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Walter A. Starck II and Robert E. Schroede

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by WALTER A. STARCK, II
and ROBERT E. SCHROEDER

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Lutjanus griseus

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Studies in Tropical Oceanography No. 10
Rosenstiel School of Marine and Atmospheric Sciences
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Contribution No. 1205 from the University of Miami,
Rosenstiel School of Marine and Atmospheric Sciences

Biology of the Gray Snapper, *Lutjanus griseus* (Linneaus), in the Florida Keys

by WALTER A. STARCK, II

Acknowledgments

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Harvey R. Bullis, Jr. of the United States Fish and Wildlife Service, made available data on the gray snapper taken during exploratory fishing by the Fish and Wildlife Service.

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The author's wife, Jo, assisted in all phases of the study.

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Recent observations on snappers made during the course of work on a study of the structure of the fish fauna of Alligator Reef have been included. This work is supported by National Science Foundation grant GB-3628 of which the author is principal investigator.

Investigations of the feeding habits of the various species of *Lutjanus* and *Ocyurus chysurus* reported in the present study were carried out in coordination with a study of the feeding habits and mechanisms of selected reef fishes supported by National Science Foundation Grant GB-1456 of which C. Richard Robins is principal investigator.

Introduction

The snappers (family Lutjanidae) comprise a large group of generally medium-sized predaceous fishes common in tropical and warm temperate seas. They feed largely on crustaceans and fish and, with few exceptions, are species of shore and shelf waters occasionally entering fresh water. They are excellent food fishes and are important commercially in many areas. though several species (not including *Lutjanus griseus*) have been involved in cases of ciguatera fish poisoning (Randall, 1958). Many species are also sought as game fishes.

As with most tropical marine fishes, little is known about their biology and the group needs systematic review. Estimates based on various literary sources indicate about 23 genera in the family, of which *Lutjanus* is by far the largest with over 70 recognized species. Due to the uncertain taxonomy, however, these figures are only estimates.

The present paper constitutes a report on a study, made primarily during 1962–63, on the biology of the gray or mangrove snapper, *Lutjanus griseus* (Linnaeus). This study was carried out mainly in the vicinity of Lower Matecumbe Key and Alligator Reef in the Florida Keys.

The gray snapper is the most abundant and widespread species of *Lutjanus* in the western Atlantic. It is especially abundant in the Florida Keys where the extensive grass beds of Florida Bay and the nearby Florida reef tract combine to afford excellent habitats for both young and adults. Longley (Longley and Hildebrand, 1941:115) wrote of the gray snapper at the Dry Tortugas, Florida, “This is the commonest of Tortugas snappers and in many respects the dominant fish in the local fauna.”

The habitat, color pattern, morphology, and feeding habits of seven related species are also discussed for comparison with the gray snapper in order to elucidate the niches occupied and adaptations for them among closely related and competing species.

1. Relationships; Nomenclature; Economic Value; Geographic Range

RELATIONSHIPS

Of approximately 23 genera in the family Lutjanidae, only one, *Lutjanus*, is found in all four major tropical marine faunal regions. Three genera, *Apsilus, Etelis,* and *Pristipomoides*, are found both in the Atlantic and the Indo-West Pacific. *Pristipomoides,* in the Atlantic, is restricted to the West Indies region. The latter three genera are epipelagic species which go as deep as several hundred fathoms. One genus, *Aphareus*, is found in the Indo-West Pacific and is also recorded from the eastern Pacific. There are 10 genera restricted to the Indo-West Pacific, five restricted to the eastern Pacific, and three, *Verilus* (possibly not a lutjanid), *Rhomboplites,* and *Ocyurus*, found only in the tropical western Atlantic.

Of the more than 70 species in the genus *Lutjanus*, about 45 occur in the Indo-West Pacific region, eight or nine are found in the eastern Pacific region, four or five are recorded from the eastern Atlantic, and at least 13 from the western Atlantic. Three common western Atlantic species, *L. jocu, L. apodus,* and *L. griseus*, have also been recorded from West Africa (Metzelaar, 1919: 235 and Fowler, 1936: 792 et seq.). These West African records have been variously placed in the synonymy of nominal West African forms by some writers and recognized as distinct species by others so that their actual status is indefinite. Descriptions of *L. griseus* based on West African specimens do not agree well with western Atlantic specimens, though Fowler (1936:793) stated that a specimen he identified as *L. griseus* taken at the mouth of the Congo agrees in all respects with western Atlantic specimens.

Three western Atlantic species have close eastern Pacific cognates (Jordan, 1908). Of the western Atlantic species of *Lutjanus*, four, *L. buccanella*

L. campechanus, L. vivanus, and *L. purpureus,* live in deeper water (generally 20 to 150 fathoms) and are generally of reddish color. One, *L. brachypterus,* is known only from the Bahamas (James E. Böhlke, personal communication) and is a close relative of *L. synagris,* which also occurs there. Another species, *L. ambiguus,* is apparently restricted to Cuba. Poey (1860:152) suggested that *L. ambiguus* is a hybrid between *L. synagris* and *Ocyurus chrysurus,* but Rodríguez (1961:20), after histological examination of the gonads of *L. ambiguus,* concluded that it is a valid species. Of the remaining seven species of *Lutjanus, L. analis, L. apodus, L. cyanopterus, L. griseus, L. jocu, L. mahogoni* and *L. synagris,* all are inshore and reef or bank species with wide ranges throughout the West Indian area.

Ocyurus chrysurus is also a wide ranging reef and inshore species. *Ocyurus* is similar in most respects to *Lutjanus* and probably derived from it. General characters reflect its more free-swimming mode of life.

Anderson (1967) presents a key to and synopsis of the western Atlantic species of Lutjanidae, including nominal species of uncertain status.

NOMENCLATURE

Lutjanus griseus was described as early as 1743 by Mark Catesby in his book *The Natural History of Carolina, Florida, and the Bahama Islands.* He used the name mangrove snapper and the Latin appellation, *Turdus pinnis branchialibus carens.* A full page color plate was also presented.

Parra described it from Cuba in 1787 and figured it in a woodcut. He called it Caballerote, a name still used in Cuba. Since that time it has appeared rather frequently in the literature and acquired a considerable synonymy.

The synonymy used by Jordan, Evermann, and Clark (1930: 325) is given below. No additional synonyms have been noted.

Turdus pinnis branchialibus carens	Catesby, 1743: 9, pl. 9, Bahamas
Labrus griseus	Linnaeus, 1758: 283, after Catesby
Caballerote	Parra, 1787: 52, pl. 25, fig. 1, Havana
Sparus tetracanthus	Bloch, 1791: 116, Martinique
Anthias caballerote	Bloch and Schneider, 1801: 310, after Parra
Bodianus vivanet	Lacépède, 1802, pl. 4, fig. 3, Martinique
Mesoprion griseus	Cuvier (in) Cuvier and Valenciennes, 1828: 469, San Domingo, not after Linnaeus
Lobotes emarginatus	Baird and Girard, 1855: 332, Beaseley Point, New Jersey
Lutjanus stearnsi	Goode and Bean, 1878: 179, Pensacola, Florida.

Fowler (1939: 792) presents a synonymy of West African names which, because of their uncertain status, have not been included here.

Various common names have been applied to *Lutjanus griseus*. In southern Florida the name mangrove snapper is frequently used, as it was by Catesby (1743: 9). Alternative names attributed to the species by American writers are:

red snapper	(LaMonte, 1952);
lowyer	(Jordan and Evermann, 1898: 1255, Beebe and Tee-Van, 1933: 150);
mango snapper	(Robins, 1959: 22; Moe, 1963: 106);
black snapper	(a name reported from the northwest coast of Florida, Moe, 1963: 106).

The name gray snapper is preferred by the American Fisheries Society and this appears in their list of common and scientific names of fishes (Bailey et al., 1960: 26). This name is also used by many other authors.

Spanish-speaking peoples have used the names

caballerote	(Parra, 1787: 52; Jordan and Evermann, 1898: 1255; Evermann and Marsh, 1902: 170; La Monte, 1952; Schultz, 1952: 130; Duarte-Bello, 1959: 81);
pargo prieto	(Evermann and Marsh, 1902: 170; La Monte, 1952);
pargo de piedra	(Schultz, 1952: 130);
pargo moreno	(Fowler, 1953: 62);
aguadera	(Schultz, 1952: 130).

Metzelaar (1919: 61) reported the name caranchito from Bonaire and Curaçao. Carbalho (1943: 58) listed the names caranha, caranhota, caranho, and caranha de mangue or de viveiro as the common names used in Brazil. Beebe and Tee-Van (1928: 152) give the Haitian common name as carde gris. In West Africa, Copley (1952: 127) used the name green snapper and listed the local Senegambia names as oureijh, diabarrjh, and diejch. Fowler (1936: 792) also lists dienoujher diejch.

ECONOMIC VALUE IN FLORIDA

Considerable quantities of gray snappers have been taken commercially in Florida for many years. Generally, it does not support a full-fledged fishery, but it is an important seasonal adjunct to other fisheries. Brice (1898: 293) reported that as early as 1895 76,000 lb. of gray snappers were taken from the Indian River for that year. He also reported that

262,334 lb. of gray snappers and other snappers, excluding red snappers, were taken in Monroe County (the Florida Keys) during the same year.

Landings by county for various Florida counties during the year 1962 are shown in Figure 1. Figure 2 shows landings of gray snappers taken in other recent years in Monroe County and over the entire state of Florida. Monroe County generally has led the state in recent years in landings of gray snappers. In Monroe County much of the commercial catch of gray snappers is made by hook and line from small boats in the summer when large schools of adults congregate along the reefs to spawn.

Greatest economic value of the gray snapper, however, lies in the sport fishery. Sport fishermen leaving Flamingo to fish in shore waters of Ever-

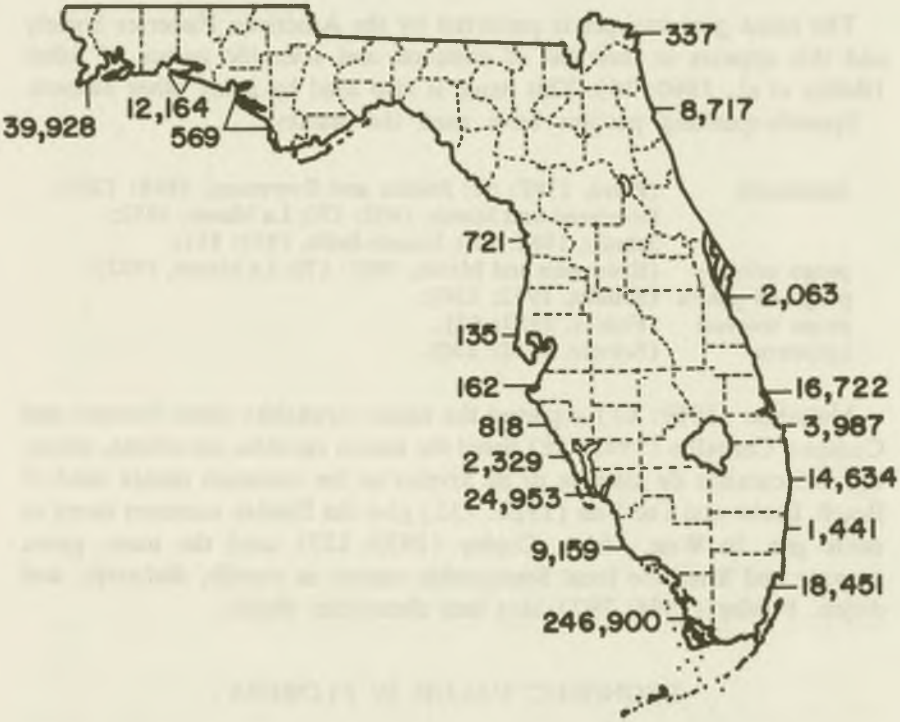

Figure 1. Catches of gray snappers (Predominantly *Lutjanus griseus* but includes a few *L. synagris* and probably other inshore relatives) for various Florida counties in 1962. Figures are in pounds. (Data from Rosen and Robinson, 1963: 6 et seq.)

glades National Park during the year beginning June 1958 were estimated to have caught about 65,500 gray snappers making up about 30% of the total catch that includes 40 species of fishes (Higman, MS; Rosen and Dobkin, MS).

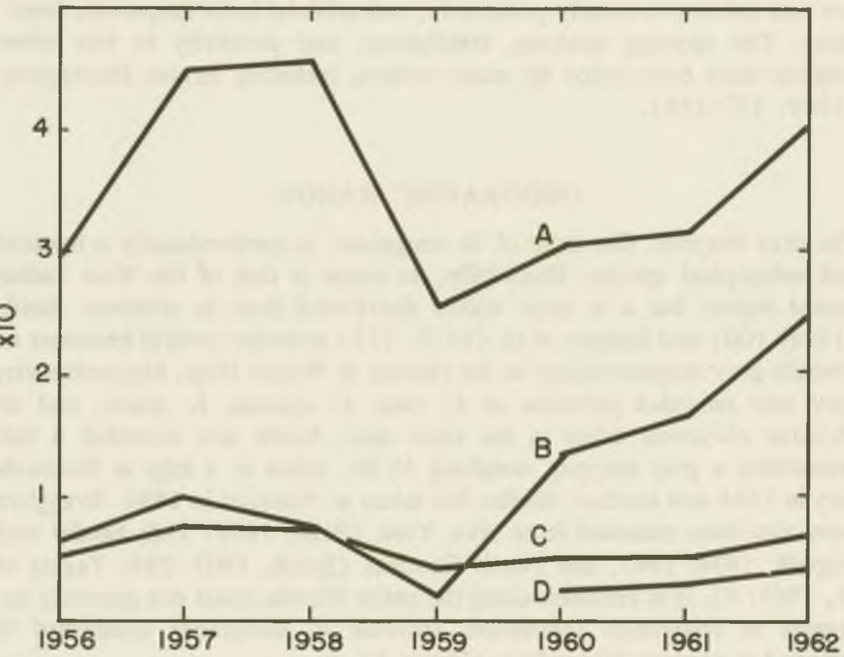

Figure 2. Florida commercial landings of gray snappers (Predominantly *Lutjanus griseus* but includes a few *L. synagris* and probably other inshore relatives) in recent years. A: Total landings for Florida in hundred thousand pounds. B: Total landings for Monroe County in hundred thousand pounds. C: Value of Florida landings in hundred thousand dollars. D: Value of Monroe County landings in hundred thousand dollars. (Data from Rosen, 1957; Rosen and Ellis, 1958; Rosen, 1959, 1960; Rosen and Robinson, 1961, 1962, 1963.)

Figures for the year beginning July 1961, the latest year available, indicate that gray snappers made up about 16% of the total sport fishing catch of an estimated 43,319 anglers at Flamingo (Higman and Yokel, MS). The smaller catch during the 1961–62 survey is attributed in part to increased salinities in estuarine waters during this period. This permitted the snappers to ascend rivers and streams beyond convenient reach of the average angler. The gray snapper clearly has more value as a sport fish than as a commercial species.

The habits and abundance of gray snappers make them readily accessible to sport fishermen in inshore waters. Availability, excellent qualities as a food, and fighting ability on light tackle make it one of the more popular sport fishes. It is commonly taken on cut bait (particularly mullet), live bait (shrimp is usually preferred), and artificial lures (especially bucktails). The sporting qualities, intelligence, and proclivity to bite when handled have been noted by many writers, including Ernest Hemingway (1949: 157–158).

GEOGRAPHIC RANGE

The gray snapper, like most of its congeners, is predominantly a tropical and subtropical species. Essentially, its range is that of the West Indies faunal region, but it is more widely distributed than its relatives. Smith (1898: 100) and Sumner et al. (1913: 757) recorded several instances of juvenile gray snappers taken in the vicinity of Woods Hole, Massachusetts; they also recorded juveniles of *L. jocu, L. apodus, L. analis,* and of *Ocyurus chrysurus* taken in the same area. Smith also recorded a fish resembling a gray snapper, weighing 25 lb., taken in a trap at Buzzards Bay in 1894 and another, similar fish taken at Newport in 1896. Stragglers have also been recorded from New York (Bean, 1903: 548; Breder and Nigrelli, 1934: 194), and North Carolina (Smith, 1907: 286; Tagatz et al., 1961: 4). It is common along the entire Florida coast but generally increases in abundance southward. Increase in abundance southward is reflected in commercial landings (Figure 1).

Texas records are few, and apparently the gray snapper is uncommon there (Baughman, 1934: 212, 1950: 249; Gunter, 1945: 62; Fowler, 1945: 375). Jordan and Dickerson (1908: 14) report a specimen from Tampico, Mexico. It is common along the coast of Yucatán and British Honduras (Bean, 1888: 205; and personal observation). Fowler (1944: 466) records it from Honduras and it is said to be a common species in Panama (Meek and Hildebrand, 1925: 511). Fowler (1953: 62) records its occurrence in Colombia, and Schultz (1952: 130) in Venezuela. It is also recorded from several locations along the Brazilian coast (Fowler, 1941: 160, compiles previous records; Carvalho, 1943: 58, records it from São Paulo). In Bermuda it is abundant (Bean, 1906: 56; Beebe and Tee-Van, 1933: 150; Bardach, 1958: 28), and it has been recorded from the Bahamas and the Greater and Lesser Antilles by many authors at numerous locations.

Metzelaar (1919: 235) compiled previous West African records; Fowler (1936: 792) recorded a specimen from the mouth of the Congo; Cadenat (1950: 316) listed ***Lutjanus griseus*** as a species recorded, but not observed by himself, in Senegal; Copely (1952: 127) gave the following locations in a list of localities for ***Lutjanus griseus***:

> Forcados, Goreé, Dakar, Babagaye, Fernando
> Poo, Cap Vert, Ashantee, Leybar, Senegal,
> Barbarie Pointe, St. Louis, St. Thomas Is.

The status of the West African records needs review.

2. Habitat; Tolerance to Temperature and Salinity; Predators; Parasites, Diseases, and Malformations; Abundance

HABITAT OF THE GRAY SNAPPER

Habitats occupied by the gray snapper vary widely. These range from inshore grass beds, mangrove areas, estuaries, and lagoons to deeper channels and offshore reefs.

Juveniles have been recorded frequently from inshore areas and waters of varying salinity. Hildebrand and Schroeder (1928: 257) recorded six specimens, from 105 to 111 mm, from Chesapeake Bay. Kilby (1955: 219) reported a number of small specimens from coastal marsh areas around Cedar Key and Bayport, Florida, and stated that they enter both the Weekiwachee River and Salt Creek where salinity is less than 2%. Springer and Woodburn (1960: 40) collected 102 specimens in the Tampa Bay area. These ranged from 14 to 164 mm standard length with only four specimens exceeding 91 mm. Most specimens were taken in grass flats from Maximo Point and Boca Ciega Bay. Grass flat vegetation there is predominantly *Diplanthera* with a small amount of *Thalassia* and *Syringodium.* Springer and Woodburn recorded the species in salinities of 3.0 to 35.0% in the Tampa Bay area and also took specimens in the St. Lucie River in salinities of less than 1%. Springer (1960) took young gray snappers in the Indian River in salinities of less than 1 to 29.4%. Tabb and Manning (1961: 619) listed the gray snapper as the most common snapper in northern Florida Bay and adjacent brackish waters of the Florida mainland, though they found no adults in this area. They collected it from fresh water of rivers tributary to Whitewater Bay and the Shark River estuary, to the highest salinities of Florida Bay. Observed salinity range in these areas was 0 to 37%. Tabb et al. (1962: 74), included the gray snapper in a list of species that are marine as adults but nearly euryhaline as larvae and juveniles. Other occurrences of gray snapper in fresh water have been recorded by the following: Herald and Strickland (1949: 105) at Homosassa Springs, Florida; Breder (1934: 70) at Andros Island, Bahamas; Eigenmann (1902: 229) from western Cuba; and Hildebrand (1939: 27) reported eleven specimens, ranging from 100 to 540 mm, from the Gatun Locks of the Panama Canal.

Adult gray snappers generally occur in deeper channels and farther offshore. Jordan and Evermann (1922: 407) stated that gray snappers were often taken at considerable depths in the company of red snappers. Longley, in Longley and Hildebrand (1941: 115), described occurrence of gray snappers about wharves, along submerged ledges of beach rock, around the greater aggregated coral heads offshore, and in some isolated gorgonian patches at the Dry Tortugas, Florida. Springer and Bullis (1956: 81), Captiva and Rivers (1960: 8), and Rathjen (1961: 130) reported catches of gray snappers by the United States Fish and Wildlife Service from the southwestern and southeastern Gulf of Mexico in depths ranging from 3 to 68 fathoms (5 to 125 m).

Captiva (personal communication) stated that most catches were made on bottom supporting sponge and alcyonarian growths. Bullis (personal communication) mentioned the possibility of misidentification in some of these reports. The extremely large size recorded for some of these fish is more characteristic of *Lutjanus cyanopterus*. Springer and Woodburn (1960: 40) commented that large adults were frequently seen on rocky reefs, at depths to 60 ft. (18 m), as far as 20 miles off the west coast of Florida. Moe (1963) gives several offshore locations along reefs off the Florida coast where mangrove snappers are taken.

A length frequency histogram of 354 specimens, from collections of the Institute of Marine Sciences of the University of Miami, is given in Figure 3A. All this material was collected from shore areas and usually from grass beds in depths less than 3 ft. Over 90% of these fish were in the 10 to 70 mm size range corresponding to the zero year class (see section on age and growth). Of particular interest among these collections is UMML 11472 having 66 specimens ranging from 12.4 to 21.8 mm standard length. This collection was made at Loggerhead Key, the Dry Tortugas, Florida, on 14 July 1961. A projecting spur of beach rock, at water level, extended about 50 m at an angle of 30° to the beach. The pocket formed between this spur and the beach was about 3 ft deep with a sandy bottom, carpeted by several inches of dead *Thalassia* blades. The small snappers were taken, after the use of poison, from the dead beds of *Thalassia* and many more were lost among the blades. All were of dark brown color

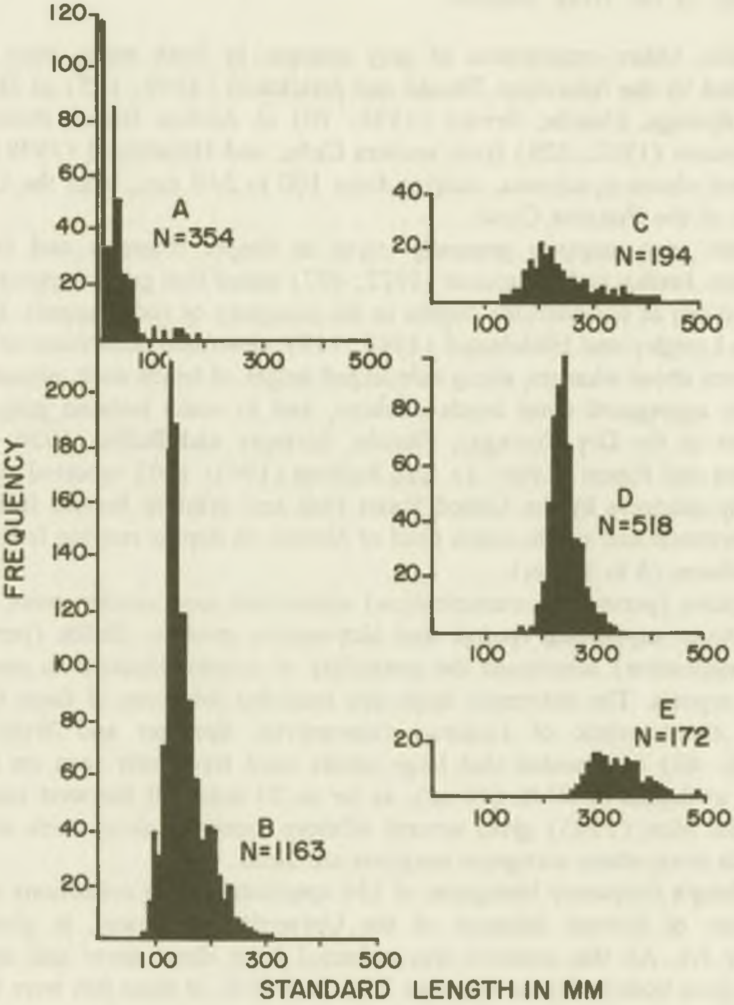

Figure 3. Length frequencies of gray snappers, *Lutjanus griseus*, from various habitats in Florida. A: Grass beds in shallow water based on material in the collections of the Institute of Marine Sciences of the University of Miami. Catalog numbers and data on this material are given in Table 1. B: Around brush, debris, and edges of channels in shallow water in the general vicinity of Lower Matecumbe Key. Based on material in collections 8 to 16 in Table 4 and fish caught for tagging in the same habitat and area. C: Inshore channels in the general vicinity of Lower Matecumbe Key. Based on material in collections 8, 17, 18, and 19 in Table 6 and fish caught for tagging in the same habitat and area. D: Alligator Lighthouse. Based on material in collections 20, 21, 22, and 25 in Table 6 and fish caught for tagging. E: Ledge at Alligator Reef. Based on collections 23 to 25 in Table 6.

similar to that of the dead grass. Stomach contents of these specimens are included in the section on food and feeding. Table 1 lists data on the UMML collections.

Inshore grass bed areas apparently form the most important nursery areas for juvenile gray snappers and are important feeding areas for adults in inshore waters. Several marine phanerogams, *Halophila engelmanni, Thalassia testudium, Diaplanthera wrightii, Ruppia maritima,* and *Syringodium filiforme,* dominate such communities depending upon local conditions. Salinities may range from fresh water (see above) to fully marine conditions as at Lower Matecumbe Key.

In the Lower Matecumbe Key area the author has collected gray snappers as small as 11.5 mm standard length in beds of *Thalassia* near shore. Grass beds in the Lower Matecumbe area are extensive, particularly on the Florida Bay side, from low water to depths of 5 or 6 ft. *Thalassia testudinum* is the dominant plant in this community which covers a large part of the Florida Bay area.

Invertebrates are extremely abundant in the *Thalassia* community and form an important part of the food for the predaceous fishes which feed in the grass beds. Moore (1963) discusses some of the invertebrates, particularly mollusks, from *Thalassia* beds in Biscayne Bay, Florida. Crustaceans are probably the most important invertebrate food of fishes, including the gray snapper (see section on food and feeding), in grass beds. Amphipods, shrimp (particularly *Penaeus duorarum*), carideans (of the families Hippolytidae, Palaemonidae, and Alpheidae), xanthid crabs, portunid crabs, and majid crabs all abound in these beds.

Fishes abundant in grass bed communities in the Lower Matecumbe Key area include pinfish (*Lagodon rhomboides*), toadfish (*Opsanus beta*), juvenile grunts (*Haemulon sciurus* and *H. plumieri*), spotfin mojarras (*Eucinostomus argenteus*), filefish (*Monacanthus hispidus*), juvenile parrotfishes (Scaridae), and rainwater killifish (*Lucania parva*).

In addition, a number of larger fishes commonly move into grass bed areas to feed, the most common of which are the nurse shark (*Ginglymostoma cirratum*), lemon shark (*Negaprion brevirostris*), bonnethead (*Sphyrna tiburo*), southern stingray (*Dasyatis americana*), ladyfish (*Elops saurus*), tarpon (*Megalops atlantica*), bonefish (*Albula vulpes*), needlefish (*Strongylura* spp.), crevalle jack (*Caranx hippos*), mullet (*Mugil* spp.), and great barracuda (*Sphyraena barracuda*).

The above list is by no means exhaustive; it includes merely the more common species collected by poison and trawl or seen in the grass bed areas. At night, when many of the larger carnivorous fishes enter the grass

Table 1. Collections of juvenile gray snappers, *Lutjanus griseus*, at the Institute of Marine Sciences, University of Miami.

UMML number	No. of Specimens	Size	Location (Fla. unless noted otherwise)	Date	Collecting method	Collector(s)
335	5	34.1–142.0	Long Key	27/10/56	Rotenone	Robins et al.
1013	2	53.7– 68.4	White City	–/4/57	Push Net	Durbin Tabb and John Gore
99	3	44.2–105.5	Largo Sound	20/10/56	Rotenone and seine	Robins et al.
246	24	23.2– 62.2	Lower Matecumbe Key	27/10/56	Rotenone	Robins et al.
318	13	12.6– 61.3	Key Largo	17/11/56	Rotenone	Robins et al.
761	1	124.5	Biscayne Bay	18/4/47	—	J. Sutton
1056	4	17.4–185.0	East Side Virginia Key	11/8/57	Seine	Robins et al.
1229	8	37.2– 62.3	Crawl Key	16/12/56	Rotenone	Robins et al.
1283	5	13.3– 36.3	Little Torch Key	24/8/57	Rotenone	Robins et al.
1842	22	10.5– 16.3	Bear Cut	9/8/56	Seine	de Sylva et al.
1872	4	40.9–122.2	Fort Pierce Inlet	–/7/57	Push net	John Galt and Durbin Tabb
2145	21	13.9– 59.3	Long Key	12/10/57	Rotenone	Robins and Manning
2658	1	106.7	Biscayne Bay	26/8/57	—	D.R. and P.H. Paulson
2737	4	57.3–152.0	Goodland	6/12/57	—	Alan Moffett and Ed Klima
2798	1	13.6	Bahia Honda Key	25/8/57	Rotenone	Robins et al.
2859	5	44.6– 75.3	Upper Matecumbe Key	23–24/2/57	—	A. Moffett and T. W. McKenney
2862	8	24.1– 61.0	Grassy Key	27/10/56	Rotenone	Robins et al.
2887	2	71.1– 87.1	Virginia Key	25/1/58	Rotenone	Robins et al.
2961	3	44.9– 55.0	Virginia Key	13/1/58	Rotenone	D.R. and P.H. Paulson
3118	3	31.7– 66.3	St. Lucie	23/9/57	Push net	Durbin Tabb

3842	14	23.3– 61.5	Key Biscayne
4101	19	30.6– 71.9	Fort Pierce
4687	1	104.0	Key Biscayne
4797	10	27.6– 69.0	Long Key
5042	50	23.5– 75.8	St. Lucie
6668	5	46.5– 75.0	Long Key
7500	1	104.2	Knight Key
7558	3	49.8– 60.6	Key Biscayne
7766	1	50.2	Long Key
7787	4	17.3– 42.8	Little Duck Key
8219	3	11.4– 12.0	Bonito Springs Beach
8236	3	11.5– 70.3	Upper and Lower Matecumbe Keys
8334	14	12.5– 24.7	Virginia Key
8401	2	62.0– 68.2	Whitewater Bay
8450	1	36.3	Anastasia State Park
8626	1	44.7	Coral Gables
8643	1	31.3	Whitewater Bay
8928	5	42.5–149.0	N. Florida Bay
9451	1	23.2	Lower Matecumbe Key
9681	3	12.0– 14.7	Bonito Springs Beach
9914	2	14.2– 14.4	British Honduras, Lighthouse Reef
11472	66	12.4– 21.8	East side, Loggerhead Key, Dry Tortugas
Uncatalogued	12	11.5– 43.6	Lower Matecumbe Key

2/11/57	Rotenone	Robins and Courtenay
15/10/57	Push net	John Gore
22/7/58	Rotenone	Robins and Courtenay
31/1/58	—	Robins et al.
11/9/57	Push net	D. Tabb and David Dubrow
31/1/58	Rotenone	Robins and Courtenay
25/8/57	—	Robins et al.
30/8/58	Rotenone	Paulson et al.
10/10/60	—	Iversen et al.
24/8/58	Rotenone	Paulson et al.
4/8/57	—	S. and R. Cissel
4/6/60	Rotenone	Starck, II and Belcher, III
26/8/58	Seine	Paulsen et al.
17/9/58	—	D. Tabb and Thomas
1/12/60	—	A. Jones
16/2/58	—	—
31/10/59	—	R. B. Manning
15–16/3/58	—	Durbin Tabb
–/9/57	Rotenone	—
13/8/57	—	S. and R. Cissel
3/7/61	Rotenone	W. A. Starck, II
14/7/61	Rotenone	W. A. Starck, II
4/8/62	Rotenone	W. A. Starck, II

beds to feed, adult gray snappers do likewise and are the commonest of these larger fishes. Twenty-four gray snappers speared in grass beds at night ranged from 143 to 388 mm and averaged 244 mm standard length. During the day these larger snappers remain in deeper water of surrounding channels (see below).

When the young snappers reach a size of about 70 to 90 mm, they begin to congregate around brush, logs, and debris on or near the grass flats, near the edges of channels, and along mangrove shorelines or any other feature that offers adequate cover, in depths of up to 6 or 8 ft, usually close to grass areas. Ledges along the edges and ends of channels through grass beds are particularly favored by such fish. These ledges are formed by currents eroding the marl bottom beneath *Thalassia* roots leaving an overhanging ledge of root mat several feet wide. Figure 3B gives the length frequency of 1163 fish taken from around debris, along channel edges, and around mangrove trees in shallow water in the vicinity of Lower Matecumbe Key. Over 90% of these fish were in the 90 to 210 mm size group, corresponding to year classes I, II, and III. Most of these fish disperse into the grass at night to feed.

The gray snapper is the dominant fish in such areas, and the schoolmaster (*Lutjanus apodus*) and the bluestriped grunt (*Haemulon sciurus*) are also often abundant. The crawfish (*Panulirus argus*) is commonly found in such areas.

Slightly larger fish, 170 to 210 mm, tend to move into the deeper water of surrounding channels and bays in depths of 10 to 20 ft. Channels are generally preferred. These channels are cut by tidal currents through marl deposits. They are bordered usually by grass flats or mangrove growths and floored by rock and calcareous sand with patches of grass and often growths of sponges and alcyonarians. Large snappers are generally more numerous along edges bordered by mangroves than along edges bordered by grass. In channels they gather around rocks, coral, ledges, wrecks, and around any other features that furnish adequate cover for fish in their size group Figure 3C shows the length frequency of 189 fish taken in channels near Lower Matecumbe Key. About 90% of these fish are in the 170 to 360 mm size group, corresponding to year classes III through VII.

A rather wide range of sizes of gray snappers is found in channels. Larger predatory fishes which feed in the grass beds are also found in the channels along with several species of wrasses (Labridae), parrotfishes (Scaridae), angelfishes (Chaetodontidae), groupers (Serranidae), snook (*Centropomus undecimalis*), lane snapper (*Lutjanus synagris*), schoolmaster (*Lutjanus apodus*), an occasional cubera snapper (*Lutjanus cyanop-*

terus), lookdown (*Selene vomer*), and spadefish (*Chaetodipterus faber*). Among crustaceans, the crawfish or spiny lobster (*Panulirus argus*), several species of spider crabs, portunid crabs, and xanthid crabs are commonly found.

Shrimp, *Penaeus duorarum*, frequently move through these channels in great numbers. A few may be found at almost any time but they are particularly abundant at night on an outgoing tide when a strong north to northwest wind prevails. At such times, most predatory fishes in the channels, including snapper, will feed heavily on them.

Many larger snappers, over 200 mm standard length, move offshore to patch reefs, wrecks, and the outer reefs. On patch reefs, 1 to 3 miles offshore, snappers of a rather wide range of sizes may be found, as in the channels, though the smallest fish are not as small as those of the channels. The patch reefs are composed chiefly of various head-forming corals, the most important of which is *Montastrea cavernosa*. The bottom in these areas is rock covered by a thin layer of sand or silt. Surrounding areas are usually mixed beds of *Thalassia* and *Halophila* and areas of sponge and alcyonarian growth. Patch reefs support a wide variety of West Indies reef organisms, with several species of parrotfishes (Scaridae), surgeonfishes (Acanthuridae), grunts (*Haemulon*), snapper (*Lutjanus*), and groupers (Serranidae), making up the greater part of the fish biomass.

Gray snappers are also frequent along the outer reefs off the Florida Keys. They are particularly abundant in the summer but many fish remain on the reefs throughout the year. Alligator Reef, off Lower Matecumbe Key, supports a great variety of West Indian reef forms. The author has collected over 300 species of fish from this area and a correspondingly large invertebrate fauna exists there. Gray snappers school during the day primarily at two locations on Alligator Reef. A large school is usually found among the underwater supports of Alligator Lighthouse or in the immediate vicinity. The water here is 4 to 10 ft (1 to 3 m) deep, with a sandy and rocky bottom. This area is exposed to breaking seas during windy weather. The immediate surrounding areas are sand, mixed *Thalassia* and *Halophila*, and coral rubble. A length frequency of 518 fish collected from this school is given in Figure 3D, corresponding to year classes III, IV, and V. About 90% of these fish are in the 200 to 280 mm size range.

About 150 yards south of Alligator Lighthouse is the beginning of a rocky ledge, 15 to 20 ft (4 to 6 m) in depth, running southwest for about 400 yards (350 m). This ledge runs parallel to the main reef tract, is 3 to 8 ft (1 to 2 m) high, and faces northwest, or inshore. Sand and coral rubble begin at the base of the ledge and continue inshore. The top of the ledge is covered with dense growth of the brown algae, *Dictyota*, stinging coral, *Millepora alcicornis*, and alcyonarians. This ledge is a point of concentration for fishes of many species (for description see Schroeder and Starck, 1964. Length frequency of 172 snappers from the ledge is given in Figure 3E, corresponding to year classes V to VIII. The fish from the ledge are considerably larger than those from the lighthouse. Over 90% of these fish are in the 270 to 400 mm size range. In numerous dives both during the day and at night, the author has failed to observe gray snappers in depths over 30 ft (9 m), though several other inshore snappers are often seen along the deeper reef at depths of 90 to 100 ft (27 to 30 m) (see below).

In the Lower Matecumbe Key area the general tendency is for fish of increasing age and size to move into more exposed areas and deeper water. Though there is some overlap, size segregation with habitat is distinct. Fish over 200 mm standard length tend to be found in a wide variety of habitats from channels and bays to offshore coral reefs and smaller fish are more closely tied to areas in, or near, grass beds.

Habitat of Other Snappers

The other common members of the family Lutjanidae, in inshore waters of this region, occupy a less broad range of habitats than does the gray snapper and are less abundant in most areas. The mutton snapper (*Lutjanus analis*) tends to frequent more open areas than the gray snapper. Juveniles are occasionally taken in grass areas around Lower Matecumbe Key, but they do not occur frequently on the Florida Bay side of the Keys. Adults are seen wandering during the day in offshore grass areas over bottom with scattered growths of sponges and alcyonarians and around coral patches from Hawk Channel to the outer edge of the deep reef where they are common in depths of about 100 ft (30 m). They also occur around small rocky patches in 150 ft (45 m) of water well beyond the outer reefs. Here (for a description see Starck and Courtenay, 1962: 161) they are sometimes taken along with red snappers.

Small schoolmasters (*Lutjanus apodus*) are frequently seen in company of gray snappers around brush and other debris near, or on, the grass flats. They also occur around rocks and wreckage in the channels, along rocky shores, on the patch reefs, and on the outer reefs. A large school is present at Alligator Lighthouse, and many are seen along the ledge at Alligator Reef. They, like gray snappers, do not go much deeper than 20 to 30 ft (6–9 m) in this area. Generally, they are more closely associated with rocky areas than is the gray snapper and are not seen in many locations in Florida Bay where gray snappers are common.

An individual cubera snapper (*Lutjanus cyanopterus*) is seen occasionally in schools of gray snappers in the channels and around patch reefs and offshore reefs. A number of cubera are present under the drawbridge at Indian Key Channel. They are seldom smaller than 350 mm and usually over 400 mm. Large individuals have been seen along the outer edge of the deep reef in 95 ft (28 m) of water. On the south coast of Cuba they are fairly common in channels with grass bottom, in depths less than 25 ft (8 m).

Juveniles of the dog snapper (*Lutjanus jocu*) are sometimes seen along the shore, especially in rocky areas. Small adults, 200 to 400 mm standard length, are most often seen in and around caverns in patch reefs and around rocky ledges offshore. Large adults, in the 20 to 30 lb. (9 to 14 kg) size range, are sometimes seen along the outer edge of the deep reef.

Only two juvenile mahogany snappers (*Lutjanus mahogoni*) have been seen in seven years of collecting on Alligator Reef. They are more common in areas farther north and south along the Florida reefs in areas of staghorn coral (*Acropora palmata*) which is almost absent at Alligator Reef.

Lane snappers (*Lutjanus synagris*) are frequently taken as juveniles in grass beds with young gray snappers. The adults occupy mud and sand bottom in bays and channels. They also commonly occur in the sandy, back reef area.

Yellowtail snappers (*Ocyurus chrysurus*) are found from the patch reefs to the outer edge of the deep reef and are apparently less closely associated with bottom types than the other snappers, although they are most common over rough bottom of coral or rocks. Juveniles occur in grass beds, particularly where finger coral (*Porites porites*) is present.

TOLERANCE TO TEMPERATURE AND SALINITY

Temperature

The wide geographic and ecologic range of the gray snapper exposes it to environmental extremes in many localities. The most important of such extremes for a tropical marine organism are low temperatures and low salinities.

Northern records of the occurrence of *Lutjanus griseus* as far as Cape Cod, Massachusetts, have been previously mentioned. Virtually all northern occurrences have been of juvenile fish taken in summer months. Such individuals undoubtedly would not survive the following winter.

Mortalities due to sudden drops in temperature have been mentioned by several authors. Storey and Gudger (1936: 642, 643) reported instances of gray snappers killed by freezes in 1917, 1928, and 1934 at Sanibel Island, Florida. In 1934 air temperature at salt water dropped to 30° F (-1° C) in a few hours after an extended warm spell [October mean at nearby Fort Myers 78.3° F (25.7° C), November 70° F (21.1°)]. Fishermen dipped up 2270 lb. (1032 kg) of stunned snapper, though on the second day individuals still alive had started to recover. In a later paper, Storey (1937: 14) included *L. griseus* in a list of fishes always hurt during freezes at Sanibel Island.

Galloway (1941: 118) described an occurrence of fish killed by cold at Key West, Florida, during the winter of 1939–40. *L. griseus, L. apodus, L. analis,* and *L. synagris* were " . . . everywhere in great numbers" and 40 tons of benumbed fish were handled by a local fish house. The mean maximum air temperature for January was 71.3° F (21.8° C) and the mean minimum was 59.4° F (15.2° C). The lowest temperature was 43° F (6.1° C) on 28 January, the day of the fish kill. Water temperature at the submarine base at Key West was 67° F (19.4° C) on 21 January and decreased to 57° F (13.9° C) by 28 January. On 26 and 27 January no dead fish were seen.

Gunter (1945: 62) recorded one dead specimen of *L. griseus* taken by a trawl in Aransas Bay, Texas, in January 1942. Water temperature was 9.1° C and salinity was 16.1%.

More recently, Springer and Woodburn (1960: 40) found two dead specimens at Cross Bayou near St. Petersburg, Florida. This occurrence was after the cold wave of 14 December 1957, at which time water temperatures were 13.0° C.

During the period of this study, a minor cold kill occurred on 14 December 1962. Fish seen in small numbers on the shores of Lower Matecumbe Key at Lignumvitae Channel included the following: *Carcharhinus leucas, Lutjanus synagris, L. jocu, L. apodus, Ocyurus chrysurus, Haemulon plumieri, H. parrai, Anisotremus virginicus, Eucinostomus* sp., *Lagodon rhomboides, Sphyraena barracuda.* Two schools of gray snappers were seen at that time in a nearby canal. These schools were tightly grouped almost motionless fish consisting of about 30 to 50 individuals. Their orientation and spacing approached the school derived pod defined by Breder (1959: 404). On 15 December three similar groups of several hundred individuals each were found in a different position in the same canal. Two schools were around brush in locations where only one or two snappers are normally seen. The largest schools were in a dead-end branch of the canal which is less than 10 ft (3 m) deep and dug into coral rocks. After several days, these schools disappeared. The fish involved were mostly in the 100 to 300 mm range of standard length. Water temperature near one of the small schools of fish on 14 December was 53° F (11.7° C). The same temperature was also recorded at that time on the ocean side of Upper Matecumbe Key. Water temperature near the large schools on 15 December was 58° F (14.4° C). At this time they readily took a baited hook.

Though no dead gray snappers were seen at Lower Matecumbe Key, Terry Starck saw several along with numerous dead bonnethead sharks (*Sphyrna tiburo*) in shallow water near Green Mangrove Key, about 5½ nautical miles away, in Florida Bay.

Judging from these records, the lower lethal limit of the gray snapper apparently falls between about 11 and 14°C. The exact point, of course, would be affected by differences in populations and size of fish, if any, acclimatization of the individual, rapidity of change, and other environmental factors such as salinity (see Doudoroff, 1957: 408).

The more northern range of the gray snapper and its absence among snappers killed by the cold at Lower Matecumbe Key, even though it is the most common lutjanid in the immediate area, indicate a lower lethal temperature, for *L. griseus* than for the other inshore species of snappers.

Salinity

Published occurrences of gray snapper in fresh water have been previously mentioned in the section on habitat. The frequent presence of gray snapper in fresh water does not mean, however, that the gray snapper, as a species, should be classed as an estuarine organism—populations exist, in Bermuda for example, where the species is never exposed to fresh or even brackish water. The preponderance of small juveniles in published records of occurrences of gray snappers in fresh water is probably due to the preference of juveniles for inshore grass beds where they are frequently exposed to low salinities, rather than any direct preference for low salinities. An indirect benefit, however, might result from low salinities which would exclude a good number of potential marine predators on, and competitors of, young snappers. Adult gray snappers in fresh water, though less frequent than juveniles, are by no means uncommon.

In Florida, certain springs and spring-fed rivers are often invaded by gray snappers (Herald and Strickland, 1949: 105; Odum, 1954; 142), particularly in winter months. These springs offer water at a constant temperature, around 70°F (21.1° C), and may be entered as a refuge from colder inshore marine waters.

Odum (1954: 142) described the gray snapper as a species limited to oligohaline or almost oligohaline water and reported the lowest chlorinity observed, where occurrence was frequent, as 50 parts per million in Chasschowitzka Springs, Florida. Fresh waters of Florida are generally high in calcium, and Black (1957: 193) pointed out that many investigators have noticed that the presence of calcium salts in fresh water greatly increased the viability of marine animals in that medium. Other factors may also affect tolerance to low salinities. Osmoregulatory failure at near lethal low temperature has been found in some fish (Doudoroff, 1957: 409). Breder (1934: 81) found that small individuals of *Lutjanus opodus* died if placed suddenly in low-salinity water which they could otherwise tolerate by gradual acclimatization. Populational differences in salinity tolerance of the gray snapper have not been investigated.

The other species of inshore lutjanids in the West Indies area have been less frequently reported from low-salinity waters. *Lutjanus jocu* was included among fish from the Gatun Locks of the Panama Canal (Hildebrand, 1939: 27) and from rivers in western Cuba (Eigenmann, 1902: 221). Tabb and Manning (1961: 620) recorded juveniles of *L. synagris* from salinities as low as 13% in northern Florida Bay.

PREDATORS

Little is known about predators of the gray snapper. Almost any of the larger carnivorous fishes in the grass beds are potential predators on young snappers. In the channels and on the reefs the most important potential predators of snappers are the great barracuda, *Sphyraena barracuda,* and the green moray, *Gymnothorax funebris.*

A barracuda was seen to strike an adult gray snapper on one occasion: A poison collection of fish was being made on the reef top near Alligator Lighthouse. Young grunts, *Haemulon aurolineatum*, affected by the poison were swimming erratically near the surface, and several snappers from a nearby school left the school and began to feed on the grunts. One of the snappers approaching a grunt was struck by a barracuda of about 20 lb. (9.1 kg) and rapidly eaten.

Morays are active at night when snappers feed. Snappers, on the reef, are occasionally seen with wounds similar to those made by morays. Barracuda have been observed to be very active at dusk in the immediate vicinity of schools of milling snapper.

Three stomachs of the cubera snapper were examined during this study, and one (411 mm standard length) taken from among a school of gray snappers was found to contain a gray snapper (158 mm standard length).

PARASITES, DISEASES, AND MALFORMATIONS

Linton (1910) reported nine species of trematodes from gray snappers at the Dry Tortugas, Florida, and Manter (1934: 175) again recorded one of these species at the Dry Tortugas from gray snapper. In a later paper (Manter: 1947) listed eight digenetic trematodes from the gray snapper at the Dry Tortugas and several differed from those in Linton's paper. Robert E. Schroeder, studied the trematode parasites of gray snapper in the Lower Matecumbe Key area and has cooperated closely with the present writer. His results are reported in the second part of this volume.

Linton (1908: 86) examined nine specimens of *L. griseus* at Bermuda and found an acanthocephalan worm, *Echinorhynchus medius,* encapsulated on the viscera. He also found an immature nematode, possibly *Ascaris*, the adults of *Heterakis foveolator* Rudolphi, another nematode, and an unidentified species of *Heterakis*. One cestode, *Rynchobarium speciosum* Linton, was found encysted on the viscera, and the cub shark (presumably *Carcharhinus leucas*) was suggested to be the adult host.

