Reproductive biology of gray snapper (*Lutjanus griseus*), with notes on spawning for other Western Atlantic snappers (Lutjanidae)

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SEDAR51-RD-11

October 2016

Reproductive Biology of the Gray Snapper (*Lutjanus griseus*), with Notes on Spawning for other Western Atlantic Snappers (Lutjanidae)

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DOMEIER, M.L., C. KOENIG and F. COLEMAN. 1996. Reproductive biology of the gray snapper (*Lutjanus griseus*), with notes on spawning for other Western Atlantic snappers (Lutjanidae) [*Biologia reproductiva del pargo prieto* (Lutjanus griseus), *con notas sobre el desove de otros pargos (Lutjanidae) del Atlantico Occidental*], p. 189-201. *In* F. Arreguín-Sánchez, J.L. Munro, M.C. Balgos and D. Pauly (eds.) Biology and culture of tropical groupers and snappers. ICLARM Conf. Proc. 48, 449 p.

Abstract

Specimens of *Lutjanus griseus* were collected from four sites off Key West, Florida, from May 1991 to January 1992. Two sites were in shallow inshore waters and two were offshore reef sites. Gonads from all specimens were macroscopically examined, and a subset was examined microscopically. A few sexually active males were found as early as late March, but females were not observed with active ovaries until mid-June. Spawning peaked in July and August and tapered off in September. The minimum size at maturity was found to be 182 mm SL for males and 198 mm SL for females. Examination of otoliths from newly settled *L. griseus* revealed that actual spawning was occurring during the new moon phases. Adult fish were observed to migrate from inshore to offshore waters during the peak of the spawning season. Observations of other species of *Lutjanus* suggest that some spawn in annual aggregations at specific sites, while others have protracted spawning seasons with no apparent spawning migration.

Resumen

Especímenes de Lutjanus griseus *fueron colectados de cuatro sitios fuera de Key West, Florida, de Mayo de 1991 a Enero de 1992. Dos sitios fueron en aguas interiores de baja profundidad y dos fueron en arrecifes de aguas marinas. Las gónadas de todos los peces fueron examinadas macroscopicamente y una submuestra fué examinada microscópicamente. Unos pocos machos sexualmente activos fueron encontrados al inicio y al final de Marzo, pero no fueron observadas hembras con ovarios activos hasta*

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la mitad de Junio. El desove presentó su máximo en Julio y Agosto, culminando en Septiembre. El tamaño mínimo de madurez fué de 182 mm de longitud estandar (SL) para machos y 198 mm SL para hembras. El exámen de los otolitos de L. griseus *recientemente reclutados reveló que el desove actual ocurrió durante las fases de luna nueva. Se observó que los peces adultos presentan una migración de aguas costeras a aguas marinas durante el pico de la época de desove. La observación de otras especies de* Lutjanus *sugiere que algunas desovan en agregaciones anuales en sitios específicos, mientras que otros presentan una época de desove protráctil sin migración aparente para desovar.*

Introduction

Snappers are a major component of the commercial, sport and subsistence fisheries in the tropical Western Atlantic and Gulf of Mexico. Although gray snapper (*Lutjanus griseus*) (Domeier and Clarke, unpubl.), red snapper (*L. campechanus*) (Arnold et al. 1978; Minton et al. 1983) (see also Collins et al., this vol.), lane snapper (*L. synagris*) (Domeier and Clarke 1992; Clarke et al. in prep.) (see also Rivera-Arriaga et al., this vol.), yellowtail snapper (*L. chrysurus*) (Soletchnik et al. 1989; Domeier and Clarke 1992; Clarke et al. in prep), and mutton snapper (*L. analis*) (Clarke et al. in prep) have been spawned in captivity, little is known of the reproductive biology and spawning habits of this group (see also Manickchand-Heileman and Philipp, this vol.). Details of reproduction and early life history are critical to effective fisheries management. Here we present new data regarding the reproductive biology of the gray snapper and report observations on the spawning habits of several other species of Western Atlantic snapper.

