles, however, feed more on shrimps (80%) than on fish.

The equation found for the relation mean weight of stomach contents and size classes is: $\overline{w} = 0.00567 \times TL^{3.5917}$, this indicates that the weight of the stomach contents is a function of about the third power of the length.

Graysbys show preference for *Chromis multilineata* (± 55%). They feed especially at sunrise and sunset. Food intake varies considerably during the year and is in general high between February and August and lower in the rest of the year. In addition, minima in food intake can be observed in January, September, and possibly in June, and maxima in October-November, February-March and July. These minima and maxima in food intake correspond with time of ring formation in the otoliths.

A significant correlation was found between food intake and condition factor during the year ($p < 0.01$).

RESUMEN

Epinephelus (*Cephalopolis*) *cruentatus* (Lacépède, 1802) [= *Petrometopon cruentatum*], es una de las más corrientes entre las cunas y los meros en los arrecifes de coral a lo largo de la costa sudoeste de Curazao. Abundan mucho a una profundidad de 7½ a 9 m. Otro máximo, menos abundante en su distribución vertical se encuentra a 30 m de profundidad. Las jóvenes se encuentran principalmente a una profundidad de 6 m en las grietas de los corales de la especie *Montastrea annularis*. La calculada cantidad de peces que se hallan actualmente resultó ser 24 ejemplares en un área de 240 m² a una profundidad de 9 m. Se midieron el porcentaje de cobertura de suelo y de la cantidad de estructuras de coral y se descubrió una estrecha correlación entre las dos. Por lo que toca el arrecife de coral estudiado en Curazao, un alto porcentaje de cobertura de suelo signífica al mismo tiempo una alta cantidad de estructura y en consecuencia de escondrijos para la cuna cabrilla. Se pudo observar una estrecha relación ($p < 0.01$) entre la cantidad promedia de *E. cruentatus* y el procentaje promedio de la cobertura del suelo de las especies de coral *M. annularis* y de *Agarcia* spp. Las dos especies de coral tienen mucha importancia sobre la distribución vertical de *E. cruentatus* por medio de su forma de crecer, lo que suministra posibilidades de refugio, cuevas y grietas. En la población hay una indicación de un movimiento hacia aguas menos profundas durante el período de desove.

En Curazao las cunas cabrillas resultan ser diurnas. Durante la noche bajan a mayores profundidades a las cuevas y grietas del arrecife. El pez más importante que sirve de alimento para la cuna cabrilla, *Chromis multilineata,* demuestra la misma distribución vertical que su consumidor y parece que su presencia se liga íntimamente con el porcentaje de cobertura de *M. annularis* y de *Agaricia.*

La examinación de los otolitos de *E. cruentatus* demuestran que cada año se forman 3 cercos cuya formación inicia en setiembre, enero y junio. Las jóvenes, empero, forman 7 cercos cada año. Las zonas translúcidas de los adultos se forman en setiembre, enero y junio, cuando la toma de alimento, factor de condición y de crecimiento corporal es poca. En los períodos que siguen a estos 3 meses, se forman las zonas opacas y esta formación coincide con la máxima toma de alimento, factor de condición y de crecimiento corporal. Posiblemente un cambio de temperatura sea un factor para la iniciación de otro cerco de crecimiento. Crecimiento en sentido longitudinal y aumento de peso de las cunas cabrillas ocurren especialmente en febrero y en un grado menor durante julio y octubre.

La ecuación de crecimiento de Von Bertalanffy para *E. cruentatus* en Curazao es:

$$L_t = 41.5\ (1 - e^{-0.13\ (t\ +\ 0.94)}).$$

La relación del largor total – largor corriente se expresa por la ecuación: $y = 1.2091 \times + 0.2326$ y resulta ser lineal. Para la relación largor – peso de las cunas cabrillas se encontró: $W = 0.0121 \times LT^{3.0821}$, y proporcionalmente queda muy cerca del cubo del largor.

El período de desove es de mayo a octubre. La cópula se efectúa particularmente en agosto y setiembre. Las hembras maduras por regla general miden 16 a 25 cm LT, a la edad de 4 y 5 años, los machos maduros entre 21.5 y 27.4 cm LT en un grupo de edad de 6 años y en menor grado a un grupo de edad de 5 y de 7 años, los en transición entre 19.5 y 23.4 cm en los grupos de edad de 4 y 5 años. Por lo que toca los en vía de transición en la serie de 19.5 y 23.4 cm se encontró una proporción de transición de un 10%. Esta proporción relativamente alta se une a un aumento de la cantidad de los machos en esta serie de largor. La transición se verifica generalmente en setiembre y en un grado menor durante julio, agosto y octubre, inmediatamente después del desove. Se observó un cociente de sexo de 2.5 : 1 para las hembras y los machos maduros. Una correlación significante ($p < 0.01$) existe entre la proporción de transición y el cociente de sexo. En términos generales una fuerte dominación femenina coincide con una transición relativamente baja y al revés.

Las hembras deshuevan sólo una vez por estación, mientras la freza de los machos sucede con más frecuencia y ellos pueden acoplar con más de una hembra.

E. cruentatus se alimenta generalmente con pececillos (75%) y en menor grado con crustáceos (18%). Los jóvenes en cambio comen más camarones (80%) que pececillos.