Four parasitic crustaceans have been reported from the gray snapper. The isopod, *Exocirolana mayana* Ives, was stated to be abundant on the gray snapper at Bermuda (Yeatman, 1957: 346). Wilson (1935: 33) took a single specimen of the copepod, *Caligus irritans*, from the mouth of a gray snapper caught at the Tortugas. Pearse (1954: 357) collected several specimens of two species of caligoid copepods, *Hatschekia albirubra* and *H. oblonga*, from the gills of *Lutjanus griseus.*

Many gray snappers have small black spots on them which appear to be caused by the cysts of a parasitic worm. Occasional individuals will be heavily infested (Figure 15).

Tumorous growths are often seen on gray snappers and they seem to increase in frequency with larger fish. Field observations indicate that about 5 to 10% of the fish at Alligator Reef have these growths. Most growths are about pea size though a few fish, perhaps 1%, have large growths, several centimeters wide (Figure 4). Growths were observed on all portions of the body except the ventral surfaces. One or more small tumors may be present. If a tumor is large, only one usually is present. Tumors have not been observed on other species of lutjanids in the area. Adult gray snappers occur in more shallow water than other snappers, and perhaps actinic damage is a contributing factor. In shallow areas gray snappers prefer shade when it is available.

One fish with a melanistic tail and caudal peduncle and another with the lower jaw partially missing have been seen.

ABUNDANCE

The relative abundance of gray snappers varies with habitat. Small snappers in grass beds may be the most abundant fish in one area and yet be entirely absent in another. Around brush, in channels, and along channel ledges at Lower Matecumbe Key gray snappers are the most abundant medium-sized carnivores. Almost every piece of brush, debris, ledge, or other suitable cover supports a population of gray snappers. Up to 200 may be present around the remains of a small tree and over 1000 may be present around a wreck or other large feature.

On patch reefs and at Alligator Reef, lutjanids are second only to grunts, Pomadasyidae, in order of abundance of medium-sized predaceous fishes. At specific locations on certain patch reefs, at Alligator Lighthouse, and at the ledge on Alligator Reef, the gray snapper is the dominant snapper. In the reef area as a whole, however, yellowtail snappers and perhaps mutton snappers are more numerous. The school at Alligator Lighthouse ranges in size from about 500 fish or less in the winter to several thousand in July and August. On the ledge at Alligator Reef, 50 to 100 fish are present during the winter months and increase in number to perhaps 500 in July and August.

The total population of gray snappers in the area covered by the map in Figure 5 would undoubtedly run into the hundred thousands.

Figure 4. Gray snapper, *Lutjanus griseus* (355 mm standard length) from ledge at Alligator Reef, Florida, with large tumor on side.

3. Color Pattern; Age and Growth; Morphology

COLOR PATTERN OF THE GRAY SNAPPER

The basic color pattern of *Lutjanus griseus* is gray dorsally with white countershading. The exposed posterior portion of each scale is typically pigmented gray to dark brown with a white border around the pigmented area; scale pigmentation creates a series of dark dotted lines on the body following the scale rows. The dark lines are separated by white areas. Above the lateral line the dark area of each scale is larger, producing a darker and more uniform pattern. Beneath the lateral line, the dark area on each scale decreases in size producing a more distinctive pattern of dark lines and white stripes. Below the level of the pectoral fin, the dark area of the scale centers decrease gradually in size and become less distinct. The ventral surface of the body is white. The dorsal fin is edged with dark brown except for the transparent posterior portion of the soft dorsal; the tips of the dorsal spines are white; the membrane between the dorsal spines and rays is pale gray. The caudal fin is pale gray to brown at the base as are the upper and lowermost rays. The center of the caudal fin is lightly pigmented, almost transparent; the posterior edge of the caudal fin is tinged with black. The anal fin is lightly pigmented and its ventral border is maroon except for the edge which is tinged with white. The pectoral fins are transparent and the pelvic fins are white. The head and iris are gray. Small specimens often exhibit a narrow blue line running from the middle of the upper jaw to the posterior tip of the operculum. A second blue line may parallel the first from the upper jaw to the ventral margin of the eye. A broad brown to black ocular stripe runs obliquely from the tip of the upper jaw through the eye to just beneath the anterior end of the dorsal fin. This stripe may appear and disappear in a matter of a few seconds.

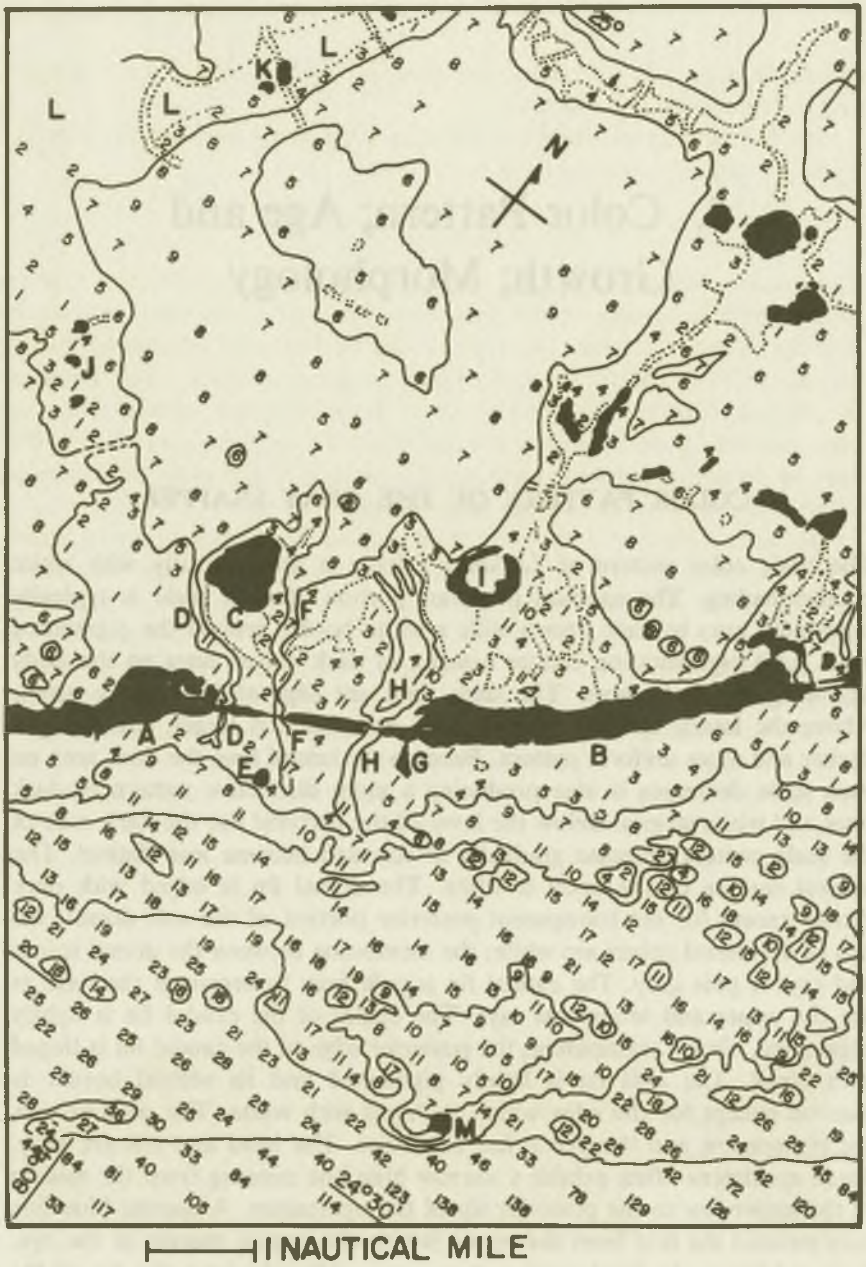

Figure 5. Map of area around Lower Matecumbe Key, Florida. A: Lower Matecumbe Key; B: Upper Matecumbe Key; C: Lignumvitae Channel; D: Lignumvitae Channel; E: Indian Key; F: Indian Key Channel; G: Teatable Key; H: Teatable Key Channel; I: Shell Key; J: Peterson Keys; K: Twin Keys; L: Twin Keys Bank; M: Alligator Reef.

The pattern described appears to be basic though various features may be intensified or reduced depending upon habitat, size of fish, light conditions, and emotional state.

Very small specimens in grass beds may be much more darkly pigmented with some pigmentation even ventrally. The fins are transparent, except for the dark outer edge of the spinous dorsal fin. The ocular stripe has a median pale portion bordered on both sides by dark lines. Faint traces of the dotted lines on the body may be evident but intermediate areas are also pigmented. The overall appearance is a uniform dark brown.

Medium-sized specimens on grass flats, around debris, and along channel edges around Lower Matecumbe Key have a pattern similar to the one described above. They are generally less heavily pigmented than small specimens from the grass, and the dotted lines on the body are very distinct, generally reddish brown. Their fins are less transparent, the dark areas of the dorsal and anal are greater, and the pelvics are white. The ocular stripe (sometimes missing) is uniformly dark and the blue subocular line is usually present though it may be variously broken. General appearance is that of a pale gray fish with dark flecks on the body.

Larger fish in channels and on the reef are generally paler. The dark area of each scale is less intense and less distinct, and the resulting dotted lines are not so obvious though still present. Intermediate areas and the ventral surface of the body are less white. The blue subocular line is usually absent. Fins are less transparent and tend to be gray. The dark area on the anal and dorsal fins may be less distinct and the pelvics also tend to gray. The overall appearance underwater is that of a uniformly gray fish (Figure 6).

Tabb and Manning (1961: 619) report that gray snappers become rich red brown to umber in the brackish waters of Coot and Whitewater bays, where humic acids often color the water a deep coffee brown.

Jordan and Evermann (1922: 407) state that gray snappers are often taken in considerable depths in the company of "red snappers" and that deep-water specimens are usually redder than shallow-water examples. Fowler (1945: 302) described a 390-mm specimen from Key West, Florida, that had the back deep red slightly tinged with brown, a golden sheen on the sides, and its undersurface brilliant red. The iris was yellow and stained red. The vertical fins were red, suffused with olive to dusky, the anal most brilliant. Paired fins were orange red.

The following color description of West African specimens was given by Copley (1952: 127): dark green above, scale centers black with a whitish edge, head, belly, and below the lateral line coppery red but the top of the

Figure 6. Color pattern of the gray snapper (*Lutjanus griseus*). Upper left: Adult snapper during day at Alligator Lighthouse. Upper right: Large juvenile snapper at night. Lower left: Large juvenile snapper at night showing blotched pattern. Lower right: Large juvenile snapper at night showing barred pattern.

head is a dark olive green. Iris dark red, tail black, other fins pale maroon. This description does not compare well with that of western Atlantic specimens.

Significance of Color Pattern

The color pattern of the gray snapper is obviously quite variable and the different patterns appear to be of adaptive significance.

Small dark fish in the grass have a color closely matching that of dead *Thalassia* blades. Medium-sized fishes are paler with dark flecks. This pattern appears to be associated with their moving from grass beds to more open areas around debris, etc. Such areas generally have a bottom of pale marl or sand with dark flecks of various material. Larger fish tend to a more uniform gray pattern which is well adapted to their habits and habitat. On the reefs and in channels, adult snappers school at varying distances above the bottom and individual fish viewed from different angles appear different against different backgrounds. Viewed from a lower level, the fish appears against the usually gray green water with which his color blends well. Fish higher above the bottom generally tend to be paler than those nearer the bottom. Seen from a higher level, the same fish appears against the bottom which may be dark grass or pale sand, marl, rock, or coral rubble; the paler bottoms are more generally the case. They are generally off-white due to growths and detritus. The gray color of *Lutjanus griseus* is a good compromise for a fish which might be seen against several such backgrounds at once, depending upon the location of the viewer.

A tendency to red in deeper waters has also been noted in some serranids (Robins and Starck, 1961: 269). Reddish colors appear as various shades of gray or brown in deeper water due to the absence of red light, hence a red phase in deeper water serves only to maintain a gray or brown color pattern.

Gray also appears on a number of other species of reef fishes which may be characterized as reef rangers (Longley, 1961: 735) or species that are found near the reef in rubble areas but not so much among the living coral. Among such fishes are several sharks, certain sea basses (Serranidae), cubera snappers, (*Lutjanus cyanopterus*), a few grunts (Pomadasyidae), chubs (Kyphosidae), some damselfishes (Pomacentridae), the doctorfish (*Acanthurus chirurgus*), and barracuda (*Sphyraena barracuda*). One grunt, *Haemulon parrai*, has a pattern very similar to *Lutjanus griseus*, and the two species often school together over coral rubble areas near the reef (Figure 31).

At dusk on Alligator Reef, large schools of various grunts, schoolmaster snappers, and gray snappers begin milling about, and all become quite pale so that it becomes difficult to see them and to distinguish the species or even the families except when a sharp silhouette is presented. With darkness, they disperse to various areas to feed.

Gray snappers exhibit at least three different color patterns at night (Figure 6): one is similar to the day pattern but paler as described above. An ocular stripe may be present. This pattern is usually associated with life in marl, sand, or rubble areas. Another is a series of six to eight pale bars which appears along the side of some individuals and seems to be associated with areas of sparse grass. And third, in heavy grass, especially when the fish are resting, a pattern of large pale blotches on a darker background has been observed. A similar blotched night pattern has also been observed in several species of grunts where it seems to be associated with areas of rocks or coarse rubble (Schroeder and Starck, 1964: 130).

Three other changes worth noting have been observed: First, individuals being cleaned of ectoparasites by the neon goby (*Gobiosoma oceanops*) at Alligator Reef were much darker when being cleaned than immediately before or after. A similar darkening has also been observed in the bar jack (*Caranx ruber*) while being cleaned by the wrasse (*Bodianus rufus*). The significance of this change is unknown. It does not appear to be associated with camouflage, for the snappers were over very pale, almost white, bottom near a small coral head while being cleaned. Perhaps the change is due to a general relaxation since freshly killed fish also become dark.

Second, death is accompanied by darkening of the body and the appearance of a reddish tinge in the normally pale ventral and lateral areas. Therefore, the above color descriptions of the gray snapper, except for the smallest specimens from the grass beds, are based on live material, underwater observations, and underwater color photographs taken both with available light and electronic flash.

Third, at Alligator Reef during the day, only occasional individuals exhibit an ocular stripe. If disturbed by a diver, the stripe rapidly disappears. When a small spotted moray (*Gymnothorax moringa*) crossed an open area of coral rubble near a large school of gray snappers, about 10 or 12 of the closest snappers approached to within a few inches of the eel and rapidly assumed the dark ocular stripe. Several other snappers in the immediate vicinity also acquired the stripe while the remainder of the school, though only a few feet away, seemed to take little notice. The eel then moved under a rock and the snappers rejoined the school where they gradually lost their ocular stripe. The eel in this case was about 80 cm long and much too large to be eaten by the snappers involved. On another occasion the same school of snappers was fed live, scaled sardines (*Harengula pensacolae*). Initially, only an occasional individual exhibited the dark stripe. After their attention was aroused by throwing over several sardines which were rapidly caught, most of the fish in the immediate area, perhaps 50, showed the ocular stripe while the main body of the school 50 to 100 ft away remained without the stripe. As long as feeding continued, the stripe remained; it became especially intense in individuals approaching a sardine. When feeding stopped, the fish gradually lost their stripe.

Function of the ocular stripe is uncertain. The stripe tends to obscure the eye and, hence, may make it more difficult for the prey to perceive if the snapper is watching it. Smaller snappers around brush, channel edges, etc., usually have the stripe during the day. In this case, the stripe might appear like a blade of dead grass or stick thus obscuring the eye and serving as camouflage for the entire fish as well as the eye. Fish in deeper channels like those on the reef only occasionaly have the ocular stripe.

Color Patterns of Other Snappers

The other common inshore snappers differ variously from the gray snapper. The cubera snapper (*Lutjanus cyanopterus*) is most similar to the gray snapper but usually darker. It is dusky gray above and paler ventrally. Dorsal, caudal, and anal fins are gray black; the soft dorsal, caudal, and anal are darker than the spinous dorsal. Pelvic fins are gray above, white below. The head and iris are dusky gray and a trace of the blue subocular line is present. This color description was based on a dead specimen taken in a channel. In life it displayed several pale bars similar to those shown in the gray snapper in Figure 6. Almost all individuals of the cubera snapper will show these bars in life. Pale gray individuals have been seen mixed in with a school of gray snappers on the reef over white bottom. That the cubera snapper has a darker color as compared with the gray snapper corresponds well with its preference for deeper water, rock ledges, etc., which are darker habitats. The red phase of gray snappers might well appear similar to the cubera in those locations.

Schoolmasters (*Lutjanus apodus*) are yellowish brown dorsally, pale below, and usually show about eight narrow vertical pale bars on the body as is the case for the cubera and gray snappers. Scales on the lower part of the side show a central orange spot which forms streaks along the scale rows. An ocular stripe similar to that of *Lutjanus griseus* is sometimes present. A blue subocular line, especially in small individuals, extends from the snout to the angle of the opercle. The iris is yellowish brown. The spinous dorsal is edged with orange and the soft dorsal, caudal, anal, and pelvic fins are orange yellow. Pectoral fins are a pale orange yellow. Individuals at Alligator Reef exhibited the pale bars on the body in sunlit areas but lost these in the shade. Fish lacking the bars rapidly acquired them when speared. Without the bars schoolmasters appear much like dog snappers. Schoolmasters characteristically school close to rocks or coral in the day and feed in rocky areas at night.

Many fishes associated with rock or coral areas are yellow. Several grunts, the yellow goatfish (*Mulloidichthys martinicus*), some chaetodontids and pomacentrids, and a number of wrasses at Alligator Reef have predominant yellow markings. Though the association of yellow and a rock or coral habitat is rather good, the adaptive significance of this association is unclear. Much yellow exists in such a habitat. Yellowish algae, sponges, alcyonarians, and coral are abundant and, in shallow areas, surface waves focus light on corals, etc., producing a continuous pattern of yellowish flashes. The fishes mentioned above, however, are readily seen by a human observer, though they are not conspicuous like a neon goby, for example.

Dog snappers are, like schoolmasters, closely associated with rocky or coral areas and display yellow in their color pattern. They are generally darker than the schoolmaster—a fact which corresponds well with their cavernicolous habits. They are also similar to the schoolmaster snapper in overall pattern though they lack the ocular stripe and pale bars on the body. The general hue is coppery red rather than yellowish brown. A mesial bronzed spot is present on the dorsal and lateral scales. The spinous dorsal has an orange band at the base and edge. The soft dorsal and pectorals are pale reddish brown; the caudal yellowish orange and the anal and pelvics tend more to orange. The blue subocular line is irregular and broken into small round and oblong spots. Beneath the eye a distinct but not sharply defined pale triangle is present.

Mutton snappers are olive green dorsally. Some scales have pale blue spots which form irregular streaks running obliquely up and back. The ventral surfaces are white tinged with red. About six pale vertical bars may be present as in the gray snapper. An irregular, blue subocular line is present from snout to opercle. The iris is red. Pelvic, anal, and lower lobe of the caudal fins are rosy. Pectoral fins are transparent tinged with red. The edge of the dorsal and upper portion of the caudal are yellowish. The caudal fin is tipped with black on the posterior border and a black spot about the size of the pupil is present just above the lateral line and below the anterior portion of the soft dorsal. Occasional large adult mutton snappers lack the lateral spot.

A red phase exists in deep water, below 100 ft (30 m). This phase is red dorsally and paler below. The blue subocular line, yellow tinge to dorsal and caudal, and black lateral spot remain. This phase is often confused with the red snapper, and Plate 20 in Evermann and Marsh (1902) labeled red snapper (*Neomaenis aya*) is a mutton snapper.

Underwater, mutton snappers appear gray green dorsally, shading to pale gray ventrally not greatly unlike the gray snapper. The greenish tendency probably reflects their tendency to occupy grass areas. In deeper water the red phase appears gray. At a distance underwater, the most conspicuous features are the pupil and black lateral spot.

Lane snappers are generally rose colored, becoming white below. Dorsally they are only slightly olive green. A series of yellow stripes are present along the sides of the body and several extend onto the head. Above the lateral line, the stripes run obliquely up and back. The lower lateral areas are yellowish. The spinous dorsal is almost transparent with a yellow band at the base and margin, soft dorsal pink with a yellow margin, caudal red with a black margin, pelvic and anal fins yellow, pectorals transparent pink. The lips and iris are red. A dark lateral spot larger than the eye is present in the same location as on the mutton snapper.

The underwater appearance of the lane snapper is that of a very pale fish against a pale background of sand or mud. The most conspicuous features are again the pupil and lateral spot.

Lack of fresh specimens does not permit a detailed color description of the mahogany snapper. The description of colors given by Evermann and Marsh (1902: 179) does not agree well with underwater observations and specimens collected by the author. Freshly killed specimens appear reddish brown, becoming red dorsally and white ventrally. The posterior border of the caudal is dark. A dark lateral spot slightly larger than the eye is present in a similar location as in the two preceding species.

Underwater, this species appears very pale, and against the sand and rubble bottoms where it is usually found the only conspicuous features are the pupil and lateral spot.

The three preceding species all wander individually or in small numbers during the day in exposed areas and all blend well with their background except for pupil and lateral spot. In these fish the pupil is the one conspicuous feature impossible to camouflage, hence a false eye has apparently evolved because of its confusion effect. The lateral spot though relatively larger in the lane and mahogany snappers is about the same absolute size in average adults of all three species.

Yellowtail snappers are pale olivaceous dorsally with a faint violet tinge. A bright yellow median stripe runs from the snout through the eye to the caudal peduncle. The median stripe increases in width caudally to include the dorsal surface of the caudal peduncle. Above this line are a number of large yellow blotches on the side of the back. Below the yellow stripe, a series of yellow lines follow the scale rows along the side of the body. The ventral lines are fainter. Between the lines are wider, pale pink intermediate areas. The dorsal fin is generally yellow, the caudal yellow, the anal pale yellow, and the pectoral and pelvic fins are transparent. The lower position of the head is rose colored with yellow spots. The iris is red.

Yellowtail snappers are a wide-ranging reef species, active both at night and in the day. They move about more freely in mid-water than do species of *Lutjanus*. Underwater, yellowtail snappers appear predominantly pale gray and yellow. In mid-water they are readily seen by a human observer though they are not attention-attracting. They blend well with yellowish alcyonarians around which they often rest. Other yellowish features of the reef environment have been discussed above. Yellowtail snappers may also exhibit a pattern of blotches similar to that described above for the gray snapper.

In considering the adaptive significance of color of these species, several factors must be considered. Color patterns within a species may vary with habitat, stress or other emotional factors, size, light intensity, viewing conditions, and death. Sexual dichromatism and breeding colors have not been noted in these fish. Because of such factors, adaptive significance is best considered on the basis of *in situ* observations. Submarine conditions may affect the appearance of a color pattern in various ways. The spectrum of incident light is increasingly attenuated by travel through water. Red is rapidly eliminated. Scattering reduces resolution and merges smaller features of a color pattern. The intensity of existing colors is also lessened to the observer by suspended particles which are generally of a pale hue giving a "muddy" appearance to color.

The rather brilliant colors of a mutton snapper viewed close up at a depth of 15 ft appear not unlike they do on the surface, though the reds and pinks are less brilliant. At a viewing distance of 30 ft in the same depth, however, a total light path, from surface to fish to observer, of 45 ft, has eliminated the reds; the smaller features, such as the blue lines on the back, have merged; and the olive green of the back appears gray green due to intervening pale-hued particles. The net result is a pale fish, gray green dorsally, which blends well with its environment.

AGE AND GROWTH

Publications on Age and Growth

Published information concerning the growth rates of tropical marine fishes is scarce. Limited data are available on the gray snapper. Croker (1962: 380) gave observed and calculated mean fork length based on scale readings of 815 fish taken near Flamingo in Everglades National Park and five fish from Biscayne Bay, Florida. Some of his data are given in Table 2.

Ingle et al. (1962) included growth among other data on tagged gray snappers and other fish from various areas in Florida. Seven gray snappers showed an average growth increment of 11.7 mm in 15 to 53 days, average 33.9, along the southwest coast of Florida. One specimen apparently decreased in length. On the southeast coast they reported 61 recoveries, for which length data are available; 12 length reductions were noted and the

Table 2. Observed and calculated mean fork lengths found by Croker (1962: 380) for *Lutjanus griseus* in Northern Florida Bay

Age Group	Number of Fish	Mean Fork Observed	Lengths in mm Calculated
	2	88	—
I	53	158	81
II	504	244	180
III	234	260	241
IV	19	318	295
V	5	357	352
VI	2	479	431
VII	1	470	456

remainder averaged a 7.5 mm increment. About 91% of the 119 fish recovered were caught within 60 days. Of 10 snappers showing the greatest length increment, only one was recorded free over 60 days.

Three gray snappers tagged by Randall (1961: 222) in the Virgin Islands were recovered in 59 to 234 days. Growth of these fish averaged 3.1 mm per month.

Age and Growth From Scales

During the present study, scales of 1289 fish were examined for annuli. One hundred and ninety-seven were rejected due to replaced centers, injuries, etc. Several scales were taken from the mid-lateral area of each specimen. On many large individuals, however, many scales have been replaced, and sometimes scales from other parts of the body had to be used.

Scale impressions on cellulose acetate were made at first, but microscopic examination of the scale itself was found to give better results. Measurements were made with an ocular micrometer from the focus anteriorly to each annulus and to the scale edge, and from the last annulus to the scale edge. One scale from each fish was utilized for this purpose.

Several features aid in recognizing an annulus: different refractive properties give a difference in shade to the annulus, lighter or darker depending upon lighting conditions. The circuli at an annulus are broken and irregular, radii often branch at an annulus, and annuli are always concentric with the scale margin.

Figure 7. Scales from a specimen of *Lutjanus griseus* 363 mm standard length, from Alligator Reef, Florida. Upper scale shows seven annuli and several intermediate marks. Lower scale is replaced.

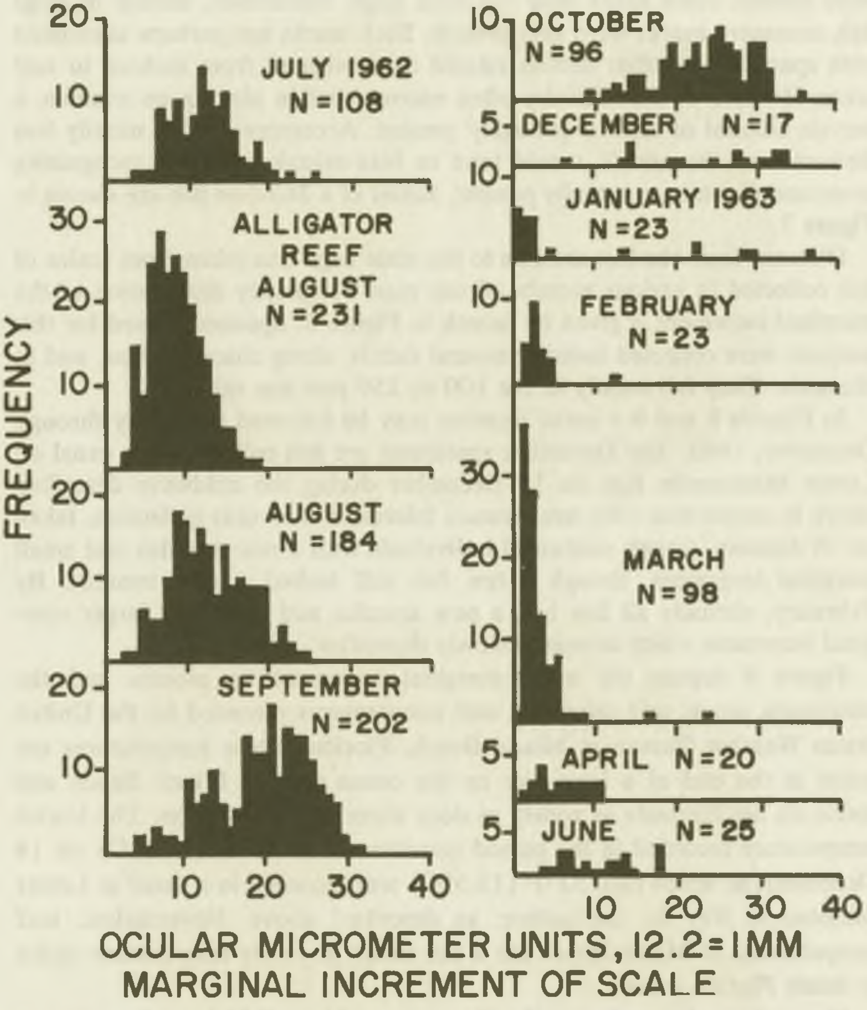

Figure 8. Frequency distribution by month of marginal increment of scales (distance from the last annulus to the scale edge) of *Lutjanus griseus* from inshore areas in the vicinity of Lower Matecumbe Key, Florida. August marginal increments of snapper from Alligator Reef showing lesser increment are also included.

In many instances annuli were very difficult to determine. The first annulus on scales from large fish was especially troublesome. Increased scale thickness in large fish probably helped obscure this annulus. Annuli were located more easily near the scale edge. Sometimes, mostly in large fish, accessory marks were also present. Such marks are perhaps associated with spawning or other factors related to movement from inshore to reef areas. Because of the difficulty often encountered in placing an annulus, a certain amount of error is probably present. Accessory marks, usually less distinct than the annuli, would tend to bias mistakes toward recognizing more annuli than are actually present. Scales of a 363-mm fish are shown in Figure 7.

Distance from the last annulus to the scale edge was taken from scales of fish collected in various months of the year. Frequency distribution of the marginal increment is given by month in Figure 8. Specimens used for this purpose were collected inshore, around debris, along channel edges, and in channels. They fall mostly in the 100 to 250 mm size range.

In Figures 8 and 9 a mean increase may be followed from July through December, 1962. The December specimens are fish collected in a canal on Lower Matecumbe Key on 15 December during the coldwave described above in connection with temperature tolerance. The next collection, taken on 19 January, largely contained individuals with a new annulus and small marginal increment, though a few fish still lacked a new annulus. By February, virtually all fish had a new annulus and a slightly larger marginal increment which increased slowly thereafter.

Figure 9 depicts the mean marginal increment by months and the maximum, mean, and minimum surf temperatures recorded by the United States Weather Bureau at Miami Beach, Florida. These temperatures are taken at the end of a long pier on the ocean side of Miami Beach and hence do not fluctuate as widely as does water in shallow bays. The lowest temperature recorded in the period considered was 65°F (18.3°C) on 14 December, at which time 53°F (11.6°C) was recorded in a canal at Lower Matecumbe Key by the author, as described above. Nevertheless, surf temperatures at Miami Beach are a fair index of yearly temperature cycles in South Florida waters.

No snappers taken during the December cold spell had yet formed new annuli, though a month later most fish examined had a new annulus and small marginal increment indicating annulus formation at or shortly after the December cold snap. Average temperatures, however, are lower in January and lowest in February.

Croker (1962: 381) found a few fish with new annuli in December 1959 more in January 1960 and all with a new annulus by February. Temperature conditions at Miami Beach during this period are given in Table 3.

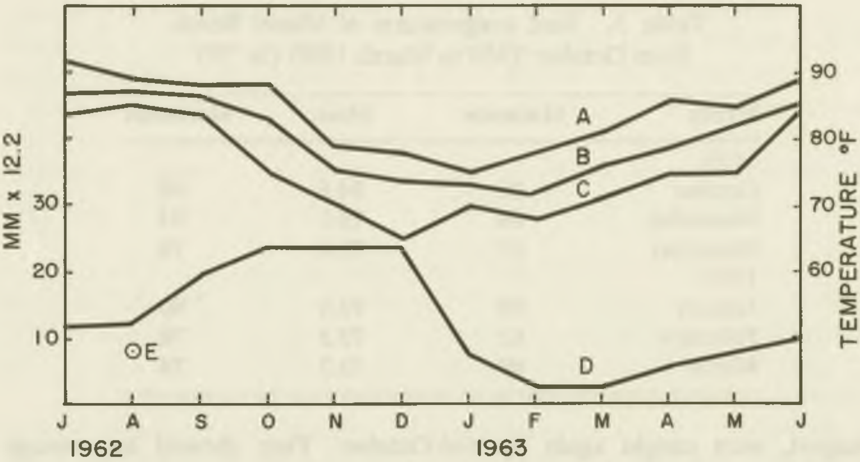

Figure 9. Relationship between temperature and marginal increment of scales in *Lutjanus griseus* (12.2 occular micrometer units = 1mm). A. B. and C: Maximum, mean, and minimum surf temperatures at Miami Beach, courtesy U.S. Weather Bureau, Miami. D: Mean marginal increment of scales by months. E: Mean marginal increment of scales from snapper caught at Alligator Reef in August 1962.

Annulus formation again follows closely a sudden drop in temperature, this time in November. Apparently annulus formation in gray snappers from Florida is initiated by sudden drops in temperature during late fall. After acclimatization has taken place, growth resumes so that a small marginal increment occurs during the succeeding period even though mean water temperature may be lower.

Figure 9 shows a marked increase in marginal increment from August to October, which is also the period of highest mean and least variable water temperature. The August increment was 12.1 ocular micrometer units, which by October had increased to 23.1. This 11.0 increase in two months is 47% of the maximum of 23.4 in December. Whether or not body growth is proportional to scale growth during this period is unknown. Van Oosten (1957: 241) pointed out that body and scale seldom grow in an absolutely fixed ratio. Calcium deposition is facilitated by higher temperatures; perhaps scale growth is thus stimulated.

Limited data from tagged fish (Table 4), however, lend support to the idea that growth is greatest in August and September. Of eight fish tagged at Alligator Reef and recovered in inshore waters, five, tagged in early

Table 3. Surf temperatures at Miami Beach from October 1959 to March 1960 (in °F)

Month	Minimum	Mean	Maximum
1959			
October	81	84.6	90
November	68	79.1	84
December	69	72.6	76
1960			
January	60	73.4	80
February	62	75.3	78
March	69	73.7	79

August, were caught again by mid-October. They showed an average monthly growth rate of 9.4 mm in fork length. Of the remaining three, two were tagged during the first half of August and one on 1 September. These fish remained at large from 100 to 285 days and averaged 6.3 mm monthly growth. Fish tagged and recovered at Alligator Reef were not considered here since they exhibited much lower growth rate than fish from inshore areas.

The mean marginal increments in August for fish from Alligator Lighthouse and the ledge on Alligator Reef are included in Figures 8 and 9. The smaller increment of fish from the reef may be due to reduced growth rate in larger fish and also reduced growth in the reef environment.

Scale size was found to be sufficiently linear in proportion to body size (Figure 10) to permit direct back calculation of standard length from scale annuli. Distance from the focus to each annulus and to the scale edge were used in back calculations of size. A nomograph was constructed for back calculations which permitted an accuracy within 1 to 2 mm in calculated standard lengths.

Several features in Figure 10 need comment. Scale size approaches zero at about 10 mm standard length. No scales were found on a 10.5-mm postlarval fish, the smallest examined. Because of the difficulty often encountered in finding an original (nonreplaced) scale on larger fish, scales from various body areas were often taken. When possible scales were taken from the mid-lateral portion of the body where they are largest, hence an increasing number of scales from other body regions in larger fish produces the appearance of proportionately smaller scales in those fish. However, if

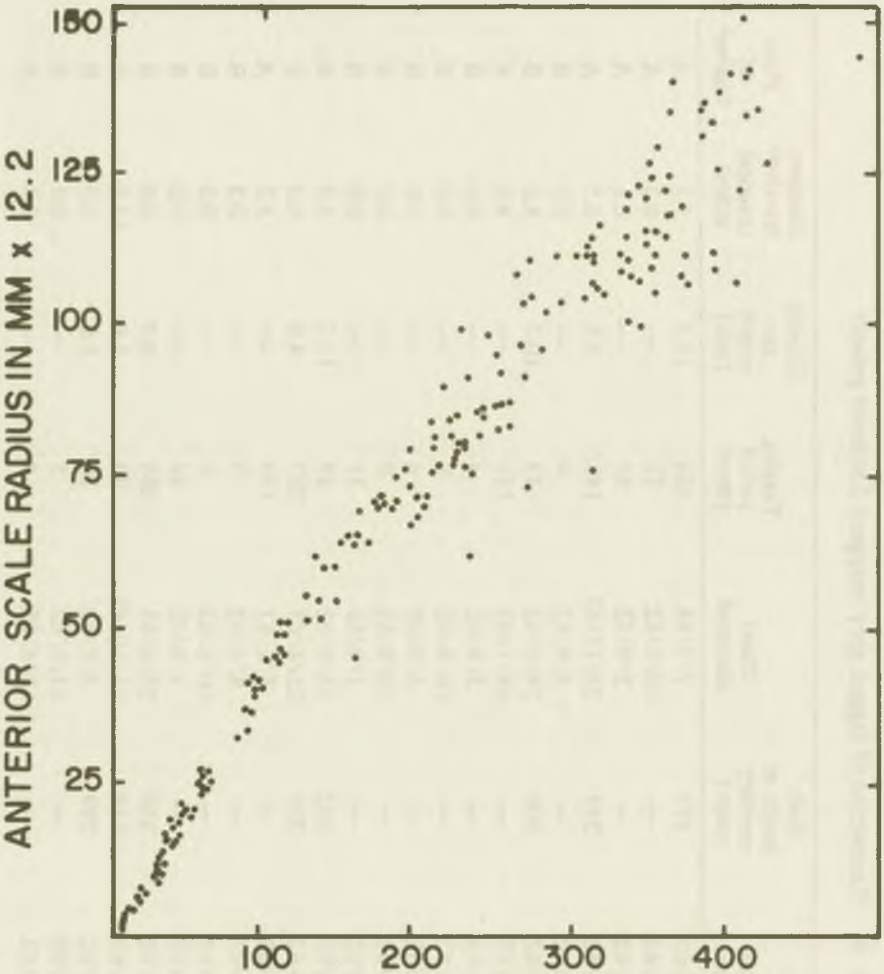

Figure 10. Anterior radius (focus to anterior edge) of scales plotted against standard length in *Lutjanus griseus.*

only fish over 90 mm standard length are considered, any true departure from linearity in the relationship between scale size and standard length is negligible as far as the effect upon back calculations of standard length from scale annuli is concerned. Scales of only three fish under 90 mm were used in back calculations of length.

Table 4. Recoveries of tagged gray snappers *Lutjanus griseus*

Tag number	Fork length at tagging (mm)	Date[1] tagged	Fork length at recovery (mm)	Date[1] recovered	Tagging period (days)	Growth per month (mm)	Distance traveled[2] (nautical miles)	Place of tagging[3]
22	140	8/7/62	274	7/7/63	364	11.2	5.1	A
28	234	10/7/62	—	30/8/62	51	—	0.3	A
44	125	8/7/62	—	2/9/62	56	—	0.1	A
69	190	6/8/62	243	28/11/62	145	4.8	0.5	A
103	362	1/8/62	—	5/8/62	4	—	0.0	B
104	298	1/8/62	306	24/8/62	23	10.7	8.0	B
105	290	1/8/62	—	19/1/63	171	—	8.0	B
107	310	1/8/62	—	5/8/62	4	—	0.0	B
115	271	1/8/62	—	10/8/62	9	—	0.0	B
124	305	1/8/62	—	5/8/62	4	—	0.0	B
135	305	1/8/62	—	10/8/62	9	—	0.0	B
144	358	1/8/62	—	1/9/62	31	—	0.0	B
145	295	3/8/62	302	22/8/62	19	11.2	3.4	B
161	290	1/8/62	325	25/4/63	267	4.0	0.0	B
168	195	19/8/62	—	5/1/63	170	—	1.5	A
171	268	1/8/62	—	8/8/62	7	—	0.2	B
184	295	1/8/62	—	10/8/62	9	—	0.0	B
185	360	1/8/62	—	5/8/62	44	—	0.0	B
199	324	3/8/62	330	25/4/63	265	0.7	0.0	B
203	305	3/8/62	319	14/10/62	72	5.9	13.5	B
228	298	3/8/62	299	3/8/62	29	1.0	0.0	B
239	307	6/8/62	—	11/8/62	5	—	0.0	B
243	272	6/8/62	—	10/8/62	4	—	0.0	B

245	300	6/8/62	—	8/8/62	2	—	0.2	B
252	302	6/8/62	—	10/8/62	4	—	0.0	B
256	368	3/8/62	—	11/8/62	8	—	0.0	B
269	294	6/8/62	—	12/8/62	6	—	0.0	B
270	370	3/8/62	—	18/8/62	15	—	0.0	B
272	273	6/8/62	—	29/8/62	23	—	3.6	B
278	328	6/8/62	—	13/8/62	7	—	12.1	B
281	278	6/8/62	—	8/8/62	2	—	0.2	B
283	274	3/8/62	294	–/11/62	ca. 100	6.0	10.0	B
284	303	6/8/62	—	10/8/62	4	—	0.0	B
291	330	6/8/62	—	11/8/62	5	—	0.0	B
292	288	3/8/62	287	1/9/62	29	–1.0	0.0	B
293	285	3/8/62	—	11/8/62	8	—	0.0	B
296	290	6/8/62	331	18/5/63	285	4.3	18.7	B
298	287	6/8/62	—	11/8/62	5	—	0.0	B
303	330	11/8/62	—	18/8/62	7	—	0.2	B
309	256	11/8/62	254	13/8/63	367	–0.2	0.0	B
312	329	11/8/62	—	18/9/62	38	—	22.0	B
315	266	11/8/62	—	19/8/62	8	—	6.2	B
330	306	11/8/62	357	5/2/63	178	8.7	3.7	B
335	298	6/8/62	—	8/8/62	2	—	0.0	B
344	288	6/8/62	288	14/3/63	220	0.0	4.7	B
351	320	11/8/62	—	18/8/62	7	—	40.5	B
355	284	11/8/62	285	1/9/62	21	1.5	0.0	B
365	271	11/8/62	290	25/4/63	257	2.3	0.0	B

1. Date is day, month, year.
2. Minimum distance by water from point of release to point of recovery.
3. Tagging locations: A. Lower Matecumbe Key; B. Alligator Lighthouse; C. Teatable Key Channel; D. Captive Fish.

Table 4—*Continued*

Tag number	Fork length at tagging (mm)	Date[1] tagged	Fork length at recovery (mm)	Date[1] recovered	Tagging period (days)	Growth per month (mm)	Distance traveled[2] (nautical miles)	Place of tagging[3]
377	283	6/8/62	307	22/10/62	77	9.5	9.0	B
378	291	11/8/62	294	1/9/62	21	4.5	0.0	B
386	309	11/8/62	—	1/9/62	21	—	13.5	B
388	286	11/8/62	—	7/8/63	362	—	0.0	Probably B
431	274	11/8/62	282[4]	15/3/63	216	1.1	0.0	B
441	153	23/8/62	—	24/8/62	1	—	0.0	C
500	169	1/9/62	168	22/9/62	21	−1.5	0.0	A
533	318	1/9/62	330	8/10/62	37	9.9	5.2	B
941	290	4/3/63	303	13/10/63	223	1.8	—	D

1. Date is day, month, year.
2. Minimum distance by water from point of release to point of recovery.
3. Tagging locations: A. Lower Matecumbe Key; B. Alligator Lighthouse; C. Teatable Key Channel; D. Captive Fish.
4. Fork length estimated from standard length by use of Figure 13.

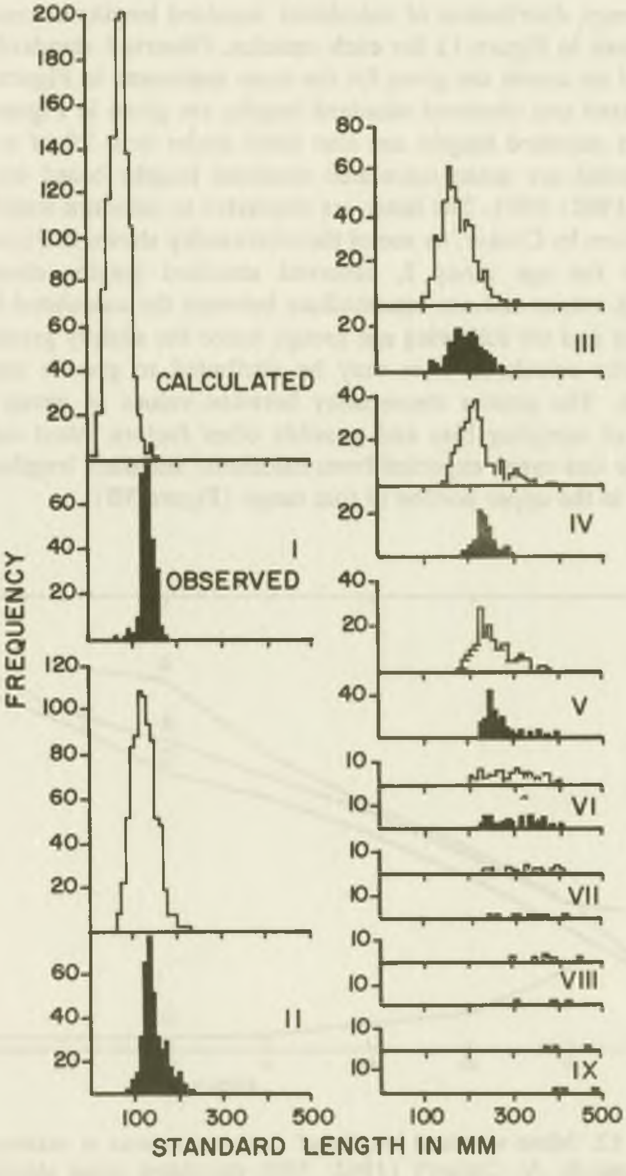

Figure 11. Frequency histograms of standard length calculated from scale annuli and of observed standard lengths of fish having scales bearing from one to nine annuli. *Lutjanus griseus* from the general vicinity of Lower Matecumbe Key, Florida.

Frequency distribution of calculated standard lengths at annulus formation is given in Figure 11 for each annulus. Observed standard lengths by age based on annuli are given for the same specimens in Figure 11. Means of calculated and observed standard lengths are given in Figure 12 (mean calculated standard lengths are also listed under item 20 of conclusions); also included are mean calculated standard lengths based on data from Croker (1962: 380). The latter are converted to standard length from fork length, given by Croker, by use of the relationship shown in Figure 13.

Except for age group I, observed standard lengths closely parallel calculated values and are intermediate between the calculated length for a given year and the following age group; hence the slightly greater observed values over calculated ones may be attributed to growth since annulus formation. The greater discrepancy between values of group I fish is a function of sampling bias and possibly other factors. Most collections of fish in the size range expected from calculated standard lengths of group I fish were in the upper portion of that range (Figure 3B).

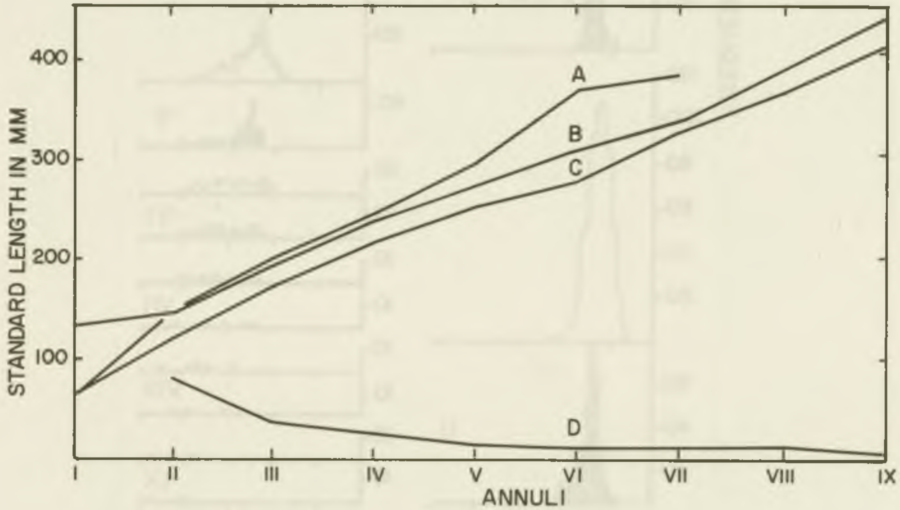

Figure 12. Mean standard lengths of *Lutjanus griseus* at various ages based on scale annuli. A: Croker's (1962: 380) calculated mean standard lengths. B: Mean observed standard lengths of snapper from Lower Matecumbe Key having scales with one to nine annuli. C: Mean calculated standard lengths at annulus formation for snapper from Lower Matecumbe Key. D: Increase in lengths over length at the previous annulus in percent.