The gray snapper is of considerable commercial importance in Florida, where hook-and-line landings for 1978 amounted to 337 t worth an estimated US $426 000 (Bortone and Williams 1986). Catches dropped to 230 t by 1990 but the economic value remained high at $731 000 (preliminary data: O'Hop, pers. comm.). The economic value of the sport fishery probably far exceeds that of the commercial fishery (Starck 1971). Peak commercial landings occur during the summer months in Florida, with the Florida Keys taking 25% of the annual catch in July alone (Burton 1992). This peak of commercial activity coincides with the peak of gray snapper spawning activity reported by Jordan and Evermann (1923) to occur in July and August, and Starck (1971) (working in south Florida) from June to September with peak spawning in June and July.

Actual spawning has not been observed but the evidence suggests that it takes place at offshore reefs and wrecks (Springer and Woodburn 1960; Starck 1971). Starck (1971) suggested that spawning periods followed a lunar cycle, occurring around the full moon. Eggs and larvae are planktonic (Barans and Powles 1977). Larvae remain in the plankton for three weeks (Domeier and Clarke, unpubl.) and settle as early juveniles in estuaries (Bortone and Williams 1986), primarily in shallow seagrass beds in Florida (Starck 1971). Gray snapper larvae have been described from laboratory-reared individuals (Richards and Saksena 1980; Clarke et al. in prep.).

Starck's (1971) comprehensive study of gray snapper covered many aspects of the life history. However, important details regarding spawning were left unanswered. This study investigates spawning season, spawning periodicity, spawning behavior, and sexual pattern of gray snapper. Data were also collected regarding certain aspects of early juvenile biology.

Materials and Methods

Site selections

Gray snapper were collected from four sites near Key West, Florida, two shallow inshore sites and two offshore reef sites representative of the wide range of habitat types known for this species. Specific sites were chosen after visually identifying areas (using SCUBA) with large numbers of gray snapper. The following are site descriptions.

Inshore Site 1 (IS1) - A large patch reef (20 m long, 7 m wide, and 3 m high in a depth of 5 m) consisting of living boulder, brain, and star coral, surrounded by sand and seagrass beds. Visibility varied greatly from poor to good (2-12 m).

Inshore Site 2 (IS2) - Boca Grande Channel between Boca Grande Keys (west of Key West in a depth of 6 m) with soft corals, sponges and one small isolated coral head. This site was subject to strong tidal currents restricting sampling to slack tides. Visibility was poor (1-6 m).

Offshore Site 1 (OS1) - A large area of reef with overhanging ledges and sand channels at a depth of 9 m, adjacent to a sloping dropoff into deepwater. The top of the reef was covered with soft corals. Visibility ranged from 10 to 20 m. Although this site produced relatively few gray snappers during initial surveys, it was selected because it was known by fishers to be a spawning ground for these fish.

Offshore Site 2 (OS2) - A large area of spur and groove reef, locally referred to as Boca Grande Bar at a depth of 15 m). Visibility ranged from 10 to 30 m.

Miscellaneous Sites - The data set was supplemented by specimens opportunistically collected at a variety of locations in southern and western Florida. Many of these collections were made by fishers unwilling to reveal the exact location of the site.

Sampling of adults

Ten gray snappers were collected by spearfishing at each of the four sites at regular intervals between 14 May 1991 and 12 September 1991, the extent of the spawning season. Collections were made at one-week intervals during the peak of spawning activity, and at two-week intervals at all other times. These sites were periodically sampled outside the spawning season until January 1992. All specimens were sexed, measured to the nearest mm standard length (SL), and gonads were removed for subsequent analysis. Most of the specimens were also weighed to the nearest gram. A subset of fish were not weighed due to faulty equipment; weights were calculated for these specimens using a derived length (cm)-weight (g) relationship (weight= $0.0281(SL^{2.998})$; n=1 026).

The large variability in visibility between sites and between sampling periods precluded reliable density comparisons between sites and sampling periods. Densities of gray snapper changed over time on a magnitude that could not be explained by repeated sampling.