La ecuación encontrada para la relación entre peso del contenido estomacal y las clases de tamaño es: $\bar{w} = 0.00567 \times LT^{3.5917}$, lo que indica que el peso del contenido estomacal es una función de aproximadamente la tercera potencia del largor.

Las cunas cabrillas demuestran preferencia para *Chromis multilineata* (± 55%). Se alimentan particularmente al amanecer y al anochecer. La toma de alimentos varía considerablemente durante el año y generalmente es elevada entre febrero y agosto y reducida por lo que queda del año. Además se puede observar mínimos en la toma de alimento en enero, setiembre y posiblemente en junio, y máximos en octubre-noviembre, febrero-marzo y julio. Estos mínimos y máximos en la toma de alimento corresponden con la época de formación de cercos en los otolitos.

Se encontró una significante correlación entre la toma de alimento y el factor de condición durante el año ($p < 0.01$).

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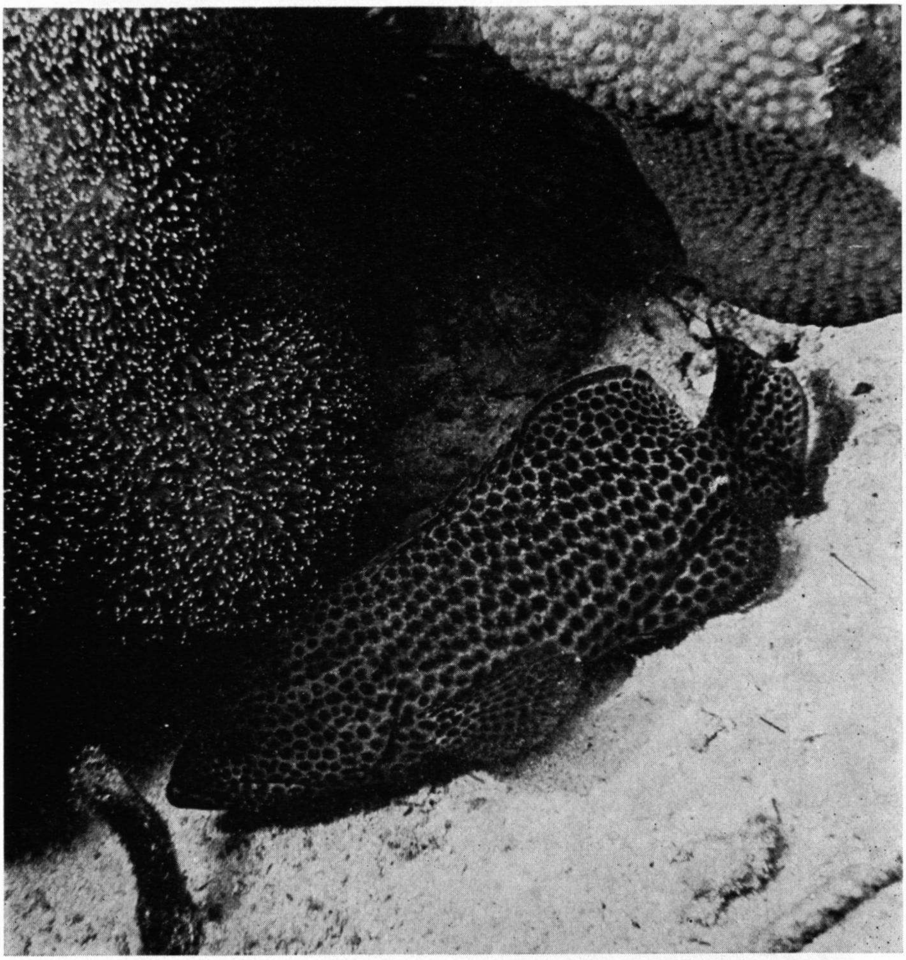
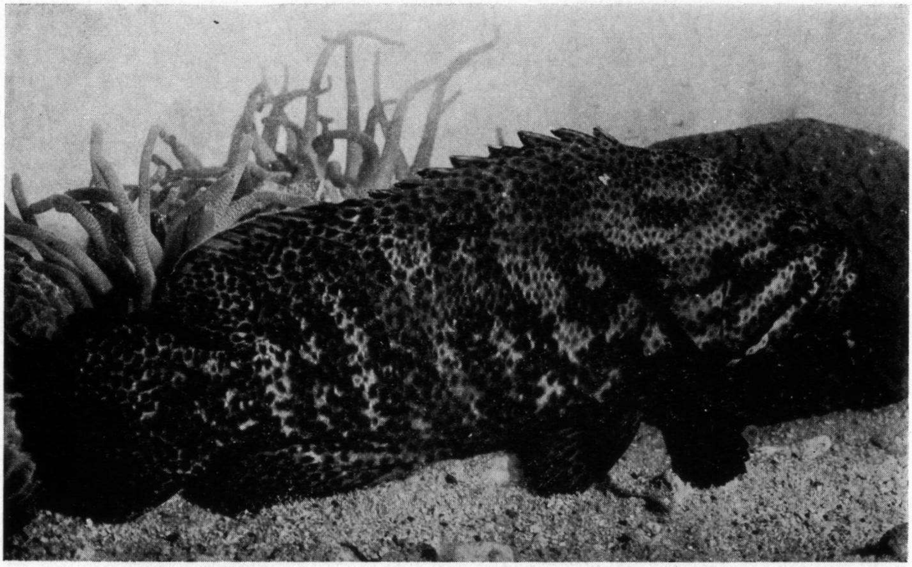
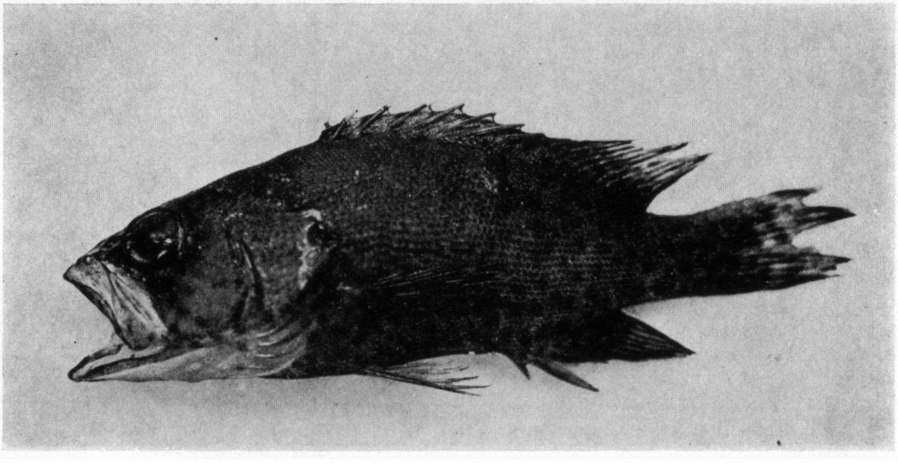