A wide range of sizes is found in any given age group. Several factors may be involved in producing such differences. Difficulty in locating annuli will result in underestimates of age in some cases and accessory marks will lead to determinations of greater age than is actually present in others. Widely differing growth rates from one area to another and even between individuals in a school were found in tagged fish (see below). Another factor involved is the wide range of sizes at the time of formation of the first annulus due to the lengthy spawning season (see the section on reproduction).

Despite the possible sources of error involved, growth rates calculated from scale analysis are reasonably close to observed growth rates of tagged

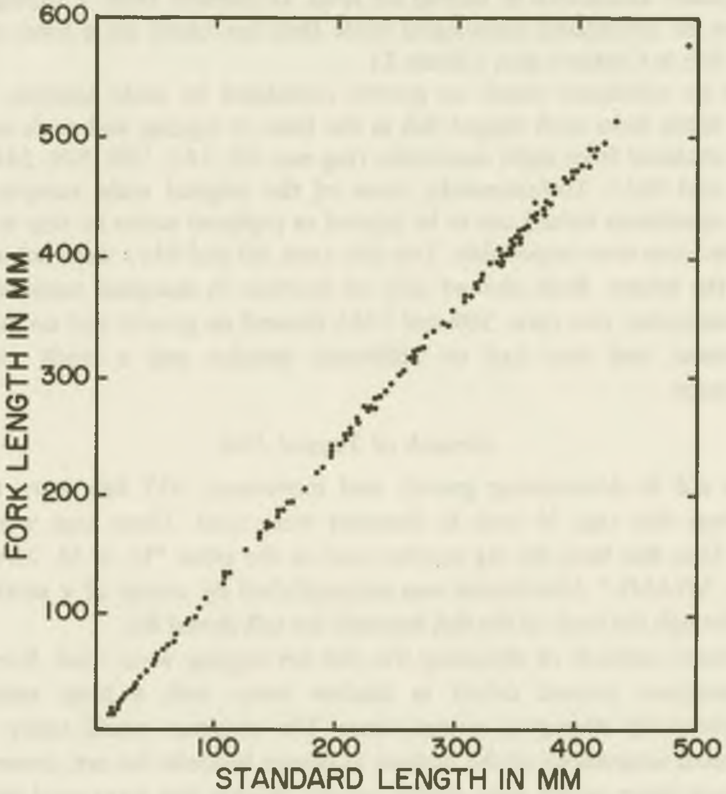

Figure 13. Relationships between fork length and standard length in *Lutjanus griseus* from Florida.

fish. Eleven tagged fish at large from 72 to 367 days showed an average increment in fork length of 3.9 mm per month or 46.5 mm per year. These fish were from 256 to 324 mm standard length when tagged; therefore, this growth rate is approximately the calculated rate for fish of their size. Fish at large from 21 to 37 days were not considered since they were at large only during the high growth period indicated for August and September and because of the greater significance of measurement error over such a short interval.

Croker's calculated values differ in several respects from those in the present study. At year I they are similar. Values are parallel but higher in years II, III, and IV and differ more widely from V to VII. A greater growth rate from I to II may be related to the rich grass beds in northern Florida Bay as opposed to the area around Lower Matecumbe Key and to the greater abundance of shrimp for food. Differences from V through VII cannot be considered meaningful since they are based on a total of only eight fish in Croker's data (Table 2).

As an additional check on growth calculated by scale analysis, scales were taken from each tagged fish at the time of tagging and scale samples were obtained from eight recoveries (tag nos. 69, 161, 199, 309, 344, 365, 431, and 941). Unfortunately, most of the original scale samples from these specimens turned out to be injured or replaced scales so that accurate comparisons were impossible. Two fish (nos. 69 and 941) were not at large over the winter. Both showed only an increase in marginal increment. Of the remainder, two (nos. 309 and 344) showed no growth and no marginal increment, and four had an additional annulus and a small marginal increment.

Growth of Tagged Fish

To aid in determining growth and movement, 912 fish were tagged. Peterson disc tags ⅜ inch in diameter were used. These tags were pale blue. One disc bore the tag number and on the other "U. of M. MARINE LAB. MIAMI." Attachment was accomplished by means of a nickle wire pin through the back of the fish beneath the soft dorsal fin.

Several methods of obtaining live fish for tagging were tried. Surrounding snappers around debris in shallow water with a large seine was unsuccessfully attempted several times. The snappers would make use of any small irregularity of the bottom to escape beneath the net; however, in the same place grunts were readily caught. Wicker fish traps used throughout the West Indies were also tried but caught very few gray snappers, although schoolmaster and other fish were obtained in quantity. Hook and line fishing using nylon monofilament line and a small hook with no sinker or leader proved to be the most productive method. Live pilchards (*Harengula* spp.) or shrimp (*Penaeus duorarum*) were far better than dead bait.

Date, exact location, several scales, standard length, and fork length were taken from each fish tagged.

Tagging, especially of larger fish, was greatly facilitated by use of an anesthetic, quinaldine. About ½ to 1 cc in 3 or 4 gal of seawater was found to be sufficient to produce anesthesia in adult snappers within 30 seconds to 1 minute. Quinaldine is not readily soluble in water and shaking or stirring is necessary. It is inexpensive in the quantities used and a mixture was generally used for several days without loss of effect. Anesthetized fish usually recovered and rejoined their school in less than a minute after release.

Of the 912 fish tagged, 232 were in the immediate vicinity of Lignumvitae Channel, 264 at Twin Key Bank, 56 at Peterson Keys, 61 at Teatable Key Channel, and 25 captive fish at Lower Matecumbe Key—to a total of 638 fish tagged in inshore areas. These fish were tagged from July through October, 1962, except for one fish in June 1962 and the 25 captive fish that were tagged in March 1963. The remaining 274 fish were tagged at Alligator Lighthouse in August 1962. The majority of inshore fish were tagged by Raymond Brooks and Terry Starck and the Alligator Reef fish by the author. Standard lengths of tagged fish were largely in the 125 to 300 mm range.

Fifty-seven recoveries of tagged fish were made (Table 4). Seven recoveries were from fish tagged at Lignumvitae Channel, one from the captive fish, one from Teatable Key Channel, and 48 from fish tagged at Alligator Reef. In addition, an estimated 30 fish from Alligator Reef were brought into the local fish market in August 1962, within three weeks of release.

Several factors contribute to the high incidence of recovery of fish tagged at Alligator Reef: a high number of tagged fish in one school, heavy fishing pressure at that spot, selective underwater recovery, better tag retention by large fish, and a high catch rate for this size fish. Recoveries were made by hook and line fishermen and by selective underwater spearing of tagged fish by the author.

A high tagging mortality and loss of tags is indicated for small inshore fish. Underwater observations within a few weeks of tagging revealed many tag-bearing fish at Alligator Reef but few to none in inshore areas. Eight months to a year later, at least five tagged fish were seen at Alligator

Lighthouse; none was seen in inshore areas where fish were released. Within a few weeks of inshore tagging, several small fish were seen with tear wounds as if a tag had been pulled out, and one tag was found on the bottom. Small fish moving about among debris and in grassbeds probably keep tag wounds irritated or rip out the tag by entangling it.

Shortly after tagging, several large fish at Alligator Lighthouse were seen with necrotic areas around the tag, but all fish examined after two months or more at large appeared well healed around the tag. Two fish were recovered in 1963 with one disc of the tag missing and the bent end of the nickle wire pin embedded in the body and healed over. Another fish had one disc of a tag completely buried in its body and healed over.

After several months, tags were covered with algae, although the legend was still legible when the growth was removed. Underwater, the tags appear as a dark spot similar to the lateral spot of the mutton snapper. A tagged fish (no. 161) at large 267 days is shown in Figure 14.

Several patterns of growth emerge from the data in Table 4. Growth data were obtained from 18 recoveries of fish tagged at Alligator Lighthouse. Nine of these fish remained at Alligator Reef and exhibited an average growth rate of 1.7 mm per month (fork length). Four of the nine were out 21 to 29 days—growth rate averaged 1.8 mm per month; the remaining five were at large 216 to 367 days with an average growth of 1.6 mm per month. The other nine recoveries of fish tagged at Alligator Lighthouse were made at various locations 3.4 to 18.7 nautical miles away. These fish averaged 7.4 mm growth per month. All but one of these fish had moved to inshore habitats. The one exception (tag no. 344) had moved to a pile of ballast from an old wreck off Lower Matecumbe Key. This habitat is similar to a patch reef and this fish was the only one of the group that left Alligator Reef that showed no growth. If this fish is not considered and if only the eight fish moving into an inshore habitat are considered, then growth averages 8.4 mm per month. Five fish in this group at large 19 to 77 days averaged 9.4 mm per month growth whereas those out 100 to 285 days averaged 4.8 mm per month, or 6.3 mm if number 344 is excluded. The overall growth rate of all 18 fish was 4.55 mm per month; this compares well with growth rate calculated from annuli. Greater growth rate of fish at large over a short period is probably a function of their being at large only during the high growth period indicated for August and September from marginal increment of scales. Randall (1961: 259) demonstrated that growth of tagged individuals of *Acanthurus triostegus* in Hawaii ceased completely during winter months.

Figure 14. Tagged gray snapper, *Lutjanus griseus* (No. 161) collected 267 days after tagging.

Reduced growth of fish that remained on the reef is probably related to greater competition for food in the densely populated and spacious reef environment.

Four other recoveries of snappers tagged in inshore areas yielded growth data. Period at large were 20, 145, 223, and 364 days and growth per month 0.0, 4.8, 1.8, and 11.2 mm respectively. The 1.8 mm growth was of a captive fish described below and the 11.2 mm growth is possibly erroneous, as information on recovery was secondhand. Three of the above 22 fish showed negative growth of 1 to 2 mm. Two were measured after some time in a freezer and negative growth may be attributed to shrinkage by desiccation. The other individual differed by only 1 mm, a not unlikely error in measurement. All were considered to show no growth for purposes of growth-rate calculations.

The effect of tagging on growth is unknown. Randall (1962: 210) stated that there is little doubt that tagging has a deterring effect on the growth of some species. That some snappers grew well when tagged means that absence of growth cannot be attributed solely to tagging. Hence, individuals showing no growth have not been excluded from calculations of mean growth.

Other Determinations of Age and Growth

Experiments on growth of captive fish were unsuccessful. A section of canal 35 by 80 ft and 2 to 4 ft deep was enclosed by a fence. Sixty-six fish from 120 to 150 mm standard length were measured and placed in the enclosure along with 25 tagged fish, in early March 1963. Brush was thrown in for cover and natural food was supplemented by feeding. The fish did well for several months until an extreme tide allowed most of them to escape. The remaining fish slowly decreased in number from unknown causes until by 13 October 1963, only one fish was found. It bore tag number 941 and had grown 13 mm in a little over seven months.

Although the experiment was unsuccessful, the method seems feasible, and the fish, while present, appeared to do well.

Determination of growth from length frequency modes is not useful with gray snappers since their habit of schooling in groups of like size and difference in habitat between different sized fish produce biased samples. The long spawning period and wide range of growth rates also obscure differences in size of fish in different year classes.

The only available data on related species are from the study by Rodríguez (1962) on the lane snapper (*Lutjanus synagris*). Using otoliths for age determination, Rodríguez found a similar growth pattern to that described above for the gray snapper.

MORPHOLOGY

Size

Records of the maximum sizes of the gray snapper are uncertain due to the confusion between it and *Lutjanus cyanopterus* (Figure 15). Captiva and Rivers (1960: 8) reported a catch of gray snappers with an average weight per fish of 20 lb. (9.1 kg). The possible misidentification of these specimens has been confirmed by Harvey Bullis (personal communication). Rathjen (1960: 130) reported on a different catch during the same experimental trawling work and he distinguished *L. griseus* from *L. cyanopterus.* The former averaged 2 lb. (.91 kg) each the latter 20 lb. (9.1 kg) each.

Erdman (1956: 317) stated that *L. griseus* grows larger than the 16 to 18 lb. (7.3 to 8.2 kg) mentioned in literature. He recorded a 30.5 lb. (13.9 kg) specimen, 36 inches (92 cm) total length, caught at La Parguera, Puerto Rico. He wrote that the local fishermen know the pargo to grow over 100 lb. (45.5 kg) though he mentioned that such large fish may be cuberas. He believed the 30.5-lb. specimen to be *L. griseus* even though the backward projection of the vomerine teeth was absent. This backward projection is characteristic of *L. griseus* and absent or reduced in *Lutjanus cyanopterus* (Evermann and Marsh, 1902: 170; Rivas, 1949: 150). Larger specimens examined, in the 3 to 5 lb. (1.4 to 2.3 kg) size range, during the present study, showed no decrease in the backward projection of the vomerine teeth.

Gray snappers were reported by Jordan (1884: 126) rarely to exceed 8 lb. (3.6 kg) at Key West, Florida. In a later work Jordan and Evermann (1922: 407) stated that gray snappers attain a length of 3 ft and weight of 18 lb. (8.2 kg) at Key West, Florida.

Figure 15. Gray snapper, *Lutjanus griseus* (274 mm standard length) and cubera, *Lutjanus cyanopterus* (440 mm). Note cysts on head and pectoral fin of gray snapper and small tumor at base of caudal fin.

Weights rarely over 8 lb. and a maximum of 18 lb. are probably closer to being correct limits for the gray snapper than the preceding weights. During the present study, large adults in the 3 to 4 lb. (1.4 to 1.8 kg) size range were frequently encountered, and the largest fish weighed was 5¼ (2.8 kg) lb. No notably larger individuals were seen among thousands of fish observed underwater.

Of the remaining species of inshore lutjanids, the cubera is the largest. Florida anglers have taken specimens weighing over 100 lb. (45.5 kg). The next largest is the dog snapper, which probably does not exceed about 30 lb. (13.6 kg), though angling records often confuse the cubera with the dog snapper, resulting in greater recorded sizes for the latter. Mutton snappers reach a size of 20 to 25 lb. (9.1 to 11.4 kg), though normal adults of this species are in the 10 to 15 lb. (4.6 to 6.8 kg) size range in comparison with average adult dog snappers which are usually less than 10 lb. Yellowtail, mahogany, and schoolmaster snappers are generally under 3 lb. (1.4 kg) when adult, and the lane snapper is usually less than 1 lb. (.45 kg).

Figure 16 gives the length-weight relationship of 233 specimens of gray snapper from around lower Matecumbe Key and Alligator Reef. Figure 17 presents the same information using the cube root of the weight and depicts a slight departure from linearity for larger specimens. This relative decrease in weight with increase in size is associated with a more elongate body in larger fish as indicated by the decreasing body depth of large fish shown in Figure 19.

Size is important to fishes in several ways: it affects the availability of

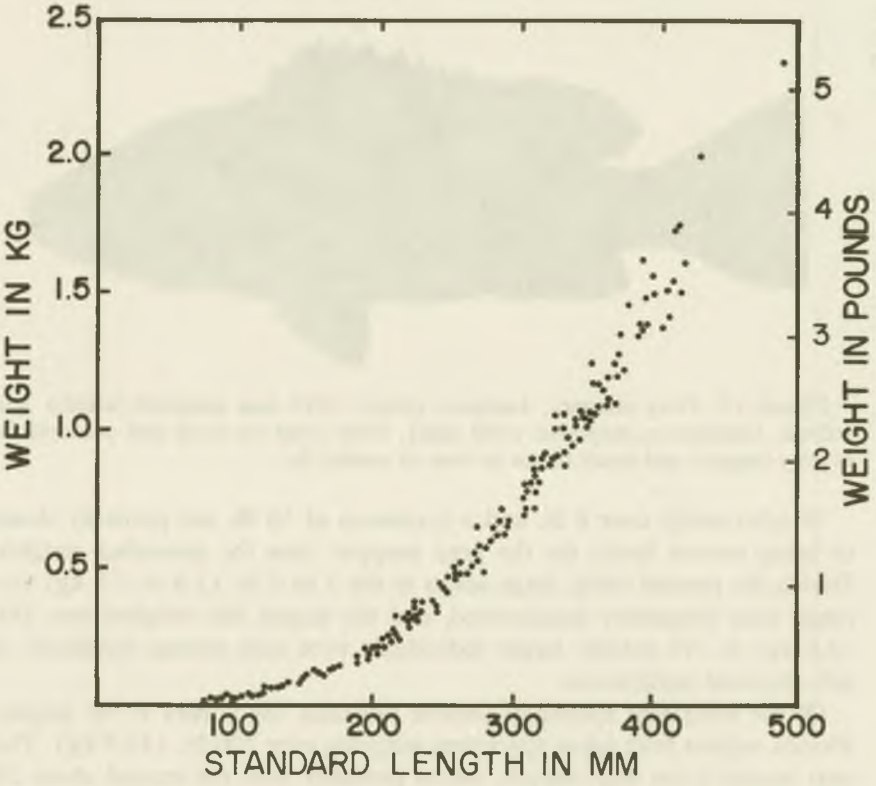

Figure 16. Length-weight relationship of *Lutjanus griseus* from the vicinity of Lower Matecumbe Key, Florida.

adequate cover, it may govern the number and size of eggs produced, it affects swimming ability, and it controls to some extent the range of

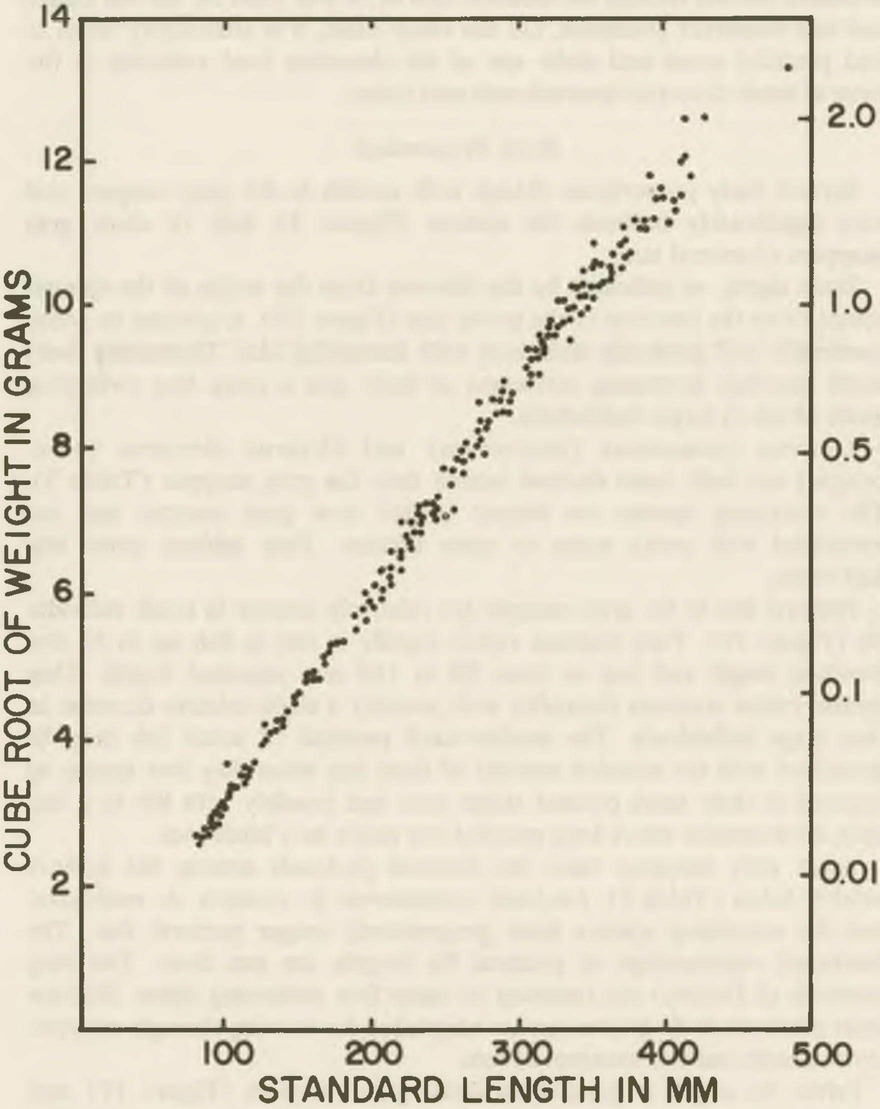

Figure 17. Length-weight relationship (using cube root of weight) of *Lutjanus griseus* from the vicinity of Lower Matecumbe Key, Florida.

predators on the fish and limits the range of effective food items. *Lutjanus griseus* is large enough to produce large quantities of eggs, to make rather extensive diurnal feeding movements, and to be free from all but the bigger and less abundant predators. On the other hand, it is sufficiently small to find plentiful cover and make use of the abundant food available in the form of small demersal invertebrates and fishes.

Body Proportions

Several body proportions change with growth in the gray snapper and vary significantly between the species. Figures 15 and 18 show gray snappers of several sizes.

Body depth, as indicated by the distance from the origin of the spinous dorsal fin to the insertion of the pelvic fins (Figure 19), is greatest in young specimens and gradually decreases with increasing size. Decreasing body depth parallels increasing tereteness of body and a more free swimming mode of life in larger individuals.

Lutjanus cyanopterus (piscivorous) and *Ocyurus chrysurus* (semi-pelagic) are both more shallow bodied than the gray snapper (Table 5). The remaining species are deeper bodied than gray snapper and are associated with rocky areas or open bottom. They seldom move into mid-water.

Pectoral fins in the gray snapper are relatively shorter in small individuals (Figure 19). They increase rather rapidly in size in fish up to 50 mm standard length and less so from 50 to 100 mm standard length. They remain rather constant thereafter with possibly a slight relative decrease in very large individuals. The smaller-sized pectoral of small fish may be associated with the rounded contour of these fins when they first appear as opposed to their more pointed shape later and possibly with life in a less open environment where long pectoral fins might be a hindrance.

Adult gray snappers have the shortest pectorals among the inshore lutjanid fishes (Table 5). *Lutjanus cyanopterus, L. synagris, L. mahogoni,* and the remaining species have progressively longer pectoral fins. The functional relationships of pectoral fin lengths are not clear. The long pectorals of *Ocyurus* are common to many free swimming fishes. Perhaps short pectorals in *L. griseus* are an adaptation for moving through crowded environments such as mangrove roots.

Pelvic fin length is greatest in small gray snappers (Figure 19) and decreases gradually thereafter. Most free-swimming fishes have small pelvic fins and the decreasing pelvic length of the gray snapper parallels the decreasing body depth and freer-swimming mode of life with increasing size.

Figure 18. Juvenile gray snappers, *Lutjanus griseus*, at various sizes. Top to bottom: UMML 1842, 10.5 mm standard length; UMML 11472, 14.4 mm; 19.9 mm; 48.5 mm. The two latter are uncataloged specimens from Lower Matecumbe Key, Florida.

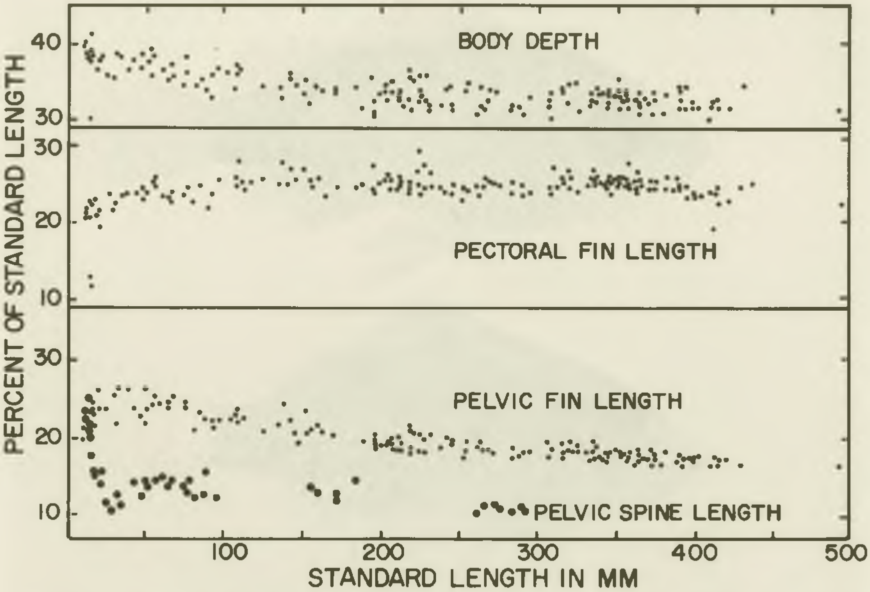

Figure 19. Body depth (origin of first dorsal to origin of pelvic fins), pectoral-fin length, and pelvic-fin length expressed as a percent of standard length plotted against standard length in *Lutjanus griseus*.

The pelvic spine is generally longer than the fin in specimens from 10 to 15 mm standard length. The spine decreases rapidly in relative size to 20 mm standard length and gradually thereafter. Strong spines are common in many postlarval fishes and probably serve to reduce predation on them by smaller organisms.

Lutjanus griseus, L. cyanopterus, and *Ocyurus chrysurus* have the shortest pelvic fins of the inshore lutjanids (Table 5) and are more shallow bodied and free swimming than the others. *Lutjanus jocu* has the longest pelvic fins and is the species most closely associated with rocky holes and caverns.

Strongly developed spines are also present in the dorsal and anal fins of young gray snappers. The relative length of these spines decreases rapidly with increasing standard length (Figure 20). The third dorsal spine of very small snappers is longer than the fourth, though the fourth dorsal spine is longest in adults. The second anal spine is longest in small juvenile snappers, and the third anal spine longest in adults. Measurements were also taken of the longest ray of the soft dorsal and anal fins (Figure 20). They are similar in that they increase rapidly in length between 10 to 15 mm standard length and reach a maximum between 50 and 100 mm standard length. Over 100 mm, they gradually decrease their relative size. The rapid increase at 10 to 15 mm is late postlarval development of individuals just settling down from a planktonic larval period. The gradual decrease throughout the adult life is again a parallel of increasing tereteness. Reduction of soft dorsal and anal fin length is found in a number of free-swimming fishes and may also be associated with the greater propulsive efficiency of a large fish over a small fish.

Young gray snappers have relatively large heads (Figure 21). Head length decreases proportionately and moderately up to 100 mm standard length and gradually thereafter. A large head in small individuals is a character common to many vertebrates. It is associated with rapid early development of the sensory systems and respiratory and feeding mechanisms.

Head lengths of the other inshore snappers are given in Table 5. *Lutjanus cyanopterus, L. analis,* and *Ocyurus chrysurus* have smaller heads than does the gray snapper. In *L. cyanopterus* and *Ocyurus chrysurus* the relatively smaller head is a function of a more elongate body. The smaller head of *L. analis* may be the result of a smaller mouth and eyes. The large head of *L. apodus, L. jocu, L. synagris,* and *L. mahogoni* are correlated with deeper bodies, larger eyes, and large mouths.

Snout length of the gray snapper is analyzed in Figure 21. Gradually increasing snout length with increasing size may be largely accounted for by decreasing eye size. Snout lengths for other lutjanids are given in Table 5. The mid-water feeding *Ocyurus chrysurus*, which has a relatively small terminal mouth, has the smallest snout length, and *L. analis,* a bottom feeder with a more ventrally situated mouth, has the longest snout length.

Orbit length is used as an index of eye size in *L. griseus* (Figure 21). The large eye of juveniles and the early rapid decrease in size becoming more gradual in large fish is the pattern found in most fish. This pattern reflects the early importance of vision. The eye must attain a certain minimal size to function effectively and likewise reaches a certain maximum size beyond which effectiveness is not increased by increasing size.

Orbit lengths of the inshore lutjanid fishes are given in Table 5. The

Table 5. Morphometric data on eight common inshore lutjanid fishes of the West Indies region. Mean values are underlined.

Origin of spinous dorsal fin to origin of pelvic fins

Percent of standard length:	29	30	31	32	33	34	35	36	37	38	39	40	41
Lutjanus griseus			2	2	$\underline{2}$	4							
Lutjanus cyanopterus	1	1	$\underline{2}$	1									
Lutjanus apodus								1	1	$\underline{3}$	3		2
Lutjanus jocu									2			$\underline{3}$	3
Lutjanus synagris										2	$\underline{3}$	3	2
Lutjanus analis			$\underline{1}$		$\underline{1}$			$\underline{3}$	2	2			
Lutjanus mahogoni						1	$\underline{7}$	1	1				
Ocyurus chrysurus		1	$\underline{4}$	2	2	1							

Pectoral-fin length

Percent of standard length:	23	24	25	26	27	28	29	30	31	32	33
Lutjanus griseus	1	$\underline{7}$	1	1							
Lutjanus cyanopterus		1		$\underline{2}$	2						
Lutjanus apodus					1	1		$\underline{2}$	2	3	1
Lutjanus jocu				1		1		$\underline{1}$	3	1	1
Lutjanus synagris				2	$\underline{2}$	2	3				
Lutjanus analis						1	2	$\underline{3}$	1	1	1
Lutjanus mahogoni					1	1	$\underline{4}$	2	1	1	
Ocyurus chrysurus						2	2	5			

Percent of standard length:	18	19
Lutjanus griseus		6
Lutjanus cyanopterus	2	1
Lutjanus apodus		
Lutjanus jocu		
Lutjanus synagris		
Lutjanus analis		1
Lutjanus mahogoni		
Ocyurus chrysurus	2	3

Percent of standard length:	32	33
Lutjanus griseus		
Lutjanus cyanopterus		
Lutjanus apodus		
Lutjanus jocu		
Lutjanus synagris		
Lutjanus analis		
Lutjanus mahogoni		
Ocyurus chrysurus	3	3

Percent of standard length:	10	11
Lutjanus griseus		
Lutjanus cyanopterus		
Lutjanus apodus		
Lutjanus jocu		
Lutjanus synagris		
Lutjanus analis		

Pelvic-fin length

20	21	22	23	24	25	26	27	28	29	30	31	32
4												
1	1											
			4	4	2							
		2			1	1	1	1		1		1
		3	2	3	2							
2	3	3										
			3	4		3						
4	1											

Head length

34	35	36	37	38	39	40	41	42	43	44
		5	4	1						
	2	1		2						
						3	2	3	1	1
				2	1		2	2	1	
				1	4	5				
	3	2	3	1						
					6	3	1			
4										

Snout length

12	13	14	15	16	17
1	8	1			
	2	2	1		
	2	1	4	3	
		3	4	1	
3	6	1			
		1		7	1

Table 5—*Continued*

Lutjanus mahogoni		2	1	3	4
Ocyurus chrysurus	5	5			

Orbit length

Percent of standard length:	5	6	7	8	9	10	11
Lutjanus griseus			5	5			
Lutjanus cyanopterus	3	1	1				
Lutjanus apodus					3	7	
Lutjanus jocu			1	1	3	1	2
Lutjanus synagris				4	4	2	
Lutjanus analis	2	5	2				
Lutjanus mahogoni						9	1
Ocyurus chrysurus	1	1	7	1			

Length of upper jaw

Percent of standard length:	11	12	13	14	15	16	17
Lutjanus griseus				10			
Lutjanus cyanopterus					2	3	
Lutjanus apodus				1	6	3	
Lutjanus jocu				2	3	3	
Lutjanus synagris				2	7	1	
Lutjanus analis		1	8				
Lutjanus mahogoni					1	5	4
Ocyurus chrysurus	2	6	2				

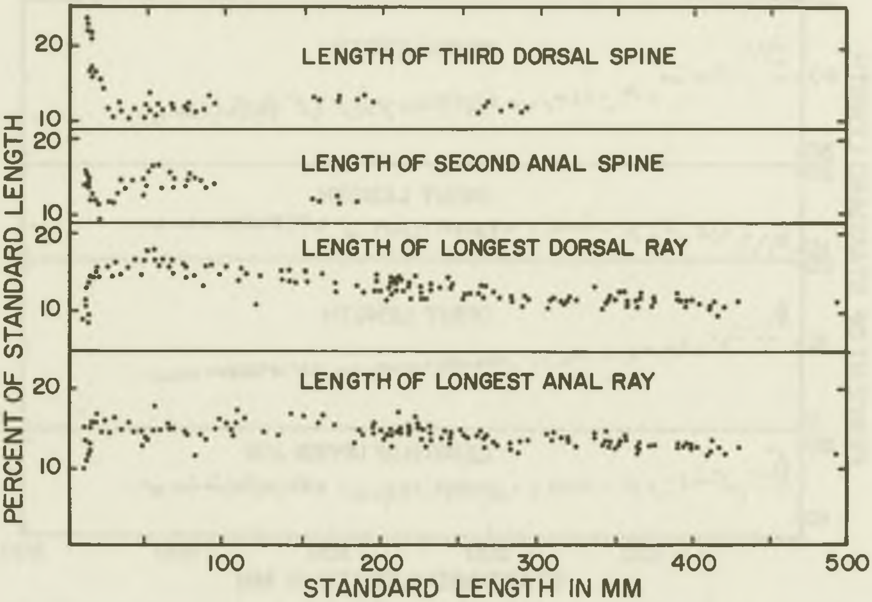

Figure 20. Length of third dorsal spine, second anal spine, longest soft dorsal ray, and longest anal ray expressed as a percent of standard length plotted against standard length in *Lutjanus griseus.*

freer swimming species (*L. griseus, L. cyanopterus,* and *Ocyurus chrysurus*) and the diurnally active *L. analis* have relatively smaller eyes than the species associated with rocky areas (*L. apodus* and *L. jocu*) or the reef dwelling *L. mahogoni.* The last two groups may have to search for their food in the shadows of the reef. The relatively large eye of *L. synagris* is possibly related to its smaller size.

The length of the upper jaw is used as an index to mouth size. It is greatest in the small gray snapper (Figure 21), and rather constant over 100 mm standard length. A larger mouth in small fish may be related to the early importance of the feeding mechanism.

The upper jaw is greatest in size in the piscivorous *L cyanopterus* and *L. mahogoni* and smallest in *Ocyurus chrysurus* a mid-water feeder on small crustaceans and fish, and *L. analis*, which feeds largely on demersal crustaceans and mollusks. The remaining generalized feeders on small demersal invertebrates and fishes have intermediate jaw lengths.

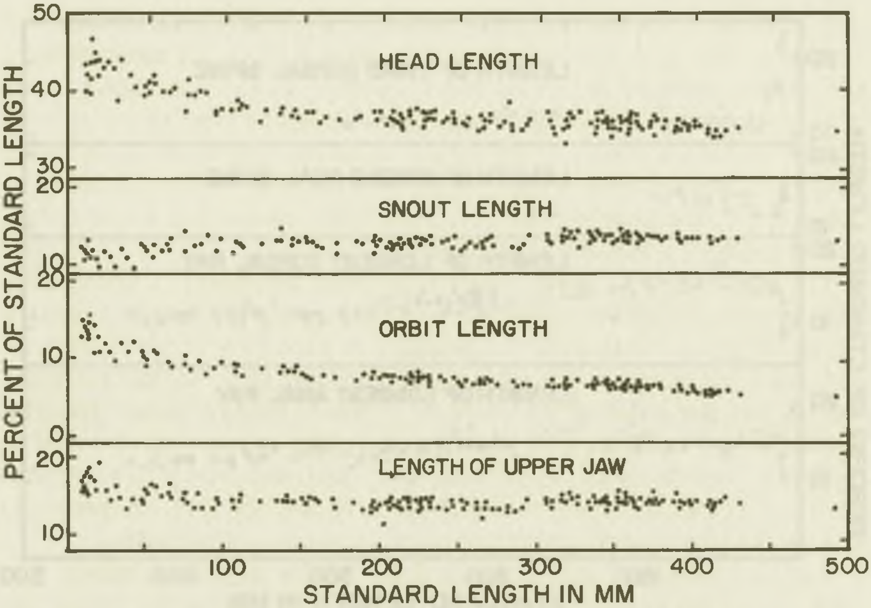

Figure 21. Head, snout, orbit, and upper jaw lengths expressed as a percent of standard length plotted against standard length in *Lutjanus griseus.*

Dentition

Dentition of most of the snappers is well developed (Figures 22 and 23). The upper jaw bears an outer row of enlarged conical teeth and an inner row of small, almost villiform teeth. Four of the outer row of teeth are enlarged as canines. The lateral two canines are the largest. The lower jaw also bears an outer row of enlarged teeth. They decrease in size posteriorly. An inner row of small almost villiform teeth is present anteriorly but disappear at less than a third of the length of the outer row of teeth. Villiform teeth are present on the vomer, palatines (pterygoids in *Ocyurus*), and hyoid bones. Pharyngeal teeth are well developed and similar in shape to the smaller teeth of the jaws.

Dentition is best developed in *L. cyanopterus, L. jocu, L. apodus,* and *L. griseus.* Canine lengths of a specimen of each of these species are 2.7, 2.6, 2.1, and 2.1% of standard length, respectively. The vomerine tooth patch has a long posterior projection in *L. apodus* and *L. jocu.* The posterior projection is lacking or short in *L. cyanopterus* (Evermann and

Marsh, 1902: 170). Palatine teeth patches are ovoid and are about one half as wide as long in *L. cyanopterus* and *L. griseus*. They are more elongate and slightly S-shaped in *L. jocu* and *L. apodus*. Teeth of the basihyal are in an elongate patch, the shorter axis of which is one third to one quarter that of the longer. Teeth of the vomer, palatines, and basihyal are finely villiform in all four species. Pharyngeal teeth are short and not as heavy as those of the jaws. They are best developed in *L. cyanopterus*. These species feed primarily on fish and crustaceans.

The dentition of *L. analis* is relatively short and heavy. Canines measured were 1.4% of the standard length. Vomerine teeth are in a roughly triangular group and those of the palatines in a small ovoid patch. Palatine and vomerine teeth of *L. analis* are larger than those of the preceding species but the palatine teeth are in a much smaller group. Basihyal dentition is in an oval patch as in the preceding species, but the median teeth are stronger. Pharyngeal teeth are short and heavy. The general condition is that of shorter and heavier teeth than those of the preceding species. Mutton snappers feed largely on crustaceans and mollusks.

Lutjanus mahogoni and *L. synagris* are similar in their dentition. The teeth are similar in shape to those of the first group above but not so well developed. Canines are 1.0 and 1.1% of standard length, respectively. The vomerine tooth patch has a short backward projection. Palatine and basihyal teeth are in narrow elongate patches.

Pharyngeal teeth are long and slender. *Lutjanus mahogoni* appears to feed on small fishes, and *L. synagris* on small fishes and invertebrates.

Ocyurus chrysurus feeds largely in mid-water on small fishes and crustacea. It has more reduced dentition than species of *Lutjanus*. Five or six teeth in front are somewhat caninelike but small. Canine length is 1.0% of standard length. The lower jaw has a single row of moderately strong teeth. The vomer bears an arrow-shaped patch as in some of the above species. A narrow ovoid of pterygoid teeth is present and the teeth of the basihyal are in two groups; a short anterior one and a longer posterior one. Vomerine and palatine teeth are better developed but fewer in number than in *L. griseus*. Pharyngeal teeth are slender and elongate.

Gillrakers are short and thick in *L. griseus, L. cyanopterus, L. apodus,* and *L. jocu*. They number six to nine on the lower limb of the arch (seven or eight in *L. griseus*). They are moderately developed in *L. analis* and *L. synagris*, eight on the lower limb of the arch in *L. analis* and 10 plus three or four rudiments in *L. mahogoni*. Gillrakers are longer in *L. synagris* and

Figure 22. Jaw dentition of five inshore lutjanids. Upper left: *Lutjanus griseus* (407 mm standard length). Upper right: *Lutjanus cyanopterus* (411 mm). Middle left: *Lutjanus analis* (401 mm). Middle right: *Lutjanus mahogoni* (305 mm). Lower: *Ocyurus chrysurus* (285 mm).

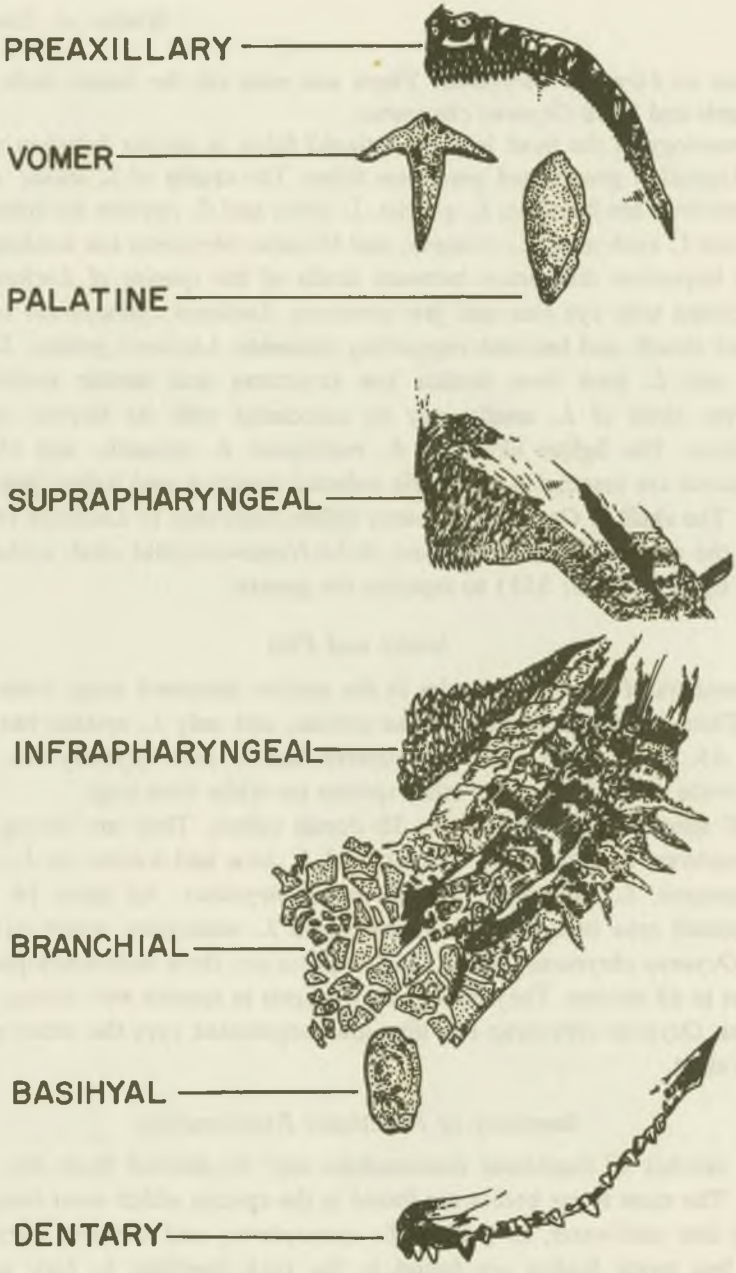

Figure 23. Exploded view of dentition of the gray snapper, *Lutjanus griseus.*

longest in *Ocyurus chrysurus*. There are nine on the lower arch of *L. synagris* and 21 in *Ocyurus chrysurus*.

Osteology of the head in these lutjanid fishes is similar between species and typical of generalized perciform fishes. The crania of *L. analis* and *L. cyanopterus* are heaviest; *L. griseus*, *L. jocu*, and *L. apodus* are intermediate, and *L. mahogoni*, *L. synagris*, and *Ocyurus chrysurus* are weakest. The most important differences between skulls of the species of *Lutjanus* are associated with eye size and jaw structure. *Lutjanus cyanopterus* has the largest mouth and heaviest supporting elements. *Lutjanus griseus*, *L. apodus*, and *L. jocu* have similar jaw structures and similar skulls. The heaviest skull of *L. analis* may be associated with its heavier internal dentition. The lighter skulls of *L. mahogoni*, *L. synagris*, and *Ocyurus chrysurus* are associated with their reduced dentition and lighter jaw structure. The skull of *Ocyurus chrysurus* differs from that of *Lutjanus* primarily in the greater anterior extension of the fronto-occipital crest, a character used by Gill (1885: 353) to separate the genera.

Scales and Fins

Numbers of lateral-line scales in the species discussed range from 41 to 51. There are 45 to 47 in *Lutjanus griseus*, and only *L. apodus* has fewer than 45. Body scales of *L. cyanopterus* and *L. jocu* typically are longer than wide while those of the other species are wider than long.

All species of *Lutjanus* have 10 dorsal spines. They are strong in *L. cyanopterus*, *L. griseus*, *L. apodus*, and *L. jocu* and weaker in *L. analis*, *L. synagris*, *L. mahogoni*, and *Ocyurus chrysurus*. All have 14 dorsal segmented rays except for *L. synagris* and *L. mahogoni*, which have 12, and *Ocyurus chrysurus*, which has 13. There are three well-developed anal spines in all species. They tend to be strongest in species with strong dorsal spines. *Ocyurus chrysurus* has nine anal segmented rays the other species have eight.

Summary of Functional Relationships

A number of functional relationships may be derived from the above data. The most terete bodies are found in the species which most frequently move into mid-water, *L. griseus*, *L. cyanopterus*, and *Ocyurus chrysurus*. The less terete bodies are found in the rock dwelling *L. jocu* and *L. apodus* and the bottom dwelling *L. synagris*. *Lutjanus analis* and *L. mahogoni* are intermediate and are bottom-ranging species.

Long pectoral fins are associated with rock dwelling, bottom ranging, and a semipelagic mode of life (*L. apodus, L. jocu, L. analis, L. mahogoni,* and *Ocyurus chrysurus*). Shorter pectorals are found in *L. griseus, L. cyanopterus,* and *L. synagris,* whose normal habitats and modes of life may require less maneuverability. Short pelvic fins in snappers appear to be associated with a more free-swimming mode of life. Head length is related to elongation of the body, mouth size, and eye size. Snout length is a function of mouth position and is longest in species with a deep body and low mouth. Eye diameter is smallest in the freer swimming species and in the diurnally active *L. analis.* Relatively large eyes are found in the two rock-dwelling species, the reef roaming *L. mahogoni* and the smallest species *L. synagris.* Large mouths seem to be related to piscivorous habits and small mouths to feeding on invertebrates. Generalized feeders are intermediate in mouth size.

Jaw dentition is heaviest in *L. cyanopterus,* followed by *L. jocu, L. apodus,* and *L. griseus.* The first is a fish eater and the remainder feed mainly on fish and crustacea. In these snappers, vomerine, palatine, and hyoid dentition is finely villiform and pharyngeal teeth moderate to small. Gillrakers are short and thick. These species feed on fishes large enough to require subduing before being swallowed, hence, the large jaw teeth. Once subdued, they are easily swallowed, therefore internal teeth are less important.

Lutjanus analis has short heavy jaw teeth and more well-developed internal teeth. This species feeds on crustaceans and mollusks that are not difficult to capture. Short heavy teeth in the jaws and internally are useful, however, to crush the exoskeleton of the prey.

The remaining species, *L. synagris, L. mahogoni,* and *Ocyurus chrysurus,* have weaker jaw dentition and moderate villiform teeth on the vomer, palatines (pterygoid in *Ocyurus*), and basihyal. The pharyngeal teeth are elongate and slender. They have moderate to long gillrakers. They feed on small invertebrates and fishes that may be ingested with a single gulp. Better developed internal teeth and longer gillrakers prevent the escape of the prey through the gill slits and aid in swallowing small prey. *L. mahogoni* has the largest mouth and apparently feeds extensively on small fish.

Slender dorsal and anal spines are found in species that wander in open areas and seldom enter caves or other similar cover (*L. synagris, L. analis, L. mahogoni,* and *Ocyurus chrysurus*).

In most of the characters considered, the gray snapper is intermediate to the other species. Size, morphometry, jaw structure, and dentition are generalized in keeping with its wide range of habitats and variety of food eaten.

4. Food and Feeding; Reproduction; Behavior

FOOD AND FEEDING

Publications on Feeding Habits

Most lutjanids are known to be rather generalized carnivores; specific information, however, on food habits is sparse. Randall and Brock (1960) reported on the food of several species of snappers from the Society Islands. Information on the food of West Indies snappers is also limited. Longley and Hildebrand (1941: 115 et seq.) recorded stomach contents of several inshore species including the gray snapper. The food of commercial red snapper (*Lutjanus aya*) in the Gulf of Mexico was discussed by Camber (1955: 27–28).

Several published accounts mention food of *Lutjanus griseus*. Longley et al. (1925: 230) is the most important of references (Longley, 1927, also mentions the same data). Their paper reported on stomach contents of 264 gray snappers and compared these to the food of 106 schoolmasters. The spider crab, *Mithrax corphe,* was found in 3.9% of the gray snapper and in 31.1% of the schoolmaster. The porcellanid crab, *Petrolisthes,* was taken by 0.76% of the gray snapper and by 34.7% of the schoolmasters. Portunid crabs, on the other hand, were found in 34.8% of the gray snapper and only 6.6% of the schoolmasters. In addition, 17 or 18 gray snappers contained specimens of the following sand-or mud-haunting crustaceans, namely, *Euryplax, Gebia, Callianassa,* and *Albunea,* of which none was found in the schoolmaster. Longley, in Longley and Hildebrand (1941: 115), mentioned 26 specimens of the gray snapper taken at 5:00 P.M. One had parts of a crab, *Portunus sebae*, in its stomach, the others nothing identifiable. Of another 27 fish, 215–415 mm long, taken between 5:00 and 5:30 A.M., six had empty stomachs, two contained little, and the remainder had recently fed well. They had eaten at least 15 fish up to 125 mm in length, two crabs "of the average size of a quarter-dollar," many small shrimps, a squid, and a large annelid.