Gonad analysis

Gonads removed in the field were macroscopically examined to determine sex, if possible, and either placed on ice for transport to the laboratory, or placed in Davidson's solution for subsequent histological work (n=122). In the laboratory, gonads were weighed to the nearest 0.1 g and frozen.

Squashes of thawed gonad tissue were microscopically examined to determine sex, identify stages of oocyte development (Moe 1969), range of oocyte size per stage, and presence or absence of atresia. Quick hematoxylin and eosin stains of new squashes were made (see Link (1980)) when sex could not be determined from unstained squashes.

Histological preparations of gonads were made following the procedures of Moe (1969) to determine gonadal development. Preserved tissue was sectioned at 10 m, mounted on slides, and stained with hematoxylin and eosin. Such preparations were required for identification of pre- or post-spawning individuals and early atritic stages. Gonads were evaluated histologically for the following:

1. Minimum size of sexual maturation and sexual differentiation;
2. Sexual pattern;
3. Description of stages of gonadal maturation; and
4. Timing of annual spawning activity.

Spawning season and periodicity

The extent and peaks of spawning activity were determined by calculating a gonosomatic index (GSI) for all specimens, and plotting them against capture dates. Spawning dates were also back-calculated by counting daily increments of otoliths from juvenile gray snapper (n=68) collected from seagrass beds by otter trawl, benthic scrape and roller frame trawl. Collections were made in 1992 between late July and mid-September. The specimens were measured to the nearest mm (SL) and either frozen or fixed in 95% ethanol to ensure preservation of otoliths. Otoliths were subsequently removed and stored in 95% ethanol. Lapilli were ground and polished, then viewed under oil immersion at 1000x. Daily increment counts (following Brothers and McFarland 1981) were made using a video-enhanced microscope.

Daily growth increments of juvenile otoliths were validated by comparing our counts with the known age of juveniles reared from the egg by Richards and Saksena (1980). A subset of 10 otoliths were read and counts confirmed by Dr. Ed Brothers.

Spawning behavior

Many dive trips were made during the summers of 1991 and 1992 in an attempt to observe courtship and spawning. Dives were made between first light and dark. These dives were made primarily during the days before and after the full moon, since Starck (1971) stated that gray snapper spawn at this time.

Observations on spawning behavior of several other Western Atlantic snappers were opportunistically made by one of us (MLD). Although this information is not quantitative, it is a valuable contribution to our knowledge of these little known species. Observations on *L. analis*, *L. synagris*, *L. chrysurus*, *L. jocu*, *L. apodus*, and *L. cyanopterus* were made on SCUBA, and additional information was gained through collecting (hook and line, spearfishing, fish trapping) and through interviewing fishers.

Results

Gonad analysis

Gonad developmental stages of gray snapper were described by histological examination of gonads. All oocyte and spermatocyte stages follow those described by Moe (1969).

- Sexually undifferentiated - Gonad is small, compact and contains undifferentiated stroma. No oocytes, seminiferous tubules, spermatogenic tissue or lumen are visible. All gonads have attached fat.

- Immature female - Gonads are small and compact with a distinct lumen. The gonads contain much stroma and scattered small previtellogenic oocytes, or many small previtellogenic oocytes. The ovarian wall is generally thin. All gonads have attached fat.
- Immature male - Gonads are small and compact with no lumen. The gonads contain developing seminiferous tubules and scattered early stages of spermatogenesis, interspersed with stroma.
- Mature inactive female - In addition to a lumen and previtellogenic oocytes, the ovaries contain a number of stage 3 oocytes (early vitellogenic) and/or indications of prior spawning. Prior spawning is indicated by a thickened ovarian wall, degenerating oocytes, or internal muscle bundles that contract the expanded ovary after spawning.
- Mature inactive male - The testes predominantly consist of the early stages of spermatogenesis, which are particularly evident at the gonad margins. A few scattered cysts of later spermatogenic stages may be present.
- Mature active female - Ovaries have a lumen and a mixture of previtellogenic oocytes and vitellogenic oocytes of stages 3,4 and 5 in varying proportions. The diameter of the gonad is relatively thin and stretched.
- Mature active male - The testes consist predominantly of later stages of spermatogenesis (stage 2 spermatocytes, spermatocids and spermatozoa). The gonad is enlarged and may contain large areas of sperm. If spawning has occurred, empty lobules may be visible and the testes will appear to be disrupted in areas.