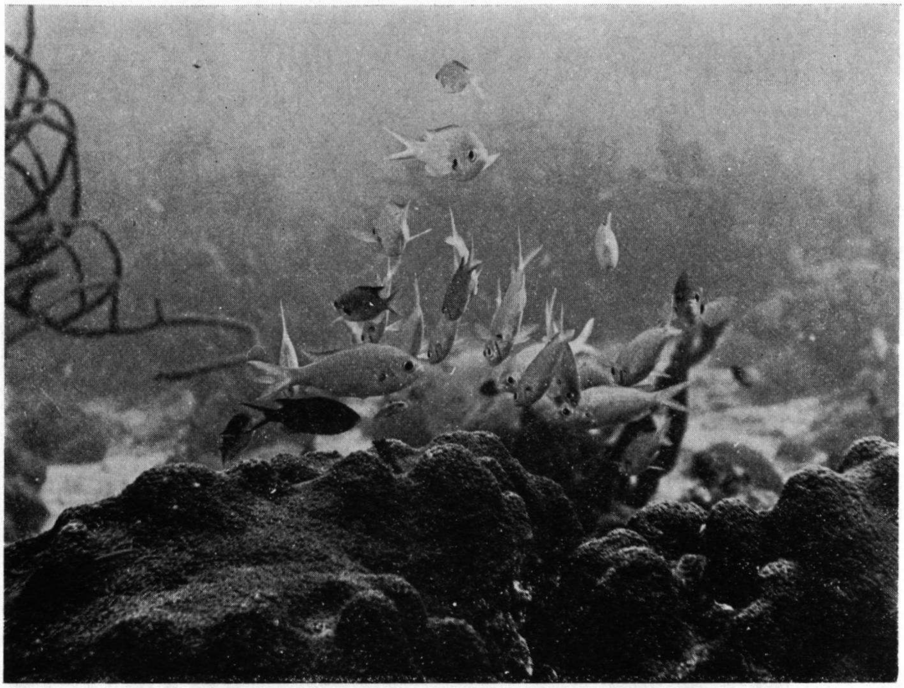
I. The Graysby, *Epinephelus cruentatus* [= *Petrometopon cruentatum*] at a depth of about 10 m in Piscaderabaai, Curaçao; about 18 cm TL. (Photo ERIK VAN DIJK).