Croker (1962: 383) examined 200 gray snappers from Florida Bay and Biscayne Bay, Florida. He found fish in 34% of the stomachs. *Anchoa* was the dominant identifiable fish. Crustaceans were found in 79% of the stomachs and shrimp occurred in 66%. Bait shrimp was 28%, other shrimp 42%, crab 27%, stomatopod 1%, and 3% was unidentified. Shrimp were primarily penaeids and crabs were grapsids.

Several other references mention stomach contents of the gray snapper. Cowles (1908: 33) and Gudger (1929: 175) report gray snappers feeding on ghost crabs (*Ocypoda arenaris*) that had been driven into the water. Breder (1948: 170) states that *L. griseus* feeds to a considerable extent on the small arboreal crabs of the mangrove trees. Probably the crabs are caught when they enter the water on the mangrove roots. Breder (1934: 70) collected two gray snappers in a freshwater lake on Andros Island, Bahamas. They had eaten fish and a dragonfly nymph. Reid (1954: 39) found penaeid shrimp and some organic detritus in the stomachs of three small gray snappers taken near Cedar Key, Florida. Springer and Woodburn (1960: 40) took 102 gray snappers in the area of Tampa Bay, Florida. These ranged from 14.0 to 164.0 mm with only four specimens exceeding 91 mm. Specimens under 60 mm were found to have eaten primarily caridean shrimp and copepods, but small fish, annelids, and insects were also included. Only fish were found in the larger specimens.

Food by Area

In the present study, 1335 gray snappers were examined for stomach contents. Of these, 636, or 48%, contained food; the remainder were empty. Included with the empty stomachs were 16 stomachs that contained items so well digested that distinction between fish and invertebrates was impossible. Sizes of specimens examined ranged from 10.5 to 489 mm standard length. Data on collections of snapper used for food studies are given in Table 6.

Very small specimens, 10.5 to 76 mm standard length, collections 1 to 7, were collected with rotenone-based fish poisons, pushnet, and seine. These collections were made by the author and other personnel of the Institute of Marine Sciences of the University of Miami. These specimens are now in the collections of the Institute and the catalog numbers are given in Table 6. They are also included in Table 1. Small fishes are killed quickly by rotenone and have little chance to feed on other organisms affected by the poison.

Larger specimens are not as readily affected by rotenone, they feed readily on smaller organisms affected by the poison and generally avoid the poison cloud. At Alligator Reef, large gray snappers have often been seen feeding on other animals killed by poison, but fewer than 10 specimens have been collected in numerous poison stations there.

Hook and line, nets, and spears were also tried. Hook and line, though more productive than poison, is slow and produces a biased sample. The unsuitability of nets to catch adult gray snappers has been previously mentioned. Underwater spearfishing, though useful for small samples, is also slow. After several fish are speared from a school, the remainder are increasingly wary.

The best method found to collect an adequate number of specimens from a single school in the early morning when stomachs are fullest was the use of a concussion device. A small CO_2 cylinder, use to inflate rubber life rafts, was filled with black gunpowder (about one pound) and ignited by a short length of dynamite fuse with a burning time of 15 to 20 seconds. The steel cylinder is rated for 1800 psi. and has a burst strength of perhaps three times that figure. The cylinder serves to contain the gases until it bursts. The resultant shock wave is much sharper than that produced by the same powder in a weaker container. When dropped into a school of snappers the fish at first scatter and then regroup around the device apparently attracted by the bubbles from the fuse. The regrouping occurs within 5 to 10 seconds, and after about 10 to 20 more seconds, the snapper begin to lose interest and disperse, hence a 15 to 20 second fuse produced best results. The effective radius is about 10 ft. Because of this small radius, proper placement results in a very low kill of other species.

Gray snappers larger than about 75 mm standard length are nocturnal feeders, hence most collections were made in early morning. Several collections were made later in the day for comparison, however, and one collection was made at night. The latter collection was made with a spear for the fish are scattered when feeding at night.

Stomach contents by collection and totals by area are given in Tables 7 to 12. Each stomach containing food was considered as 100%, and different items in the same stomach were visually estimated as a portion of the total volume of stomach contents of that fish. Total percentages for various groups were divided by the number of fish containing food. The number of stomachs containing a given item and the number of each item is also given by area and for the overall total. Figures for higher groups are

Table 6. Collections of gray snappers, *Lutjanus griseus*, used for stomach content examination

Collection numbers	Location	Habitat	A	B	C	D	E	F	G	H	I
1	Lower Matecumbe Key	Along shore	24	22	2	92	8	11.00	27/10/56	23– 62	246
2	Loggerhead Key, Dry Tortugas	Dead *Thalassia*	66	61	5	92	8	15.00	–/7/61	12– 22	11472
3	Key Biscayne	Along shore	14	14	0	100	0	—	2/11/57	23– 62	3842
4	Long Key, Fla. Keys	Along shore	10	9	1	90	10	—	31/1/58	28– 69	4797
5	St. Lucie River	Grass bed	50	38	12	76	24	—	11/9/57	24– 76	5042
6	Ft. Pierce	Grass bed	19	17	2	89	11	—	15/10/57	31– 92	4101
7	Key Biscayne	Grass and sand	21	10	11	48	52	—	9/8/56	10.5– 16	1842
Total 1–7	Florida	Grass	204	171	33	84	16	—		10.5– 76	
8	Green Mangrove Key, Fla. Bay	Bush near grass bed	39	19	20	49	51	11.30	23/8/62	189–269	
9	Shell Key, Fla. Bay	Mangrove in grass bed	108	49	59	45	55	10.00	19/1/63	109–209	
10	Lower Matecumbe Key	Brush in grass bed	165	8	157	5	95	16.00	15/2/63	116–258	
11	Lower Matecumbe Key	Mangrove in grass bed	6	3	3	50	50	7.30	2/3/63	133–181	
12	Lower Matecumbe Key	Debris in grass bed	30	24	6	80	20	7.30	20/3/63	159–304	
13	Long Key, Fla. Keys	Brush in grass bed	57	51	6	89	11	7.00	24/4/63	92–293	
14	Lignumvitae Bank	Debris in grass bed	83	58	25	70	30	6.30	6/6/63	82–189	
15	Lower Matecumbe Key	Brush in grass bed	58	12	46	21	79	15.00	22/6/63	75–193	
16	Lower Matecumbe Key	Grass bed	24	14	10	58	42	22.00	10–14/3/63	137–338	
Total 8–16	Florida Keys	Debris in grass bed	570	238	332	41	59	—		75–338	
Total 1–16	Florida	Grass	774	409	365	53	47	—		10.5–338	
17	Lignumvitae Channel	Wreck in channel	110	72	38	65	35	8.30	24/4/63	146–414	
18	Lignumvitae Channel	Wreck in channel	10	4	6	40	60	8.30	4/8/63	165–419	

Total Channel	Lignumvitae Channel	Wreck in channel
19	Rabbit Key, Fla. Bay	Mangrove channel
Total 1–19	Florida	Inshore
20	Alligator Lighthouse	Coral reef
21	Alligator Lighthouse	Coral reef
22	Alligator Lighthouse	Coral reef
Total 20–22	Alligator Lighthouse	Coral reef
23	Ledge at Alligator Reef	Coral reef
24	Ledge at Alligator Reef	Coral reef
Total 23–24	Ledge at Alligator Reef	Coral reef
25	Various offshore areas	Coral reef
Total 20–25	Various offshore areas	Coral reef
Total 1–25	Florida	Various

A. Number of Specimens.
B. Number of Stomachs with Food.
C. Number of Stomachs Empty.
D. Percent of Stomachs with Food.
E. Percent of Stomachs Empty.

120	76	44	63	37	—		146–419
4	2	2	50	50	13.00	28/7/63	261–365
898	487	411	54	46	—		10.5–419
159	62	97	42	58	7.45	21/8/63	185–311
89	54	35	63	37	7.45	3/8/63	190–300
11	1	10	9	91	10.00	25/8/62	232–317
259	117	142	45	55	—		185–317
67	8	59	12	88	11.30	26/8/62	294–498
73	20	53	27	73	7.30	2/8/63	251–430
140	28	112	20	80	—	1962–63	251–489
39	4	35	10	90	—	June–Aug. 63	271–472
437	149	288	34	66	—		185–472
1,335	636	683	48	52	—		10.5–472

F. Approximate time of collection.
G. Date of collection day, month, year.
H. Standard length in mm.
I. UMML catalog numbers.

Table 7. Stomach contents in mean percent of food volume of postlarval and young juvenile gray snappers, *Lutjanus griseus*, from Florida

Items	Collection Numbers							Total percent	Stomachs containing item	Number of items
		2	3	4	5	6	7			
Copepod		0.2					40.0	2.4	6	42
Amphipod	45.6	99.6	0.9	12.2		8.2	1.0	43.0	83	441
Isopod					0.3			0.1	1	1
Shrimp										
Penaeus	2.7					4.1		0.8	2	2
Alpheidae	1.4			12.2				0.8	3	3
Palaemonidae					76.5		10.0	18.5	34	130
Total caridean	11.4		40.4	12.2	76.5		49.0	25.2	50	158
Total shrimp	14.1	0.2	40.4	45.5	79.1	47.0	49.0	32.1	67	178
Cancroid crab					2.6	4.7		1.1	2	2
Grapsoid crab			16.4					1.3	5	29
Pagurid crab					1.8			0.4	1	2
Total crab	8.9		16.4		4.4			4.0	13	40
Barnacle			0.1					.01	1	1
Total Crustacea	92.5	100.0	72.7	83.3	94.3	95.2	90.0	93.0	167	724
Fishes										
Anchoa			5.7					0.5	1	1
Gobiidae					1.8			0.4	1	1
Total fishes	7.5		23.6	16.7	5.7	4.8		5.5	13	15
Unidentified eggs			3.8				10.0	0.9	8	—

generally larger than the sum of their components. This is because many food items were identified only to the higher groups.

Table 7 includes stomach contents of post-larval and small juvenile fish from various inshore locations. All collections with habitat data available were from grass beds. Crustacea predominate (93%) with amphipods and shrimp most prominent. Carideans of the family Palaemonidae are the most abundant shrimp, and most identifiable specimens were *Percilimenes americanus and P. longicaudatus.* Occasional specimens of *Leander tenuicornis* were also seen as were a few examples of the hippolytid, *Tozeuma carolinensis.* Copepods were prominent only in one collection containing the smallest (postlarval) fish.

The next group of collections (Table 8) was made around mangrove roots, brush, and other debris in grass beds around Lower Matecumbe Key. Depths were less than 6 ft. Most fish were large juveniles. Crustacea (69.4%) again predominate but by a lesser margin. Shrimp and crabs are the most important crustacea. *Penaeus,* chiefly *P. duorarum,* makes up most of the shrimp. Identifiable alpheid shrimp were all *Alpheus heterochaelis.* Xanthid crabs appeared to be mainly *Panopeus herbstii* and *Neopanope packardii.* Identifiable portunid crabs were either *Callinectes ornatus* or *C. sapidus.*

Fish make up 29.1% of the total food volume in this group and toadfish (*Opsanus beta*) are the most abundant identifiable fish.

This group of collections differs from the first group in several respects. Penaeid shrimp replace carideans in importance. Amphipods are absent. Crabs and fish play a more important role.

Table 9 gives the stomach contents of large snappers from an inshore channel near Lower Matecumbe Key. Crustacea still dominate but by an even lesser margin (59.5%). Portunid crabs of the genus *Portunus* (probably *P. gibbesi*) are predominant (40.5%). Spider crabs (3.6%) seem to be mainly *Pitho anisodon.*

The polychaetes were identified as the bristle worm, *Hermodice carunculata.*

Fish (36.5%) play a more important role than in the previous groups. Toadfish are again the most numerous identifiable fish. Eels were of the family Ophichthidae.

This group differs from the previous two, summarized in Table 10, in that crustacea are reduced from 79.3 to 59.5% and that crabs are dominant among crustacea. A larger percentage and greater variety of fish are also eaten, although toadfish make up the biggest proportion in both groups.

Table 8. Stomach contents in mean percent of food volume of gray snappers, *Lutjanus griseus,* from around debris in grass beds near Lower Matecumbe Key, Florida

	Collection Numbers										Stomachs contain-	Number of
Items	8	9	10	11	12	13	14	15	16	Total percent	ing item	items
Gastropod	5.3	2.0								0.8	2	2
Holothurian									10.7	0.7	2	2
Isopod							0.5			0.1	2	2
Shrimp												
Penaeus		44.9	25.0		29.4	7.4			28.2	16.0	45	48
Alpheidae		2.0			2.1	0.7	12.7		7.1	4.2	15	16
Palaemonidae									7.1	0.4	1	1
Total caridean		2.0		66.7	2.1	0.7	12.7		14.2	5.4	18	39
Total shrimp	5.3	48.9	25.0	66.7	33.6	9.3	18.2		42.5	26.0	75	101
Spider crab						2.8	10.3			3.1	10	11
Cancroid crab												
Xanthidae						22.6	19.2	8.3		10.2	38	60
Portunidae												
Callinectes		3.1			8.3	13.8			20.4	5.6	18	20
Total portunid		3.1			8.3	13.8	0.3		20.4	5.7	19	21
Total cancroid		3.1			10.4	36.4	19.5	8.3	20.4	15.9	46	81
Total crab	5.3	9.2	12.5		14.6	47.0	31.2	8.3	24.0	23.7	67	105
Stomatopod	5.3					1.6				0.8	3	3
Panulirus argus	10.5									1.6	2	2
Total crustacea	39.6	66.5	37.5	66.7	48.2	83.6	89.6	8.3	66.5	69.4	174	250
Total invertebrates	44.9	68.5	37.5	66.7	48.2	83.6	89.6	8.3	77.2	70.9	177	254

Fishes				
Anguilliformes				
Lucania parva		1.1		
Pipefish	4.7	1.0		
Gobiosoma rubustum				
Callionymus				
Scaridae				
Opsanus beta		10.2	12.5	
Total fishes	55.2	31.4	62.5	33.3

2.1					0.2	1	1
		0.9			1.1	3	5
0.8		0.9			0.9	4	4
4.2					0.4	1	1
2.9					0.3	1	3
				1.4	0.1	1	1
32.5	2.9	6.4	8.3	14.3	9.2	26	29
51.9	16.4	10.4	91.7	22.8	29.1	80	100

Table 9. Stomach contents in mean percent of food volume of gray snappers, *Lutjanus griseus,* from Lignumvitae Channel, Florida

Items	Collection numbers 17	18	Total percent	Stomachs containing items	Number of items
Octopus	2.2	5.0	2.4	3	3
Polychaete worm	1.7		1.6	2	2
Shrimp					
Penaeus	0.1		0.1	1	1
Alpheidae	1.4		1.3	1	1
Total Shrimp	4.5		4.3	6	6
Spider Crab	3.8	1.2	3.6	6	6
Cancroid crab					
Portunidae					
Portunus	42.7		40.5	33	41
Callinectes	0.1		0.1	1	1
Total portunid	42.8		40.6	37	42
Total cancroid	44.2		41.9	39	44
Total crab	51.1	1.2	46.8	47	50
Total crustacea	62.7	26.3	59.5	60	64
Total invertebrates	66.6	31.2	63.5	61	69
Fishes					
Anguilliformes	4.2	25.0	5.2	5	5
Pipefish		25.0	1.3	1	1
Labridae	1.4		1.3	1	2
Monacanthus	0.7		0.7	1	1
Opsanus beta	19.3	18.8	19.2	17	18
Total fishes	33.4	68.8	36.5	34	35

Table 10. Stomach contents in mean percent of food volume of all gray snappers, *Lutjanus griseus,* from grass beds (collections 1–16) and from all inshore areas (collections 1–19)

Items	Total percent from grass beds	Total percent from inshore areas
Gastropod	0.5	0.4
Octopus		0.4
Polychaete worm		0.2
Holothurian	0.3	0.3
Copepod	1.0	0.8

Table 10—*Continued*

Items	Total percent from grass beds	Total percent from inshore areas
Amphipod	18.0	15.1
Isopod	0.1	0.1
Shrimp		
Penaeus	9.6	8.1
Alpheidae	2.8	2.5
Palaemonidae	8.0	6.7
Total caridean	13.7	11.7
Total shrimp	27.3	23.5
Spider crab	1.8	2.1
Cancroid crab		
Xanthidae	6.3	5.3
Portunidae		
Portunus		6.3
Callinectes	3.3	2.8
Total portunid	3.3	9.2
Total cancroid	9.7	14.5
Grapsoid crab	0.6	0.5
Pagurid crab	0.2	0.1
Total crab	15.5	20.2
Stomatopod	0.4	0.4
Panulirus	0.5	0.4
Barnacle	0.005	0.004
Total Crustacea	79.3	75.9
Total invertebrates	80.1	77.3
Fishes		
Anguilliformes	0.1	0.9
Anchoa	0.2	0.2
Lucania parva	0.6	0.5
Pipefish	0.5	0.6
Gobiosoma robustum	0.2	0.2
Total Gobiidae	0.4	0.3
Callionymus	0.2	0.1
Labridae		0.2
Scaridae	0.05	0.04
Monacanthus		0.1
Opsanus beta	5.4	7.6
Total fishes	20.6	22.8
Unidentified eggs	0.4	0.3

Table 11. Stomach contents in mean percent of food volume of gray snappers, *Lutjanus griseus*, from Alligator Reef, Florida

Items	Collections from Alligator Lighthouse		Total[1] percent	Collections from ledge at Alligator Reef		Total percent	Total[2] percent from Alligator Reef	Stomachs containing item	Number of items
	20	21		23	24				
Octopus	1.6	0.2	0.9				0.7	2	2
Isopod							0.01	1	1
Shrimp									
Penaeopsis goodei		10.7	5.8		2.5	1.8	4.9	11	12
Alpheidae	0.1	0.1	0.1				0.1	2	2
Stenopus hispidus		1.9	0.9				0.7	1	1
Total shrimp	10.3	12.7	11.2		2.5	1.8	9.8	21	24
Spider crab	3.7	0.9	2.4	12.5	5.0	7.1	1.8	6	6
Cancroid crab									
Portunus sp.	0.8	13.5	6.6		5.0	3.6	6.6	10	11
P. spinimanus	1.6	1.9	1.7				1.3	2	3
Total portunid	13.6	19.1	15.9		12.5	12.5	14.9	24	32
Total crab	17.7	20.0	18.6	12.5	17.5	20.0	16.9	30	39
Stomatopod	0.6		0.3				0.3	1	1
Panulirus				37.5		10.7	2.0	3	3
Total Crustacea	39.1	44.6	39.3	62.5	20.0	33.9	37.4	66	82
Total invertebrates	40.7	44.8	41.5	62.5	20.0	33.9	38.1	67	84
Fishes									
Anguilliformes	4.0	1.9	3.8				3.0	4	4
Pipefish			3.8		2.5	1.8	0.3	1	1
Mugil (bait)					10.0	7.4	1.3	2	2

Synodus	0.8		0.4
Jenkinsia			
Mullidae	1.6		0.8
Rypticus	0.8		0.4
Serranus tabacarius		1.9	0.8
Labridae	1.6		0.8
Scarus croicensis	0.8		0.4
Haemulon	5.2	5.6	5.3
Acanthurus	1.6		0.8
Lactophrys			
Balistes	0.8	5.2	2.0
Total fish	59.3	55.2	58.8
Unidentified eggs		1.9	0.8

[1] Includes collection 22.

[2] Includes collection 25.

			0.3	1	1
			0.7	1	1
			0.7	1	1
			0.3	1	1
			0.7	1	1
			0.7	1	1
			0.3	1	1
12.5		3.6	5.4	9	10
			0.7	1	1
	5.0	3.6	0.7	1	1
	5.0	3.6	2.2	5	6
37.5	80.0	64.3	61.9	96	107
			0.7	1	—

Because of the difference in size between fish from Alligator Lighthouse and the ledge a short distance away, separate totals are also given (Table 11). Fish (61.0%) are more numerous than crustacea in stomachs of snapper from the reef; *Haemulon, Balistes,* and ophichthid eels are the most numerous. The mullet (*Mugil*) were represented only by heads and were almost certainly bait discarded by fishermen.

Crustacea (37.4%) are made up chiefly of shrimp and portunid crabs. *Penaeopsis goodei* is the most abundant shrimp and *Portunus* the most numerous crab.

Stomach contents of fish from Alligator Lighthouse differ from those of fish from the ledge in that shrimp are more abundant in fish from the light and spider crabs and *Panulirus* more numerous in fish from the ledge. These differences may be attributed to the larger size of fish from the ledge.

The greater variety of fishes in stomachs of snappers at Alligator Lighthouse is a result of the larger sample from that location.

The *Portunus* sp. in the Table is probably *P. ordwayi*, a species common on the reef. Identifiable spider crabs were all *Chorinus heros*, and identifiable crawfish were *Panulirus guttatus*. The unidentified eggs were similar to those of the sergeant major, *Abudefduf saxatilis.*

Comparison of stomach contents between snappers collected at Alligator Reef and those from inshore areas reveals a greater proportion of fish in stomachs from the reef (61.9% as opposed to 22.8%) and a lesser proportion of crustacea (37.4% vs. 75.9%). Comparison with similarly sized fish from Lignumvitae Channel shows a less marked but still distinct difference in stomach contents. Types of food organisms are similar from inshore to offshore, but probably no one species is common to these two groups of stomach contents.

Food by Size

Average percentages of various foods by volume for stomach contents are given for each 10 mm increment of standard length and are shown in Figure 24.

Copepods are important only in very small fish in the 10 to 20 mm size range and then only in the smallest of these. Amphipods make up the biggest part (about 85%) of the food of 10- to 20-mm fish and become rapidly less important in 20- to 70-mm fish.

Palaemonid shrimp comprise about 30% of the food of 20- to 500-mm fish and slightly more than 14% in 50- to 70-mm individuals. The remaining carideans are found in small numbers in fish up to 300 mm.

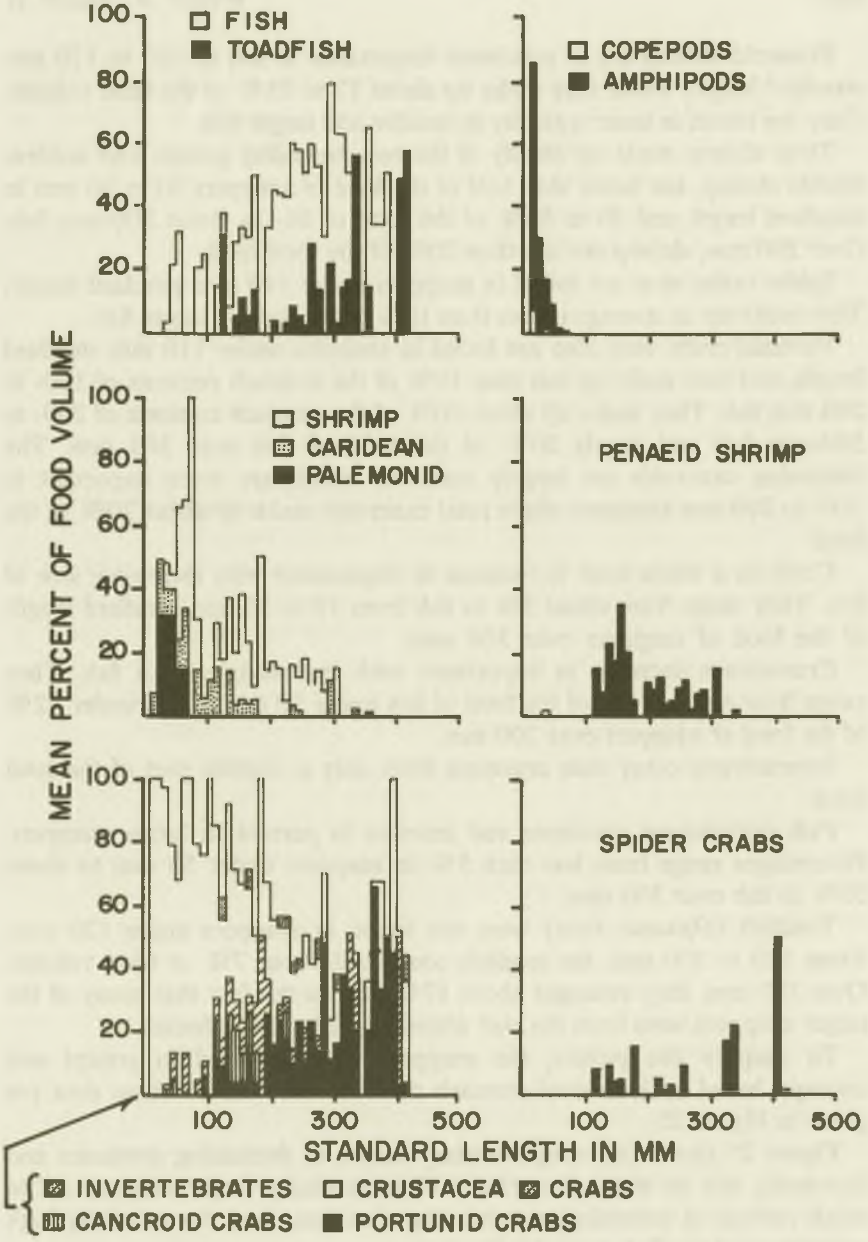

Figure 24. Stomach contents by mean percent of volume for the gray snapper, *Lutjanus griseus,* in 10 mm groups of standard length. Snappers are from collections in Table 6.

Penaenid shrimp are of maximum importance in fish of 130 to 170 mm standard length, where they make up about 17 to 35% of the food volume. They are found in lesser quantity in smaller and larger fish.

Total shrimp made up chiefly of the two preceding groups and unidentifiable shrimp, are better than half of the food of snappers 20 to 80 mm in standard length and 20 to 30% of the food of 80- to about 200-mm fish. Over 200 mm, shrimp are less than 20% of the total food.

Spider crabs were not found in snappers under 110 mm standard length. They make up an average of less than 10% of the food of larger fish.

Portunid crabs were also not found in snappers under 110 mm standard length, and they make up less than 10% of the stomach contents of 100- to 200-mm fish. They make up about 20% of the stomach contents of 200- to 300-mm fish and nearly 30% of the food of fish over 300 mm. The remaining cancroids are largely xanthids, which are more important in 100- to 200-mm snappers where total cancroids make up about 20% of the food.

Crabs as a whole tend to increase in importance with increasing size of fish. They range from about 3% in fish from 30 to 50 mm standard length of the food of snappers over 300 mm.

Crustaceans decrease in importance with increasing size of fish. They range from nearly 96% of the food of fish under 50 mm to just under 42% of the food of snappers over 300 mm.

Invertebrates other than crustacea form only a neglible part of the total food.

Fish complement crustacea and increase in percent in larger snappers. Percentages range from less than 5% in snappers under 50 mm to about 55% in fish over 300 mm.

Toadfish (*Opsanus beta*) were not found in snappers under 120 mm. From 120 to 300 mm, the toadfish comprised about 7% of food volume. Over 300 mm, they averaged about 17% despite the fact that many of the larger snappers were from the reef where toadfish are not found.

To simplify this picture, the snappers were arranged in groups and averages based on individual stomach contents were made. These data are given in Figure 25.

Figure 25 shows the complementary nature of decreasing crustacea and increasing fish in stomach contents of increasingly larger snappers. The small portion of invertebrates other than crustacea and the relatively high percentage of toadfish may also be seen.

Figure 25 also gives percentages of several of the more important crustacea in stomach contents. Copepods are found in only the smallest size

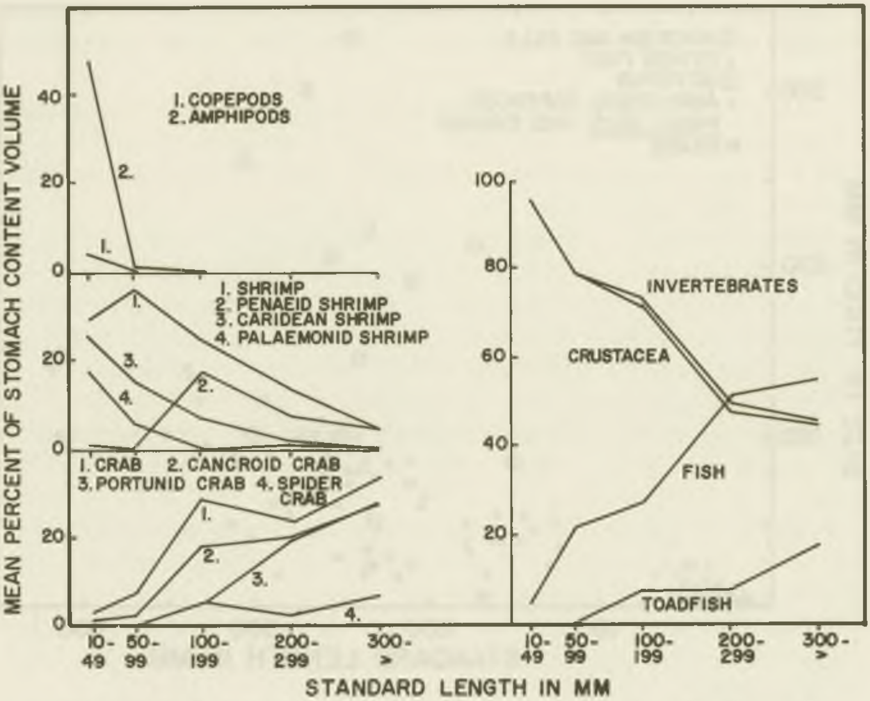

Figure 25. Stomach contents of various sized gray snappers, *Lutjanus griseus*, by mean percent of food volume. Snappers are from collections in Table 6.

group and, as mentioned above, are important only in fish in the lower end of the 10 to 20 mm size group.

The difference between total shrimp and caridean shrimp in 50- to 100-mm fish is due to unidentified shrimp, most of which are probably carideans since all identifiable shrimp are of this group. The declining importance of shrimp in the food of larger fish and the partial replacement of carideans by penaeids are evident.

The difference between portunid and cancroid crabs is made up largely of xanthids, which are replaced by portunids in the stomachs of snappers over 200 mm standard length. Crabs are more important food items of larger gray snappers.

The general impression is that postlarval and perhaps larval snappers feed mainly on copepods and amphipods, with amphipods becoming more important in very small juveniles. Caridean shrimp, crabs, and fish replace amphipods in the diet of larger juveniles and penaeids replace carideans in

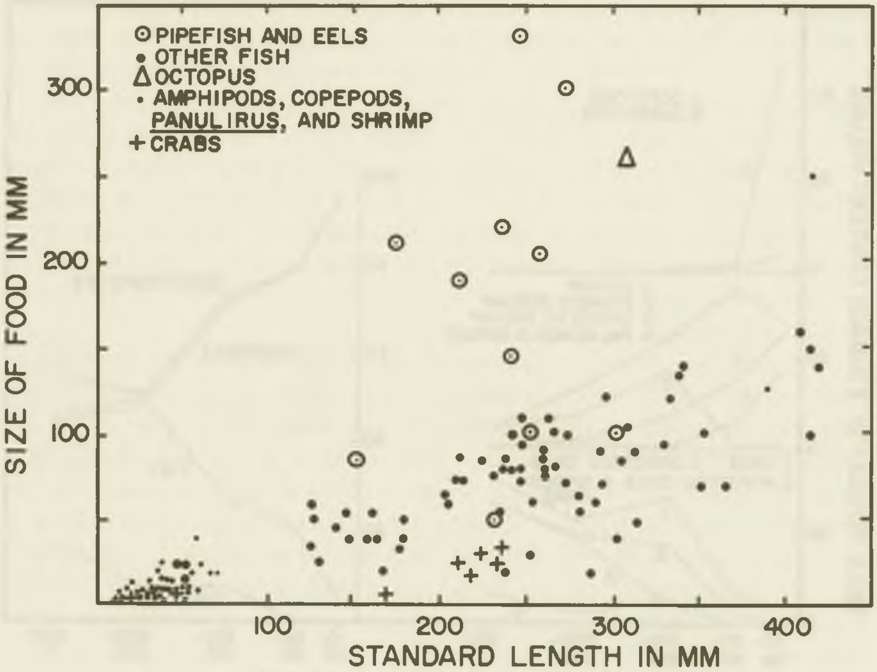

Figure 26. Size of food items eaten by the gray snapper, *Lutjanus griseus.*

the largest juveniles. Crabs and fish increase in percentage in adult snappers of increasing size, and shrimp decrease in percentage. Crabs are mainly xanthids at first, then they are gradually replaced by portunids. A tendency to fewer numbers of larger crustacea per stomach is also apparent in large snappers. No general changes in food habits with season were noted. Certain seasonal phenomena, however, may affect fish in localized areas. Pink shrimp (*Penaeus duorarum*) occasionally go through channels in large numbers on the outgoing tide at night. The runs are often associated with strong north or northwest winds in late fall or winter, and snappers and other fish feed extensively on the shrimp at such times.

Anchovies sometimes form extremely dense schools, probably associated with spawning (most individuals are ripe), in certain inshore areas during late summer or early fall. Gray snappers feed on these schools even in the day and frequently bulge with anchovies they have eaten.

Size of food items (Figure 26) follows several patterns. Elongate, pliable items such as eels, pipefishes, and octopus may exceed the predators' standard length. The longest item was an eel, 135% of the snapper's standard length. Shrimp, amphipods, *Panulirus*, etc., as large as 60 to 70% of the predators' standard length, may be eaten because of their folding crustacean abdomen. Fishes other than eels and pipefishes may be taken as large as about 45 to 50% of standard length. Crabs found in stomachs were less than 15% of standard length, though pieces of large *Callinectes* were found in several stomachs. Most items fall in the 8 to 45% of standard length group for snapper of all sizes. Measurements for food fishes were taken by standard length. Shrimp, etc., were measured from tip of telson to tip of rostrum or base of antennae, whichever was greater. Crabs were measured by carapace width.

Size, defenses, habits, and habitat both of predator and of prey determine the availability of a food organism to a given fish. Abundance of the prey and preference of the predator are also important.

When the overall food of the gray snapper is considered (Table 12), the effect of these factors becomes apparent. Successive dominance of copepods, amphipods, caridean shrimp, penaeid shrimp, and cancroid crabs among crustaceans and the increasing importance of fish are brought about by increasing size of the snapper and governed by the other factors. Individuals of each of these groups of food organisms average larger than individuals of the preceding group.

Crustaceans fall into two main groups: small species of copepods, amphipods, and shrimp (mainly carideans), which live in grass beds, and larger species of crabs and shrimp (mainly penaeids), which live on more open areas of mud, sand or rubble, and sparse grass.

Fishes eaten may be divided into three groups: slow-moving demersal forms, diurnal species, which rest on the bottom at night, and abundant nocturnal forms, which usually are species that occupy more open bottom, where the larger crustaceans eaten by snappers are also found. Some of the fishes, however, also live in grass beds. Slow-moving demersal fishes include the eels, pipefish, *Synodus*, gobiids, *Rypticus, Lactophrys, Monacanthus, Callionymus,* and *Opsanus beta.* Diurnal species that rest at night include mullids, *Serranus tabacarius*, labrids, scarids, *Acanthurus*, and *Balistes. Haemulon* is abundant nocturnally in open areas where gray snapper feed. *H. flavolineatum* and *H. chrysargyreum* are the two most abundant species in such areas at Alligator Reef. Of the remaining fish, *Lucania parva* is common in the grass beds, and *Anchoa* spp. are abundant in many inshore locations.

Percentages of full stomachs in collections made at various times of day are given in Figure 27. Collections of 10 or seven fish are not considered.

Table 12. Stomach contents in mean percent of food volume of all gray snappers, *Lutjanus griseus,* examined

Items	Total percent	Stomachs containing items	Number of items
Gastropod	0.3	2	2
Octopus	0.5	5	5
Polychaete worm	0.2	2	2
Holothurian	0.2	2	2
Copepod	0.6	6	42
Amphipod	11.6	83	441
Isopod	0.1	4	4
Shrimp			
Penaeus	6.2	48	51
Penaeopsis goodei	1.1	11	12
Total penaeid	7.4	59	63
Alpheidae	1.9	21	22
Palaemonidae	5.1	35	131
Total caridean	9.0	71	200
Stenopus	0.2	1	1
Total shrimp	20.3	170	309
Spider crab	2.0	22	23
Cancroid crab			
Xanthidae	4.1	38	60
Portunidae			
Portunus sp.	6.4	43	52
Portunus spinimanus	0.3	2	3
Callinectes	2.1	19	21
Total portunids	10.6	80	96
Total cancroid	14.6	111	158
Grapsoid crab	0.4	5	29
Pagurid crab	0.1	1	2
Total crab	15.5	158	234
Stomatopod	0.3	4	4
Panulirus	0.3	5	5
Barnacle	0.003	1	1
Total crustacea	66.9	470	1122
Total invertebrates	67.9	476	1133
Fishes			
Anguilliformes	0.9	10	10
Anchoa	0.1	1	1

Table 12—*Continued*

Items	Total percent	Stomachs containing items	Number of items
Lucania parva	0.4	3	5
Pipefish	0.5	6	6
Mugil (bait)	0.3	2	2
Synodus	0.1	1	1
Jenkinsia	0.2	1	1
Gobiosoma robustum	0.2	1	1
Total Gobiidae	0.3	2	2
Callionymus	0.1	1	3
Mullidae	0.2	1	1
Rypticus	0.1	1	1
Serranus tabacarius	0.2	1	1
Labridae	0.3	2	3
Scarus croicensis	0.1	1	1
Total Scaridae	0.1	2	2
Haemulon	1.2	9	10
Acanthurus	0.2	1	1
Lactophrys	0.2	1	1
Balistes	0.5	5	6
Monacanthus	0.1	1	1
Opsanus beta	5.8	43	47
Total fishes	31.7	225	259
Unidentified eggs	0.4	9	—

Rate of Digestion

About 80% of the snappers from inshore areas near Lower Matecumbe Key had food in their stomachs at 6:30 A.M. to 7:30 A.M.; by 4:00 P.M. this figure had decreased to less than 10%. A collection made at about 10:00 P.M. had 58% of the stomachs with food. Snappers from Alligator Reef followed a similar rate but the percentage of stomachs with food is lower throughout. Stomachs contained food in 84% of small snappers from grass beds even though they were collected during the day. Only two of these collections had time data available. They are plotted in Figure 27.

The above data indicate diurnal feeding for small juvenile snappers and nocturnal feeding for larger juveniles and adults. Also, stomach contents of snappers collected in the morning contain only food from the previous night. An increasing percentage of empty stomachs in fish of increasing size

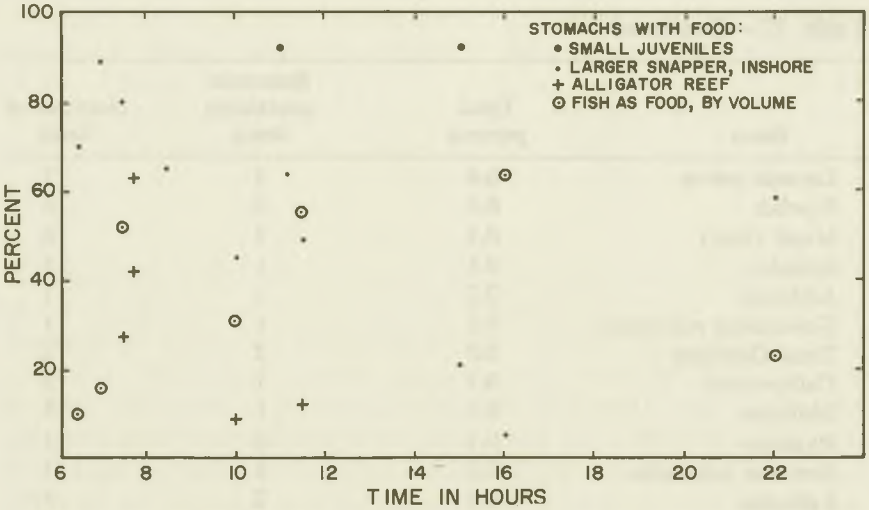

Figure 27. Percent of gray snappers, *Lutjanus griseus,* with food in their stomachs from collections made at various times of day and mean percent by volume of fish in the food of gray snappers taken at various times of day.

parallels the decreased growth rate of larger fish. The lower proportion of fish containing food from Alligator Reef as opposed to similar sized fish from inshore areas (collection 17) correlates well with the reduced growth rate of fish in the reef environment.

Fishes in stomach contents of snappers collected in early morning vary from freshly ingested to well digested but most are intact with patches of skin missing. Crustaceans are generally intact. By midday, fish have lost all skin and the body walls are eaten away. By late afternoon only bones are left. By noon crustaceans are fragmentary, and by late afternoon have largely disappeared. Food in various stages of digestion in early morning collections and night observations indicate feeding occurs throughout the night.

Longley, in Longley and Hildebrand (1941: 116), reported on feeding various fish and crabs to schools of snappers in two experiments. One group was examined after 2¼ hours. In this group digestion had proceeded far enough on the fishes to destroy the color pattern and in most instances to erode the abdominal wall. The crabs, however, remained virtually unchanged. The second group, killed after 3½ hours and examined 1 hour later, had some of the food reduced to fragments—all fish had more or less disintegrated—but on the crabs digestion had scarcely begun.

For several hours, crustacea resist digestion better than fish. Once the exoskeleton has been digested, however, crustaceans rapidly disappear, whereas the vertebral column of fish is recognizable over a much longer period. As a result, collections taken late in the day show an apparent high percentage of fish (Figure 27). Data are from collections 8 to 16 not including collections of fewer than 10 fish.

Feeding Movements

Night observations were made in attempts to determine the nocturnal movements of snappers. In inshore areas, observations were made chiefly from a boat in shallow areas. A limited number of underwater observations were also made. In inshore areas snappers seem to disperse into numerous habitats at night. They were seen in channels and in grass beds both in areas where they are found in the day and several hundred yards from the nearest point of daytime concentration. Limited observations on tagged fish and general impressions of schools indicate that most snappers return to the same point of diurnal concentration.

A considerable number of night observations were made at Alligator Reef. Over 50 night dives, using scuba gear, were made from February 1962 to August 1963. These dives were made for varying purposes and on various parts of the reef.

Sight observations were made with the aid of 6-v, 30-w, sealed-beam spotlights powered by nickel-cadmium batteries in underwater cases. These lights are used as headlamps, miner fashion, and permit underwater visibility up to 40 or more feet, depending upon water clarity. For popular accounts of these night-diving operations, see Schroeder and Starck (1964) and Starck and Schroeder (1965).

Because the two schools of gray snappers on Alligator Reef are composed of fish of different size, and because they always return to the same location during the day, it is possible to tell with considerable certainty from which school and from where a fish comes.

Snappers from the ledge at Alligator Reef were occasionally observed at night along the ledge. They were seen more commonly on the open rock bottom just offshore of the ledge. This area supports scattered small coral heads, alcyonarians, and sponges. None, however, was seen along the inside edge of the deep reef in a depth of 50 ft (15m) about 200 yards (180 m) farther offshore. Large snappers from the ledge school were also seen at night in the mixed rubble, sand, and grass bottom beginning at the ledge and extending perhaps 200 yards inshore. Some of these large snappers were also seen at night close to Alligator Lighthouse in the area occupied by smaller fish in the day.

Four night transects of 300 each, originating at Alligator Lighthouse, were made. Direction was maintained by magnetic compass, and distance measured by means of a model airplane propeller attached to a mechanized counter. Four trials over a measured distance resulted in an accuracy of 50±2m with this device. Snappers were counted in each 50-m segment of a transect, and bottom type noted.

No snappers were seen along the northern transect over fine calcareous sand bottom. Three gray snappers were seen during the eastern transect. One each was seen in the second through fourth 50-m segments, which had mixed bottom of rock, grass, and sand. The last two segments were chiefly sand, and no snappers were seen. The southern transect was largely over rubble and grass bottom, and it crossed the ledge in its terminal segment. Three gray snappers were seen, one over rock bottom near the light in the first segment and one each in the ultimate and penultimate segments over rubble and grass bottom and near the ledge. No gray snappers were seen on the western transect, which was mainly over sand and grass bottom.

Snappers from the school at Alligator Lighthouse were seen during other dives over rubble and grass bottom ¼ to ½ mile southwest and west southwest of the lighthouse. They were also seen on a small rocky patch supporting sponge and alcyonarian growths with some *Thalassia* along the edge about ½-mile northeast of the lighthouse.

In summary, gray snappers at Alligator Reef feed over open bottom of sand, rubble, or rock supporting alcyonarians, sponges, and *Thalassia.* They avoid open sand areas though they may cross them to get to preferred locations. They also avoid the deep reef and areas of rock or coral outcroppings. Nocturnal ranges of fish from the school at Alligator Lighthouse and the ledge overlap.

An order of magnitude estimate of population density in areas preferred at night is one fish per 1000 square meters. With this density, a dispersal of at least 1 to 2 km up and down the reef from Alligator Lighthouse would be required to account for the 2000 to 3000 fish estimated to occupy the reef by day in the summer.

Selection of Food

Trawl sampling of areas where snappers feed were made both inshore and offshore. A small frame trawl of 21 by 64 inches with ½-inch stretch mesh netting was used. Nine night trawls in grass bed areas near Lower Matecumbe Key were made. Trawls lasted from 3 to 5 minutes and covered about 100 yards. All organisms available as food for the gray snapper were counted. This excluded echinoids and large holothurians, which are common on the grass flats, and the small mollusks, largely *Astrea* and *Cerithium*, which were more numerous than all other organisms taken. A total of 983 potential food items were collected.

Variability between trawl catches seems to be associated chiefly with depth. Trawls in depths of about 6 ft where grass is sparse took more echinoids, holothurians, and spider crabs, and fewer *Penaeus, Lagodon,* and *Opsanus*. A greater variety of fish was usually found in the grass in deeper water.

Because of the mesh size, copepods, amphipods, and most caridean shrimp were not taken, hence comparison is made with snappers from collections 8 to 16 (Table 7). The comparison is made in percent by number of items found (Table 13).

A positive selection of this group of snappers for crustacea and a negative selection for fish and invertebrates other than crustacea are noted. Crabs seem to be taken in about the same numbers by both trawl and snappers; snappers, however, eat mainly portunids and xanthids, whereas the overwhelming majority of crabs from trawl catches were spider crabs (chiefly majids). Portunid crabs frequent more open bottom in the grass beds; xanthids also occupy such open areas as well as brush or other debris. The result is that these crabs are more readily found by snappers than the spider crabs, which are well camouflaged and usually live in the deep grass.

Pinfish (*Lagodon*), a quick-moving and deep-bodied little fish, is the most abundant fish of the shallow grass beds, but was never found in stomach contents of snapper. Speed and body shape probably protect it.

Penaeus, the commonest shrimp, and *Opsanus*, the second most numerous fish in trawls, are eaten by snappers in about the same proportion as they occurred in the trawls.

Holothurians are normally avoided by snappers as they are both readily available and abundant in the environment, though only two were found in snappers.

Haemulon, Monacanthus, and *Eucinostomus* are common in the grass beds but not eaten by snappers in this area; the first two are eaten by the large snappers in the channels and on the reef. Scarids are also common in the grass beds but only one was found in this group of snappers.

Table 13. Comparison between stomach contents of gray snappers, *Lutjanus griseus*, and trawl catches in percent of total number of items. Trawls and snappers from debris and grass beds near Lower Matecumbe Key

Items	Percent in trawl	Percent in snappers	Less than 1% in trawl 0 in snappers	Less than 1% in snappers 0 in trawl
Invertebrates	55	72	*Hippocampus*	Isopod
Crustacea	47	71	Asteroid	Eel (non moray)
Fish	45	28	Ophiuroid	*Callionymus*
Crab	34	30	*Chilomycterus*	
Spider crab	31	3	*Lutjanus* sp.	
Lagodon	13	—	*Lactophrys*	
Shrimp	11	28	*Apogon*	
Penaeus	10	14	*Portunus*	
Opsanus beta	9	8	*Diplectrum*	
Holothurian (small)	7	0.6	*Ocyurus*	
Haemulon	7	—	Clinidae	
Monacanthus	4	—	*Harengula*	
Eucinostomus	4	—	*Mycteroperca*	
Scaridae	4	0.3	*Synodus*	
Cancroid crab	4	23	*Gymnothorax*	
Portunid	2.3	6	*Bothus*	
Callinectes	1.7	6	*Carapus*	
Xanthid crab	1.4	17	Oxystome crab	
Alpheid shrimp	1.4	4		
Gobiidae	0.6	0.3		
Lucania	0.5	1.4		
Stomatopod	0.4	0.8		
Panulirus	0.3	0.6		
Pipefish	0.2	1.1		
Gastropod (large)	0.1	0.6		

Total number of items in trawl catches = 983
Total number of items in stomach contents = 354

The remaining organisms in the first column of Table 13 were taken in such small numbers in both snapper stomachs and trawls that the differences can not be considered significant.