Gonads were generally undifferentiated in fish smaller than 140 mm SL. The smallest sexually differentiated male was 120 mm SL, and the smallest sexually differentiated female was 140 mm SL. The size of first maturity was 182 mm SL for males and 198 mm SL for females. Although small sample size precluded separate analyses of maturation by sex, we calculated a combined maturity curve for both sexes for size classes 100-300 mm SL (n=80) because both sexes mature at about the same size. Ninety percent of gray snappers mature by the time they reach 200 mm SL and 100% are mature at 240 mm SL.

All gray snapper gonads have stored fat attached to the gonads during the nonreproductive season; during the spawning season sexually mature fish lose this fat as it is mobilized for gametogenesis and spawning.

Sexual pattern

Gray snapper are clearly gonochorists, based on the similarity in size of sexual maturation of the sexes, the overlap between the sexes in size-frequency distributions, and the absence of individuals undergoing sexual transition. Testes had a typical gonochore structure lacking the ovarian-type lumen characteristic of many hermaphroditic (protogynous) species. One adult male exhibited a few, very small previtellogenic oocytes within the testes, but this characteristic is found in many gonochoristic species (Sadovy and Shapiro 1987), and is assumed to be unrelated to sexual pattern in the absence of any other indications of sex change.

The sex ratio of gray snapper was slightly skewed towards females at 1.2 females:1 male (n=889, size range 145-497 mm). A subset of all fish greater than 350 mm also had a sex ratio of 1.2:1.

Spawning season

Spawning began in late May and continued into early September (Fig. 1; n=664). A few ripe males were found as early as late May, but most males were ripe by late June. Females were never collected running ripe, although microscopic examination of ovaries revealed a few hydrated eggs in several specimens during the months of July and August. Clear peaks in GSI appear to be related to the lunar cycle for fish collected at the offshore sites. The first peak coincides with the new moon in mid-June, a second peak occurs on the following full moon late in June, and a third peak with the new moon in July. Each of these three peaks is successively larger than the previous one. The fourth and largest peak occurs on the last quarter moon in early August. The mean GSI of inshore specimens are lower than those of offshore specimens collected at the same time and do not show any pronounced peaks until the last quarter moon in August, although GSI gradually increases from June through August.

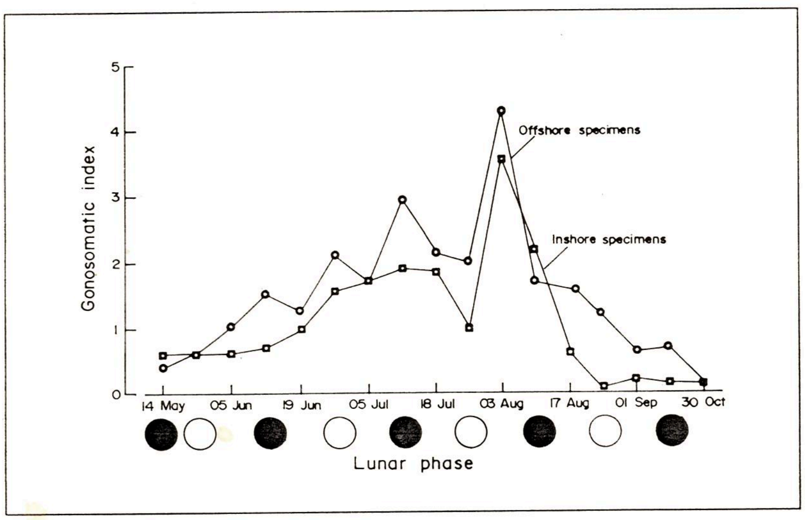

Fig. 1. Mean gonosomatic index (GSI) of *Lutjanus griseus* in inshore and offshore waters of Florida. [*Indice gonadosomático medio (GSI) de* Lutjanus griseus *en aguas interiores y aguas marinas de Florida.*]