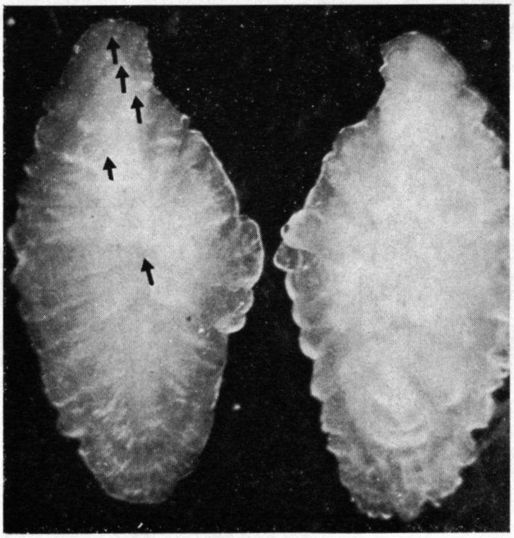




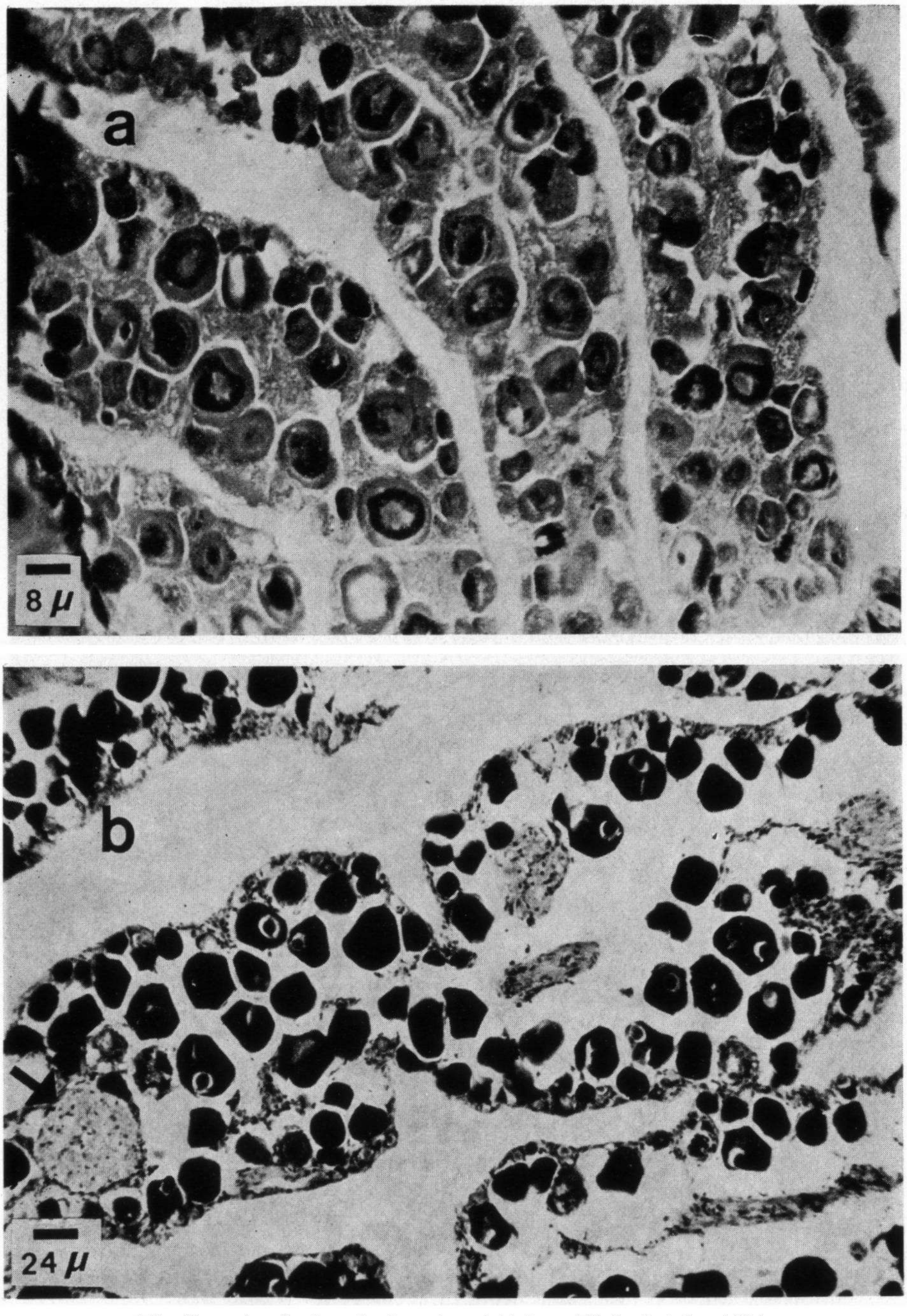
IIa. *Epinephelus cruentatus* with banded pattern, Portomaribaai, Curaçao; 26.2 cm TL.

IIb. Juvenile of the Graysby, taken at Portomaribaai on 13 January 1978 at a depth of 7½ m with the aid of Quinaldine, a fish poison; 5.9 cm TL. The otoliths of this specimen are shown in Plate IIIb. (Photo AUBREY TIEL).