A second group of organisms were each less than 1% of the total trawl catch and not found in snappers. Most of these were fish, and the preference of these snappers for food other than fish, coupled with the small percentages of fish in this group, account for their absence in stomach contents.

A third group of organisms including isopods, eels (ophichthid), and *Callionymus* comprised less than one percent of the items found in stomach contents and were not found in the trawl catches. All of these organisms have been taken on the grass flats around Lower Matecumbe Key at other times.

Four, 3-minute trawls were made at night on Alligator Reef. A total of 80 organisms was collected. Two trawl-hauls from *Thalassia* revealed *Portunus ordwayi* and *Chorinus heros* (a spider crab) to be the most abundant organisms. Two trawls on open sand bottom caught mostly sand dollars, *Penaeopsis goodei,* and *portunus spinimanus.*

Portunus sp. (probably *P. ordwayi*) and *Penaeopsis* were the commonest identifiable crustacea in snappers from the reef and were most numerous in the trawls. *Chorinus heros* and *Portunus spinimanus* were found in smaller numbers in the trawls and in still smaller numbers in snapper stomachs.

The overall impression is that food preference or selection by the gray snapper is not very specific in keeping with its wide range of habitats and relatively nonspecialized physical makeup.

Food of Other Snappers

Stomach contents of the other species of inshore lutjanids are presented for comparative purposes. Information came from specimens in the collection of the Institute of Marine Sciences of the University of Miami, collections made by the author, and data furnished by John E. Randall, then of the University of Puerto Rico. The number of stomachs containing an item are given after each item for every species.

Of seven specimens of *Lutjanus cyanopterus* (410–765 mm) two were empty and five contained fish remains: *Lutjanus griseus*, 1; *Haemulon*, 1; scarids, 2; *Diodon*, 1. The apparent preference of this species for fish is in keeping with its large mouth, heavy dentition, terete body, and large size.

Fifty-four specimens of *L. jocu* (65–630 mm) revealed the following: Empty, 20/Fishes, 22—scarids, 5; mullids, 2; *Haemulon*, 2; *Holocentrus,* 2; moray, 1; atherinids, 1; dussmierines, 1/Invertebrates, 19/ Crustacea, 15—crabs, 8; *Panulirus guttatus*, 2; shrimp, 2; scyllarid, 1/ Mollusk, 4—*Octopus,* 3; *Strombus,* 1. The food of *L. jocu* indicates generalized feeding on fishes, crustacea, and mollusks close to or on the reef.

One hundred and thirty-five specimens of *L. apodus* (140–445 mm) had these stomach contents: Empty, 65/Fishes, 57—scarids, 4; pomacentrids, 4; *Aulostomus*, 2; serranids, 2; scorpaenids, 2; *Amanses*, 1; mullid, 1; labrid, 1; eel, 1/Invertebrates, 25/Crustacea, 24—crab, 8; shrimp, 4;

stomatopod, 2; pagurid crab, 1/*Octopus*, 1/Eggs (*Abudefduf*), 1. These stomach contents are similar to those of *L. jocu* but with a greater emphasis on small fishes. A rocky feeding area is suggested and night observations confirm this. Longley et al. (1925: 231) listed several crustaceans prominent in the food of the schoolmaster, and Hildebrand (in Longley and Hildebrand, 1941: 118) listed several additional food items from the schoolmaster at the Dry Tortugas.

Only 10 stomachs of *L. synagris* (63–102 mm) were examined. None was empty. Two contained fish: *Anchoa*, 1/Crustacea, 9—alpheids, 3; crab, 1. Rodriguez (1962: 83) reported on 207 stomachs of *L. synagris* with food. Fish were in 66 stomachs, crustacea in 55, annelids 25, mollusks 3, algae 5, and unidentifiable 53. The algae was probably ingested incidentally along with other food. The stomach contents are in accordance with the preference of this species for open sandy or muddy bottom in inshore areas. A high percentage of stomachs with food indicates at least some diurnal feeding.

Stomach contents of 50 specimens of *L. analis* (204–620 mm) produced the following data: Empty, 10/Fishes, 17—*Diodon,* 2; *Fistularia,* 1; scarid, 1; *Sphoeroides,* 1; *Acanthurus,* 1; *Monacanthus,* 1/Invertebrates, 35/Crustacea, 29—portunid crab, 7, spider crab, 6; calappid crab, 6; stomatopod, 1; pagurid crab, 1; shrimp, 1; *Panulirus argus,* 1/Mollusk, 13—conch, 10; *Octopus,* 2; *Fasciolaria,* 1; murex, 1. The stomach contents of this species show a preponderance of crustacea and mollusks, the shells and exoskeletons of which explain the short, heavy dentition of the mutton snapper. The food items here are mostly found in open areas of grass, sand, rubble, and rock where mutton snappers are seen in the day. A relatively small number of empty stomachs indicates at least some diurnal feeling. Even fish collected during the afternoon contained food. Hildebrand (in Longley and Hildebrand, 1941: 119) mentioned small grunts and shrimps as predominating in 29 stomachs of mutton snapper at the Dry Tortugas.

Thirty-two specimens of *L. mahogoni* (81–280 mm) were examined, of which 15 were empty. Food items were as follows: Fishes, 13—*Pomacentrus*, 1; *Saurida*, 1; atherinid, 1; *Holocentrus*, 1/Invertebrates, 6 /Crustacea, 6—shrimp 2, portunid 1/*Octopus* 1. The mahogany snapper apparently feeds chiefly on small fishes and probably in the rather open reef area where it is usually seen.

Of 55 specimens of *Ocyurus chrysurus* (149–394 mm) collected during the day, 14 had empty stomachs and nine contained only bait. Twenty-three stomachs contained planktonic organisms, crustacea were in 13, larval fish in 5, and very small cephalopod in 1. Demersal crustacea were in five stomachs: crab, 3; spider crab, 2; shrimp, 2; *Penaeopsis,* 1; stomatopod, 1. Twelve stomachs had large fishes one of which was a labrid of 95 mm and the remainder were elongate silvery fishes too digested for positive identification. The yellowtail snapper feeds largely on plankton and small mid-water fishes supplemented to some extent by demersal crustaceans and fishes. Fresh stomach contents are found throughout the day but nocturnal feeding is also important. Commercial fishermen who fish for yellowtail snappers do so mainly at night.

On the basis of feeding habits, the inshore snappers may be divided into several groups in the Lower Matecumbe Key area. *Lutjanus synagris* and *L. analis* are predominately invertebrate eaters in open areas, with the former more common near shore and the latter farther offshore.

Lutjanus jocu, L. apodus, L. mahogoni, and *L. cyanopterus* are largely fish-eaters though all but *L. cyanopterus* also eat a fair amount of crustaceans. The first two occupy rocky areas but are of widely different sizes. The third is found in open areas between coral on the reef; the fourth and largest species, occupies a wide range of habitats preferring deep channels, ledges, and coral patches. Juvenile *Lutjanus griseus* feed mainly on crustaceans and adults feed to a greater extent on fish. They tend to feed in open areas over a variety of bottom types and appear to be the most generalized of the snappers in feeding area and feeding habits. *Ocyurus chrysurus* is predominately a mid-water feeder on small organisms over reef areas. *Lutjanus griseus, L. apodus, L. jocu,* and *L. mahogoni* are largely nocturnal feeders. The cubera probably also belongs in this group, but less information is available. As adults, all feed largely on fish.

Lutjanus synagris, L. analis, and *Ocyurus chrysurus* eat mostly invertebrates and feed to some extent in the day though they also feed at night.

REPRODUCTION

Sex Ratio

No external sexual dimorphism was discovered in the gray snapper; hence, determination of sex was possible only by examination of the gonads. The gonads lie in the dorso-posterior portion of the body cavity. The sexes are readily recognized except for small specimens less than about 75 mm standard length. Ovaries are round, tubular structures as in most fishes and the testes are flattened, ribbonlike organs that lack the distinct lumen possessed by the ovary. Three anomalous adult males with asymmetrical testes were found. One of these had one testis 58 mm and the other 120 mm. long.

Of 722 specimens examined (Table 14), 336 were females and 386 were males. Croker (1962: 382) examined 770 fish from Florida Bay and found 404 females and 366 males. Croker's fish were comparable in size to the fish from inshore areas—other than channels—in the present study. Inshore areas, other than channels, had almost equal ratios between the sexes. Two collections from Lignumvitae Channel had 100 females and 70 males, whereas collections from the reef had 170 females to 259 males. Miscellaneous small collections—11 specimens or fewer—from the reef vary in sex ratios. Of four larger collections from the reef containing 67 to 158 specimens, three are predominately males, and one (collection no. 21) had a slight majority of females. This collection was made on 3 September 1963, on the day of full moon. Of 47 females, 41 were freshly spent.

Apparently the sex ratio in the gray snapper is about equal, as evidenced by the collections of small fish from inshore areas other than channels. In the channels, adult females predominate, and adult males are most numerous on the reef except during the full moon period when females arrive to spawn.

For the total sample used in the present study and for Croker's sample, the null hypothesis that the sex ratio of the gray snapper is equal can be accepted at the 95% confidence level. If only fish from inshore channels and those from the reefs are considered, however, this null hypothesis must be rejected at the 95% level of confidence according to chi-square analysis.

Spawning Cycle

The smallest mature female was a freshly spent fish at 195 mm standard length; also several ripe females between 200 and 210 mm were collected. The smallest ripe male examined was 185 mm standard length; two ripe males from 190 to 200 mm were also seen. Ripe males larger than 200 mm were common. The number of fish and size ranges examined indicate that these minimum sizes at maturity are probably close to correct. Apparently, males mature at a slightly smaller size than females.

Frequency histograms of standard length were made for males and females from each collection, and no significent difference in size of the sexes was found. However, four fish larger than 430 mm standard length were collected and all were females. The largest was 489 mm. Perhaps females reach a slightly greater maximum size than do males. Croker (1962: 382) found no consistent differences in the mean lengths of males and females of the same age in the most abundant age group he examined.

Table 14. Gonad state and sex of gray snappers, *Lutjanus griseus*, collected in the vicinity of Lower Matecumbe Key, Florida

Date[1]	Females						Males					Location	Collection[2] number	Standard lengths (mm)
	I	II	III	IV	Spent	Total	I	II	III	IV	Total			
23/8/62	7	12	1			20	1	11	2	4	19	Green Mangrove Key Fla. Bay	8	189–269
25/8/62		1	6			7		1		3	4	Alligator Lighthouse	22	232–319
26/8/62			3	12	8	23				44	44	Ledge at Alligator Reef	23	294–489
19/1/63	12					12	10	1			11	Shell Key, Fla. Bay	9	114–203
15/2/63	10	3				13	8				8	Lower Matecumbe Key	10	116–258
10–14/3/63	3	9				12	10	2			12	Lower Matecumbe Key	16	137–338
20/3/63	10	7				17	9	4			13	Lower Matecumbe Key	12	159–304
24/4/63	9	3				12	11				11	Long Key, Fla. Keys	13	141–293
24/4/63	6	26	30			62	18	21	9		48	Lignumvitae Channel	17	146–414
5/6/63		2				2					—	Ledge at Alligator Reef	25	322–355
5/6/63		1				1			1		1	Alligator Lighthouse	25	306–310
5/6/63			1			1					—	Patch reef off L. Matecumbe Key	25	472
6/6/63	5					5					—	Indian Key Channel	14	142–172
7/6/63			3			3				2	2	Ledge at Alligator Reef	25	346–440
16/6/63			2			2				1	1	Crocker Reef	25	304–370
29/6/63			4			4					—	Ledge at Alligator Reef	25	288–394
4/7/63			2			2				2	2	Ledge at Alligator Reef	25	290–450
28/7/63		1				1			2	1	3	Rabbit Key, Fla. Bay	19	261–365
1/8/63				3		3				4	4	Ledge at Alligator Reef	25	271–380
2/8/63		1		21		22			1	50	51	Ledge at Alligator Reef	24	251–430
7–8/8/63				1	1	2				6	6	Ledge at Alligator Reef	25	286–378
21/8/63		1	1	48	5	55				103	103	Alligator Lighthouse	20	185–311
3/9/63		2		4	41	47	2	1	1	38	42	Alligator Lighthouse	21	190–300
4/9/63	2	3			3	8	1				1	Lignumvitae Channel	18	165–419
			Total females =			336		Total males =			386			

1. Day, month, year.
2. Corresponds to collection numbers in Table 6.

Jordan and Evermann (1922: 407) stated that gray snappers spawn in July and August, usually on the shoals. Data on gonad state throughout the spawning period were fewer than desired in this study. Two factors hindered the collection of adequate samples of adult fish during the spawning season. Because the adult fish are found primarily on the exposed offshore reefs, weather conditions often prevented collections for several weeks. The second factor is that the fish tend to congregate in a limited number of places and continuous sampling may result in the dispersion of the school. The latter effect has occurred in past years due to heavy pressure by spear fishing, hook and line fishing, and other fishing efforts. For these reasons, sampling during the present study was restricted to only one or two large collections from each school and a limited number of small samples.

Gonads of fish examined were assigned to one of four states described below:

	Female	Male
State I	Ovaries glassy, about one mm in diameter ¼ to ⅓ length of body cavity.	Testes colorless, about one mm wide, ⅓ to ½ length of body cavity.
State II	Ovaries pinkish, two to six mm in diameter, ⅓ to ½ length of the body cavity, fat deposits generally present attached to and anterior to the ovaries.	Testes pinkish to white, opaque, one to six mm wide, ½ to ¾ length of body cavity, fat deposits usually present adjacent to and anterior to the testes.
State III	Ovaries yellowish, six to 30 mm or more in diameter, ½ to ¾ length of body cavity, fat deposits usually present as in state II but larger.	Testes white, six to 15 mm wide, about ¾ length of body cavity, fat deposits as in state II but larger.
State IV	Ovaries pale orange to white, size as in state III or smaller if partially spent, free eggs in the lumen, fat deposits reduced or absent.	Testes white, size as in state III or smaller if partially spent, milt flows from the testes when light pressure is applied, fat deposits reduced or absent.

An additional state (spent) in the females is also recognized.

Entirely spent females have collapsed; their flaccid ovaries contain gelatinous material consisting of eggs in the process of resorption. Data on state of gonads from various collections are given in Table 14. Collection numbers in this table correspond with those in Table 4.

Female fish of adult size had ovaries in states I and II from January through March, 1963. States II and III fish were prominent in April, and state III fish dominant in June. July samples are too small to be meaningful, though of 22 females collected at Alligator Reef on 2 August 1963, 21 were state IV. Hence, state IV probably is reached by most fish in July. Females from the remaining August collections are predominately state IV, and two collections in early September contained mostly spent females.

Male fish of adult size were states I and II in January through March, 1963, and a collection of 24 April contained a number of males with states II and III testes. Males from collections from June through early September are chiefly state IV. Ripe males from the two early September collections had flaccid testes apparently in the process of resorption and several fish had gonads regressed to state I.

Croker (1962: 382) found no ripe fish among 790 snappers from northern Florida Bay, though most of these fish were above the minimum size at maturity. Four fish from Rabbit Key in Florida Bay were collected on 28 August 1963. One female and two males had state II gonads, and one male was ripe. All were well over the minimum size at maturity. Few other fish of comparable size were seen at that location. Apparently, gray snappers spawn only in offshore areas, and the adult fish that remain inshore generally have undeveloped gonads.

Gonad lengths and weights of adult fish indicate that spawning occurs more than once during the spawning season. Five female snappers from 310 to 472 mm standard length had ovaries 80 to 120 mm long, and three of these had ovaries 114 mm and greater at standard lengths of 346 mm and longer. The weight of the ovaries from the largest fish was 121 g. These fish were collected from 5 to 16 June 1963, in offshore areas. Five males collected during the same period were state IV. Testes were 120 to 135 mm long at standard lengths of 304 to 383 mm. Eight additional fish were collected from the ledge at Alligator Reef on 29 June and 4 July. Six were state III females, 288 to 450 mm standard length with gonad lengths ranging from 60 to 120 mm. The remaining two fish were state IV males, 301 and 310 mm standard length with testes of 118 and 120 mm. The gonad sizes of the above fish are larger than those of fish from the large collection of 2 August 1963 from the ledge at Alligator Reef. Gonad lengths and weights of fish from the latter collection are given in Figure 28. Apparently, some spawning occurred during the period from 5 June to 2 August 1963.

The wide range of ovarian weights of state IV fish in the 26 August 1962 collection also indicates the presence of partially spent fish.

A collection on the ledge of Alligator Reef on 26 August 1962 (see Figure 28), contained large fish (294 to 489 mm standard length) than did the collection of 2 August 1963 (251 to 430 mm standard length). The 1962 collection had fish with a rather wide range of gonad sizes. Large fish similar to those in the 1962 collection were again present at the ledge on 22 August 1963. The presence of larger fish at a later date could be due to either an exchange of population or to the emigration of the smaller individuals from the existing population. The latter effect probably plays some part since the school of large fish seems to be about half the size of the first group. Possibly, the larger fish spawn more times than the smaller ones and, hence, remain on the reef later.

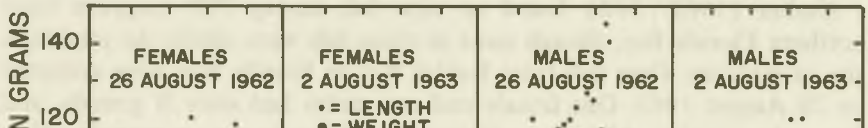

Figure 28. Lengths and weights of state IV and spent gonads of gray snappers, *Lutjanus griseus*, from the ledge at Alligator Reef, Florida.

Two collections of fish from the school at Alligator Lighthouse were made. These fish are smaller than either group at the ledge. Standard lengths ranged from 185 to 311 mm.

The first collection, on 1 September 1963 contained 55 females and 103 males. The females were predominately state IV. Five spent fish were also taken but they did not appear to be freshly spent.

Collections and field observations resulted in increasing suspicion that spawning probably occurred only during short periods, possibly during or near full moon. Randall and Brock (1960: 12) state that *Lutjanus vaigiensis* in the Society Islands apparently spawn at about the time of full moon, hence lunar periodicity in the spawning of gray snapper would not be unique.

Previous attempts to collect gray snappers near time of full moon had been thwarted by weather and other factors. A collection from the school at Alligator Lighthouse was successfully attempted on 3 September, the morning after the night of full moon. This collection contained 47 females and 42 males. Twenty one of the females were freshly spent fish. The state IV males had generally flaccid testes apparently in the early stages of resorption.

The contrast between sizes of gonads from 21 August and 3 September are apparent in Figure 29.

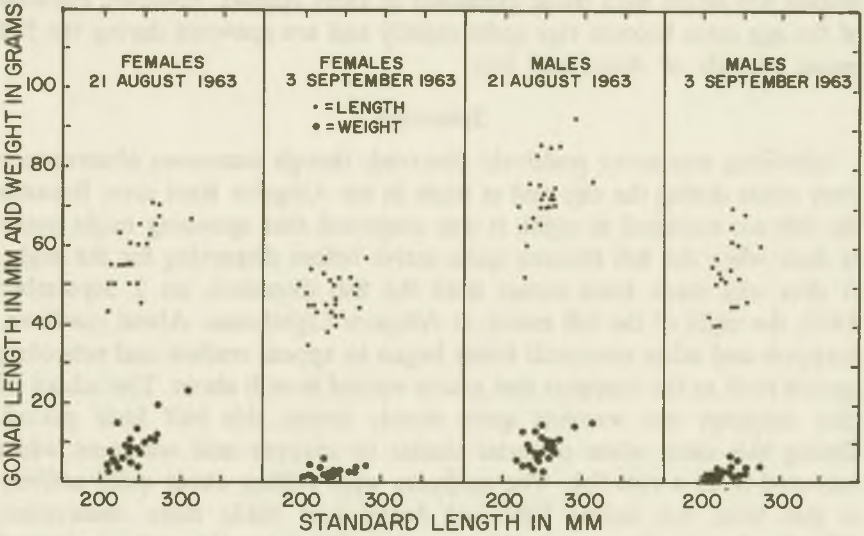

Figure 29. Lengths and weights of state IV and spent gonads of gray snappers, *Lutjanus griseus*, from Alligator Lighthouse.

Relationship between gonad length and weight is not consistent. The longest gonad is not necessarily heaviest. Values of gonad length and weight at the same standard length are from the same individuals.

Occurrence of Small Juveniles

Frequency histograms of 279 small gray snappers from inshore areas in the collections of the Institute of Marine Sciences of the University of Miami are presented by month of collection in Figure 30. Fish in the 10 to 20 mm range of standard lengths are prominent in July and August. Only one fish in this size range was taken in June, two in October, and five as late as November. These were the smallest fish taken in collections from grass beds, the smallest of them, at 10 to 11 mm, showed postlarval characteristics. Since the length of the larval life of *Lutjanus griseus* is unknown it is impossible to state precisely the relationship that the occurrence of juveniles has to the spawning period. Gosline (1955: 466) noted the absence of *Lutjanus* in Hawaii, though no limiting factors are apparent among the ecological conditions there. Randall and Brook (1960: 9) suggested that the absence of *Lutjanus* in Hawaii is due to a relatively short planktonic life. Thus, peaks of occurrence of small snappers in July and August may stem from spawning peaks during June and July. Gonad size of snapper for June and July, though data are limited, supports this, for gonads are larger than those examined in early August. Possibly, portions of the egg mass become ripe quite rapidly and are spawned during the full moon periods of June and July.

Spawning

Spawning was never positively observed, though numerous observations were made during the day and at night in the Alligator Reef area. Because the fish are scattered at night, it was suspected that spawning might occur at dusk when the fish become quite active before dispersing for the night. A dive was made from sunset until the fish dispersed, on 2 September 1963, the night of the full moon, at Alligator Lighthouse. About sundown, snappers and other nocturnal fishes began to appear restless and schooling species such as the snappers and grunts started to mill about. The school of gray snappers was watched quite closely during this half hour period. During this time, white material similar to snapper milt was seen when squeezed from a ripe fish. The snappers were milling about quite actively at that time, but failing light and heavy seas made close observation difficult. A collection made the next morning from this school showed mostly spent fish (Table 14 and Figure 29).

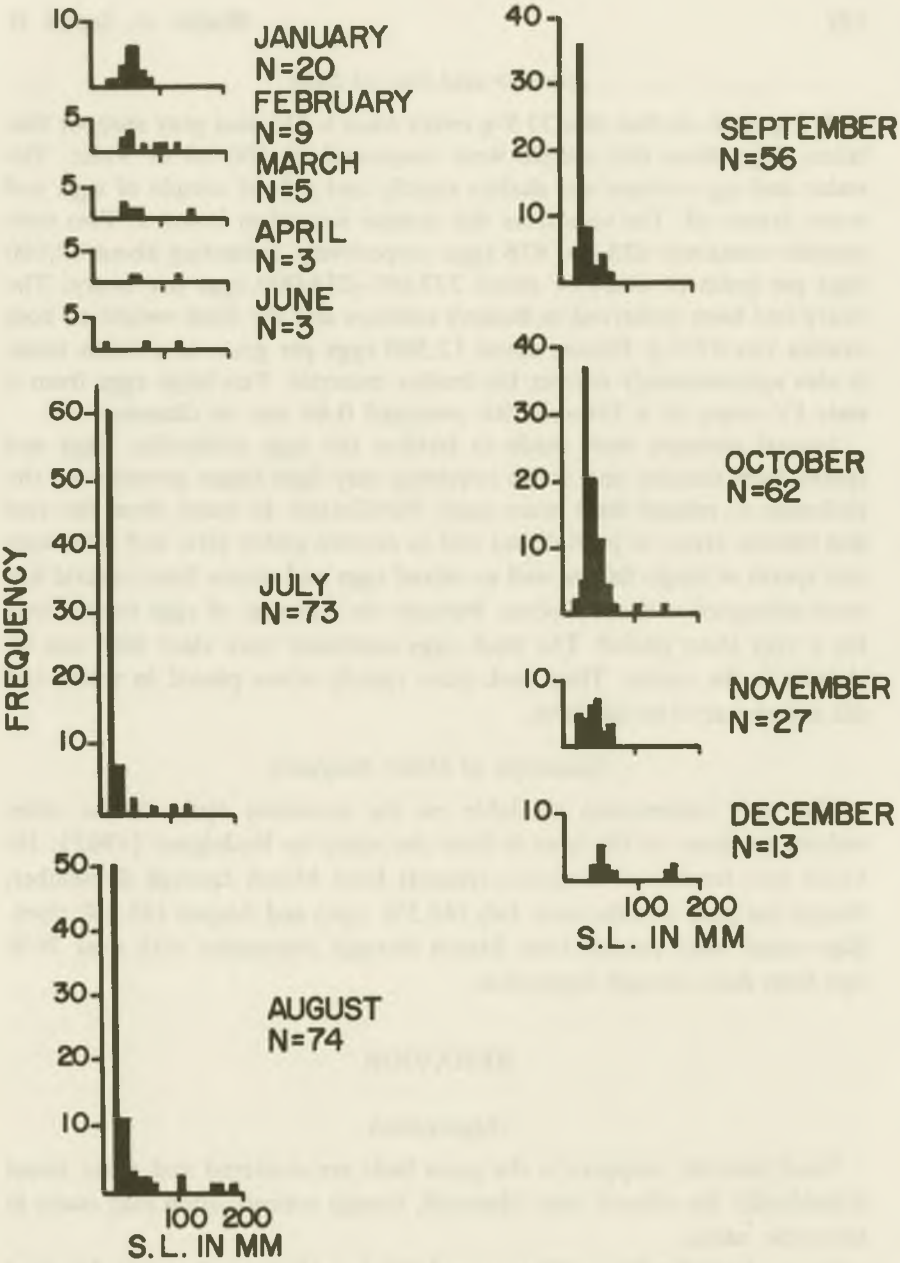

Figure 30. Length frequency, by month of collection, of small gray snappers, *Lutjanus griseus,* in the collections of the Institute of Marine Sciences of the University of Miami (see Table 1).

Number and Size of Eggs

A 1-g cross section of a 21.9-g ovary from a 315-mm gray snapper was taken. Eggs from this sample were suspended in 100 ml of water. The water and egg mixture was shaken rapidly and a 5-ml sample of eggs and water drawn off. The eggs from this sample were then counted. Two such samples contained 623 and 626 eggs, respectively, indicating about 12,500 eggs per gram of ovary or about 273,000–274,000 eggs per ovary. The ovary had been preserved in Bouin's solution and the fresh weight of both ovaries was 47.2 g. Hence, about 12,500 eggs per gram of ovarian tissue is also approximately correct for fresher material. Ten large eggs from a state IV ovary of a 354-mm fish averaged 0.44 mm in diameter.

Several attempts were made to fertilize the eggs artificially. Eggs and sperm from females and males requiring only light finger pressure on the abdomen to release them were used. Fertilization in water from the reef and inshore areas, in petri dishes and in aerated gallon jars, and from eggs and sperm of single fish as well as mixed eggs and sperm from several fish were attempted without success. Perhaps the ripening of eggs occurs only for a very short period. The fresh eggs examined were clear with one oil globule in the center. They sank quite rapidly when placed in water and did not appear to be adhesive.

Spawning of Other Snappers

The only information available on the spawning cycle of the other inshore snappers of this area is from the study by Rodríguez (1962). He found ripe females of *Lutjanus synagris* from March through September, though the peak months were July (46.3% ripe) and August (48.4% ripe). Ripe males were present from March through September with over 70% ripe from June through September.

BEHAVIOR

Aggregation

Small juvenile snappers in the grass beds are scattered and move about individually. No schools were observed, though concentration may occur in favorable areas.

Larger juveniles that gather around debris and along channel edges had only weak schooling tendencies. The attraction appears to be cover rather than mutual attraction between the fish. Hence, when cover is abundant they will be more or less scattered. Adult fish in channels and on the reef form definite schools in which the individuals are oriented generally in the same direction and move together. When disturbed, some individuals from such schools may seek cover if it is available, and a school may split into two or more groups. School coherence is greatest in areas of reduced cover.

Schools of gray snappers on the reef often float in mid-water. They stay in the same general areas but the exact location of a school varies. At times, fish in one area may be in one school and at other times split into several schools. When moving from one location to another, snappers usually swim close to the bottom. A school often elongates while moving, so that it seems to flow from one point to another rather than move as a unit. Scattered individuals are frequent, usually close to cover or mix in with a school of fish of different species. Other species of fish also are often found in schools of gray snappers. The pale gray grunt, *Haemulon parrai*, commonly mixes with gray snappers, sometimes in considerable numbers (Figure 31).

Schooling seems to result from the accumulation of snappers in favorable areas and is strongest when cover is limited. Its chief advantage is probably the confusion effect that makes it difficult for a predator to get an

Figure 31. Mixed school of *Lutjanus griseus, Haemulon parrai, Haemulon sciurus,* and *Mulloidichthys martinicus*, at Alligator Lighthouse.

effective optical fixation on any one fish (see Breder, 1959: 414). The confusion effect is apparent to anyone who has tried to spear fish from a school.

With the approach of darkness, decreasing light and increasing hunger produce an increasing restlessness in nocturnal fish like snappers and grunts. They mill more and more and become quite pale. Finally, about ½ hour after sunset, at about the time light becomes too low for effective human observation, the schools disperse.

The dense schools of snappers described in the section on tolerance to temperature are similar to those described by Breder and Nigrelli (1935) for the sunfish, *Lepomis auritus*. They state in the summary that schooling may be considered as a primary impulse with cases of nonschooling as inhibitions of it caused by feeding, reproduction, or other requirements. Any cessation of such influences causes an immediate reappearance of the schooling habit. They stated further that adverse conditions, generally, allow aggregating effects to appear, and that the results to the individuals and species may be valuable, neutral, or harmful. They listed temperature, light, CO_2, fright, and various toxic substances as factors that cause aggregations.

The schooling of snappers on the reef during the day can be attributed to noninhibition of the schooling impulse conditioned by light and perhaps by fear of predators. Dispersal of the schools at night may be attributed to inhibition of the schooling impulse caused by feeding requirements and conditioned by reduced light.

In the same system, the dense schools or pods of smaller snappers during the cold spell can be attributed to adverse temperature conditions.

A third sort of aggregation has been observed in the gray snapper. They tend to accumulate around docks and other areas where refuse and fish scraps are discarded. These groups often contain fish of widely varying sizes in contrast to natural schools. These aggregations are mechanical assemblages brought about by concentration in a favorable area.

Migrations

Juvenile snappers are seen in favorable locations throughout the year and no large movements are suspected, though they may temporarily be driven from some locations by extreme temperatures or storm conditions.

Adult snappers are seen in reduced numbers at inshore locations in summer when they are most abundant on the reef. During fall, winter, and spring this situation is reversed. The summer concentration of adult fish on the reef apparently is associated with spawning, though a lesser number of fish remain on the reef throughout the year.

During fall, winter, and spring the group of snappers at Alligator Lighthouse comprises an estimated 500 individuals. The number increases during June and July, and a maximum of perhaps 3000 fish are present in early August. On 2 September 1963, over 1000 snapper were seen at Alligator Lighthouse, though on 4 September and thereafter fewer than 500 were seen. Field observations followed the same pattern for two years.

A similar situation occurred at the ledge on Alligator Reef. On 8 June 1963, about 50 snappers were seen. They were similar in size to the large fish taken at Alligator Lighthouse (i.e., about 300 mm standard length). On 29 June, 300 to 500 fish were present including a number in the 400 mm size class. The average size fish in this school increases later in the season. On 22 August 1963, fish in this school averaged about 350 mm standard length as opposed to about 300 mm on 2 August 1963. The larger fish numbered about 200 to 300, hence the larger average size may be due in part to disappearance of smaller fish. The impression, however, is that a greater absolute number of large fish are present.

Results from tagging confirm the nonmigratory nature of small fish and the seasonal inshore to reef movements by adults. The tagging done during this study is discussed in the section on growth (see Table 4).

Of the 613 juvenile and young adult snappers tagged in inshore areas, exclusive of captive fish, eight recoveries were made. One fish (tag no. 22) had moved from Lower Matecumbe Key to Alligator Reef. However, this datum is suspect because of the apparent extreme growth. Four of the remaining fish were recovered at locations differing from their point of release. The distance traveled varied from 0.1 to 1.5 nautical miles. No particular pattern of movement was present. Two of these fish were released at points differing from point of capture, and one fish had left a dock during late summer when fish scraps are not discarded and most of the snappers there leave. The last fish had left an exposed position on a shallow bank for a protected creek during the fall. An additional total of about 20 sightings of tagged snappers were made over a period of several weeks at inshore locations where numbers of tagged fish had been released.

Of 274 gray snappers tagged at Alligator Lighthouse in August 1962, 48 recoveries were obtained and an additional 30 fish were estimated to have been brought into the local fish market during the same month by fishermen fishing at Alligator Lighthouse.

Movements fall into two patterns: First, some fish apparently remained at Alligator Reef throughout the year, and recoveries were made as much as

367 days later. Recoveries made in the summer of 1963 could, of course, have gone inshore for the winter and returned, but this seems unlikely for recoveries made in March and April. Second, a number of tagged fish began to be caught in inshore areas as soon as seven days after tagging, and

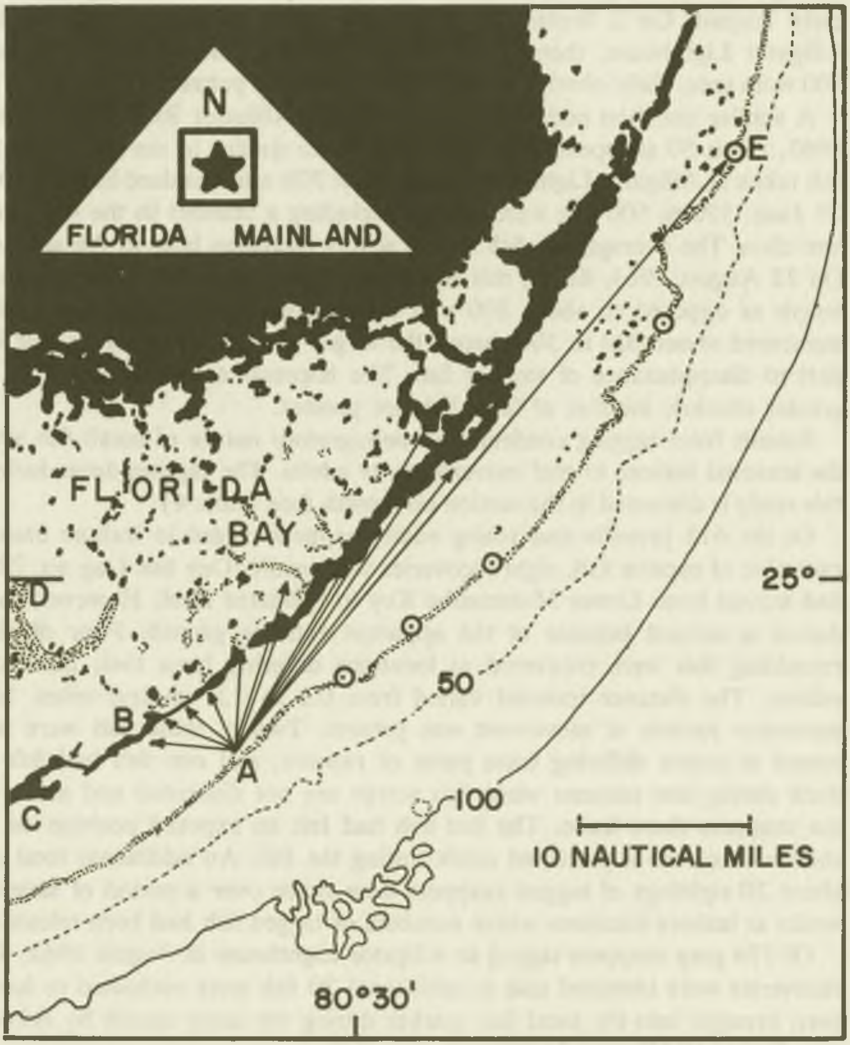

Figure 32. Recovery areas of tagged gray snappers, *Lutjanus griseus*, leaving the area of Alligator Lighthouse. A: Alligator Reef; B: Lower Matecumbe Key; C: Long Key; D: Rabbit Keys; E: Pacific Reef.

recoveries from inshore areas were occasionally made as much as 285 days later, in May 1963. Inshore recoveries of fish tagged at Alligator Lighthouse were scattered throughout the northwest to northeast quadrant from Alligator Reef (Figure 32).

The greatest distance from point of release was 40.5 nautical miles in seven days (tag no. 351).

Recruitment of snappers from the school at Alligator Lighthouse to the school on the ledge is indicated by the recovery of a tagged fish from the ledge (tag no. 303) and the sighting of a tagged fish in the school at the ledge on 7 July 1963.

Bardach (1958: 142) tagged 33 gray snappers and recovered a total of 17 on five occasions. He reports that the entire group is continuously on the move though they remain on or near the same reef.

Randall (1962: 222) reported tagging six gray snappers in the Virgin Islands. Three were caught again, one twice and another three times. All were recovered at or near the place of tagging and were at large one month or more.

Ingle et al. (1961: 16) reported recoveries of seven out of 22 tagged gray snappers along the southwest coast of Florida. Only one fish was caught more than five miles from the release site. This one specimen traveled less than 10 miles. Mean distance traveled was six miles in 15 to 53 days. Along the southeast Florida coast, of 532 fish tagged 121 gray snappers were recaptured (Ingle et al., p. 25). The greatest distance traveled in this case was 20 miles in 37 days. This was the only instance of movement over 10 miles. Ninety-seven and one-half percent of recoveries were made less than five miles from the point of release.

The results of studies by Bardach and Randall are similar to those of the present study for fish remaining on the reef throughout the year. Reef populations of the gray snapper tend to vary in exact location but remain in the same area.

The recoveries reported by Ingle et al. parallel those of the present study in that snappers in inshore areas generally move only short distances and movements show no particular pattern. These movements are apparently related to factors such as aggregations in favorable areas, movements to more or less sheltered locations depending upon weather, and shifts in habitat with increasing size.

Feeding Behavior

Food is taken in three ways by the gray snapper. Immobile food items such as a small dead fish may be gently picked up with the mouth especially if no other snappers are present. If a school is present, however, even immobile objects may be struck. Often around docks several fish may strike at food and just miss before one finally takes it. The near misses appear to be testing behavior.

A second method of taking food is by sucking the item into the mouth by a rapid expansion of the gill covers and branchial membranes. This method is used on small items and may be combined with a strike if the items move. When catching shrimp on the surface at night, the sucking action creates a loud pop.

Striking of prey usually occurs when feeding on larger, active food organisms. An item too large to swallow may be torn apart by violent lateral shaking. Pieces of *Callinectes* from crabs clearly too large to have been swallowed whole were found in the stomachs of a few snappers, and a large snapper on the ledge at Alligator Reef was seen to tear off the head of a French grunt (*Haemulon flavolineatum*) after the grunt has been stunned by rotenone. The great majority of food, however, is swallowed whole.

Vision

Reighard (1908) carried out a number of experiments at the Dry Tortugas, Florida, in which atherinids (*Atherina laticeps* = *Atherinomorus stipes*) were dyed various colors and certain colors were made unpalatable by different means. He found that after a brief experience, colored atherinids rendered unpalatable were no longer taken as food by gray snappers, although normal atherinids were readily taken. After a considerable number of experiments with various colors, some associated with unpalatability and others not, he concluded that gray snappers discriminate certain colors, form associations with great rapidity, and retain these associations for a considerable time.

Longley also carried on extensive experiments (at the Dry Tortugas) designed to provide information on the ability of the gray snapper to distinguish color patterns. These experiments are reported upon in Carnegie Institution of Washington Year Book Nos. 22, 23, 24, and 29. Hildebrand, (Longley and Hildebrand, 1941: 117–118) summarized the results of these experiments. *Atherina laticeps* was again used as food. Two patterns were painted on the atherinids with silver nitrate; one consisted of a dark lateral stripe and the other of two dark crossbars. A series of experiments using these patterns with one pattern or the other rendered unpalatable resulted in the conclusion that gray snappers can distinguish beween the two color patterns and that they can learn to avoid one or the other.

Sound

Lutjanus griseus was listed by Moulton (1958: 358) among fishes that make no sound or only chewing sounds during a study of the acoustical behavior of various fishes in the area of Bimini, in the Bahamas.

Sound perception has also been briefly investigated. Several years ago, the author carried out a simple experiment. A group of gray snappers around a dock were noticed to be attracted by a spray of water on the surface. Tuna fishermen use a similar spray to attract tuna. Presumably, droplets of water hitting the surface approximate the sound of small fishes showering, though in the case of snapper at the dock, conditioning may have occurred since sprayed water was also used to wash fish entrails from the dock. In the experiment, water was sprayed on the surface attracting the snapper and they were fed. An underwater recording of the spray and feeding sounds was made and played back by an underwater speaker after the fish had dispersed. They were immediately attracted to the speaker when playback began and remained for several seconds until a human voice on the recording tape cut in, at which time they quickly departed.

Parasite Removal

Gray snappers were seen on two occasions to submit to parasite removal by small fishes. Both ocurrences involved large adults on the ledge at Alligator Reef. In one incident several neon gobies (*Gobiosoma oceanops*) living on a small coral head cleaned several snappers in succession. A snapper would approach the coral head, become quite dark, and come to rest on the pale bottom beside the head. The gobies would transfer from the coral to the snapper, which would lie still except for trembling of the fins. After a short period the snapper would leave and the process would be repeated by another snapper.

The other occurrence involved three snappers in a crevice between two large rocks which were attended by two small Spanish hogfish (*Bodianus rufus*). The snappers did not respond to the smaller fish.

Reighard (1908: 319) described two observations in which young porkfish (*Anisotremus virginicus*) emerged from coral crevices and swam a distance of 6 to 8 inches to nibble at the surface of a gray snapper.

Gray snappers at Alligator Reef have also been seen to engage frequently in another activity that may be associated with the presence of ectoparasites. A fish will approach the bottom in a sandy area, roll over on its side, and rapidly swim along the sand for several caudal oscillations. Often it is followed by several other fish in quick succession at the same spot. A flash of white from the side of the fish makes this activity quite noticeable. Possible spawning activity was suspected at first, but careful examination of the spot revealed no eggs and nothing was seen to be released.

5. Discussion; Summary of Life History; Management Recommendations; Conclusions

DISCUSSION

The most striking features of the gray snapper are its wide geographic and ecologic ranges combined with its abundance throughout much of these ranges. Though the other inshore lutjanids may have extreme geographic ranges similar to the gray snapper, they are not found as commonly at these extremes as is *Lutjanus griseus* nor are their normal ranges so extensive. None of the other species appears to have the wide ecologic range of the gray snapper, and certainly none is as abundant through so wide a range of habitats. Longley, (Longley and Hildebrand, 1941: 115) described it as in many respects the dominant fish in the local fauna at the Dry Tortugas, Florida.

The wide ranges and abundance of the gray snapper are reflective of its generalized nature, which permits it to occupy successfully a number of environments. Normal geographic range and some evidence from cold kills in areas where several species of snappers are found indicate a greater tolerance to low temperature than exists in the other species. Frequency of occurrence in fresh water indicates tolerance to a wide range of salinities. The color pattern of *L. griseus,* though less well adapted for certain specific situations than (the pattern of) other snappers, is not conspicuous in any of its habitats and blends very well with several. Its ability to change pattern as well as tone also reflects its adaptability. Morphometric studies again point to its intermediate or generalized character. Among the characters examined the only morphologic exceptions to this are in the length of the paired fins. The short pelvic fins appear to be associated with a tendency to mid-water swimming, and the short pectoral fins may be an adaptation to movement through brush and mangrove roots. Dentition and mouth size fall between that of the fish-eating cubera snapper and the largely crab eating mutton snapper. Food of the gray snapper is composed of crustaceans and fish, with the former most important to the small snapper and the latter to large snapper.

In short, the gray snapper may be said to be adapted for a generalized environment. Bays, estuaries, and lagoons comprise such an environment, and gray snappers usually dominate such areas in their range. Their generalized nature also allows them to compete successfully in more specialized environments such as coral reefs.

Despite the generalized nature of *Lutjanus griseus*, there is no eastern Pacific cognate. Jordan (1908), in a partial list of geminate species from the West Indies region and the tropical eastern Pacific, includes four such pairs of lutjanids: *L. cyanopterus* and *L. novemfasciatus, L. apodus* and *L. argentiventris, L. analis* and *L. colorado*, and *L. synagris* and *L. guttatus.* An abundance of rocky coasts and considerable open rock, sand, and mud bottom in the tropical eastern Pacific favor the presence of the species listed. *Lutjanus jocu, L. mahogoni*, and *Ocyurus chrysurus* are closely tied to coral reefs and absence of cognates in the almost reefless eastern Pacific is not surprising. Paucity of coral reef, estuarine, inshore grass bed, and shallow bay habitats is probably related to the absence of *Lutjanus griseus* in that area.

SUMMARY OF LIFE HISTORY

The life history of *L. griseus* as interpreted by this study is as follows. Spawning adults congregate at certain locations along th outer reef tract in June, July, and August. Spawning occurs near the time of full moon and probably more than once in a given individual. The eggs are demersal, and larval development is apparently rapid. Postlarval snapper with elongate dorsal and pelvic spines and little pigmentation enter the grass beds at a standard length of about 10 mm. Young snappers remain in the grass beds until they reach a length of about 80 mm. They are darkly pigmented at 10 to 20 mm and gradually develop their adult pattern thereafter. In the grass they are nonschooling and feed during the day.

Copepods, amphipods, and palaemonid shrimp are successively important as the snappers increase in size. At first annulus formation in early winter, they average 68 mm standard length.

Fish of 80 mm begin to concentrate around debris and channel edges in shallow water where they are common up to 200 mm standard length.

They feed at night in surrounding areas and eat largely penaeid shrimp, cancroid crabs, and small demersal fish.

Fish of 170 mm and larger are abundant in channels and around reefs or wrecks. With increasing size, they feed more on fish and larger crustacea such as portunid crabs. They feed nocturnally and may range a mile or more from their place of daytime concentration.

Maturity occurs at 175 to 180 mm standard length or about three years of age. Ripe fish migrate to the reefs in summer and return inshore after spawning. Some fish remain on the reef throughout the year. The oldest individuals encountered had nine annuli and averaged 407 mm standard length.

Several of the more abundant predaceous reef fishes of the West Indies region share with the gray snapper a life history involving juvenile development in nearshore areas, especially grass beds. Certain pomadasyids, serranids, and lutjanids are among these fishes. All are medium to large predators that, as adults, feed on prey too large to be eaten when juveniles. As a result, they must occupy two or more ecological niches in respect to feeding as they increase in size. Inshore grass beds offer the juveniles of such species an abundance of small food organisms, adequate cover, and fewer predators and competitors than the reef environment. Herbivorous and plankton-feeding reef fishes are able to eat the same food as small juveniles as they do when adults, and usually live on reefs as juveniles and adults.

MANAGEMENT RECOMMENDATIONS

At present, this species is underexploited and no restrictive measures are needed now or in the immediate future. If protective measures should be required at some future time, protection might be best implemented in two areas where gray snapper are especially vulnerable. Grass beds are essential to the young fish and should be protected. In Monroe County, however, the grass bed area enclosed by Everglades National Park is probably more than adequate for that purpose since rather small grass bed areas can support rather large populations of adults such as at Bermuda. The second vulnerable point is found at certain reefs where spawning schools concentrate in summer. These populations may suffer heavily from fishing pressure. About 40 fish out of 274 tagged at Alligator Lighthouse were caught by fishermen within two to three weeks of release.

The most important approach to management of this species, though, can be a positive one rather than the negative one of restriction. Properly placed artificial reefs in both inshore and offshore areas and even brush in inshore areas would contribute substantially to the habitat available to adults. Grass bed area and juvenile populations appear to be out of proportion to the area of habitat available to adult fish. Much potential feeding ground is unavailable to adults because of lack of cover for daytime concentrations. Artificial cover could open these areas to gray snapper populations.