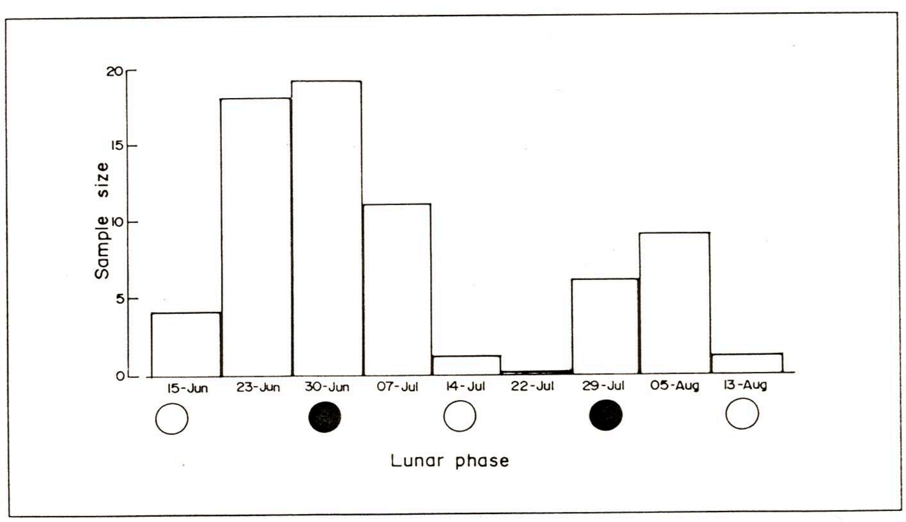

Fig. 2. Back-calculated spawning dates of *Lutjanus griseus* relative to date and lunar phases. [*Fechas de desove retrocalculadas de* Lutjanus griseus *asociada a fechas y fases lunares.*]

Spawning dates back-calculated by reading daily increments of juvenile gray snapper otoliths (Fig. 2) corroborated spawning periods delimited by GSIs. Spawning takes place in June, July and August, with peaks of spawning around the new moon and a decline in spawning activity around the full moon of each month. The relatively small number of samples from spawnings in July and August is due to decreased sampling effort. Since sampling was discontinued in mid-September, representative specimens from the new moon spawning in August were not obtained.

Spawning migration

During the course of this study, movement of adult gray snapper from inshore to offshore sites was observed. Initially, large fish were especially numerous at IS2 while very few gray snappers were present at OS1. As the spawning season progressed large specimens disappeared from the inshore sites and began to appear at the offshore sites. Movement of gray snappers from inshore areas to offshore areas became clear as the time required to attain our weekly samples increased at the inshore sites and decreased at the offshore sites. Fig. 3 plots the mean standard length for each sampling period at inshore and offshore sites (two inshore sites were combined and two offshore sites were combined; n=664). Prior to the onset of the spawning season, the mean SL of inshore samples was actually higher than that of offshore samples; as the spawning season progressed the mean standard length of the samples increased at offshore sites. At the end of the spawning season, the means are again similar. This