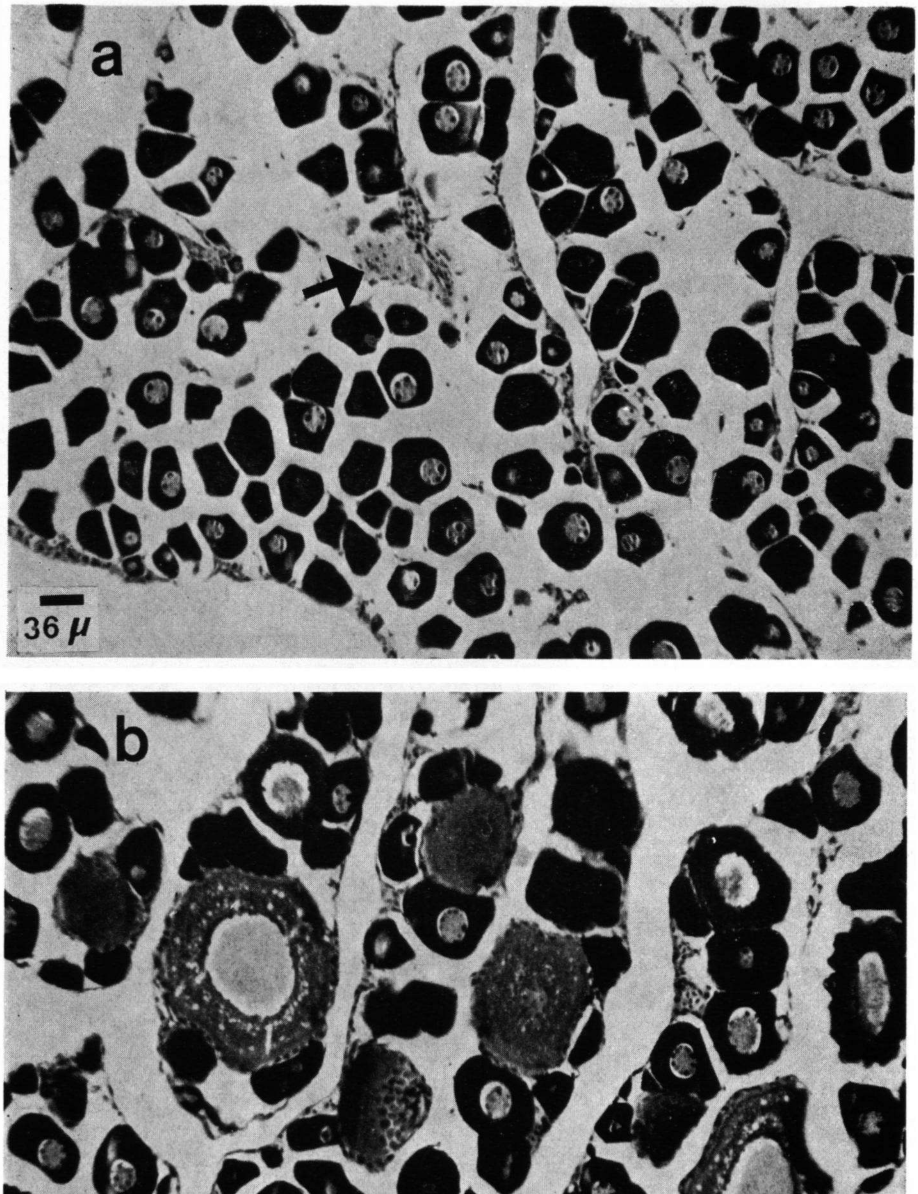




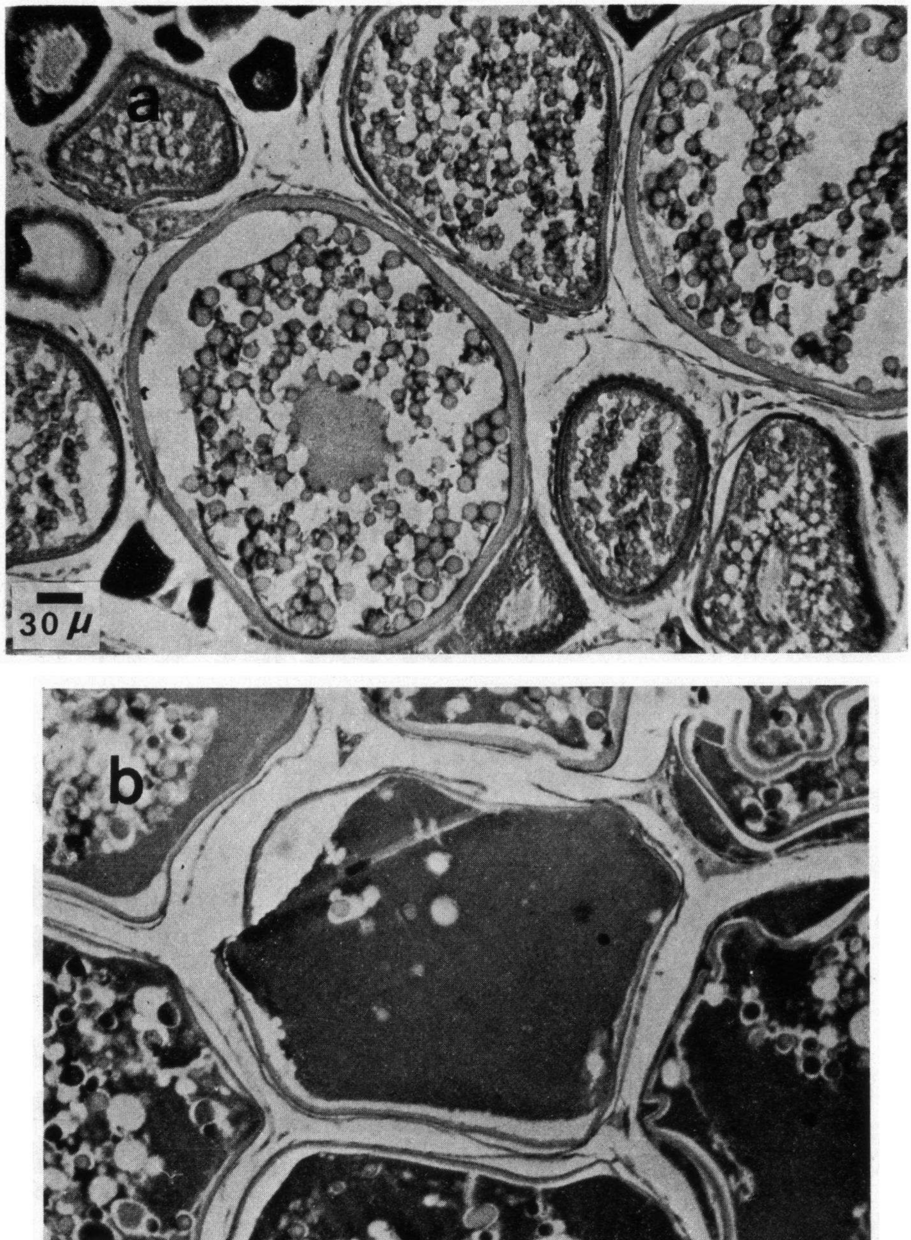
IIIa. Aggregation of *Chromis multilineata* above the coral *Montastrea annularis*; southwest coast of Curaçao at a depth of about 10 m. (Photo BART DE BOER). IIIb. Otoliths (2.7 mm long) from a juvenile Graysby with 4 growth rings, collected 13 January 1978; TL 5.9 cm. Each arrow indicates the beginning of a new growth ring.