The gray snapper is a species that conservationists in South Florida have often used for an example of a fish easily taken and often depleted by spearfishermen in certain areas. It is true that the abundance and habits of the gray snapper together with its food qualities make it a species often taken by spearfishermen. However, considerable use of spears as well as hook and line and other methods during the present study and over previous years lead the author to believe that spearfishing is overrated as a method for taking gray snapper. Spearing is most useful when selection is desired but in terms of catch per unit of effort hook and line is usually several times as effective. Hook and line fishing also has the advantage that it can be used under a much wider range of conditions than can underwater spearing.

CONCLUSIONS

1. The family Lutjanidae comprises a large group of generally medium-sized predaceous fishes common in warm seas. For the most part snappers are shelf species, and some are important commercially as food fishes.

2. The family contains an estimated 23 genera, six of which occur in the West Indies region. *Lutjanus* is the largest genus with over 70 species, 14 of which are found in the West Indies region.

3. *Lutjanus griseus* was described as early as 1743 by Catesby and has a synonymy of at least eight names based on western Atlantic specimens. The most frequently encountered English common names are gray snapper and mangrove snapper.

4. Commercial landings of the gray snapper in Florida have varied between about 252,896 to 456,137 lb., worth $40,078 to $76,140, from 1956 through 1962. Monroe County usually leads the state in production. Limited information on sport fishery landings indicates that the economic value of gray snapper as a sport fish far exceeds its commercial value.

5. *Lutjanus griseus* has been recorded from Woods Hole, Massachusetts, to São Paulo, Brazil. It is common throughout the West Indies faunal

region. Several eastern Atlantic records exist but the systematic status of the eastern Atlantic species and its synonyms is uncertain.

6. Juvenile gray snappers of 10 to 70 mm standard length are common in shallow-water grass beds and often in low salinities. At 70 to 90 mm standard length they begin to congregate around brush, debris, and channel edges and are common at such locations from 90 to 210 mm standard length. Fish over 170 mm tend to move into channels. Individuals occupying reef and wreck areas farther offshore usually are 200 mm or larger. Gray snappers occupy a wider range of habitat than do the other common inshore lutjanids in this region.

7. Records from cold kills of gray snappers indicate a lethal low temperature limit between 11 and 14°C. During cold periods they move into deeper water and form dense schools.

8. Gray snappers of all sizes have been reported from fresh water with chlorinities as low as 50 parts per million. High calcium content is probably important to snappers in fresh water.

9. Barracuda, *Sphyraena barracuda*, and the green moray, *Gymnothorax funebris*, are considered the most important potential predators of gray snappers on the reefs. One small gray snapper was taken from the stomach of a cubera snapper, *Lutjanus cyanopterus.*

10. A number of trematodes, one acanthocephalan worm, three nematodes, and one cestode have been reported as endoparasites of *L. griseus.* (Robert E. Schroeder, of the Department of Zoology of the University of Miami, presents in the second part of this book a companion study of the trematode parasites of gray snapper at Lower Matecumbe Key.). Four ectoparasitic crustacea are recorded from *L. griseus*, one isopod, and three copepods.

11. Tumorous growths are seen on 5 to 10% of large snappers at Alligator Reef. A lower incidence is seen in smaller fish.

12. Gray snappers are among the dominant medium-sized predators in most areas where they occur. Several thousand are present in two schools at Alligator Reef in summer.

13. The basic color pattern of the gray snapper is gray dorsally with white countershading. Shade may vary from pale gray to dark reddish brown. Dark shades are found among small juveniles in grass beds and adults from mangrove swamps or estuaries where the water is dark brown. Pale fish are seen in channels around Lower Matecumbe Key and on the reefs. A general reddish color has been reported for gray snappers from deeper water.

14. The color pattern of gray snappers matches in general tone the variety of environments where it is found. Patterns of bars or blotches seen at night match the pattern of areas where they commonly feed.

15. The ocular stripe is displayed when interest is fixed upon another organism or when feeding and is believed to function in obliterating the eye.

16. The color pattern of the other inshore snappers are believed to be adapted for blending with their various environments. Gray (*L. griseus* and *L. cyanopterus*) is found in the two species which occupy a wide variety of habitats. Yellow (*L. apodus, L. jocu,* and *Ocyurus chrysurus*) is associated with species found in rocky or coral areas where yellowish coral, alcyonarians, sponges, and algae are prominent. Pink or reddish hues figure prominently in the pattern of the three species (*L. synagris, L. analis,* and *L. mahogoni*) that wander in open areas during the day. Viewed in their natural habitat these pinks appear gray.

17. Selective absorption of various colors, scattering, and suspended material alter significantly the underwater appearance of a color pattern.

18. Annulus formation on scales occurs in late fall or early winter after a sudden drop in water temperature. Scales of 1289 snappers were examined and 197 rejected due to replaced centers, etc.

19. Estimates of growth based on monthly marginal increment of scales and limited data from tagged fish indicate reduced growth in winter and maximum growth in August and September.

20. Back calculations of growth from scale annuli resulted in the following mean standard lengths at annulus formation: Annulus I, 68 mm; II, 123; III, 171; IV, 219; V, 252; VI, 287; VII, 324; VIII, 372; IX, 407. Growth rates of 11 tagged fish (256–324 mm) at large 72 to 367 days averaged 46.5 mm per year.

21. Nine hundred and twelve gray snappers were tagged and 57 recoveries made. Forty-eight recoveries came from 274 fish tagged at Alligator Lighthouse, and an additional 30 tagged fish from Alligator Lighthouse were estimated to have been brought into the local fish market within three weeks of tagging.

22. A high tagging mortality is suspected for small fish.

23. Growth rate of nine snappers released and recovered at Alligator Lighthouse averaged 1.7 mm per month after 21 to 367 days at large. Nine other fish released at Alligator Lighthouse and recovered 3.4 to 18.7 nautical miles away averaged 7.4 mm growth per month in 19 to 285 days at large. Reduced growth of fish remaining on the reef is attributed to greater competition for food in the densely populated reef environment.

24. Gray snappers rarely exceed 8 lb. (3.6 kg). Most records of greater size are believed to result from confusion with cubera snapper.

25. *Lutjanus griseus* is intermediate in size and most body proportions to other inshore lutjanids. Only lengths of the paired fins are extreme. Short pelvic fins are associated with a somewhat free-swimming mode of life. Short pectoral fins are perhaps an adaptation to moving through mangrove roots, submerged brush, etc.

26. Fin spination is well developed in very small individuals and probably serves as a defense mechanism.

27. Small gray snappers have proportionately larger heads, eyes, and mouths than do larger fish, which are more terete of body. These changes are believed to be associated with the early importance of the sense organs of the head and the feeding mechanism, resulting in rapid development of these systems in small individuals. Increasing tereteness of body in larger snappers is paralleled by a freer swimming mode of life and increasing tendency to feed on fish.

28. Dentition, especially canine, is best developed in *L. cyanopterus*, *L. jocu*, *L. apodus*, and *L. griseus* in that order. All feed extensively on fish and some crustaceans as adults. *Lutjanus analis* has relatively short, heavy dentition and feeds largely on crustacea and mollusks. *Lutjanus mahogoni* and *L. synagris* have reduced dentition similar in shape to the first group of species. These two feed on small invertebrates and fish. *Ocyurus chrysurus* has the least developed dentition and eats largely plankton and small mid-water fishes and crustacea.

29. Stomach contents of 1335 gray snappers from 10.5 to 489 mm standard lengths were examined. Food was found in 638 specimens, or 48%. Crustacea, predominantly amphipods and palaemonid shrimp, are the main food (93% of mean food volume) of juvenile snappers from grass beds. Slightly larger snappers from around brush and debris in grass beds had 69.4% crustacea, chiefly *Penaeus duorarum*, xanthid crabs, and portunid crabs. Fish made up 29.1% of food volume, and *Opsonus beta* was the commonest fish. Snappers (largely adults) from an inshore channel contained 59.5% crustacea (mainly *Portunus* sp.) and 36.5% fishes (*Opsanus beta* again the commonest). Adult snappers from Alligator Reef ate mainly fish (61.9% made of several species, of which *Haemulon* spp. were the commonest). Crustacea were chiefly shrimp and portunid crabs.

30. Copepods, amphipods, palaemonid shrimp, penaeid shrimp, and portunid crabs successively dominate the crustacea eaten by gray snappers as they increase in size. Fish assume an increasing role in the diet of large snappers.

31. Most food items are swallowed whole and most range in size from 8 to 45% of standard length though elongate forms such as eels may be eaten even if longer than the snapper.

32. Juvenile gray snappers from grass beds feed in the day while larger snappers are nocturnal feeders. Stomachs examined in later afternoon were almost entirely empty.

33. Schools of gray snappers break up at dusk and disperse into surrounding areas to feed. Large gray snappers may range a mile or more at night from points of diurnal concentration.

34. The feeding habits of gray snappers are not highly selective and are more generalized than those of other species of snapper.

35. The overall sex ratio of the gray snapper is about equal though mature females predominate in inshore channels and males predominate on the reef.

36. The smallest mature female was 195 mm standard length and the smallest mature male was 185 mm standard length among 722 specimens examined.

37. No significant difference in size of sexes was noted though the four largest fish (430 to 489 mm) were females.

38. Ripe females were common in July and August, and spent females common in early September. Spawning occurs more than once and probably around the time of full moon.

39. The occurrence of small juveniles indicates some spawning as early as June.

40. A 315-mm female gray snapper was estimated to have about one-half million eggs.

41. Schooling behavior is strongest in adult fish and is greatest in areas of reduced cover. Schools of mixed species including gray snappers are common.

42. Small snappers from inshore areas show no directed seasonal movements other than being driven from certain exposed locations by low temperatures or storms. Adult gray snappers migrate to the offshore reefs to spawn in summer. A much smaller population of gray snappers are year round residents of the reefs. Tagged snappers move as much as 40.5 nautical miles in seven days following the fall breakup of the summer schools at Alligator Reef.

43. Gray snappers occasionally submit to removal of ectoparasites by other fishes. The latter include the neon goby (*Gobiosoma oceanops*), Spanish hogfish (*Bodianus rufus*), and juvenile porkfish (*Anisotremus virginicus*).

44. The wide geographic and ecologic range of *L. griseus* is attributed to its generalized nature.

45. Restrictive measures for the protection of this species are not needed at present or in the immediate future.

46. Adult populations of gray snappers could probably be substantially increased by proper placement of man-made cover.

Abstract

Investigations into the life history of the gray snapper, *Lutjanus griseus* (Linnaeus), in the vicinity of Lower Matecumbe Key, Florida, are reported and comments made on information about this species from other areas. Habitat, color pattern, morphology, feeding habits, and other factors relating to seven other common inshore lutjanids of the West Indies region are discussed for comparison with the gray snapper.

Relationships, nomenclature, economic value, predators, parasites, diseases, and malformations of the gray snapper are briefly summarized.

Habitats of various sizes of gray snappers are described for specimens from 10.5 to 470 mm standard length, and frequency histograms of standard length from 2396 fish are given by habitat.

Occurrence of both juvenile and adult gray snappers in water of less than one part per thousand salinity is found to be common, and a lower temperature limit of 11 to 14°C is suggested by data from cold kills.

Color patterns of various sizes of gray snappers are discussed in relation to habitat, activity, and time of day. Both underwater and surface appearance are described.

Age determination and back calculation of standard length from scales of 1092 snappers were made and compared with growth of 22 tagged fish. Mean standard length was calculated at 68 mm for fish at age I and 407 mm for fish at age IX, the oldest found.

Size, body proportions, dentition, and other morphological features are treated in relation to ontogenetic development and related to the biology of the fish.

Feeding habits based on stomach contents of 1335 gray snappers of 10.5 to 489 mm standard length are discussed in relation to habitat, size of

snapper, size of food organism, rate of digestion, and selectivity. Night observations on feeding movements are also presented.

Sex ratios, size at maturity, spawning cycle, occurrence of small juveniles, spawning aggregation, and number of eggs produced are discussed. Field observations, gonad examination of 722 fish, and collections of over 250 small juveniles are correlated.

Several aspects of behavior are also included. Aggregations of snappers and factors concerning them are dealt with. Changes in populations and movements of 56 tagged fish are discussed. Feeding behavior and information on vision and sound are summarized. Observations are given on parasite removal by three other species of fish.

Suggestion for further research and recommendation concerning management of the species are made.

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Ecology of the Intestinal Trematodes of the Gray Snapper, *Lutjanus griseus,* Near Lower Matecumbe Key, Florida, With a Description of a New Species

by ROBERT E. SCHROEDER

Introduction

The ecology of the digenetic trematodes of tropical marine fishes has seldom been studied. Parasitologists have directed most of their attention toward taxonomy, and most ecological investigations have been limited to the life cycles of a few common species. This paper presents a quantitative ecological study of the digenetic trematodes found in the intestine of the gray snapper, *Lutjanus griseus* (Linnaeus).

The gray snapper (Figure 1) is a convenient host organism because it is easily collected from a wide variety of habitats throughout the year. The life cycles of its more common trematodes have been outlined, and their intermediate hosts are common and easily collected. The gray snapper and the intermediate hosts occupy shallow coastal waters, so both organisms and habitats are accessible.

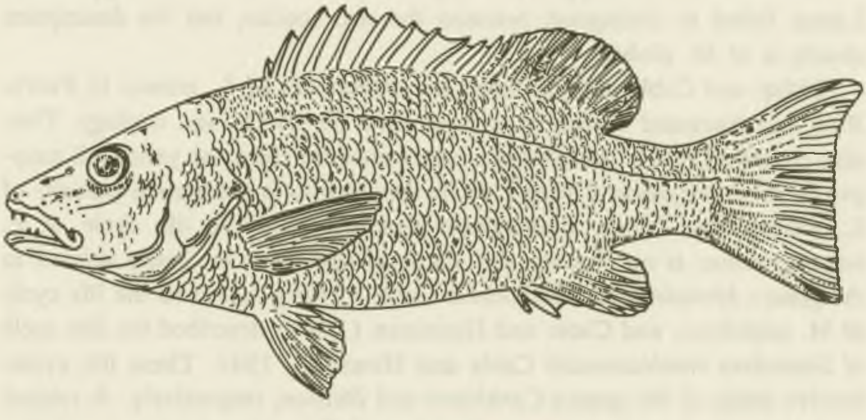

Figure 1. *Lutjanus griseus* (Linnaeus)

Lutjanus griseus is numerous in widely differing environments. It is found in water which is virtually fresh (Tabb, Dubrow, and Manning, 1962), in mangrove swamps, on shallow marine grass beds, and along offshore coral reefs. In theory, fish from these differing habitats should have materially differing trematode faunas. Results of this study show that they do.

Longley (1927) reported that *L. griseus* assembles along the reefs during the day in large, loosely associated schools that do not forage actively. The schools break up at night, and the fish feed individually over broad areas of open bottom. Similar observations are reported by Schroeder and Starck (1964).

Starck (1964) examined the stomach contents of several large series of *L. griseus.* His data on fish of various sizes suggest the importance of diet in determining the nature of gray snapper trematode populations. He also studied the movements, spawning, and nocturnal feeding behavior of *L. griseus,* and his data were useful in evaluating the results of the present study.

Six of the nine trematode species found in *L. griseus* near Lower Matecumbe Key were described by Linton (1910) from fish collected at the Dry Tortugas. These six species were *Metadena globosa, Hamacreadium mutabile, H. gulella, Helicometra execta, Helicometrina nimia,* and *Stephanostomum casum.* Not all of the six were described from *L. griseus,* but all except two were found in lutjanid fishes.

Manter (1947) described *Metadena adglobosa* from *Lutjanus apodus* and *L. griseus* at the Dry Tortugas. Specimens are included on the slide that contains the holotype of *M. globosa* (Linton, 1910). Apparently, Linton failed to distinguish between the two species, but his description clearly is of *M. globosa.*

Siddiqi and Cable (1960) listed the trematodes of *L. griseus* in Puerto Rico and discussed certain aspects of their life cycles and ecology. They also described *Paracryptogonimus neoamericanus* from the yellowtail snapper *Ocyurus chrysurus* (Bloch). *P. neoamericanus* is a common parasite of *L. griseus* near Lower Matecumbe Key, Florida. The life cycle of *P. neoamericanus* is not known, but *Paracryptogonimus* is closely related to the genera *Metadena* and *Siphodera.* Cable (1956) described the life cycle of *M. adglobosa*, and Cable and Hunninen (1942) described the life cycle of *Siphodera vinaledwardsii* Cable and Hunninen, 1942. These life cycles involve snails of the genera *Cerithium* and *Bittium,* respectively. A related snail probably is the first intermediate host of *P. neoamericanus.*

McCoy (1929, 1930) studied the life cycles of two parasites of *L. griseus*: *Hamacreadium mutabile* Linton, 1910, and *H. gulella* Linton, 1910. He described the larval forms, infection of intermediate hosts, and host specificity. Both trematodes utilize the same snail hosts, *Astraea tecta americana* (Solander), and will use almost any small fish as a second intermediate host.

Manter (1934) outlined the probable life cycle of *Helicometrina nimia* Linton, 1910, a common parasite of *L. griseus* and other fish on the offshore reefs. This trematode is related to the genus *Hamacreadium,* but it utilizes various shrimp species as second intermediate hosts. The life cycle of the closely related *Helicometra execta* Linton, 1910, probably is similar—a hypothesis that is supported by the work of Palombi (1929, who studied the life cycle of *Helicometra fasciata* in the Mediterranean.

The life cycle of *Stephanostomum casum* (Linton, 1910) is unknown, but life cycles of several species of *Stephanostomum* have been described. Martin (1939) discussed the probable life cycle of *S. tenue.* Wolfgang (1955) and Stunkard (1961) discussed the probable life cycles of *S. baccatum* and *S. dentatum,* respectively. The cercaria described by Stunkard was so unlike that of Wolfgang that Stunkard doubted Wolfgang's identification. His observations supported those of Martin's. The snail host of *S. dentatum* belongs to the genus *Nassarius,* which is widespread in Florida waters.

References to parasite ecology, other than life cycles, in the literature are fragmentary. The most thorough coverage of the subject can be found in the textbook by Dogiel, Petrushevski, and Polyanski (1958), translated from the Russian. The Soviet parasitologists derived many concepts that proved applicable to the present study.

Some of these concepts were foreshadowed in earlier papers. Van Cleave and Mueller (1934) studied the worm parasites of Oneida Lake fishes in New York, and reported some interesting ecological observations. Oneida Lake is a freshwater habitat in a temperate climate, but the kinds of ecological factors that were important are similar to those in tropical marine environments. Seasonal changes were significant and different for various parasite species. More trematodes were found in fish from areas with large snail populations than in fish from areas with small snail populations. When fish migrated, their parasite populations changed characteristically.

Similar findings were reported by Holl (1932), who made a comparative study of the parasites of sunfish and bullheads in ponds, lakes, and rivers. Fish from each habitat had characteristic parasite populations, although habitats apparently of the same type in different locations varied considerably. More recently, Chubb (1964) studied the occurrence of Acanthocephala in the fish of a freshwater lake in Wales. The ranges of intermediate hosts, fish migrations, and seasonal changes all proved to be significant in determining the nature of parasite populations.

Lumsden (1963) discussed the role of fish host ecology in the distribution of the Haploporidae. His observations supported the concept of "ecological bridges" as proposed by Manter (1957). Manter stated that euryhaline fishes might have played a role in linking the trematode fauna of coastal freshwater and marine fishes. Shireman (1964) added further substantiation to the hypothesis in reporting the possible role of mullet in linking some trematodes of "freshwater and marine fishes on a circumtropical basis." Ramsey (1965) speculated that a trematode of two species of freshwater sunfish may be dependent in completing its life history on an intermediate host of the brackish estuarine environment, lending further support to Manter's (1957) "ecological bridge" theory that trematodes of marine fishes become adapted to freshwater fish hosts in a permanently freshwater environment.

In the present study, 836 specimens of *Lutjanus griseus* were collected and examined for intestinal trematodes during a period of nine months. Collections were taken regularly from four different habitats in the vicinity of Lower Matecumbe Key, Florida. Among the factors investigated were size and sex of host, differences between habitats, migrations of hosts, seasonal changes, and host feeding behavior. Small collections were taken at various locations on Biscayne Bay, Miami, and in the saltwater drainage canals of south Dade County to study fish from other environments than those found in the Florida Keys. In addition to the collections of *L. griseus,* 63 specimens of *L. apodus* (Walbaum), four of *L. analis* (Cuv.), five of *L. jocu* (Bloch & Schneider), 20 of *Ocyurus chrysurus* (Bloch), and 81 nonlutjanid fishes of 32 species were collected and examined.

Collections of known and potential intermediate hosts of the trematodes found in *L. griseus* were taken from the same localities as the other fish collections. Snails were examined for production of cercariae. Small fish were exposed in the laboratory to these cercariae to discover if they could serve as second intermediate hosts.

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The author especially wishes to express his appreciation for the aid given him by his wife, Jean, who is fast becoming a parasitologist in her own right. Her artistic talents, countless hours at the microscope and typewriter, and unfailing moral support were invaluable contributions.

1. Materials and Methods; Collection Stations

MATERIALS AND METHODS

Eight stations, chosen to represent different habitats, were located at snapper assembly areas in the vicinity of Lower Matecumbe Key, Florida. Fish were collected repeatedly at these stations from June 1963 to February 1964. Snail collections were taken from the areas surrounding the stations.

Fish also were collected at five locations in Biscayne Bay, Miami. The collections were too small to yield statistically significant data, but they were interesting because the same trematodes were found in gray snappers from Biscayne Bay as in those from near Lower Matecumbe Key.

Almost all snappers were taken on a hook and line. On the advice of local commercial fishermen, handlines were used—they proved to be much faster than rod and reel. Best results were obtained when the hook was tied directly onto the end of a 30 lb. monofilament line, without leaders or sinkers. During the day, gray snappers school at various points that provide cover (Longley and Hildebrand, 1941), and collections were taken from such daytime schools. Fish in these schools are not actively foraging, but will take shrimp readily. Properly chummed, they go into a feeding frenzy and may be caught as fast as they can be pulled in. A 50-fish sample usually was caught in less than an hour. The fish were brought to the dock alive and were kept in a live-car to await examination.

The snappers were allowed to remain in the live-car 24 to 48 hours before being examined, thus reducing the amount of material in the intestine and making examination much easier. Trematode populations of the fish examined immediately after capture did not differ significantly from those of fish kept in captivity for 48 hours.

The fish were killed and examined for metacercarial cysts, copepods in the mouth, and gill copepods. Then they were opened on the right side and the intestine and five pyloric caeca were removed, slit lengthwise, and shaken in a bowl of 1% saline solution. Saline solution made by dilution of seawater to 1% salinity proved easier to obtain and more satisfactory than Ringer's solution or a 1% NaCl solution. Intestinal trematodes of *L. griseus* will live 24 hours or longer in 1% seawater at room temperature.

Fish were numbered consecutively upon examination. The standard length, sex, state of ripeness, collection locality and date, locations of cysts, copepods, and other data were noted. The populations of the various trematodes, nematoes, and cestodes were identified with the aid of a microscope. The resultant data were transferred to 5 by 7 inch McBee Keysort cards for initial processing. Later these data were coded on computer cards. Statistical analyses were made with the aid of a computer.

The known snail hosts were collected from the feeding areas surrounding the daytime assembly points of the gray snappers. Three techniques were used to collect snails: large numbers were collected with a hardware cloth trawl to determine the incidence of infection with trematodes; a Peterson bottom sampler was used to determine the densities of snail populations; snails also were hand collected when convenient, both from the boat and by using gear.

All snails were isolated overnight at room temperature to identify those which produced cercariae. Those which did not were cracked in fingerbowls of seawater to locate latent positives. Infected snails were kept in aquariums to study cercarial production. Cercariae released by the snails were used for laboratory infections of second intermediate hosts and to study cercarial behavior.

Bottom samples taken with the Peterson dredge were dumped into a floating sifter of ⅛ inch mesh hardware cloth tied alongside the skiff. Samples were sifted and the snails counted after each five to ten samples, depending on the amount of material being brought up in the dredge.

Small fish of several species were exposed to various cercariae. After allowing the metacercariae to mature, these fish were fed to wormed snappers. The snappers and small fish were anaesthetized in quinaldine; then the small fish were pushed into the snappers' stomachs with forceps.

Fish exposed to cercaria in the laboratory included the following species: *Cyprinodon variegatus* Lacepede, *Gambusia affinis* (Baird & Girard), *Gerres cinereus* (Walbaum), various *Haemulon* species, *Atherinomorus stipes* (Muller and Troschel), *Lucania parva* (Baird & Girard), *Lutjanus griseus* (Linnaeus), *Poecilia latipinna* Lesueur, *Opsanus beta* (Linnaeus), and *Sphyraena barracuda* (Shaw).

L. parva, C. variegatus, P. latipinna, and *O. beta* were used in attempts to infect wormed gray snappers. Controls were unexposed fish fed to wormed gray snappers.

Ten snappers, wormed by an anal injection of carbon tetrachloride, were kept in a live-car for three weeks and then killed to discover if they were acquiring trematode infections in captivity.

Initial attempts at ridding snappers of their parasites involved anaesthetizing the fish with quinaldine and then pipetting anthelminthics directly into their stomachs. Several vermifuges were tried, including piperazine adipate, arecoline, tetrachlorethylene, carbon tetrachloride, and such veterinary combinations as Vermiplex and Anthex. The results were not consistent. Some fish were negative when examined, while others had as many trematodes as the controls.

Observation of the fish as they recovered from the anaesthetic suggested that most of them had regurgitated the medicine almost as soon as they could right themselves. This led to attempts at feeding the fish anthelminthics in their food. The results were not consistent until live pilchards *(Harengula sp.),* whose swim bladders had been injected with Vermiplex, were fed to the snappers.

The injected pilchards were badly crippled and easily caught by the snappers in the live-car. Fish that had eaten injected pilchards were free of trematodes when examined 24 hours later. The effectiveness of this method was seen when the snappers, irritated by the medicine, partially regurgitated the pilchards, then reswallowed them.

Live pilchards were not always available and other methods were tried. Insertion of small worm capsules into pieces of fresh shrimp was ineffective, as was injection of Thiobendazole into the stomach and into the intestine via the anus. Good results were obtained by inserting a long needle as far as possible into the intestine via the anus, and injecting 1 to 3 cc of carbon tetrachloride. The difficulty with this method is that sufficient carbon tetrachloride to kill the trematodes also killed about half the snappers.

Snappers wormed with carbon tetrachloride are sick and unwilling to feed for approximately a week. Droplets of carbon tetrachloride were found in the caeca as much as five days after treatment. Fish treated in this fashion were not exposed in the laboratory until a week or more after they had resumed feeding.

Three methods were used in the exposure of snail hosts to infection: eggs were dissected from live trematodes and fed to snails; gray snapper intestinal contents were sedimented several times to remove soluble material and then put into small aquaria with snails; infected fish were kept in live-cars with snails. These attempts were all unsuccessful.

Eggs obtained from dissected trematodes were observed for varying periods of time to determine if they would hatch. Egg samples were kept in syracuse dishes, or sealed in deepwell slides, in seawater. None of these eggs hatched or showed signs of development. At the end of two weeks, eggs of Cryptogonomidae (*Metadena globosa, M. adglobosa, M. obscura, Paracryptogonimus neoamericanus*) appeared unchanged. Those of *Hamacreadium mutabile* and *H. gulella* were disintegrating.

COLLECTION STATIONS

Fish were collected at 13 stations in the initial phase of the study. Four of these were located in Biscayne Bay or in saltwater drainage canals that empty into Biscayne Bay. The remaining nine stations were located near Lower Matecumbe Key, Florida. Eight of these were found to represent four differing habitats, with two stations in each habitat. These eight stations were visited repeatedly. The dates, locations, and sizes of all collections are presented in Table 1.

Alligator Light and Alligator Ledge

Alligator Light Station and Alligator Ledge Station were located on Alligator Reef, about 6 km east of Lower Matecumbe Key. Together, they constitute the offshore stations.

Alligator Lighthouse, standing on the reef top in about 2 m of water, is an assembly point for large numbers of gray snappers at most times of the year. The bottom is hard coral rubble. There are patches of sand and the marine grass *Thalassia* on the seaward side, and a large expanse of sand and *Thalassia* on the shoreward side.

Four hundred meters to the south, an inner ledge of Alligator Reef runs northeast and southwest for several hundred meters. The reef platform stretches seaward in about 4 m of water. The ledge is 2 to 3 m high, with coral rubble at the base. Coral rubble on the landward side blends into sand, rubble, and *Thalassia* bottom in 7 to 8 m of water that extends shoreward for some distance. The largest gray snappers school along the ledge to spawn in the summer months.

Indian Key and Lignumvitae Channel Wreck

Indian Key Station and Lignumvitae Channel Wreck Station constitute the inshore stations. Indian Key is about 1 km east of the north end of

Table 1. Numbers of gray snappers taken at each South Florida station

	1962			1963										1964		Total
Station Month	8	9	12	1	2	4	6	7	8	9	10	11	12	1	2	
Alligator Lighthouse	17	1	3						51	35			20			127
Alligator Ledge		1					5	15	46	2						69
Indian Key						9				9	101		15	10		144
Channel Wreck	1	3								10	21		18			53
Matecumbe Canal		1	4		1		3		1	2	11		15	47		85
Lignumvitae Key	4			10	5		12	19			68	4	23	2	15	162
Pederson Bank Slough							39	4	22		23	7				95
Twin Keys								1	23					52		76
Rabbit Key								4								4
Salinity Dam													10			10
Ragged, Sand Key				10												10
Norris Cut			1													1
Total number collected:																836

Lower Matecumbe Key. It is bordered to the west and north by shallow *Thalassia* beds that may be exposed at low tide. Immediately east of Indian Key is a hard bottom area 200 m wide, where sponges and gorgonians grow in about 1 to 2 m of water. Except when strong offshore winds roil the water, this area serves as the daytime assembly point for large schools of gray snappers and is the location of Indian Key Station.

About 1 km southwest of Indian Key, Ligumvitae Channel runs through the shallows and opens into Florida Bay above Lower Matecumbe Key. It is a wide channel, bordered by grass flats which are exposed at extremely low tides. Near the channel mouth, the remains of a large wooden barge lie on the bottom in about 4 m of water. This wreck was the location of the Lignumvitae Channel Wreck Station (hereinafter referred to as the Channel Station), and is an assembly area for *L. griseus.* The substrate surrounding it consists of *Porites* rubble, with occasional patches of sand and *Thalassia.* The flats to the east are largely soft bottom covered by dense *Thalassia,* with scattered areas of hard rubble and sparse *Thalassia.* To the west, the flats are mainly *Porites* rubble on which grow sparse beds of *Thalassia,* patches of *Halimeda,* and sponges. A large population of the snail *Astraea tecta americana* is found in this area, in some places reaching a density of 60 per square meter.

Lignumvitae Key and Lower Matecumbe Canal

The Lignumvitae Key Station and the Lower Matecumbe Canal Station constitute the bayside stations. The Lignumvitae Key Station is located in a canal cut through mangroves that border Lignumvitae Key, and the Canal Station is located in a canal through mangroves that border the west side of Lower Matecumbe Key.

Lignumvitae Key is a large island that lies approximately 1 km north of Lower Matecumbe Key. It is situated on the edge of a wide area of soft, *Thalassia*-covered banks that lie to the north and west of Lower Matecumbe Key in Florida Bay. Most of the island's southern and eastern shores are occupied by a deep stand of mangroves through which is cut a canal deep enough to be navigated in a skiff. During the days snappers often assemble in these canals in considerable numbers.

The Canal Station is located in a similar but larger canal cut through mangroves on the northwest side of Lower Matecumbe Key. In this canal, fallen mangroves and hurricane wreckage are favorite daytime assembly points for gray snappers.

Trematode faunas at these two stations are similar, although they are separated geographically and located differently in relation to the channels leading to the Atlantic side of the Keys. The similarities between the two habitats apparently are more important than their different locations.

The two areas differ in that the canal bottom at Lignumvitae Key is bare mud, while canal bottoms at Lower Matecumbe Key are largely sand and shell, with flourishing *Thalassia* beds. No snails were collected from the Lignumvitae canal, but *Thalassia* close to the island harbors dense populations of *Cerithium eburneum* (Bruguire). *C. eburneum* and a few specimens of *C. variabile* (Adams) were trawled from the Matecumbe Canal Station.

Pederson Bank Slough and Twin Keys

The Pederson Bank Slough Station and the Twin Keys station are several kilometers apart. In spite of their geographical separation, the two stations are very similar. Although many differing habitats occur in the Twin Keys area, the Twin Keys and Pederson Slough collections are so similar in their trematode populations that they are considered together as the back bay stations.

The Pederson Bank Slough is a *Thalassia* area in the middle of Pederson Bank, about 500 m southwest of Lignumvitae Key. It is an area of more than 40 hectares in extent, surrounded by the much shallower tidal flats of Pederson Bank. The bottom is soft sand and mud. Thick growths of *Thalassia* are interspersed with patches of bare sand at a depth of 1 to 2 m. Dead mangrove trees and hurricane wreckage in the deeper spots serve as snapper assembly points during the summer, but are abandoned after the first winter coldwave.

Twin Keys are a pair of small mangrove-covered islands about 5 km northwest of Lignumvitae Key. They are located on a vast area of shallow banks which include Pederson Bank.

This area is transversed by two navigable channels. One runs between Twin Keys and the other runs to the south of them. The channel bottoms are soft mud and sand, alternating with dense growths of *Thalassia* and pockets of dead grass.

The Four Habitats

The offshore stations are a summer spawning ground for large schools of gray snappers. Spawning ceases around the first of September, and the area is abandoned by all except the largest fish until the following spring.

The inshore stations are occupied by gray snappers of all but the largest sizes throughout the year. There appears to be a considerable amount of fish movement between these stations and Florida Bay.

Like the inshore stations, the bayside stations are occupied throughout the year by gray snappers of a wide variety of sizes. Occasionally very

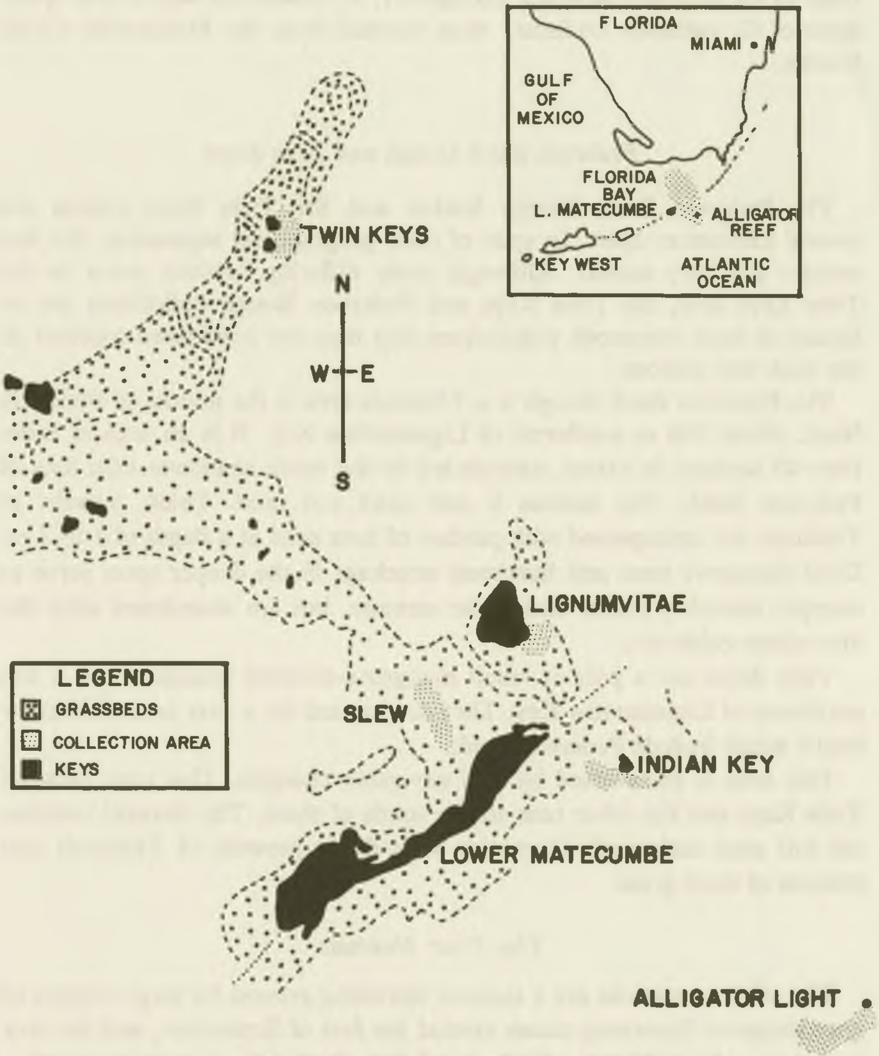

Figure 2. Map showing Lower Matecumbe Key and collection areas.

small snappers less than 100 mm standard length are seen at these stations.

In summer the back bay stations harbor dense schools of small gray snappers. Larger fish are found there in September. After the first cold-wave of winter the shallowest assembly points are abandoned, but the deeper ones harbor snappers throughout the year.

Gray snappers were not observed at the Slough Station assembly points later than November, but were present in the deeper canal between Twin Keys in January.

The eight stations that represent these four habitats are shown on the map in Figure 2.

2. The Definitive Host; Intestinal Trematodes of *Lutjanus griseus*

THE DEFINITIVE HOST

The gray snapper *Lutjanus griseus* (Linnaeus) is the most common carnivorous fish in the vicinity of Lower Matecumbe Key. It is found in habitats that range from the shallow *Thalassia*-covered banks of Florida Bay to the offshore reefs that border the Florida Atlantic coast. In other areas such as the Panama Canal, Andros Island in the Bahamas, and the Florida Gulf Coast, it has been reported from virtually fresh waters.

During the day, gray snappers school at shallow water assembly points that afford cover, such as coral reefs, gorgonian beds, mangrove swamps, or wreckage. Bardach (1958) reported that schools of gray snappers on coral reefs are constantly on the move but stay near the shelter of the reef. Similar observations were made by Starck (1964) and the author at Alligator Reef.

With the coming of night, these daytime schools break up and the snappers scatter over nearby areas of open bottom to feed. Large fish may wander several kilometers in the course of a night's foraging. The fish usually return to the previous day's assembly point in the morning, but may join another school at a different assembly point.

Longley (1925) studied the feeding habits of the gray snapper and concluded that large snappers depend on fish for a greater proportion of their diets than do small snappers. Starck (1964) made similar observations on fish collected near the stations used in the present study. Such a dietary change with increasing size could not help but affect the parasite populations in the fish.

Longley and Hildebrand (1941) studied the effects of learning on the feeding habits of the gray snapper and discovered that small snappers rapidly learn to distinguish between variously marked food fishes. They also observed that gray snappers soon learn to eat unusual foods, such as bread and table scraps. Possibly, learned feeding patterns have a measurable effect on the parasite populations of individual snappers. This factor may be significant when snappers migrate from one area to another.

Starck (1964) and the author have observed that gray snappers make definite migrations in response to various stimuli. In the early spring, the larger fish move offshore to spawn and remain on the offshore reefs for a large part of the summer. Around the beginning of September spawning ceases, and the offshore stations are abandoned rather abruptly. Thereafter, larger-than-average fish appear at the inshore and bayside stations.

With the onset of cold weather, shallow assembly points on the *Thalassia*-covered banks of Florida Bay are abandoned and the fish move into deeper water. At this time, the incidence of Florida Bay trematodes in fish collected at the inshore stations increases. This indicates that the move to deeper water carries many Florida Bay snappers to the Atlantic side of the Keys.

Assembly points are abandoned when their waters are disturbed by strong winds and choppy waves. No gray snappers were collected at the Indian Key Station, for example, when strong easterly winds disturbed the water there. When the winds were westerly, this assembly point was protected by Indian Key, and gray snappers schooled there in great numbers.

Nine species of trematodes representing three families were found in the intestine and pyloric caeca of gray snappers collected near Lower Matecumbe Key. These trematodes are listed in Table 2. As the numbers of trematodes found in the fish varied widely, the levels of infection with each trematode were scaled in four categories from “light” to “very heavy.” The numerical limits of these categories are different for each trematode (see Table 3). One trematode found in the gray snapper near Lower Matecumbe Key is a new species and is described as *Metadena obscura.*

Gray snappers collected in this study measured from 44 mm to nearly 500 mm standard length. For the purpose of comparing the trematode populations found in fish of different sizes, collections were divided into three size categories. Category 1 included fish of 200 mm standard length and under. Category 2 included fish of 201 mm to 250 mm standard length. Category 3 included all fish over 250 mm standard length.

Gray snappers very seldom exceed a standard length of 500 mm and a weight of 3 kg. Reports of much larger fish usually refer to the cubera snapper, *Lutjanus cyanopterus*, which often is mistaken for the gray snap-

Table 2. Intestinal trematodes of 836 gray snappers from the vicinity of Lower Matecumbe Key, Florida

Parasite	Percentages of fish infected with each trematode	Location in fish
Cryptogonimidae:		
Metadena adglobosa	76	caeca
M. globosa	33	intestine
M. obscura	10	caeca
Paracryptogonimus neoamericanus	7	intestine
Allocreadiidae:		
Hamacreadium mutabile	51	caeca
H. gulella	5	caeca
Helicometra execta	0.6	caeca
Helicometrina nimia	7	caeca
Acanthocolpidae:		
Stephanostomum casum	18	intestine

Table 3. Key to the numbers of trematodes of each species in each degree of infection from "light" to "very heavy," found in gray snappers collected near Lower Matecumbe Key, Florida

	Degree of infection			
Species	Grade 1, light	Grade 2, medium	Grade 3, heavy	Grade 4, very heavy
Metadena adglobosa	1–20	21–200	201–500	501+
Metadena obscura	1–3	4–10	11–20	21+
Metadena globosa	1–3	4–10	11–20	21+
Paracryptogonimus neoamericanus	1–2	3–5	6–8	9+
Hamacreadium mutabile	1–3	4–12	13–20	21+
Hamacreadium gulella	1–3	4–10	11–20	21+
Helicometrina nimia	1–3	4–10	11–20	21+
Helicometra execta	1–	–	–	–
Stephanostomum casum	1–3	4–7	8–12	21+

Table 4. Mean standard lengths and their standard deviations by month of gray snappers collected in four habitats near Lower Matecumbe Key, Florida

Area	Month	Mean size (std. length mm)	Standard deviation
Offshore:	June–July	340	55.9
	Aug.	269	52.9
	Sept.	221	34.3
	Dec.	197	27.5
Inshore:	Sept.	204	78.5
	Oct.	155	20.4
	Dec.–Jan.	158	49.4
Bayside:	June–July	174	61.5
	Oct.	182	24.7
	Dec.–Jan.–Feb.	178	32.2
Back bay:	June–July	158	28.4
	Aug.	139	20.5
	Oct.–Nov.	196	37.0
	Jan.	168	23.9

per. Mean sizes and standard deviations of the gray snappers collected from each habitat during each month are listed in Table 4.

The sex of gray snappers does not appear to be related to the nature of their trematode populations. The differences between the incidences of *M. adglobosa, M. globosa, H. mutabile,* and *S. casum* in male and female snappers are insignificant. A comparison of trematode incidences in fish of different sexes is presented in Table 5.

THE INTESTINAL TREMATODES OF *LUTJANUS GRISEUS*

The Offshore Stations

The trematode populations of the gray snapper at the two offshore stations were quite similar to each other throughout the year. The incidences of the nine intestinal trematodes in the gray snapper from the Alligator Lighthouse Station and the Alligator Ledge Station are presented in graphic form in Figure 3.

The incidences of all but two trematodes were higher at Alligator Ledge than Alligator Lighthouse. This is understandable, for the average size of

Table 5. Percentages of male and female gray snappers infected with four species of trematodes at the bayside, inshore, and offshore stations near Lower Matecumbe Key, Florida

	Bayside		Inshore		Offshore	
	Males	Females	Males	Females	Males	Females
	(101)	(112)	(84)	(99)	(104)	(67)
M. adglobosa						
Adult	90	92	64	66	53	48
Juvenile	42	38	16	10	4	6
Total	92	93	64	67	53	48
M. globosa						
Adult	29	42	55	58	31	25
Juvenile	1	5	1	7	1	1
Total	30	43	56	59	31	25
H. mutabile						
Adult	25	23	68	56	37	31
Juvenile	13	20	66	59	17	18
Total	32	36	85	77	45	39
S. casum						
Adult	6	3	20	18	11	12
Juvenile	9	10	4	9	12	15
Total	15	13	22	25	22	27

the fish from Alligator Ledge was much larger than that of fish from Alligator Lighthouse. Large fish would be more likely to be infected than small fish because they range farther when feeding, eat a larger quantity of food, and include a larger proportion of fish in their diets. These factors should increase their chances of feeding on second intermediate hosts.

The difference between the incidences of *Metadena adglobosa* at Alligator Lighthouse and Alligator Ledge was inconsequential. *M. adglobosa* is a trematode of the Florida Bay beds of *Thalassia,* and may be acquired near the offshore stations seldom or not at all. The low incidence of juvenile worms at the offshore stations indicates that *M. adglobosa* is brought offshore by fish migrating to the breeding grounds.

Metadena obscura was not recognized as a separate species until the final phases of the study, so figures for its incidence are almost meaningless. It can only be stated that it was not numerous at any station.

The incidence of *Helicometrina nimia* was considerably higher in fish from Alligator Lighthouse than in fish from Alligator Ledge. A possible explanation lies in the tendency of small gray snappers to feed more

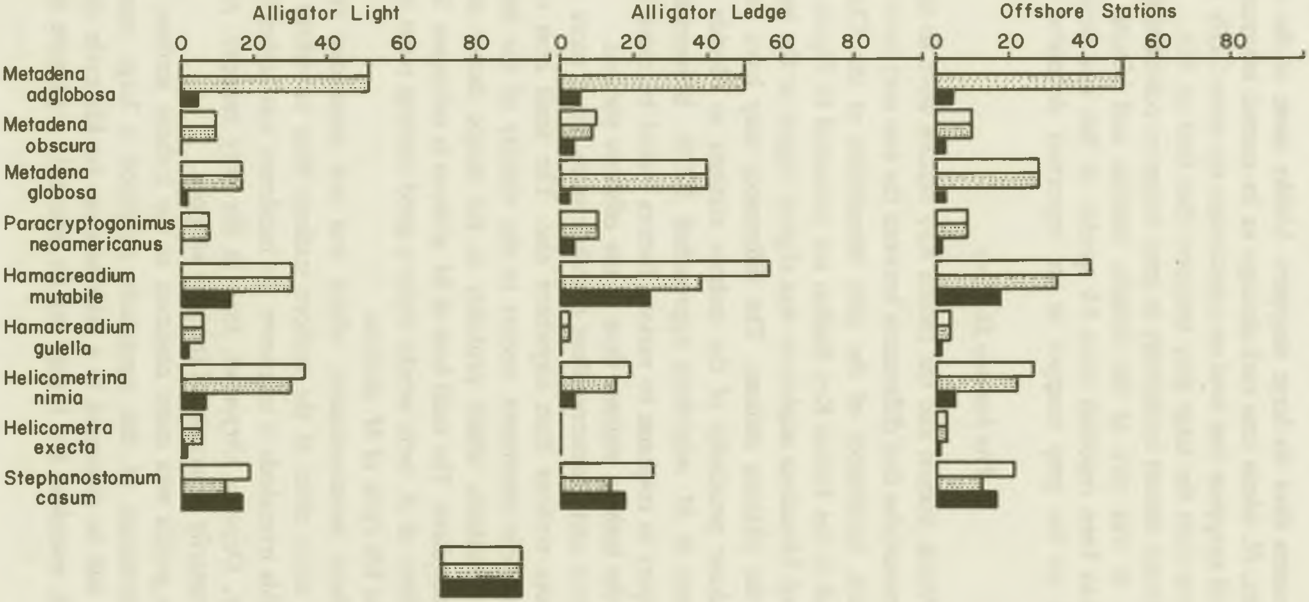

Figure 3. Percentages of gray snappers infected with each trematode at Alligator Light and Alligator Ledge Stations. Combined data presented under offshore stations. Data for adult and juvenile trematodes of each species are graphed in combination as total infections and separately as adult parasites and juvenile parasites.

heavily on crustaceans than do large snappers. Unlike most of the other snapper trematodes, *H. nimia* uses reef shrimps as its second intermediate hosts, and the small snappers that feed on crustaceans are more likely to be exposed to infection than the large gray snappers that feed on fish.

H. nimia was found almost exclusively in gray snappers collected at the offshore stations. It was rare at the inshore stations and absent from Florida Bay. It has been reported from 14 species of fish and probably does not depend on the gray snapper as an important definitive host.