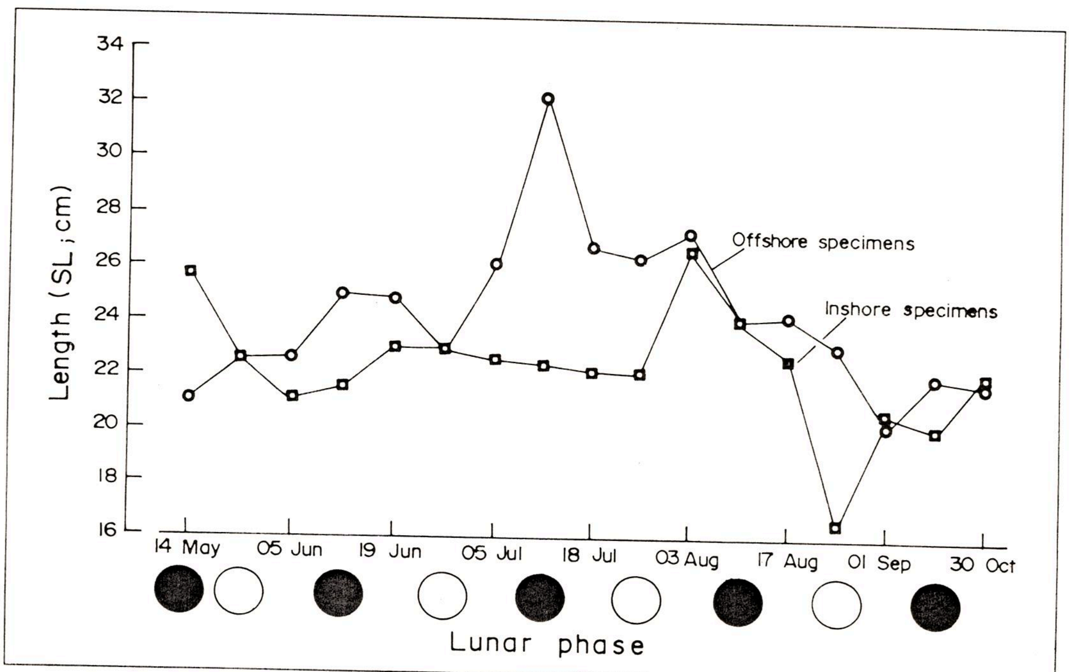

Fig. 3. Average standard length of *Lutjanus griseus* captured in inshore and offshore waters in Florida relative to date and lunar phases. [***Longitud estándar promedio de* Lutjanus griseus *capturado en aguas interiores y aguas marinas en Florida, asociada a fechas y fases lunares.***]

supports our observation that many adult gray snappers migrate to offshore reefs to spawn.

Despite repeated diving, actual spawning behavior was never observed.

Reproductive strategies of other western Atlantic snappers

As discussed in the methods section, observations of spawning strategies for several Western Atlantic lutjanids were made over the last several years (by MLD). Each species for which we have information to add is reviewed and updated relevant to its specific reproductive biology.

Mutton Snapper (*Lutjanus analis*)

Adult *L. analis* are found in a variety of habitats, from shallow grass beds and patch reefs to deep barrier reefs. They are a solitary fish, rarely found in groups or schools outside the spawning season. However, during the spawning season, they form dramatic spawning aggregations that may persist for several weeks. They exhibit high site-fidelity, spawning at exactly the same location and on the same days of the lunar calendar year after year. Aggregations may form and dissipate at a particular site during two consecutive months of the late spring. Three such aggregations were observed: one at Riley's Hump in the Dry Tortugas near the time of the full moon in May and June; one off West Caicos, Turks and Caicos, during the full moons of April and May; and the third off English Cay, Belize, between the full and last quarter moons of April and May. All three sites are located on the edge of a steep drop-off.

Many mutton snappers were collected by spearfishing and a single female with expressable hydrated eggs was collected at dusk near Riley's Hump, suggesting that spawning occurs near this time. Several evening dives made at West Caicos and the Dry Tortugas to observe spawning were unsuccessful. Thousands of snappers were observed milling around the bottom and in the water column but none spawned. It may be that mutton snapper spawn after dark.

Several fish were collected by hook-and-line at West Caicos and brought back to the laboratory where they were induced to spawn via hormone injection, confirming that the fish observed in the aggregation were in spawning condition.

Dog Snapper (*Lutjanus jocu*)

Dog snappers are solitary reef fish that appear to occupy a home range; individual specimens of dog snappers inhabited the same ledge or crevice of a reef over extended periods of time. Based on a single observation of a spawning aggregation off English Cay, Belize, on 19 July 1992 (between full and last quarter moon), it appears that dog snappers spawn in large aggregations. The site consisted of a spur of reef that began in 5 m of water and sloped down to over 35 m.