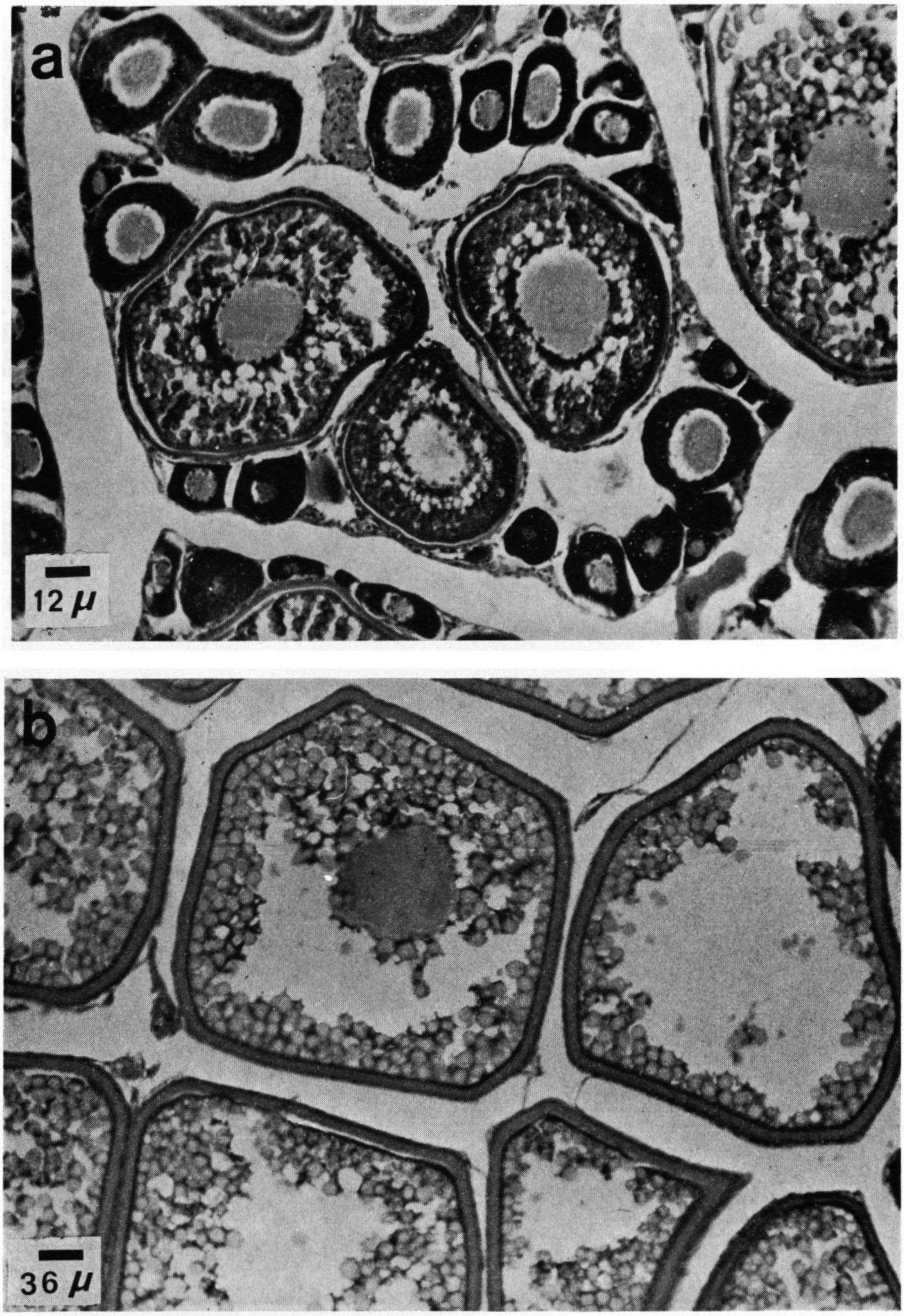
IVa. Oogonia of a female Graysby of 14.3 cm TL in October 1974.
IVb. Oocytes of stage I from a female Graysby of 17.9 cm TL in October 1973. The arrow indicates an atretic body.



Va. Oocytes of stage 2, from a female of 18.0 cm TL in April 1973. The arrow indicates an atretic body.
Vb. Oocytes of stage 3, from a female of 21.0 cm TL in May 1973.