The Inshore Stations

The Channel Wreck Station and the Indian Key Station were so similar in incidences of trematodes that differences between the two may have been sampling variations. Incidences of the nine trematodes at the Channel Wreck Station and at the Indian Key Station are presented in Figure 4.

The incidence of *Metadena adglobosa* was slightly higher at the inshore stations than at the offshore stations. The differences may have been a function of the closer proximity of the inshore stations to Florida Bay, where the incidence of *M. adglobosa* approached 100%. Movements of Florida Bay snappers in response to various factors would be more likely to carry them to the inshore stations than to the offshore stations.

Metadena globosa and *Hamacreadium mutabile* were much more common at the inshore stations than anywhere else. The snail host of *H. mutabile, Astraea tecta americana,* occurs in the vicinity of the inshore stations in great numbers, which probably is the major factor in the parasite's prevalence there. The snail host of *M. globosa* is unknown. Snails that share the habitat of *A. tecta* would make a good starting point in the investigation of the life cycle of *M. globosa.*

Paracryptogonimus neoamericanus, which was not numerous at any station, occurred more often at the inshore stations than anywhere else. The life cycle of this trematode is unknown. Its incidence was higher in the yellowtail snapper, *Ocyurus chrysurus,* than in the gray snapper, and it probably is not primarily a parasite of the gray snapper.

Hamacreadium gulella was more common at the inshore stations than elsewhere. The incidence of this trematode exhibited a large seasonal fluctuation which will be discussed in a later section. Its life cycle closely parallels that of *H. mutabile*, but it may not be primarily a parasite of the gray snapper.

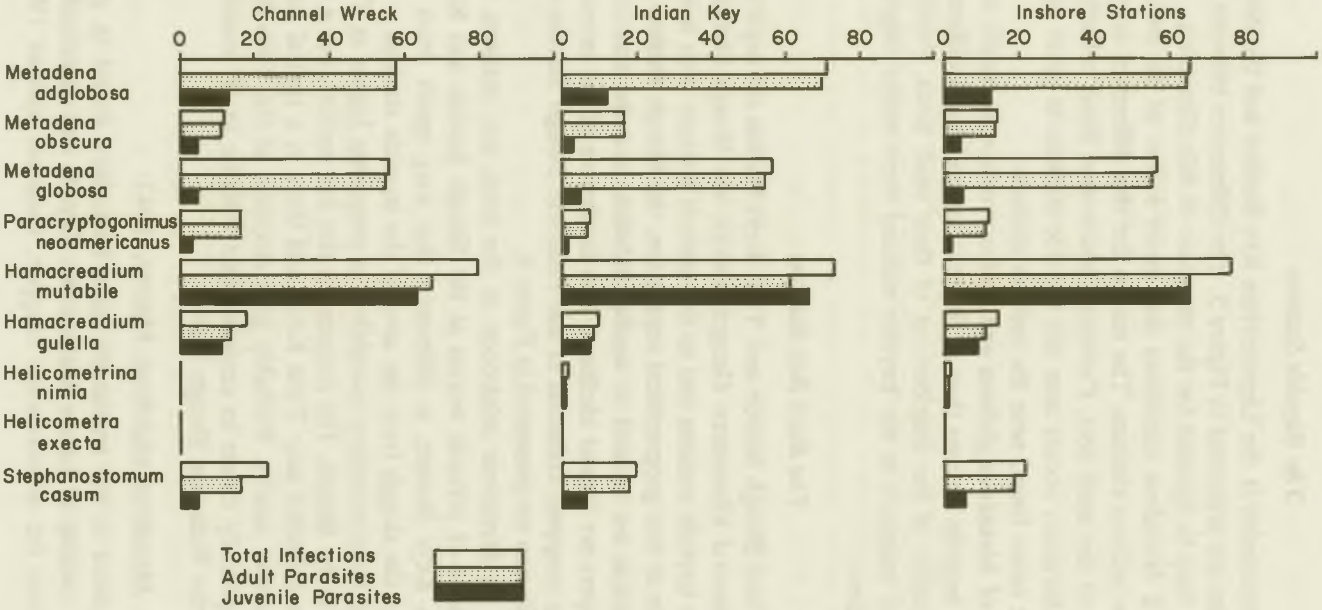

Figure 4. Percentages of gray snappers infected with each trematode at the Lignumvitae Channel Wreck and at Indian Key Stations. Combined data presented under inshore stations. Data for adult and juvenile trematodes of each species are graphed in combination as total infections and separately as adult parasites and juvenile parasites.

The Bayside Stations

Incidences of trematodes at the Lignumvitae Key Station and the Matecumbe Canal Station are presented in Figure 5. The differences between the two are slight and may be ignored for the purposes of this discussion.

The incidence of *Metadena adglobosa* was much higher at the bayside stations than at the inshore stations. The reason for this difference may lie in the distribution of the snail host, *Cerithium eburneum*. Snail collections revealed that *C. eburneum* occurs near the bayside stations in great numbers, but is almost never found near the inshore stations.

The incidences of *Metadena globosa* and *Hamacreadium mutabile* were much lower at the bayside stations than at the inshore stations, a difference that may be a function of the distributions of their snail hosts. Possibly, many infected gray snappers at the bayside stations were recent migrants from the inshore area.

The Back Bay Stations

The Pederson Bank Slough Station and Twin Keys Station are separated by a distance of several kilometers. Geographically, the Slough Station is much closer to the bayside stations and to the inshore stations than it is to Twin Keys. In spite of this geographical separation, the Slough Station and the Twin Keys station are located in similar habitats, and the trematode faunas of the snappers are almost identical. The incidences of the intestinal trematodes of gray snappers collected at the Pederson Slough Station and at the Twin Keys Station are presented in Figure 6.

The incidences of *Metadena adglobosa* at the back bay stations was 100%. The incidence of juvenile worms at the Slough Station was lower than at the Twin Keys Station, a difference that may result from the migration of fish to the slough from the area of the bayside stations.

The incidence of *Hamacreadium mutabile* was somewhat higher at Twin Keys Station than at the Slough. The reasons for this are unclear, but a few *Astraea tecta* were collected near Twin Keys, and there is a typical hard-bottom *A. tecta* habitat nearby. Probably gray snappers at the Twin Keys Station are geographically closer to environments suitable to *H. mutabile* than snappers at the Pederson Slough Station.

Metadena adglobosa Manter, 1947

Metadena adglobosa is the trematode most frequently found in gray snappers from the vicinity of Lower Matecumbe Key. It was described by Manter (1947) from the schoolmaster snapper, *Lutjanus apodus* (Wal-

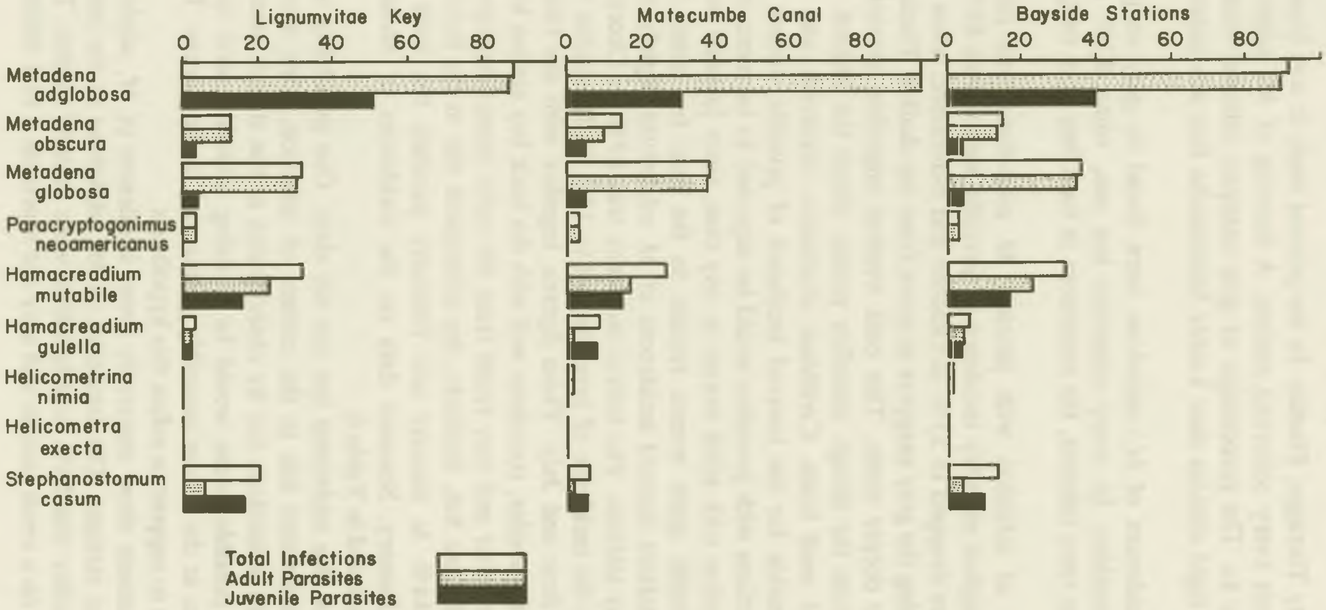

Figure 5. Percentages of gray snappers infected with each trematode at Lignumvitae Key and Matecumbe Canal Stations. Combined data presented under bayside stations. Data for adult and juvenile trematodes of each species are graphed in combination as total infections and separately as adult parasites and juvenile parasites.

baum), at the Dry Tortugas, Florida. In the present study it was found in gray snappers from every collecting station. A drawing of *M. adglobosa* appears in Figure 8a. The percentages of gray snappers infected with *M. adglobosa* at the eight stations near Lower Matecumbe Key are presented in Figure 7.

The higher incidences of *M. adglobosa* were found in gray snappers from back bay stations. In every collection but one, when 97% of a monthly collection were infected, the incidences in back bay gray snappers were 100%.

The incidence of infection with juvenile *M. adglobosa* was not so consistent. The highest monthly incidence of juvenile worms was 89% in August. The figure dropped to 33% in October and November, when cold weather was causing the gray snappers to move from the shallow *Thalassia*-covered banks to deeper water. This cold weather migration carried the snappers away from the slough assembly points, where the highest incidence of infected snail hosts, *Cerithium eburneum,* occurred, and may have been responsible for the lowered incidence of juvenile worms. The incidence of infections with juveniles would be expected to be more variable than the infection with adult worms in any case, since juvenile worms mature rapidly while adult worms remain in the host for some time.

The bayside stations showed incidences of *M. adglobosa* slightly lower than the back bay stations. The lowest incidence was 89% in December. At the same time the incidence of juveniles fell to 11% in December from a 73% peak in June and July. These figures, together with the October 36% incidence of juveniles, correlates well with the back bay station low of October and November and may result from the same cause: immigration of inshore and offshore fish. Similarly, the subsequent rise in the incidence of juveniles to 44% in January and February parallels the back bay stations rise in January. Seasonal data on the incidences of *Metadena adglobosa* are presented in Table 6.

The reasons for this midwinter rise are not clear. One possibility is the return of cold-acclimated fish to the centers of infection. This was not borne out by snail collections nor by observations at the slough assembly points. Another possible cause would be a rising infection level in the intermediate hosts at the winter assembly points and feeding areas. There are no data either to support or refute this hypothesis.

The inshore stations show materially lower incidences of *M. adglobosa* than the back bay stations. The incidence of *M. adglobosa* at the inshore stations in September was 55% and juveniles were entirely absent. These figures are based on a small sample and may not represent a real difference

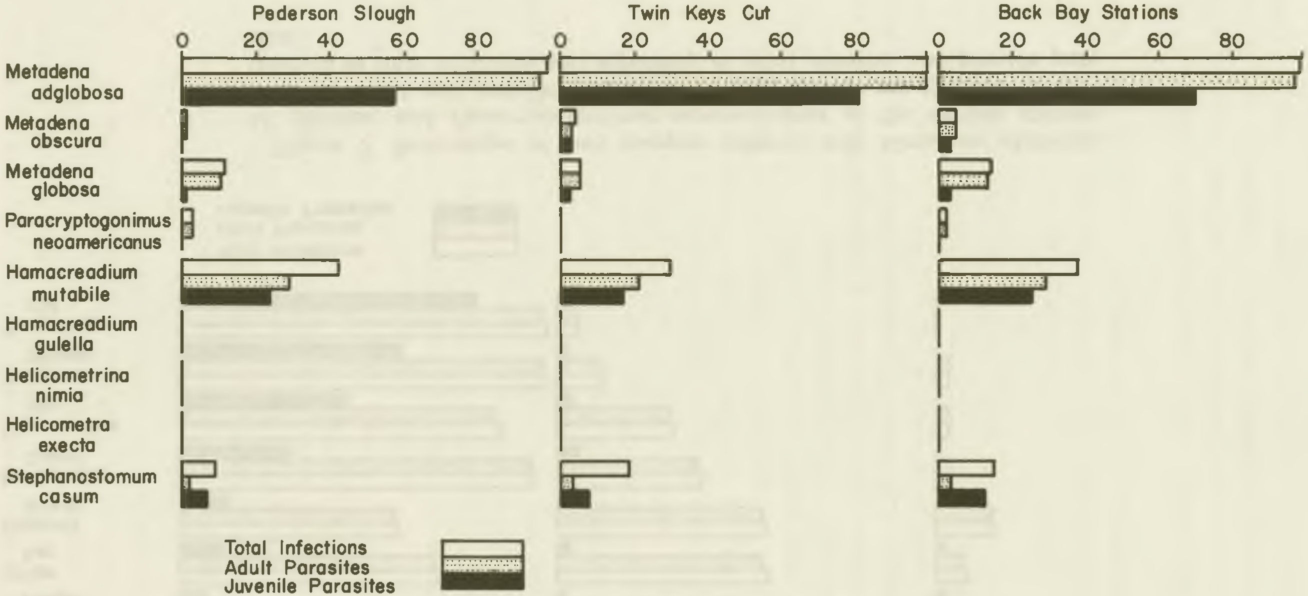

Figure 6. Percentages of gray snappers infected with each trematode at Pederson Slough and Twin Keys Cut Stations. Combined data presented under back bay stations. Data for adult and juvenile trematodes of each species are graphed together as total infections and separately as adult parasites and juvenile parasites.

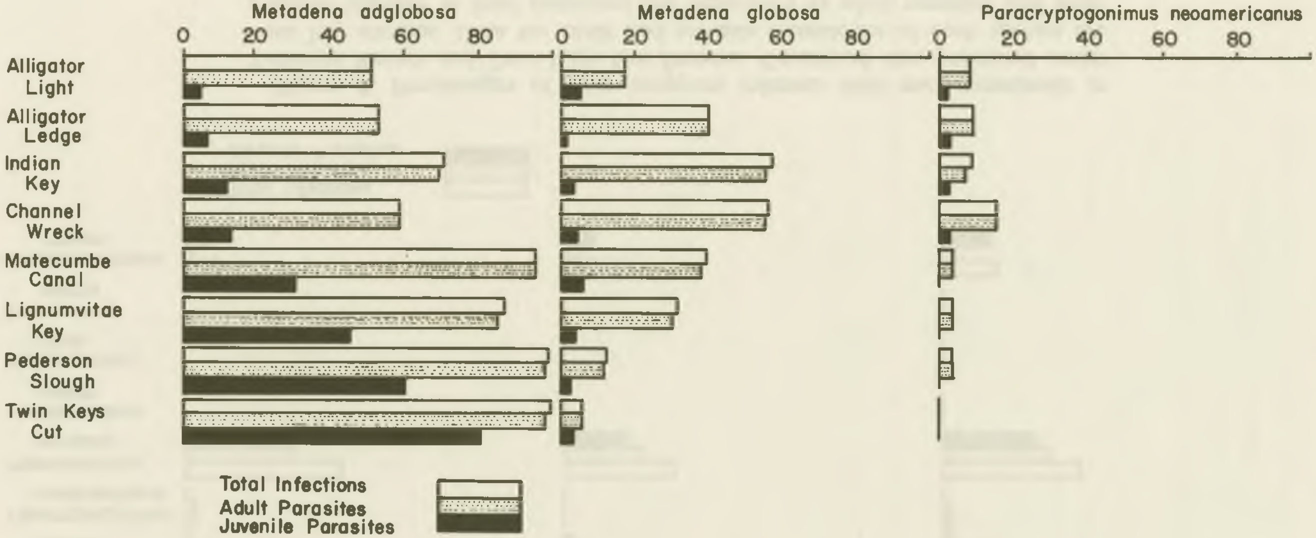

Figure 7. Percentages of gray snappers infected with *Metadena adglobosa, M. globosa,* and *Paracryptogonimus neoamericanus* at the various stations. Data for adult and juvenile trematodes of each species are graphed in combination as total infections and separately as adult parasites and juvenile parasites.

from the October incidences of 64% total infections and 14% infected with juvenile worms. The December and January high of 77%, with 14% infected with juveniles, does suggest that the rise in incidence is real. Such a rise might result from the random immigration of Florida Bay fish after the end of the post-spawning migration. *Ceritheum eburneum,* the only snail found naturally infected with *M. adglobosa,* rarely was collected near the inshore and offshore stations and was very common near the back bay stations. Similarly, naturally infected fish intermediate hosts never were collected near the offshore and inshore stations, but *Lucania parva*, which was found naturally infected with *M. adglobosa,* was the most common fish taken by trawl in the slough. Probably a large proportion of the *M. adglobosa* at the Atlantic side stations was acquired in Florida Bay.

The incidence of infections by *M. adglobosa* at the offshore stations was slightly lower than at the inshore stations. A drop in total incidence from 60% June and July to 32% in September at the offshore stations may or may not be real; the June and July collection consisted of only 20 fish.

The incidences of juvenile *M. adglobosa* of 25% in June and July, none in August, and 8% in September parallel the trend only roughly. The trend, if real, could reflect an attrition in the infections that had been brought offshore from Florida Bay with the offshore spawning migration. The December rise to 75%, based on only 20 fish, parallels the inshore rise from September to December and January, possibly for the same reason. Cold weather movements to deeper water may accentuate the random

Table 6. Percentages of gray snappers infected with *Metadena adglobosa* near Lower Matecumbe Key during various months of the year

	Offshore				Inshore		
	June–July	Aug.	Sept.	Dec.	Sept.	Oct.	Dec.–Jan.
No. of fish	20	97	37	20	20	121	43
Adult worms	60	52	32	75	55	64	74
Juvenile worms	25	0	8	5	0	14	14
Total infections	60	52	32	75	55	64	77

	Bayside				Back bay			
	June–July	Oct.	Dec.	Jan.–Feb.	June–July	Aug.	Oct.–Nov.	Jan.
No. of fish	34	83	37	64	43	45	30	52
Adult worms	94	88	89	92	100	100	97	98
Juvenile worms	73	36	11	44	63	89	33	77
Total infections	97	90	89	92	100	100	97	100

immigration from Florida Bay to the Atlantic side stations, once the post-spawning movements are over.

Fish sizes at Alligator Lighthouse and Alligator Ledge differ considerably, and differences in the parasite populations might be expected. In August, 50 fish averaging 237 mm standard length were collected from Alligator Ledge Station. The incidences of *M. adglobosa* at Alligator Light and Alligator Ledge were 51% and 52%, respectively, indicating that fish size was of little importance to *M. adglobosa* populations at the offshore stations (see Table 11). Indeed, fish size does not seem to have been of much importance in determining the incidence of *M. adglobosa* at any station.

In general, the locality of a collection was a great deal more important than fish size, sex, or season of the year in determining the incidence of *M. adglobosa.* The highest incidences were found in collections from the shallow Florida Bay beds of *Thalassia,* where dense populations of *Ceritheum eburneum,* the snail host of *M. adglobosa,* and *Lucania parva,* a fish intermediate host, were found.

Winter collections of *C. eburneum* from near summer assembly points on Pederson Bank slough revealed a much lower incidence of *M. adglobosa* infection than did summer collections. Only one snail of the 390 collected in February was infected. Snails kept in aquaria since the preceding summer still were producing cercariae, so infected snails probably neither die out nor lose their infections. The turnover in the population of adult snails would have to be improbably high to account for this seasonal decrease in the incidence of *M. adglobosa.*

A probable explanation lies in the fact that the summer snail collections were taken by trawling as close to the Pederson slough assembly points as possible. In such areas the rate of new infection should be high and the density of infected snails much higher than in the slough generally. With the abandonment of the assembly points by the gray snaper in cold weather, random movements of the infected snail would spread them throughout the area, and lack of new infections would allow the incidence of infected snails near the assembly points to fall accordingly.

Metadena globosa (Linton, 1910)

The highest incidences of *Metadena globosa* were found at the inshore stations. In September, 65% of the inshore station collection (only 20 fish) had adult *M. globosa*, and 10% had juveniles. These figures do not differ significantly from the October figures of 60% total incidence and 3% incidence of juveniles, based on a sample of 121 fish. The drop to 47%

total positives in a December and January collection of 43 fish may have been a sampling variation. A drawing of *M. globosa* appears in Figure 8B. Incidences from the eight stations are presented in Figure 7, and seasonal incidences are presented in Table 7.

The difference between the *Metadena globosa* incidences of infection at the Alligator Ledge and Alligator Lighthouse Stations probably is real and may reflect the difference in fish sizes. The August incidence of 18% infected with *M. globosa* at Alligator Lighthouse is significantly lower than the incidence of 65% found at Alligator Ledge in June and July, even when the small size of the Alligator Ledge collection is considered (20 fish). It is also significantly lower than the Alligator Lighthouse figure of 30% for August. As most other parasites occurred in a larger percentage of Alligator Ledge fish than Alligator Lighthouse fish, the large offshore fish probably do have a higher incidence of *M. globosa* than the small ones.

The still higher incidences of *M. globosa* in the small fish from Indian Key Station, however, indicate that the size difference is important only within a local fish population, and subordinate to differences in habitat. Infections by juvenile trematodes, usually a good key to where parasites are acquired, are everywhere so low that they provide no clue.

Bayside incidences of *M. globosa* were consistently lower than those on the Atlantic side of the Keys, and did not vary appreciably with season. The lowest incidence at the bayside stations, 32%, was recorded in June and July, together with a high incidence of juveniles of 9%. The highest incidence, 38%, occurred in January and February, and again in December, but with a 0% incidence of juveniles during these periods. There appear to have been no significant seasonal changes in the occurrence of *M. globosa* over this period.

Incidences of *M. globosa* were consistently low at the back bay stations. Except for a spectacular jump to 50% incidence in October and November, the range was 4 to 8%. The atypical 50% incidence in October and November occurred in gray snappers collected at the Slough Station and probably represented a collection of immigrants from the inshore area. These fish were considerably larger than others collected in the slough and obviously represent a different population. Seasonal incidences of *M. globosa* at the various stations appear in Table 7.

The proportion of incidence of juveniles to incidence of adults was outstandingly lower in *M. globosa* than in *M. adglobosa* at all stations. This indicates that there is a fundamental difference between their life cycles. The low incidence of juvenile *M. globosa* suggests the parasite may be long-lived compared to *M. adglobosa*, and the differences of the two

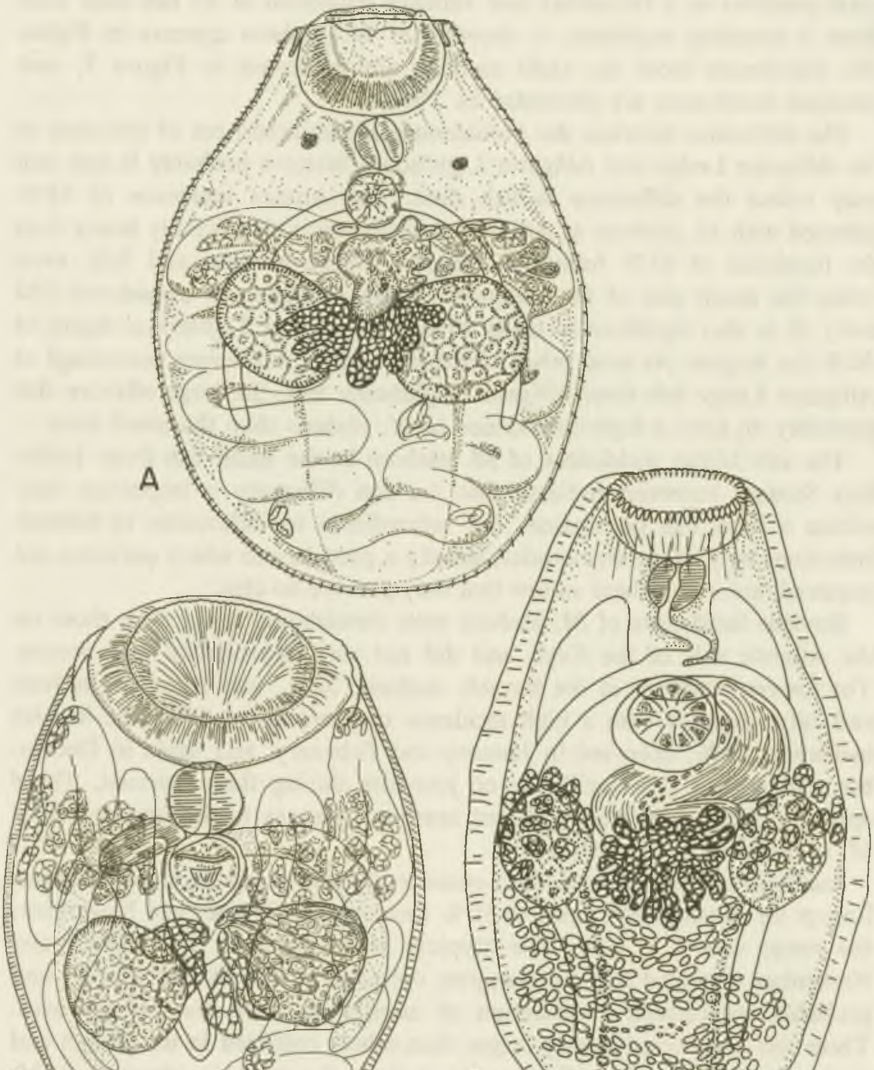

Figure 8. A. *Metadena adglobosa* Manter, 1947
B. *Metadena globosa* (Linton, 1910)
C. *Paracryptogonimus neoamericanus* Siddiqi & Cable, 1960

species indicate that they utilize different snail intermediate hosts. The most common species of *Ceritheum* near the stations having the highest incidence of *M. globosa* is *C. litteratum* (Born), and an investigation of the life cycle of *M. globosa* should start with this snail. *C. litteratum* was collected from this area, but produced no cryptogonomid cercariae. The question could be investigated by examining a larger snail collection and the laboratory exposure of the snails in aquaria.

Paracryptogonimus neoamericanus Siddiqi and Cable, 1960

Paracryptogonimus neoamericanus resembled *M. globosa* in seasonal and geographic distribution. Its incidence was not high at any station, but it was more common at the inshore stations than anywhere else.

Paracryptogonimus neoamericanus was rare in Florida Bay. Small numbers were found only at the bayside stations and at the Slough Station in October, when the post-spawning movements of the gray snappers might have brought it in from the Atlantic side of the Keys. A drawing of *P. neoamericanus* appears in Figure 8C. Incidences at the various stations are presented in graphic form in Figure 7.

Small incidences of *P. neoamericanus* were found at the offshore and inshore stations at all seasons, ranging from a high incidence of 35% collected offshore in June and July to a low incidence of 3% collected offshore in September. Juvenile worms were found at the offshore stations only in August, when one fish in a collection of 97 from the Alligator Lighthouse Station contained juveniles.

Table 7. Percentages of gray snappers infected with *Metadena globosa* near Lower Matecumbe Key during various months of the year

	Offshore				Inshore		
	June–July	Aug.	Sept.	Dec.	Sept.	Oct.	Dec.–Jan.
No. of fish	20	97	37	20	20	121	43
Adult worms	65	24	14	35	60	59	47
Juvenile worms	5	0	0	0	10	3	5
Total infections	65	24	14	35	65	60	47

	Bayside				Back bay			
	June–July	Oct.	Dec.	Jan.–Feb.	June–July	Aug.	Oct.–Nov.	Jan.
No. of fish	34	83	37	64	43	45	30	52
Adult worms	29	36	38	36	7	4	47	8
Juvenile worms	9	4	0	3	2	2	3	0
Total infections	32	36	38	38	7	4	50	8

The September inshore collection revealed a total incidence of 20% and a juvenile incidence of 10%. These were the highest inshore incidences of *P. neoamericanus.* In October, a collection of 121 fish showed a 11% total incidence and a 2% incidence of juveniles. The data for offshore and inshore stations indicates that *P. neoamericanus* usually is acquired inshore. The drop in total incidence from June and July to September, and the subsequent rise in December, follows the same pattern as that of *M. adglobosa, M. globosa,* and *H. mutabile.* Together with the absence of juvenile trematodes, it suggests that *P. neoamericanus* is carried to the offshore stations in the spring by fish moving out to spawn.

Paracryptogonimus neoamericanus was found in much higher incidences in *Ocyurus chrysurus* than in *L. griseus. L. griseus* probably is not the primary definitive host. Its high incidence inshore suggests that the snail host may be found on hard-bottom areas similar to those occupied by *C. litteratum and A. tecta.* Its obviously close relationship to the genus *Metadena* indicates that the cercaria probably is a biocellate lophocercous form that encysts in fish. Seasonal incidences of *P. neoamericanus* are presented in Table 8.

Velasquez (1961) discussed *Metadena apharei* (Yamaguti, 1942), from a species of *Lutjanus* in the Philippines, claiming that the worm possesses a circumoral coronet of spines. If true, this indicates a close relation between *Metadena* and *Paracryptogonimus.* The two genera are very similar in most respects, but are placed in different subfamilies largely on the basis of the heavy cuticle and oral coronet of *Paracryptogonimus.*

The author's observations of many *Metadena* lead him to doubt the reality of the oral coronet described by Velasquez. Members of the genus possess a circumoral row of gland ducts that look very much like spines under certain circumstances. This structure was studied carefully because of the taxonomic implications of an oral coronet in *Metadena*, and its true nature was determined by a study of serial sections and of living specimens.

Hamacreadium mutabile Linton, 1910

Hamacreadium mutabile was the second most common trematode collected, and it appeared at every station during every season of the year. In most cases the incidence of juveniles of *H. mutabile* was almost as high as that of the adults, although the incidence of adults nowhere was higher than 85%. The reason for this may be a high rate of loss in heavy infections, noted by McCoy (1929) in the course of experimental life cycle studies of the genus. A drawing of *H. mutabile* appears in Figure 10A.

Incidences of *H. mutabile* at the various stations are presented in Figure 9.

The snail host of *H. mutabile, Astraea tecta americana,* is an inhabitant of hard-bottom *Thalassia* habitats. The typical habitat varies from exposure at low tide to a depth of 4 m. Sparse *Thalassia* grows through *Porites* rubble (finger coral), interspersed with patches of live *Porites,* sponge, and the calcareous alga *Halimeda. Astraea tecta* usually occurs on blades of *Thalassia,* but a few individuals are found on *Halimeda* or *Porites* rubble. Population densities may be as high as 60 adult snails per square meter. This bottom is highly heterogeneous in structure, with snails grouping in small microhabitats.

Typical colonies of *A. tecta* occur in the shallows on both sides of the Channel Station and along a line between Indian Key and the channel. Infection rates in the areas that were collected were very low, as only one positive snail was recovered. This snail was infected with *H. gulella.* None infected with *H. mutabile* was recovered there.

The channel bottom was trawled, but no *A. tecta americana* was recovered, although typical *Porites* rubble was brought up in large quantities. Small colonies of heavily infected snails that did not happen to be picked up by the trawl may occur on the channel bottom.

Seasonal variations in the offshore incidence of *H. mutabile* paralleled those of *M. globosa* and *M. adglobosa.* Incidences at the Alligator Lighthouse and Alligator Ledge Stations in August did not differ appreciably. Offshore incidence fell from 85% in June and July to 42% in August

Table 8. Percentages of gray snappers infected with *Paracryptogonimus neoamericanus* near Lower Matecumbe Key during various months of the year

	Offshore				Inshore		
	June–July	Aug.	Sept.	Dec.	Sept.	Oct.	Dec.–Jan.
No. of fish	20	97	37	20	20	121	43
Adult worms	35	6	3	10	20	11	7
Juvenile worms	0	1	0	0	10	2	0
Total infections	35	6	3	10	20	12	7

	Bayside				Back bay			
	June–July	Oct.	Dec.	Jan.–Feb.	June–July	Aug.	Oct.–Nov.	Jan.
No. of fish	34	83	37	64	43	45	30	52
Adult worms	0	7	0	0	0	0	3	0
Juvenile worms	0	0	0	0	0	0	0	0
Total infections	0	7	0	0	0	0	3	0

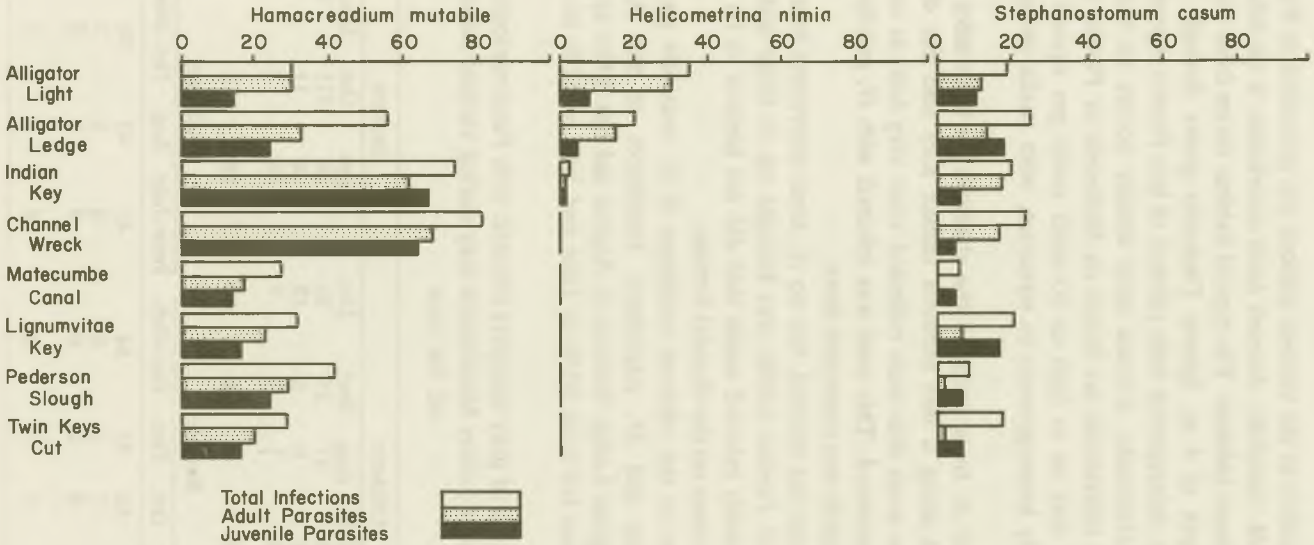

Figure 9. Percentages of gray snappers infected with *Hamacreadium mutabile, Helicometrina nimia*, and *Stephanostomum casum* at the various stations. Data for adult and juvenile trematodes of each species are graphed in combination as total infections and separately as adult parasites and juvenile parasites.

and to a low of 16% in September, then rose to 40% in December. Possibly this resulted from highly infected fish moving offshore to spawn in the spring and early summer and losing their parasites by the time of the post-spawning inshore migration in September. A selective inshore movement may occur. Those fish remaining at the offshore stations after spawning may represent a permanent population that never moves inshore. Starck's tagging data supports this hypothesis. Seasonal incidences of *H. mutabile* are listed in Table 9.

Fish size does not appear to be a primary factor in determining the incidence of *H. mutabile* offshore. The average size of gray snappers collected at the offshore stations fell steadily from June and July to September, but rose markedly in December. The August collections consisted of an Alligator Lighthouse collection of 237 mm mean standard length, and an Alligator Ledge colection of 311 mm mean standard length. The Alligator Ledge fish did not differ significantly from the smaller Alligator Lighthouse fish in total incidence, and were only slightly higher in incidence of juveniles. The two collections resemble each other much more closely than they resembled collections from preceding and following months. Large offshore gray snappers did appear to have a slightly higher incidence of *H. mutabile* than small ones, but size was less important than season.

Inshore incidences of *H. mutabile* were highest in September, coincident with the offshore low. A high incidence of both adults and juveniles was found in October, when 83% of a sample of 121 fish were infected and 69% had juveniles. The differences between this collection and the small September collection may be a sampling variation. These figures are consistent with the hypothesis that fish moving back inshore after spawning are those that moved offshore in the spring, taking *H. mutabile* with them.

The lowest inshore incidence, in December and January, coincided with the lowest incidence in *M. globosa* and the highest in *M. adglobosa,* supporting the hypothesis that these changes resulted from Florida Bay fish moving into deeper water in the cold weather. Immigrants from Florida Bay would have low incidences of *H. mutabile* and *M. globosa,* and a very high incidence of *M. adglobosa.*

Bayside incidences of *H. mutabile* do not show significant seasonal changes, with the possible exception of a slight drop in both juvenile and adult incidences in January and February. This drop is small enough to be a sampling variation, but does fit in with the presumed cold weather movements of the fish.

Table 9. Percentages of gray snappers infected with *Hamacreadium mutabile* near Lower Matecumbe Key during various months of the year

	Offshore				Inshore		
	June–July	Aug.	Sept.	Dec.	Sept.	Oct.	Dec.–Jan.
No. of fish	20	97	37	20	20	121	43
Adult worms	65	36	14	30	70	71	30
Juvenile worms	55	13	5	15	35	69	53
Total infections	85	42	16	40	85	83	63

	Bayside				Back bay			
	June–July	Oct.	Dec.	Jan.–Feb.	June–July	Aug.	Oct.–Nov.	Jan.
No. of fish	34	83	37	64	43	45	30	52
Adult worms	26	25	22	19	44	16	37	19
Juvenile worms	24	14	22	12	40	16	33	13
Total infections	35	36	30	30	53	24	47	27

Scarcity of the snail host in Florida Bay, especially near the bayside stations, indicates that most of the bayside *H. mutabile* were acquired on the Atlantic side. The drop in adult infections at the inshore stations from 71% in October to 30% in December and January is not easily creditable to sampling variation. When the fact that juvenile infections only fell from 69 to 53% in the same period is considered, it does appear that uninfected fish were moving in from some other area and rapidly becoming infected.

Back bay stations cannot be combined conveniently for the consideration of *H. mutabile* incidences. June and July collections were from the Slough Station, a typical back bay station, but 6 km east of Twin Keys and only 1 km west of Lower Matecumbe Channel. August collections were split nearly equally between the Slough Station and the Twin Keys Station. October and November collections were from the Slough Station and the January collection was taken at Twin Keys. Slough Station collections for the entire year had a total incidence of 42%, an adult incidence of 34%, and a juvenile incidence of 30%, while Twin Keys had a total incidence of 29%, and adult incidence of 20%, and a 16% incidence of juveniles.

The August back bay collections, taken from both the Twin Keys and Slough Stations at the height of offshore spawning, averaged smallest in fish size and lowest in incidences of infection with *H. mutabile*. Differences between the two stations were slight. The August Twin Keys collection resembled the January Twin Keys collection more closely than it did the slough collection in August. It was, however, more like the August slough collection than like either of the two other Twin Keys collections.

The Twin Keys Station is far from Pederson Slough Station and the bayside stations, and *H. mutabile* at Twin Keys probably does not originate on the Atlantic side. Several hard-bottom areas were seen in the vicinity of Twin Keys that closely resemble the *Porites* rubble-*Thalassia* beds and gorgonian stands near the Channel and Indian Key Stations.

An occasional *A. tecta americana* was taken when trawling *Thalassia* beds near Twin Keys. Very probably a complex of environments exists in the Twin Keys area that complements the inshore-bayside stations complex near Lower Matecumbe Key.

The high incidence of infections with juvenile *H. mutabile* and the high proportion of heavy infections with juveniles may be a function of cercarial behavior. Cercariae of *Hamacreadium* do not swim, but attach themselves to the substrate, so they do not scatter widely from the site of emergence. It would be interesting to know how rapidly they emerge. Should the movements of the snail be slow and emergence rapid, a day's cercarial production would be concentrated in a small area and small fish encountering them would stand a good chance of becoming heavily infected.

The cercaria's habit of attaching to the substrate also makes the behavior pertinent to its availability to the second intermediate hosts. As most of the snails are found on blades of *Thalassia*, the cercariae probably are located there too, and fish that come into contact with the grass would be much more vulnerable to infection. The grass-dwelling blennies, gobies, and toadfish are obvious possible vectors, as they tend to rest on the substrate.

The toadfish, *Opsanus beta,* often was taken in the trawl near the inshore stations. No natural infections with *H. mutabile* were found, but only a few toadfish were examined. Starck (1964) reported that fish constituted 36 to 37% of the stomach contents of snappers collected at the Lignumvitae Channel Wreck Station, and that the most common fish in their stomachs were toadfish. The behavior of cercariae of *Hamacreadium* suggests that only a small proportion of the vector population is heavily infected. Therefore, metacercariae could easily be overlooked if only a few toadfish were examined, but snappers that eat toadfish regularly could pick up a heavily infected one occasionally.

Very little is known about the feeding movements or food preferences of individual snappers. Longley and Hildebrand (1941) report that snappers learn rapidly to eat all kinds of unusual foods, such as scraps of bread or garbage. The high correlation between heavy infection with adults and juveniles might be the result of certain individuals developing an especial taste for toadfish or some other vector. Another possibility is that individual fish return to feed in the same area night after night; those that feed in an area having a highly infected vector population are continually reinfected.

McCoy (1930) suggested that wrasses, especially the reef-dwelling species of *Halichoeres* and *Thalassoma*, are important vectors of *Hamacreadium* because they burrow into sandy bottoms at night. Neither genus is plentiful in the Indian Key area, and neither was seen near the Channel Wreck Station. Wrasses that burrow into the sandy bottoms to sleep would contact only a small fraction of the bottom area covered by toadfish and blennies.

Helicometrina nimia Linton, 1910

Helicometrina nimia is primarily a parasite of fish on the offshore reefs. It was found in 34% of the gray snappers collected at the Alligator Lighthouse Station and 19% of those from the Alligator Ledge Station. Incidences of juveniles were low, being 7% at Alligator Lighthouse and 3% at Alligator Ledge. A drawing of *H. nimia* appears in Figure 10B. The incidence of *H. nimia* at the various stations is presented in Figure 7. An occasional *H. nimia* was found in fish from the inshore stations and, more rarely, from the bayside stations. These probably were brought in from offshore by fish returning from spawning. None was collected at the back bay stations.

Helicometrina nimia has been reported from a large number of definitive hosts. Manter (1934) listed 14 fish species of six families in which it had been found. This suggests that *L. griseus* is not an important host, although the worm does mature sexually and probably can complete its life cycle. Probably the gray snapper does not maintain *H. nimia* for very long, for few fish appear to bring it back inshore in the post-spawning movement. Manter (1934) offered evidence that Miller's Cercaria "J" (1925) is *H. nimia.* He obtained cotylocercous cercariae somewhat similar to those of *H. mutabile* from one of 34 *Columbella mercatoria* (Linnaeus). These cercariae penetrated two shrimp of the genera *Alpheus* and *Lysmata.* Metacercariae that appeared to be the same species were found as natural infections in such shrimp and proved to be *H. nimia* in experimental infections. Shrimp of the genus *Alpheus* are found along the reefs in great numbers. Their characteristic claw-popping often makes an underwater background sound on Alligator Reef that is much like fish frying.

Columbella mercatoria and related snails are numerous on the reef and in the coral rubble of the back-reef area of Alligator Ledge Station. Although intermediate hosts were not collected systematically nor examined for infection, it was noted that typical alpheid shrimp sounds are rare

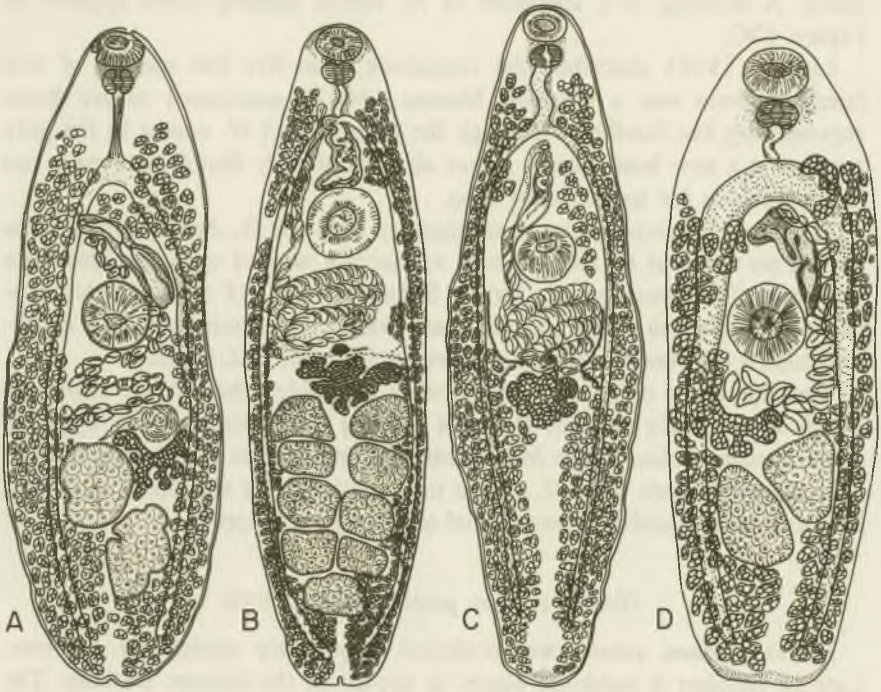

Figure 10. A. *Hamacreadium mutabile* Linton, 1910
B. *Helicometrina nimia* Linton, 1910
C. *Helicometra execta* Linton, 1910
D. *Hamacreadium gulella* Linton, 1910

or absent near the inshore and Florida Bay stations. This information is given for what it is worth. There are no data available on the specificity of *H. nimia* cercariae for second intermediate hosts, and alpheid shrimp of various species occur throughout the gray snapper's range near Lower Matecumbe Key.

Helicometra execta Linton, 1910

Helicometra execta was found only at the offshore stations on a few occasions. The specimens exhibited a wide variation in the number of testes, as described by Linton (1910). According to Linton, *H. execta* may have one or two testes, or testes may be entirely absent. In the present study all these variations were observed, plus one specimen having three testes. A drawing of a specimen of *H. execta* lacking testes appears in Figure 10C.

Linton (1910) described the trematode from five fish species of two families. None was a snapper. Manter (1947) mentioned twelve hosts representing five families. Although the discovery of *H. execta* in the gray snapper is a new host record, it was obvious already that *H. execta* is not highly specific for its definitive host.

Possibly *L. griseus* is not a satisfactory host for *H. execta.* Individuals having no testes at all still produce apparently normal eggs, but this does not imply that these eggs are fertile. Should the lack of testicular development be a function of the parasite's maturation in an unsatisfactory definitive host, it may not be able to complete its life cycle in *L. griseus.*

The life cycle of *H. execta* probably resembles that of *H. nimia,* to which it is closely related. Palombi (1929) described the life cycle of *Helicometra fasciata* in the Mediterranean, finding that a shrimp served as second intermediate host. *H. execta* may utilize a reef shrimp as its vector host and be an incidental parasite of offshore gray snappers.

Hamacreadium gulella Linton, 1910

Hamacreadium gulella was collected only rarely during the summer. Late in October it suddenly began to appear at the inshore stations. The reason for this sudden appearance is unclear.

One possible explanation is that it was not distinguished from *H. mutabile* until October. This is improbable. Its appearance was known, its presence was expected, and its absence was a cause of puzzlement and concern. When it did begin to appear regularly, it was easily recognized. A drawing of *H. gulella* appears in Figure 10D.

Another possibility is that small gray snappers are not satisfactory hosts for *H. gulella.* McCoy (1930) reported that heavy infections of *H. gulella* are lost rapidly from gray snappers. He was puzzled that two closely related species with identical life cycles should infect the same intermediate hosts when he discovered that *H. mutabile* and *H. gulella* both infect the gray snapper.

Possibly the inshore gray snappers are not good enough hosts to support an *H. gulella* population, and that some other fish is the important definitive host. If this is true, then *H. gulella* may have been absent from the inshore stations until this hypothetical definitive host moved into the area and infected the snails. Allowing for the probable development period, this would put the appearance of the hypothetical host at sometime in September, when the post-spawning inshore migration was occurring. The bearers of *H. gulella* then might be large offshore gray snappers.