During two dives at this site in the early afternoon, several large groups of fish, totalling over a thousand individuals, were observed schooling on the bottom and occasionally forming tight balls that rose up into the water column approaching the surface. Ten fish were collected by spear, 6 males and 4 females. All the males were running ripe and the females had large, well developed ovaries but no observable hydrated eggs. The lack of a laboratory and a means of refrigeration precluded a more detailed study of the ovaries. Experience in collecting ovaries and inducing spawning in other species of snapper allow the conclusion that females present in this aggregation were ready to spawn.

Cubera Snapper (*Lutjanus cyanopterus*)

This is the largest species of Western Atlantic snapper, attaining weights in excess of 57 kg (Robins et al. 1986). Despite its size, it is perhaps the least studied species of this region. It is one of the few snappers that enters water that is nearly fresh (e.g., the intra-coastal waterway on the east coast of Costa Rica). Cubera snappers are also found on both shallow and deep reefs, and in mangroves.

According to anecdotal accounts by fishers and divers, this species also spawns in aggregations. Three aggregation sites have been found by fishers off the coast of south Florida. Two of these sites (Key West and Dry Tortugas) are wrecks located in 67-85 m of water. The third is a deep reef in the Miami area. D. DeMaria (pers. comm.) has observed and collected Cubera snapper from these wrecks during spawning aggregations. The aggregations of Cubera snapper in Florida have far fewer fish, less than 100 to a few hundred, than aggregations of other snapper species reported here.

Similar aggregations occur in Belize off Buttonwood Cay and Cay Bokel (Cabral, pers. comm.). The Belizean sites are in much shallower water (10-30 m) than the Florida sites and may contain greater numbers of individuals. Both the Florida and Belizean aggregations occur during the months of June and July (full moon to last quarter).

Yellowtail Snapper (*Lutjanus ocyurus*)

This is a small planktophagous species of *Lutjanus* (=*Ocyurus*, see Domeier and Clarke 1992), abundant throughout the tropical western Atlantic. Although juvenile yellowtail snapper can be found over sandy bottom inshore, adults occur primarily over coral reefs. This species can be found feeding well off the bottom in large schools, or seen swimming over the reef as a solitary fish.

Extensive year-round collecting of this species shows a protracted spawning season lasting from March through September in south Florida. Other investigators have found this species to have a protracted, if not year-round spawning season in other parts of the Caribbean (Piedra 1965; Munro et al. 1973; Thompson and Munro 1974/1983; Erdman 1976; Soletchnik et al. 1989).

Yellowtail snappers do not exhibit any migration or aggregation related to spawning.

Lane Snapper (*Lutjanus synagris*)

This is a small, reef-dwelling species that occurs in tight schools close to the bottom.

Extensive collecting of this species at all times of the year reveals a similar spawning pattern to that of the *L. chrysurus* snapper. In south Florida, *L. synagris* have been found in spawning condition from March through August. Other investigators have found this species to have a protracted and/or continuous spawning season (Rodriguez-Pino 1962; Erdman 1976; Reshetnikov and Claro 1976; Erhardt 1977).

Lane snappers show an interesting pattern of distribution in that they can be common at a particular location year after year, but can be rare at other locations in the vicinity. This suggests that individual schools of lane snappers have strict home ranges and do not migrate or aggregate for the purpose of spawning.

Discussion

Our study of the gray snapper was consistent with previous work for first size of maturity (Croker 1962) and time of spawning season (Jordan and Evermann 1922; Starck and Schroeder 1971). Our finding that they spawn around the new moon is contrary to the findings of Starck and Schroeder (1971) who reported gray snapper spawning on the full moon. Their conclusions were based upon the presence of spent ovaries in specimens collected shortly after a full moon in early September. Our study suggests that these fish had spawned a few weeks prior to their collection and were finished spawning for the year.