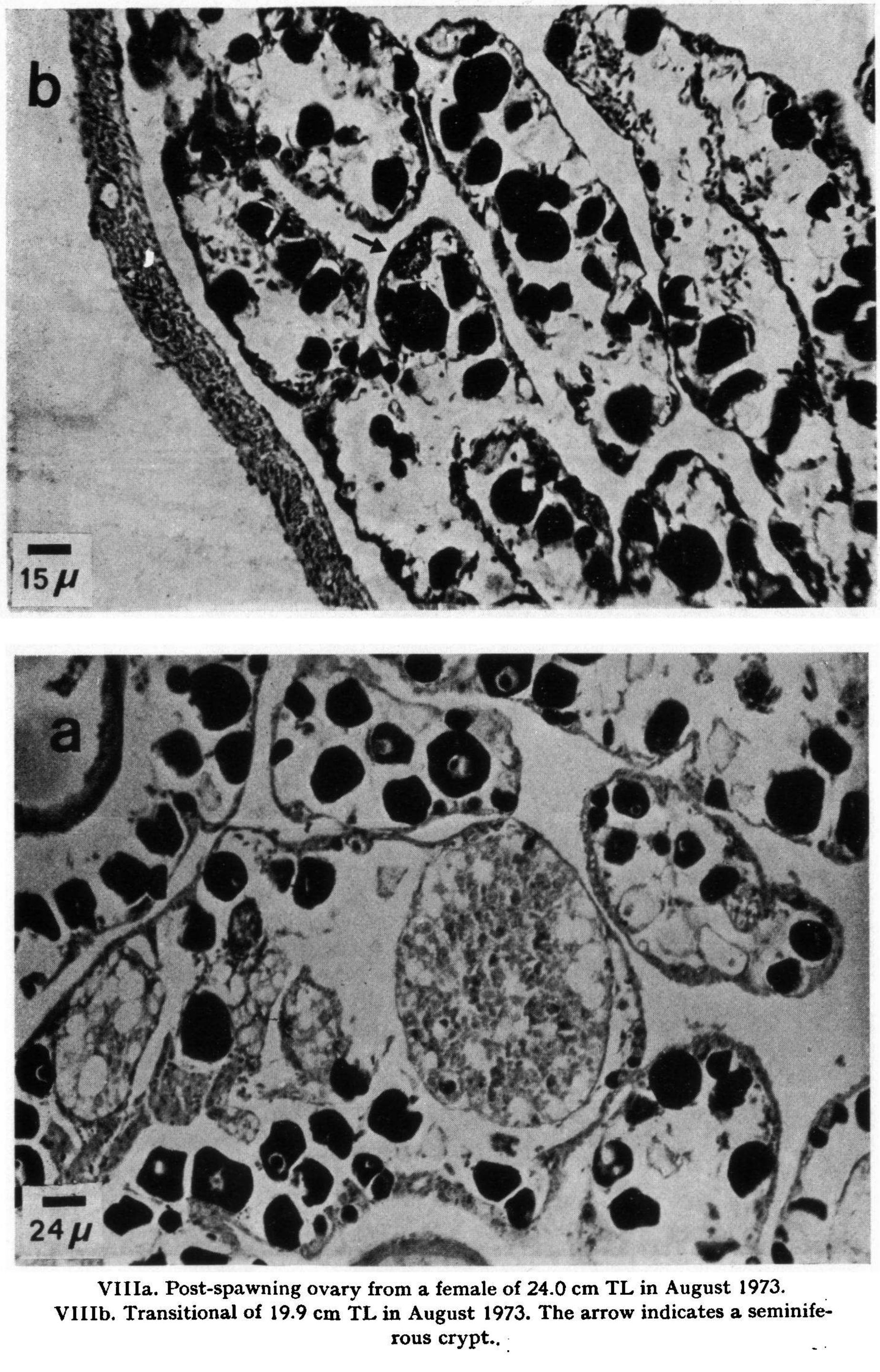


VIa. Oocytes of stage 4, from a female of 22.4 cm TL in August 1974.
VIb. Oocytes of stage 5, from a female of 21.0 cm TL in July 1973.