A more probable host is *Lutjanus cyanopterus*, the cubera snapper, which resembles *L. griseus* so closely that the two often are confused. *L. cyanopterus* is a much larger fish, sometimes attaining a weight of more than 50 k. Although it was not collected in this study, it is common under Keys bridges and along the deeper offshore reefs. McCoy's observations on *H. gulella's* intolerance of crowding would be understandable if *H. gulella* primarily inhabited the commodious caeca of *L. cyanopterus*. This also would explain the speciation of *H. mutabile* and *H. gulella* as adaption to slightly different hosts.

Stephanostomum casum (Linton, 1910)

Stephanostomum casum exhibited less variation in incidence from one station to another than the other trematodes. Its incidence on the Atlantic side of the Keys was a little higher than in Florida Bay, but adult and juvenile parasites were found at all stations during almost every season of the year.

The seasonal incidence of *S. casum* at the offshore stations fell into the familiar pattern of highest incidence occurring in June and July and lowest incidence in September, with a subsequent rise in December. Offshore incidences of juveniles of *S. casum* did not follow this pattern, being relatively unchanging in all seasons. The highest juvenile incidence was in June and July, but the next highest was in September, and the lowest was in December. The seasonal changes in the incidence of juveniles are of questionable significance when the small sizes of the collections that exhibited the extreme incidences are considered.

The total incidence at the inshore stations did not show changes beyond probable sampling variations. Extremes in the range of incidences of juveniles of *S. casum* involved so few fish that no reliable conclusions can be drawn. The incidences of adults of *S. casum* do not show proportional seasonal differences. A drawing of *S. casum* appears in Figure 12A. The incidences of *S. casum* at the various stations are presented in graphic form in Figure 9.

Bayside station incidences exhibited a considerable drop in January and February, in both adults and juveniles of *S. casum*. The samples are large enough to make it unlikely that the differences were sampling variations. The drop is paralleled by a drop at the inshore station in the incidence of juveniles of *S. casum*. No similar drop is seen at the other stations. The drop in incidence at the bayside station during the middle of winter may have been a function of the cold-weather movements of the gray snapper.

There were some differences between the Twin Keys Station and the Slough Station. Incidence at the Slough Station was a little lower than anywhere else, being 3% for all collections, with no juveniles in October and November. In June and July, adults were absent from the Slough Station, and juvenile *S. casum* incidence was 19%.

The Twin Keys collections were roughly comparable to the bayside stations, showing a total incidence of 21%. Twin Keys Station had a 12% juvenile *S. casum* incidence and 15% adult incidence in January when the bayside stations total incidence had fallen to 5%. The seasonal incidences of *S. casum* at the various stations are listed in Table 10.

Studies by Martin (1939), Wolfgang (1955), and Stunkard (1961) on the life cycles of various species of *Stephanostomum* all report snail hosts belonging to the genus *Nassarius*. This genus is widely distributed in Florida waters. An investigation of the life cycle of *S. casum* might begin with studies of the cercariae from *Nassarius albus* (Say, 1826) and *N. vibex* (Say, 1822). Warmke and Abbott (1961) reported that *N. albus* is common on mud bottoms and is dredged down to 30 m. According to Warmke and Abbott, *N. vibex* is a common sand or mud flat species. The range of either species may encompass that of *L. griseus* near Lower Matecumbe Key. Robert Work of the Institute of Marine Sciences (personal communication) reports that both species are common in the Florida Keys. The distribution of *S. casum* infections in *L. griseus* collected in the Lower Matecumbe Key area indicated that the most widely distributed species of *Nassarius* there would be the most probable snail host of *S. casum.*

Metadena obscura sp. n.

Distribution data on *Metadena obscura* sp. n. were not gathered until halfway through the study because at first it was not distinguished from *M. adglobosa*. Such data as were gathered indicate that *M. obscura,* like *M. globosa,* was most common on the Atlantic side of the Keys.

While scanning thousands of *Metadena* under the dissecting microscope, it became apparent that "*M. adglobosa*" occurred in two distinct forms. The common one obviously was *M. adglobosa* (Manter, 1947), but occasional specimens were larger, even as juveniles, and differed in body outline, both at rest and when contracting. This rarer form was studied and found to differ from *M. adglobosa* in the structure of the genital sac, the

Table 10. Percentages of gray snappers infected with *Stephanostomum casum* near Lower Matecumbe Key during various months of the year

	Offshore				Inshore		
	June–July	Aug.	Sept.	Dec.	June–July	Oct.	Dec.–Jan.
No. of fish	20	97	37	20	20	121	43
Adult worms	15	13	3	10	20	19	19
Juvenile worms	20	11	14	10	15	6	2
Total infections	35	25	14	20	35	21	21

	Bayside				Back bay			
	June–July	Oct.	Dec.	Jan.–Feb.	June–July	Aug.	Oct.–Nov.	Jan.
No. of fish	34	83	37	64	43	45	30	52
Adult worms	0	6	5	3	0	4	3	4
Juvenile worms	15	12	14	2	19	16	0	12
Total infections	15	18	19	5	19	20	3	15

distribution of uterine eggs, the number of ovarian lobes, and the location of the acetabulum. A drawing of *M. obscura* and drawings of sagittal sections of *M. obscura* and *M. adglobosa* appear in Figure 11.

Diagnosis (based on 20 specimens): Cryptogonimidae. *Metadena*. Body ovoid, truncate posteriorly; 470 to 660 (520) long by 320 to 460 (370) wide. Cuticle spined; spines 2 to 3 long, evenly distributed over body surface. Oral sucker terminal, retractile, 104 to 150 (122) wide; surrounded by numerous evenly spaced gland cell ducts that open around oral sucker at anterior end of body. Prepharynx approximately 20 long. Pharynx spherical, 35 to 41 (37) in diameter. Esophagus approximately 20 long. Eyespot pigment present at level of esophagus. Ceca 2, ending blindly in posterior ⅓ of body. Anterior body containing numerous gland cells with ducts opening on surface. Genital sac pore in anterior ¼ of body, immediately followed by large, folded genital sac lined with heavy spines 10 long and connecting with acetabular aperture. Acetabulum approximately 40 long, dorsal to genital sac, not visible except in sectional material. Testes 2, 62 to 94 (79) wide, rounded, slightly posterior to midbody, ventral to ceca, approximately one testicular diameter apart. Seminal vesicle large, convoluted; often extending both slightly anterior and posterior to genital sac. Ovary submedian, partially overlapping testes ventrally, with 10 to 15 digitform lobes, approximately 100 long by 140 wide. Uterus extending anteriorly on each side almost to level of genital sac pore. Vitelline follicles coarse, forming transverse band dorsal to ovary and testes; extending slightly anterior to ovary and testes, posteriorly and along

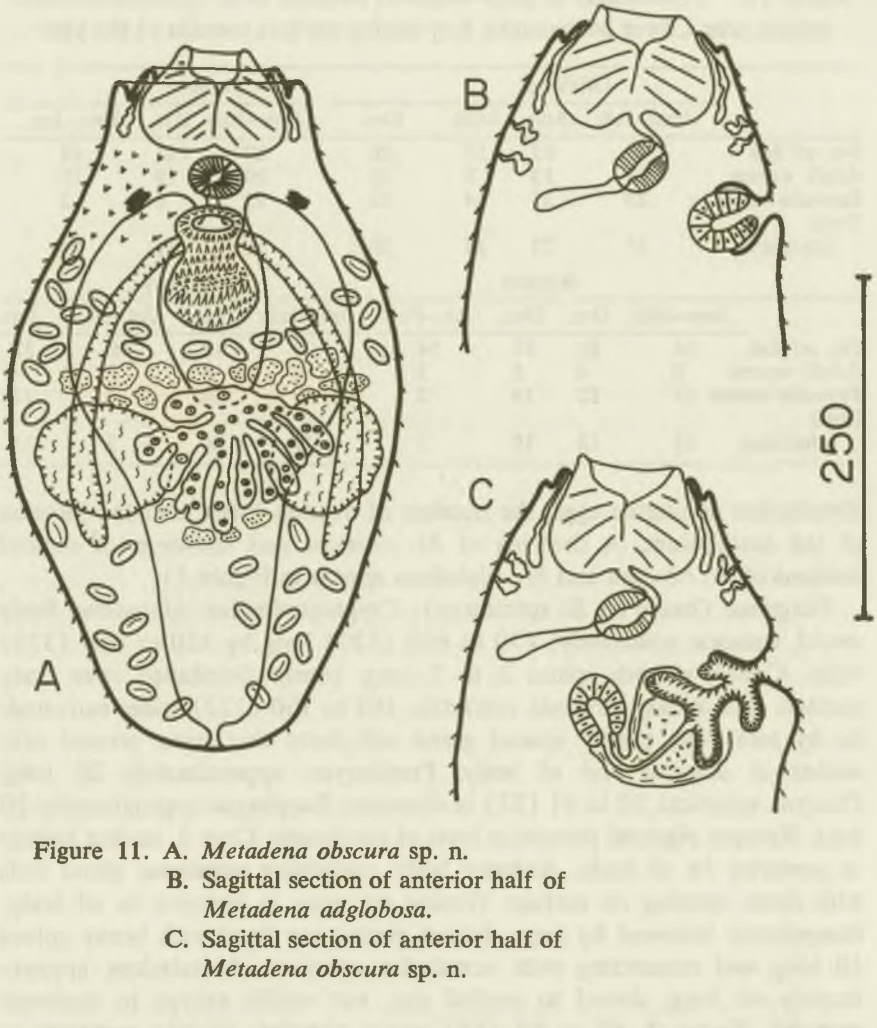

Figure 11. A. *Metadena obscura* sp. n.
B. Sagittal section of anterior half of *Metadena adglobosa.*
C. Sagittal section of anterior half of *Metadena obscura* sp. n.

median line to posterior edge of ovary. Mature uterine eggs 16 to 18 (17) long by 9 to 10 (9.5) wide. Excretory bladder large, Y-shaped, forking at level of testes, with branches extending anteriorly to level of pharynx.

Host: *Lutjanus griseus* (Linnaeus)
Habitat: Intestine and pyloric caeca
Locality: Lower Matecumbe Key, Florida
Holotype: U. S. Nat. Mus. Helminth. Coll. No. 60044

Trematode Incidence and Host Size

The question of the importance of host size is so bound up with the habitat, season, and migrations that it is difficult to discuss separately. The largest fish were taken at the offshore stations and the smallest in Florida Bay. Where there are sufficient data to draw conclusions, host size appears to be less important than habitat or seasonal changes in determining the incidence of the various trematodes.

In general, the larger fish have a greater variety of parasites than the smaller ones, other factors being equal. The larger fish probably range farther when feeding and visit a broader variety of habitats. They probably also eat a wider variety of foods, as they can eat larger organisms than can smaller fish. Large gray snappers are more piscivorous than smaller ones and therefore are more likely to pick up fish-borne parasites. This is pertinent because most snapper trematodes utilize small species of fish as intermediate hosts. Large snappers are usually older than smaller ones. Because they have been feeding longer, they have had a greater opportunity to become infected than small fish, especially as they also eat more food in a given period of time.

The incidences of trematodes in gray snappers of different sizes caught at the offshore stations are presented in Table 11. These data indicate that size was less important than time of year in determining the incidences of the various trematode species. Fish of different sizes caught at the same time of year were more alike in trematode populations than were fish of the same size caught at varying times of the year.

The incidence of *M. adglobosa* went down as the snappers grew. This probably is a result of the absence of the trematode's intermediate hosts from habitats frequented by large gray snappers. The occasional large fish taken in Florida Bay were heavily infected with *M. adglobosa.*

Fish smaller than 100 mm do not school at assembly points in large numbers. According to Starck (1965), *L. griseus* is a solitary inhabitant of the *Thalassia* beds until it is near 100 mm standard length. These small snappers are hard to collect in quantity, so their parasitology was not investigated in this study. The few that were collected indicate that fish of 50 mm standard length from the Slough Station already were infected with *M. adglobosa.* The question of the size at which various parasites are acquired is pertinent and should be investigated.

The services of the Computing Center of the University of Miami were utilized to calculate correlation coefficients between fish size and degree of infection with three trematodes, *M. adglobosa, M. globosa,* and *H. muta-*

bile. The degree of infection was indexed on a scale of 0 to 4 (see Table 3). Correlation coefficients were calculated separately for juvenile and adult parasites at each station during each season.

Correlation coefficients between the degree of adult *M. adglobosa* infection and fish size ranged from +0.72 at the offshore stations in December to +0.19 at the back bay stations in August. The balance of the correlations fell between −0.26 and +0.19. There were only three positive correlations, all in the back bay area. These data indicate that fish size was of some slight importance in determining the presence of and degree of infection

Table 11. Percentages of gray snappers in different size categories infected with various trematodes at the offshore stations

Station:	Alligator Ledge		Alligator Lighthouse		
Collection month:	June–July	Aug.	Aug.	Sept.	Dec.
No. of fish:	20	47	50	37	20
Mean standard length in mm:	312	311	237	219	193
Metadena adglobosa					
Adults	60	51	52	32	75
Juveniles	25	0	0	8	5
Total	60	51	52	32	75
Metadena globosa					
Adults	65	30	18	14	35
Juveniles	5	0	0	3	0
Total	65	30	18	14	35
Paracryptogonimus neoamericanus					
Adults	45	11	2	3	
Juvenile	0	2	0	0	
Total	45	11	2	3	10
Hamacreadium mutabile					
Adults	65	38	34	14	30
Juveniles	55	17	10	5	15
Total	85	47	38	16	40
Helicometrina nimia					
Adults	5	21	44	30	15
Juveniles	0	4	8	8	0
Total	5	25	48	32	15
Stephanostomum casum					
Adults	15	13	14	3	10
Juveniles	20	11	12	14	10
Total	35	23	26	14	20

with adults of *M. adglobosa,* small fish tending to be more heavily infected than larger ones.

Correlation coefficients between the degree of infection with juveniles of *M. adglobosa* and size of fish were similar to those for adults. They ranged from −0.40 at offshore stations in December to +0.25 at offshore stations in June and July. Most correlations were negative and quite low.

Metadena globosa correlations between degree of infection and fish sizes range from −0.30 at offshore stations in September to +0.40 at back bay stations in August. Both extremes could be the result of sample variations. There is no discernable pattern to the balance of the correlations. Low positive and negative correlations are about equally divided among the other stations and seasons.

So few juveniles of *M. globosa* were found that correlation coefficients between fish size and degree of infection would have to have extreme values to indicate a relationship. Correlations between fish size and degree of infection with juveniles of *M. globosa* ranged from −0.33 to +0.30 and indicate that fish size had no more to do with infection by juveniles than with infection by adult worms.

Correlations of degree of infection with adults of *H. mutabile* with fish size ranged from −0.18 at the inshore stations in October to +0.62 at the bayside stations in June and July. There were twelve positive correlations. The negative correlations were both inshore, where the incidences of *H. mutabile* were highest and infections heaviest. Bayside station and back bay station positive correlations were highest. These data indicate that fish size had nothing to do with infections by adults of *H. mutabile* on the Atlantic side of the Keys, but that large fish were somewhat more likely to be infected than small fish in Florida Bay.

As *H. mutabile* utilizes small bottom-dwelling fish as second intermediate hosts (McCoy, 1929, 1930), the tendency may be for large snappers, which eat a higher percentage of fish than the small snappers, to pick up the infection more often. Another factor may be the wandering of large infected fish into Florida Bay from the inshore areas.

Correlations between fish size and degree of infection for juveniles of *H. mutabile* ranged from −0.21 at the inshore stations in December and January to +0.69 at the bayside stations in June and July, and are similar to the data for adults of *H. mutabile.* There were three negative and eleven positive correlations, all quite low.

Correlation coefficients were calculated to determine whether collections that had a high incidence of a parasite were inclined to have a high proportion of heavy incidences. Grades of infection higher than Grade 1 were defined as heavy infections. Correlations were calculated between high incidences and high heavy incidences for *M. adglobosa, M. globosa,* and *H. mutabile*. Separate correlations were calculated for juvenile and adult trematodes in each of the gray snapper size categories. The results of these calculations are presented in Table 12. Also presented in Table 12 are correlations between the incidence of heavy juvenile infections and the incidence of heavy adult infections for each of the three trematodes.

These data indicate that infected gray snappers from a population in which the incidence of infection was high was more likely to be heavily infected than were infected gray snappers from a population in which the incidence of infection was low. The data also indicate that snappers heavily infected with adults of *M. adglobosa* or of *H. mutabile* were more likely to support heavy infections of juvenile worms of the same species than snappers that were not heavily infected with adult worms. This is not true of *M. globosa,* where so few juveniles were collected that no reliable conclusions can be drawn.

The correlation between the incidences of heavy infection of adults of *M. adglobosa* and heavy infections of juveniles of *M. adglobosa* in *L. griseus* smaller than 201 mm standard length was +0.93. The correlation of fish of 20 mm to 250 mm standard length (size category 2) was +0.85, and in fish of more than 250 mm standard length (size category 3) the

Table 12. Correlation coefficients between the incidences of various trematodes and the incidences of heavy infections with these trematodes at all stations

Parasite	Snappers of 200 mm standard length or less	Snappers of 201 mm to 250 mm standard length	Snappers of 251 mm standard length or longer
Metadena adglobosa, adult	+0.42	+0.56	+0.38
Metadena adglobosa, juvenile	+0.39	+0.68	+0.54
Metadena globosa, adult	+0.28	+0.19	+0.63
Metadena globosa, juvenile	+0.33	+0.00	+0.99
Hamacreadium mutabile, adult	+0.43	+0.25	+0.32
Hamacreadium mutabile, juvenile	+0.86	+0.30	+0.42
Correlation coefficients between heavy infections with juveniles and heavy infections with adults			
Metadena adglobosa	+0.93	+0.85	+0.97
Metadena globosa	+0.49	−0.08	+0.81
Hamacreadium mutabile	+0.95	+0.84	+0.94

correlation was +0.97. Similarly high correlations were found between the incidences of heavy infections with adult and juvenile *H. mutabile*. These data indicate that heavy infections of adult and juvenile parasites almost always occur together.

Gray snappers of less than 201 mm standard length (size category 1) tend to have heavier infections at stations where the incidence of infection was high than at other stations. The tendency was highest for juvenile *H. mutabile* and lowest for the adults of *M. globosa* but all correlations were positive.

The correlations were slightly lower for fish between 201 mm and 250 mm standard length (size category 2), but the tendency was for a high incidence of infections and a high incidence of heavy infections to be found together. The low correlation was for juvenile *M. globosa,* with a correlation coefficient of 0.00. The differences between the correlations for size category 1 and size category 2 snappers may be a sampling variation.

Fish of the largest size category exhibited a difference from the smaller fish that is difficult to explain. Correlations between high incidence and high heavy incidence for *M. globosa* were the highest of all, instead of the lowest. For adult *M. globosa,* the correlation coefficient between high incidence and heavy infection was +0.63. For juveniles, the correlation was +0.99. Correlations for the other parasites were lower. This difference may be a sampling variation. Incidences of *M. globosa* were never high, and heavy infections were very rare.

These correlation data may be summarized by saying that there is a tendency for high incidences of infection to include high intensities of infection, and for heavy infections by adults to be accompanied by high intensities of infections by juveniles. These tendencies are more apparent for *M. adglobosa* and *H. mutabile* than for *M. globosa*. The reason is probably that incidence of the former two parasites were much higher than incidences of the latter.

In concluding this section, it should be noted that the sampling method used in this study produces a strong sampling bias toward the smaller fish at an assembly point. On numerous occasions large gray snappers were observed to approach the bait cautiously, while the small fish rushed in and were caught.

Seasonal Changes in Trematode Populations

Forty-seven fish from the Alligator Ledge Station in August resembled 50 fish from Alligator Lighthouse Station in the same month, a great deal more than did the 20 fish caught at the Alligator Ledge Station in June and

July. The only really significant difference between the August Alligator Lighthouse and Alligator Ledge collections was that the fish from Alligator Lighthouse had twice as many individuals of *Helicometrina nimia.*

The June and July collection and August collection from Alligator Ledge Station consisted of snappers of almost exactly the same size (average mean standard lengths 311 mm and 312 mm), while the August Alligator Lighthouse collection was considerably smaller (237 mm). It appears that fish size is less important than season in determining the incidence of most offshore station trematodes. This is borne out, insofar as the data can be trusted, by the subsequent collections in September and December. Unfortunately, these collections numbered only 37 and 20 fish, respectively. They exhibited a decline in fish size to an average of 219 mm in September and 193 mm in December, but the overall pattern of a progressive drop in incidence of trematodes from June and July to September was broken by a steep rise in December.

The rise in incidence of *H. nimia* as summer progressed is not surprising when the nature of the offshore spawning movements are considered. As *H. nimia* was rather strictly a parasite of the offshore reef fishes, gray snappers moving offshore would arrive on the reefs uninfected, and the incidence of *H. nimia* would increase with the length of their stay.

The high incidence of *H. nimia* in small fish probably resulted from changes in feeding habits with growth. Longley and Hildebrand (1941) and Starck (1965) state that *L. griseus* feeds increasingly on fish as growth progresses. *H. nimia* utilizes reef shrimp of several species as vectors (Manter, 1934). The larger fish are probably less likely to feed on these small shrimp, if observations on the relationship between feeding and fish size are correct.

There was a drop in fish size and a drop in *H. nimia* incidences in September and again in December. *H. nimia* differed from all other parasites offshore in failing to show a December rise. This may have been a sampling variation, or may have resulted from an autumn and winter movement offshore by the smaller fish. Should this be true, the small offshore migrants would be expected to carry inshore and Florida Bay parasites with them and to have low incidence of *H. nimia.* Supporting evidence is the winter abandonment of the Pederson Bank Slough assembly points by the gray snapper.

Metadena adglobosa exhibited significant seasonal changes at the offshore stations. The drop in incidence from 60% in June and July to 32% in September and the subsequent rise to 75% in December correlate well with the post-spawning inshore migration at the beginning of September and probable offshore movements with the onset of cold weather. The inshore station low incidences of 55% in September and rise to 74% in December and January were consistent with the offshore changes.

These data support the hypothesis that gray snappers rarely acquire *M. adglobosa* on the Atlantic side of Lower Matecumbe Key. The incidence of juveniles was very low at both the offshore and inshore stations at any season, compared to the Florida Bay stations, and lowest in August and September when the general snapper movement was toward Florida Bay. The hypothesis also is supported by the small number of snail hosts of *M. adglobosa* that were found on the Atlantic side.

Seasonal changes in incidences of adults of *M. adglobosa* at the Florida Bay stations were slight. The bayside stations exhibited a drop in the incidence of infections by juveniles from 73% in June and July to 36% in October and 11% in December. Infections by juveniles at the back bay stations were highest in August with 89%, and lowest in October and November with 33%. This difference is significant, even though the collections numbered only 45 and 30 fish, respectively. The influx of fish from the Atlantic side after spawning could account for this drop in juvenile incidence. The average size of fish caught in October and November was larger than those caught in the summer.

The winter abandonment of the Florida Bay shallow-water assembly points may have been another factor in reducing the winter incidence of infections by juveniles of *M. adglobosa.* In summer, these areas were the site of heavily infected snail populations. The movement of the snappers into deeper water would reduce their opportunity to feed on the *Lucania parva* that inhabit the shallow *Thalassia* beds. *Lucania parva* was one of the two fishes found naturally infected with *M. adglobosa* metacercariae.

The incidence of adults of *M. adglobosa* at the Florida Bay stations did not change significantly throughout the year. The bayside stations varied from 94% in June and July to 88% in October. The back bay stations had an incidence of 100% except in October and November when it was 97%. Virtually all Florida Bay gray snappers appear to have been infected with adults of *M. adglobosa* all year, especially in the back bay areas away from the channels that run between Florida Bay and the Atlantic.

Unlike *M. adglobosa, M. globosa* is largely a parasite of snappers on the Atlantic side stations. The highest incidences were recorded from the inshore stations at a time when incidences were lowest at the offshore stations. The figure of 65% incidence of adults in the June and July offshore sample of 20 fish may have been a sampling variation. Otherwise, the movement of inshore fish to the offshore spawning grounds could have been a factor in the high incidence offshore in June and July. Unfortunately, data for the inshore stations in June and July are lacking, and these stations appear to have been a center of high incidence of *M. globosa.*

Bayside gray snappers showed no seasonal changes in incidence of *M. globosa.* The figures were considerably lower than those for inshore fish, and probably were maintained by movements of inshore fish into the bayside station areas. Inshore station fish also underwent only slight seasonal changes in incidence of *M. globosa.*

Gray snappers from the back bay stations showed a uniformly low incidence of infection with *M. globosa* throughout the year. Total incidences ranged from 4 to 8% except for a surprising jump to 47% adult and 50% total incidence in a 50-fish sample collected in October and November. This was too big a change to be attributed to sampling variation. Movements are found in Florida Bay within a kilometer of the Twin Keys movement of a highly infected population of unknown origin into the area may account for this midwinter high incidence. Many differing environments are found in Florida Bay within a kilometer of the Twin Keys Station, where these fish were taken. Some of these environments bear a strong resemblance to the hard-bottom sites common near the inshore stations. Movements of fish from such an area as a result of cold weather, the activities of seine fishermen, or other factors may have resulted in their being collected at the Twin Keys Station.

Incidences of infections by *H. mutabile* at the offshore stations exhibited a seasonal pattern similar to those of *M. adglobosa* and *M. globosa.* Total incidence of *H. mutabile* was 85% in June and July, 42% in August, and down to 16% in September. The changes are not attributable to sampling variation, even considering the small size of the June and July collection, and were paralleled by the figures for the incidence of infections by juveniles. The December rise to 40% total incidence from 16% in September suggests that in midwinter infection levels begin to rise to the level of the high summer incidences.

The inshore stations collections for September revealed an *H. mutabile* incidence of 85%. Although based on only 20 fish, this figure is supported by the October figure of 83% based on 125 fish. The December and January incidence dropped to 63%, probably as a result of the cold-weather movements of Florida Bay fish. This hypothesis is supported by the fact that the incidence of juveniles is not so much reduced (53% from 69%).

The incidences of *H. mutabile* at the bayside stations did not change significantly with season. A slight drop in December and January correlates well with the inshore station drop at the same time, and both may have resulted from a general snapper movement into deeper water with the onset of cold weather. Such a movement would reduce random movements into the Florida Bay area from inshore areas. Considering the sizes of the collections, the drop also may be a result of sampling variation.

The two back bay stations differed considerably in incidences of *H. mutabile*. Pederson Bank Slough collections were significantly higher in incidences of *H. mutabile* than Twin Keys collections. This difference may have been a function of the closer proximity of the Slough Station to the Atlantic side of the Keys, of seasonal changes, or of other factors. It may be significant that *H. mutabile* incidence in the small August collections from the two stations did not differ appreciably.

As far as can be concluded from these data, seasonal changes in parasite populations are a function of fish movements related to spawning and to responses to cold weather. The parasites acquired by snappers differ from habitat to habitat. Fish moving from one habitat to another take parasites with them. In the new habitat the original parasites are gradually lost and new ones, typical of the new habitat, are acquired.

3. Intermediate Hosts of Trematodes

The Snail Hosts

Large populations of *Astraea tecta americana,* the snail host of the two species of *Hamacreadium,* were found in the vicinity of the inshore stations. The distribution of these snails was very uneven. Typically, they were found on hard-bottom areas of *Porites* rubble, in which sparse *Thalassia* and *Halimeda* grew between the finger coral *Porites porites* and various sponges. Most snails were found crawling on blades of *Thalassia,* although some were on the calcareous alga *Halimeda* and a few on the *Porites* rubble. Populations densities varied considerably with slight differences in the substrate, being as high as 60 per square meter in isolated patches and averaging about 30 per square meter throughout the whole habitat. In these areas, *Cerithium litteratum, Modulus modulus, Tegula fasciata, Fasciolaria tulipa, Murex pomum,* and other snails were also found.

An extensive area of variable depth and bottom between Indian Key and the channel mouth was inhabited by scattered colonies of *A. tecta.* Sampling this area with the Peterson dredge produced unsatisfactory results because the jaws of the dredge so often were propped open by shells or *Porites,* allowing most of the contents to spill. Some parts of this area had populations of *A. tecta* as dense as 40 per square meter, while others were entirely uninhabited. Areas in which *A. tecta* occurred were precisely the ones where the Peterson dredge most often was fouled, so few data were gathered for labor expended.

Of 4854 specimens of *A. tecta* collected by trawling and hand-collecting in this area, only one produced *Hamacreadium* cercariae, identified as *H. gulella* Linton, 1910. This was in strong contrast with a collection of 256

A. tecta hand-collected from logger-head sponges that lay directly under the schooling snappers at Indian Key. Three snails of this group produced the cercaria of *H. mutabile*.

This suggests strongly that gray snappers acquire most of their *Hamacreadium* by casual feedings on bottom fishes at the daylight schooling areas, rather than while foraging elsewhere at night. Of course, this factor obviously would vary considerably from station to station, but certainly these snails that live directly under the assembled fish were much more likely to become infected than snails in the surrounding flats.

The most common snail at the Indian Key Station was *Cerithium litteratum*. Similarly, this snail was numerous in the *Porites* rubble bottom near the site of the Channel Station. Two-hundred specimens of *C. litteratum* were hand-collected from each location, but none yielded cercariae.

The most common species of *Cerithium* taken while trawling the area between Indian Key and Channel Stations was *C. algicola*. Occasionally a *C. litteratum* was found, but this snail appears to prefer harder bottoms. Small numbers of *C. variabile* were taken in some trawls, but *C. eburneum* was rare. The most common snail was *Modulus modulus*, which sometimes came up in the trawl in great numbers, but none of the several thousand that were isolated and crushed produced cercariae. About 500 specimens of *C. algicola* and 200 specimens of *C. litteratum* taken there were isolated and crushed, but the only cercariae recovered were small stylet cercariae resembling those of microphallids found in local fish-eating birds.

Cerithium eburneum, rare near the inshore stations, was the most common snail in the *Thalassia* areas near Lignumvitae Key and in the Pederson Bank slough. Of 250 specimens of *C. eburneum* trawled from the slough assembly points in late July, eight produced cercariae of *M. adglobosa*. In early August, six out of 100 specimens of *C. eburneum* collected there were infected, so the collections indicated that from 3% to 6% of the snails were infected in the summer. A collection of 390 specimens of *C. eburneum* taken in the middle of February yielded only one snail infected with *M. adglobosa*, indicating that the level of infection is much lower in winter.

Cerithium eburneum infected with *M. adglobosa* were kept in a wide-mouth gallon jar for nine months, and produced cercariae every time they were isolated. The snails were observed to crawl quite slowly, feeding on the algae growing on the surface of the jar. Supplementary feeding was unnecessary.

Cerithium variabile (Adams) also was collected in Pederson Bank Slough, amounting to about 5% of the ceriths taken there. Although *C.*

variabile is listed as the host of *M. adglobosa* by Cable (1956), none of those collected yielded cercariae. It is more common than *C. eburneum* near the inshore stations, and it may account for much of the *M. adglobosa* on the Atlantic side. Some malacologists (e.g., Abbot, 1958) consider *C. variabile* to be a subspecies of *C. eburneum,* and it may be closely enough related to *C. eburneum* to harbor *M. adglobosa*, even if the trematode is highly specific for its snail host.

Attempts to infect snails experimentally were unsuccessful. *C. eburneum*, *C. algicola*, *C. litteratum*, and *A. tecta* were kept in aquaria with feces from fish infected with *M. adglobosa, M. globosa, P. neoamericanus,* and *H. mutabile.* All these snails died or remained uninfected. Several *A. tecta* consumed eggs dissected from *H. gulella* and *H. mutabile* then survived for two months in aquaria without developing infections. None that survived to be examined by crushing or isolation produced cercariae of any kind.

Twenty-one of 100 specimens of *A. tecta,* kept in a live-car with heavily infected snappers for two weeks, survived until crushed four weeks later. None was infected. In this case, the snails were observed to assemble on sides of the live-car, just under the waterline. When placed on the bottom of the live-car, they soon crawled back onto the sides again. This would not be conducive to bringing snails and eggs into contact. That none of the snails became infected indicates that *Hamacreadium* species do not have swimming miracidia. When sacrificed, the snappers kept in the live-care proved to be heavily infected with adults of *Hamacreadium,* chiefly *H. mutabile.* Mortality of the *A. tecta* in the live-car was 79%. Possibly, minimal conditions so weakened the snails that all that became infected died. This experiment should be run again when better methods have been developed for keeping *A. tecta* in captivity.

The failure of the attempt to infect these snails experimentally probably was a result of faulty technique. Future attempts should account for the possibility that a maturation period is needed before the trematode eggs become viable. Better aquarium techniques must be developed for keeping the snails in captivity. The present data leave no room for doubt that these snails are indeed the molluscan hosts of these snapper trematodes, and doubtless they can be infected experimentally.

Thalassia beds on the bottom of the Lower Matecumbe Key canal were inhabited by *C. eburneum.* In a collection made during the summer, five out of aproximately 300 snails produced cercariae of *M. adglobosa.* It is interesting that *Lutjanus apodus* caught at this station all contained huge infections of *M. adglobosa*, much heavier than those found in *L. griseus* from any area.

Only one trawling expedition was made to Twin Keys, in late February. The results were disappointing. A day was spent trawling the *Thalassia* beds near the channel mouths on the east side of the bank. Large quantities of dead *Thalassia* and algae repeatedly blocked the trawl. Only about 100 specimens of *C. eburneum* and five of C. *algicola* were collected, and none of them yielded cercariae.

The bank that borders the channel through Twin Keys was too shallow to trawl. The boat was poled across it, and 90 specimens of *C. eburneum* and 10 of *C. algicola* were hand-collected. All of them were free of infection. Shells of *C. variabile* were picked up, but all of them were occupied by hermit crabs. All of the hand-collected snails were crawling on *Thalassia* blades. Every shell found lying on the bottom either was empty or occupied by a hermit crab.

Eight juveniles of *Astraea tecta* were taken in the trawl at Twin Keys, showing that the species is present there. On later trips, areas of coral rubble were observed at the west ends of the channels across the banks. Such areas may well harbor considerable *A. tecta* populations.

Second Intermediate Hosts

Cercariae of two trematodes found in *L. griseus* were identified. *Cerithium eburneum* from Pederson Bank slough and from the canal at Lower Matecumbe produced a cercaria that closely resembled *Cercaria caribbea* XV of Cable (1956). This cercaria was identified by Cable as *Metadena adglobosa.* In the present study it attached to every small fish exposed to it. The life cycle was completed in wormed snappers using *Cyprinodon variegatus* and *Poecilia latipinna* as laboratory second intermediate hosts. Captive snapper also were infected when fed with naturally infected *Lucania parva* and *Opsanus beta.*

An *Astraea tecta americana,* collected in 10 cm of water from the west side of the Lower Matecumbe canal at low tide, when crushed, liberated cercariae and sporocysts of *Hamacreadium gulella.* The cercariae attached to every small fish exposed to them, and the life cycle was completed using *Cyprinodon variegatus, Poecilia latipinna, Lucania parva*, and *Opsanus beta* as second intermediate hosts.

The life cycle of *Hamacreadium gulella* was described by McCoy (1930) in considerable detail. He identified the cercaria of *H. gulella* as Cercaria "B" of Miller (1925), and supplemented Miller's description. The cercaria recovered from *A. tecta* in the present study closely fit his description, except that staining with Harris' Hematoxylin revealed the presence of well-developed caeca not described by McCoy. The behavior of this cercaria also was the same as that of the cercaria of *H. gulella* of McCoy.

Cercarial Behavior

Cercariae of *Metadena adglobosa* began to emerge from naturally infected *C. eburneum* at about 6:30 A.M. Observations were made toward the end of March and the time of emergence may vary seasonally. Emergence proceeded at a fairly constant rate until about 7:40 A.M. One snail that was kept in captivity for nine months was isolated repeatedly and produced between 2000 and 3000 cercariae whenever it was isolated. Productivity varied with the snail and others produced as few as 700 cercariae per day. Some snails produced cercariae more slowly than others and still were releasing a few as late as 9:30 A.M. A drawing of the cercaria of *Metadena adglobosa* appears in Figure 12B.

Almost all the cercariae were positively phototactic when first released, and negatively phototactic by mid-afternoon. They usually swam in straight lines toward or away from the light. Swimming stopped if the water was agitated gently. The cercariae did not appear to be attracted to their intermediate hosts and often would swim right past suitable laboratory hosts although missing only by a cercaria-length or so. These cercariae were short-lived, and nearly all ceased to swim by 8:30 P.M. the day of emergence.

Cercariae often would strike the host and swim away without attaching. Then they would swim in short bursts stopping to extend and flex the body violently in a characteristic fashion. This behavior often led to attachment.

Older cercariae, although still swimming, often had trouble making contact, and bounced off the host repeatedly. No cercaria was observed to penetrate successfully after about 4:00 P.M. In resting position, older cercariae also did not curl the tail so tightly as young individuals, the tail being held in a J-shaped curve at the tip. Such "tired" cercariae were not observed to make successful contact.

If a cercaria blundered into a small fish, it attached itself by the oral sucker, and the tail dropped off at once. The body extended away from the surface of the host and squirmed about actively as penetration progressed.

The cercaria appears to penetrate only the epidermal or perhaps mucous coating of the host's scale. None was observed to penetrate

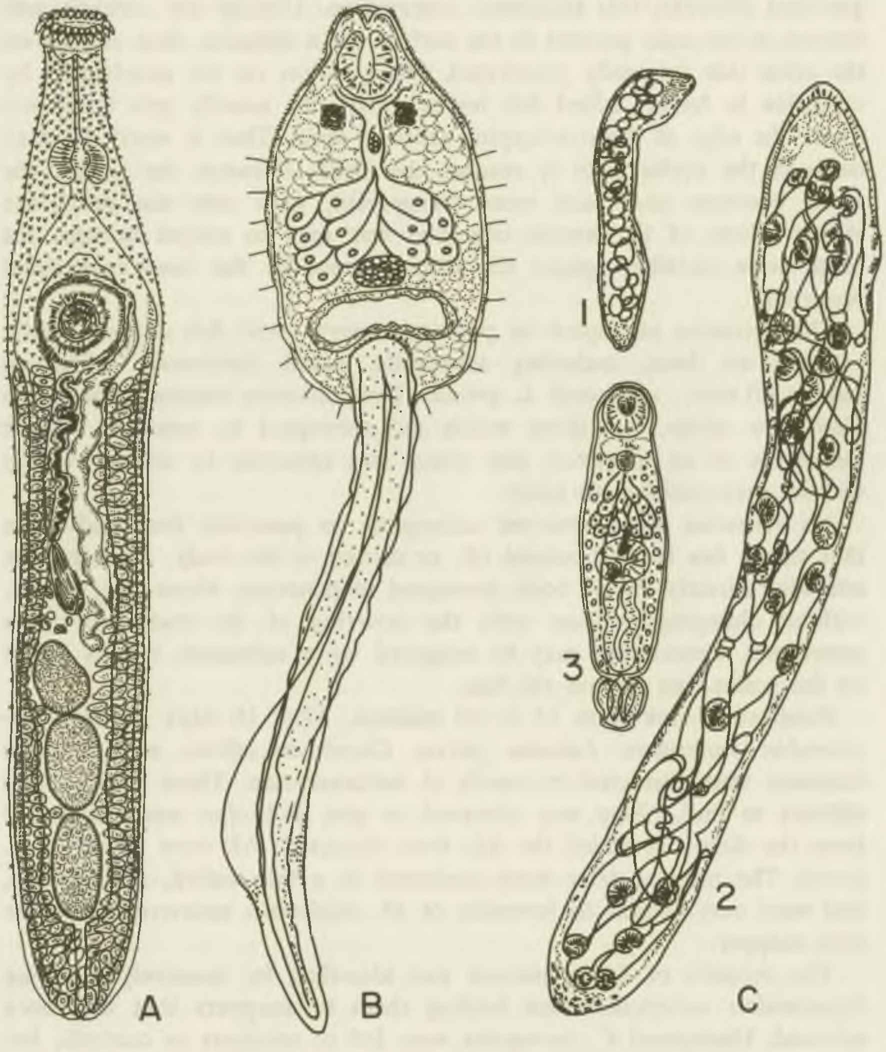

Figure 12. A. *Stephanostomum casum* (Linton, 1910)
B. Cercaria of *Metadena adglobosa.*
C. Larval stages of *Hamacreadium gulella*:
1. Immature sporocyst.
2. Mature sporocyst.
3. Cercaria.

through a scale. Cercariae will attack freshly detached scales of *Cyprinodon* and *Poecilia*; this facilitates observation. Usually the cercaria will burrow in the scale parallel to the surface for a distance, then emerge on the same side originally penetrated. Observations on the penetration by cercariae in freshly killed fish indicate that this usually gets the worm under the edge of the overlapping anterior scale. Then it works forward between the scales until it reaches the body. Between the scales, the worm becomes more and more transparent, until only the ocelli are visible. None of the worms observed was seen to encyst because the ocelli were invisible against the skin pigment by the time encystment occurred.

The cercariae attempted to penetrate every small fish experimentally exposed to them, including atherinids, small *Sphyraena barracuda* (about 50 mm), and small *L. griseus*. Few cercariae became attached to *Gambusia affinis*, but those which did attempted to penetrate. Under the scales of an atherinid, one worm was observed to wander widely without ever reaching the body.

No cercariae were observed attempting to penetrate fins, and those that struck fins either bounced off, or moved to the body. All cercariae attaching directly to the body attempted to penetrate where they struck, without changing position until the covering of the scale had been penetrated. Penetration may be triggered by a substance that is found on the scales, but not on the fins.

Penetration took from 15 to 30 minutes. After 10 days, exposed *Cyprinodon variegatus, Lucania parva, Gambusia affinis,* and *Poecilea latipinna* were dissected in search of metacercariae. These proved very difficult to find. None was observed *in situ,* but nine were recovered from the dishes in which the fish were dissected. All were found in *L. parva.* The metacercariae were contained in a thin-walled, flexible cyst, and were very similar to juveniles of *M. adglobosa* recovered from the gray snapper.

The cercaria of *M. adglobosa* was identified by massively exposing *Cyprinodon variegatus*, then feeding them to snappers that had been wormed. Unexposed *C. variegatus* were fed to snappers as controls, but they produced no infection. *C. variegatus* exposed to large numbers of cercariae in a small container produced infections of six to more than 30 juvenile *M. adglobosa* when fed to wormed snappers. The development time required for metacercariae to become infective was not determined. All experimentally exposed intermediate hosts were kept at least two weeks before being fed to the wormed snappers.

Cercariae of *Hamacreadium gulella* were obtained from *Astraea tecta americana* by crushing the snail, but nothing was learned about emergence time. Although no direct count was made, one snail contained at least 1000 cercariae sufficiently mature to attempt penetration.

The cercaria of *H. gulella* attaches to the substrate by its short sucker-like tail and extends the body, waving about with the water movements. When a small fish touches the oral sucker the worm almost always attaches, usually to the fish's anal or pelvic fins. Then it actively crawls to the fin root and may penetrate there. Some crawl about the body for a time, then force their way under the edge of a scale and worm forward to the body. Encystment was not observed in those entering under scales because they disappeared from sight before it occurred. The cercaria and sporocyst of *Hamacreadium gulella* are illustrated in Figure 12C.

A few cercariae penetrated the fins of fishes. They attached by the oral sucker, extended the body at an angle of 90°, and squirmed about actively. Inside the fin membrane, they turned and burrowed parallel to the surface for three or four cercaria-lengths, then gradually formed thin-walled cysts. Development was not followed because penetration was observed in freshly killed fish. Cercariae required about 10 minutes for penetration of fins, while 20 minutes or more were required for penetration of the fish's body.

Only small numbers of the cercariae of *H. mutabile* were recovered from a single snail, most of which were preserved for study. A small fish was exposed to the remainder, but an attempt at infecting a previously wormed snapper was thwarted by the premature death of this single experimental host.

Most cercariae that penetrate fins shed their tails as they drew themselves completely into the fin membrane. A few shed the tail inside the membrane but did not include it inside the cyst.

When crawling, the cercariae of *H. mutabile* does not use the tail for attachment. It moves inchworm fashion, using the oral and ventral suckers and feeling about actively with the anterior end.

Cercarial behavior is an important part of trematode ecology because it is intimately bound with adaption to a habitat. In this study, the nature of cercarial behavior was only briefly investigated. A more thorough examination of the subject would contribute much to the knowledge of the ecology of marine trematodes.

Summary

Gray snappers were collected from eight stations comprising four habitats over a nine-month period and were examined for intestinal trematodes. The incidence of each trematode was calculated for each habitat at each time of year.

Snails were collected in the vicinity of the various stations and examined for larval trematode infections. Special attention was given to snails known to harbor snapper trematodes. When possible, some index of infection levels and snail populations was derived.

The habitat in which fish were caught was more important in determining the nature of their trematode populations than fish size, sex, or season of the year. The reasons for this probably involved the distribution of intermediate hosts, and most especially the snail hosts.

Metadena adglobosa Manter, 1947, was most common in gray snappers from shallow Florida Bay *Thalassia* beds, where its snail host, *Cerithium eburneum* (Bruguiere), was most plentiful. Snappers in this area were small, and as a result *Metadena adglobosa* were found more often in small fish than large fish, when all collections were considered. *M. adglobosa* was usually found in the pyloric caeca of *L. griseus.*

Metadena globosa (Linton, 1910) was most common at the inshore stations. Its distribution suggests that its snail host is different from that of *M. adglobosa. M. globosa* was remarkable for the low incidence of juvenile worms.

Metadena obscura sp. n. was described from the pyloric caeca and intestine of *L. griseus.* Although superficially similar to *M. adglobosa*, it differs in a number of characters, the most important of which are the enlarged spines of the genital sac.

Paracryptogonimus neoamericanus Siddiqi and Cable, 1960, was most common in fish from the inshore stations. It was usually found in the

intestine of *L. griseus*, but occasionally was in the pyloric caeca. Few juveniles were found. In this and its distribution, it resembled *Metadena globosa.*

Hamacreadium mutabile Linton, 1910, also was most common at the inshore stations. Large populations of the snail host, *Astraea tecta americana* (Solander), were found near the stations having the highest incidences of *H. mutabile.* One snail infected with *H. mutabile* was collected.

Hamacreadium gulella Linton, 1910, was found only rarely until late October, when it began to appear regularly in inshore fish. A possible explanation is that it was brought into the area by another definitive host. Four *Astraea tecta americana* that were infected with *H. gulella* were collected.

Helicometrina nimia Linton, 1910, was most common in snappers from the offshore stations. It was very rare at other stations. *H. nimia* was not specific for snappers, and was reported from many nonlutjanid species. The gray snapper was not an important definitive host.

Helicometra execta Linton, 1910, was found in the gray snapper only rarely, and only at the offshore stations. It is probably an accidental parasite of *L. griseus*, and largely dependent on other hosts. It may be unable to complete its life cycle in *L. griseus.* Its presence in the gray snapper is a new host record.

Stephanostomum casum (Linton, 1910) was found at all stations in about the same percentage of gray snappers, suggesting that its intermediate hosts are widely distributed. *Nassarius albus* (Say) or *N. vibex* (Say) may be the snail host. *Nassarius* species are hosts to other *Stephanostomum* species. Both *N. albus* and *N. vibex* are widely distributed in habitats of the gray snapper.

The data indicate that seasonal changes in parasite populations of *L. griseus* near Lower Matecumbe Key were a function of spawning migrations and cold weather movements.

Many parasites probably appear in unusual habitats through movements of the host. Migrating fish carry parasites into new habitats. In a new habitat the original parasites are gradually lost, being replaced by species characteristic of the new environment.

Examination of a collection of 178 fish of 41 species other than *L. griseus* indicates that the trematodes of *L. griseus* except *Helicometrina nimia* and *Helicometra execta* are family specific for the Lutjanids. *H. nimia* and *H. execta* have been reported from many families, and are unimportant in L. *griseus.*

Abstract

Gray snappers were collected from four different habitats and examined for trematodes. The incidence of each trematode was calculated for each habitat during each season. Intermediate hosts of the trematodes were also collected.

It was found that the habitat in which gray snappers reside is more important than their size, sex, or the season of the year in determining the nature of their trematode populations. This may be the result of the intermediate host distribution being regulated by the habitat.

Seasonal changes in trematode populations result from fish movements, such as spawning migrations or movements in response to cold water. The differences between the trematode populations of large and small snappers probably are a function of their residing in different habitats and eating different organisms. The sex of gray snappers has no discernable effect on their trematode populations.

Metadena obscura sp. n. (Cryptogonimidae) was found in the pyloric caeca and intestine of *Lutjanus griseus* (Linnaeus).

Nine species of trematodes were found in the intestine and pyloric caeca of *Lutjanus griseus* near Lower Matecumbe Key: *Metadena globosa, M. adglobosa, M. obscura, Paracryptogonimus neoamericanus, Hamacreadium mutabile, H. gulella, Helicometrina nimia, Helicometra execta,* and *Stephanostomum casum.*

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