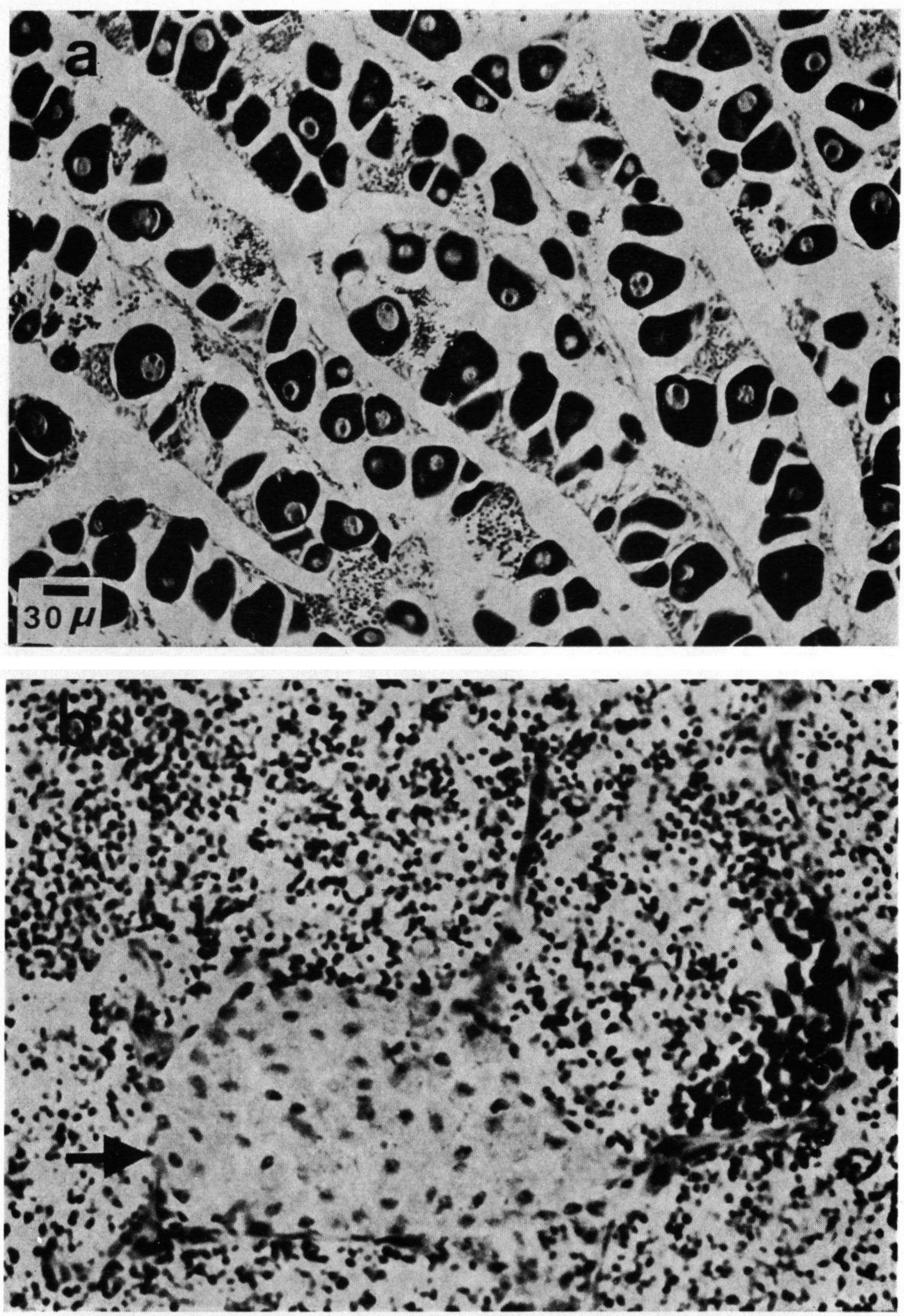


VIIa. Mature ovary with oocytes in stage 3, from a female of 21.0 cm TL in July 1974.

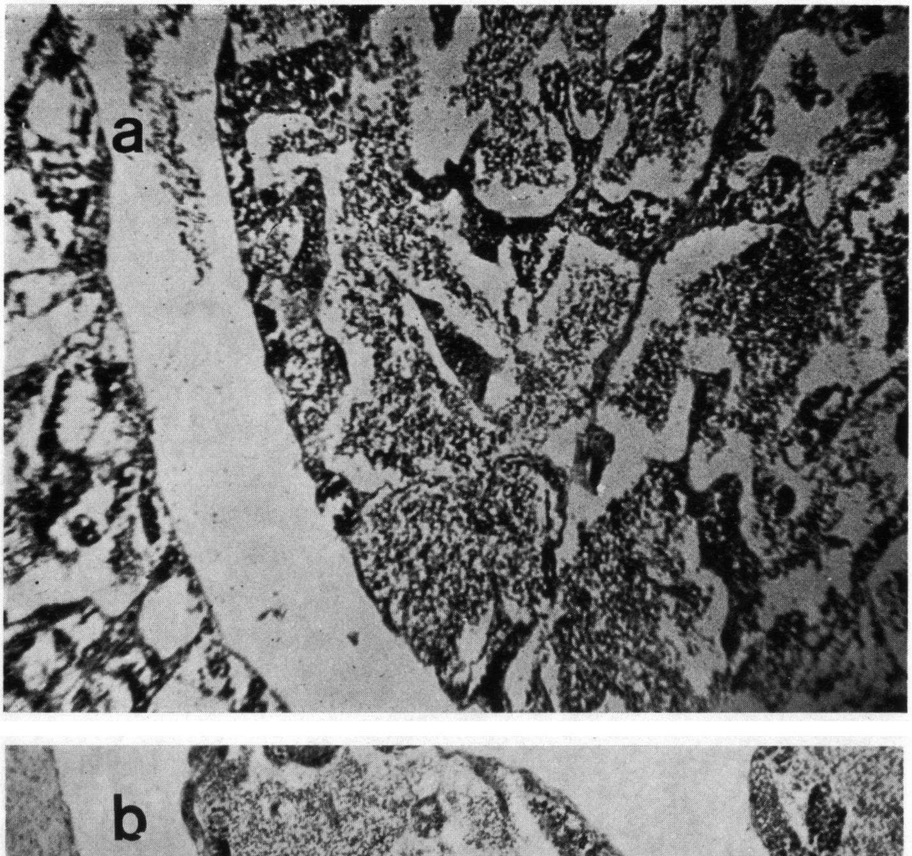
VIIb. Mature ovary with oocytes in stage 4, from a female or 23.8 cm TL in July 1973.



VIIIa. Post-spawning ovary from a female of 24.0 cm TL in August 1973.
VIIIb. Transitional of 19.9 cm TL in August 1973. The arrow indicates a seminiferous crypt..



IXa. Mature inactive testis from a male of 19.9 cm TL in April 1973.
IXb. Ripening mature testis from a male of 27.2 cm TL in June 1974.
The arrow indicates an old atretic body.



Xa. Ripe testis from a male of 26.1 cm TL in July 1973.
Xb. Gonad of a partly spawned male of 25.9 cm TL in August 1973. Note the relatively thick muscular tunica and some empty crypts.