Many dives were made at all times of the daylight hours during the spawning season to observe spawning. Although dives were concentrated around the full moon due to Starck's (1971) report of spawning activity at this time, some diving was accomplished at all phases of the lunar calendar. Our failure to witness spawning may be a result of our concentrated effort around the full moon, or it may suggest that gray snappers spawn at night. The lack of specimens with hydrated eggs supports the suggestion that they spawn at night, since all specimens were collected during the day.

Grimes (1987) concluded that snappers exhibit two basic spawning strategies that are directly related to whether the population occurs over a continental or insular habitat. Continental populations exhibit extended summer spawning seasons, while insular species reproduce year-round with spring and fall peaks (Grimes 1987). This study found a new snapper spawning strategy, the spawning aggregation, that occurs over both insular and continental habitats. It is true that habitat differences can cause variation of occurrence and length of spawning season between populations of the same species, but we suggest that spawning strategies are species specific rather than habitat dependent.

Two spawning strategies seem evident among Western Atlantic lutjanids:

1. Schooling species that have protracted spawning seasons and do not migrate or aggregate for the purposes of spawning (e.g., *L. chrysurus* (Piedra 1965; Munro et al. 1973; Thompson and Munro 1974/1983; Erdman 1976; Soletchnik et al. 1989), *L. synagris* (Rodriguez-Pino 1962; Erdman 1976; Reshetnikov and Claro 1976; Erhardt 1977), *L. apodus* (Munro et al. 1973; Thompson and Munro 1974/1983).
2. Solitary species that migrate and aggregate for the purpose of spawning over a very short time period (i.e., a few days or weeks) (e.g., *L. analis*, *L. jocu*, *L. cyanopterus*).

Mahogany snapper (*L. mahogani*) may be found to be a Strategy 1 spawner due to its similarity in behavior and habitat utilization to *L. synagris*.

Spawning aggregations have been well documented for many species of grouper (Serranidae) (see Sadovy et al., in press), but have not been previously reported for lutjanids. The nature of snapper spawning aggregations is extremely similar to that of groupers. In fact, many sites that are used by groupers for spawning are used by snappers but at different times of the year. For example, the Belize site used by mutton snapper is also used by Nassau grouper (*Epinephelus striatus*), yellowfin grouper (*M. venosum*), and Jewfish (*E. itajara*) (Cabral, pers. comm.). As with groupers, snappers begin to arrive at the spawning site approximately one week prior to the peak spawning activity (deduced from peak density of fish at site) and linger at the site after spawning for another week. Also similar to groupers, an aggregation may occur during two consecutive months of the year, although one month usually has a greater number of fish participating in the aggregation.

In both the Lutjanidae and the Serranidae it is the larger species that aggregate to spawn. These large predators require more spatial and nutritional resources to survive than smaller fish. Increased space between individuals creates difficulty in finding mates during the spawning season. Formation of annual spawning aggregations at permanent sites provides an efficient mechanism for overcoming this problem. The brevity of the spawning may limit periods of intense cospecific competition for food.

Smaller species of lutjanids require fewer resources per individual and can form schools year-round. Membership in a school enhances reproductive success. Schooling species are limited in the duration of the spawning season only by the availability of food and the physiological constraints of the eggs and larvae.

The gray snapper does not fit well into either of the described spawning strategies. This species has adapted to a variety of habitats, including inshore areas that can vary widely in temperature and salinity. It is possible that the adult stage has evolved to tolerate a wide range of physical conditions, but the larval stage remains intolerant. The spawning migration of this species from inshore to offshore would thereby increase the survival of the offspring. This scenario would make the *L. griseus* snapper a modified Strategy 1 spawner. Another possibility is that the intermediate size of this species has allowed an intermediate spawning strategy. The *L. apodus* is a closely related species that needs further study; it too may exhibit an intermediate spawning strategy.

Spawning behavior has only been reported for two species of snappers worldwide: *L. synagris* which were observed to spawn at dusk in Florida (Wicklund 1969) and *L. kasmira* which were reported to spawn at night in captivity (Suzuki and Hioki 1979). Both species were group spawners. Although *L. chrysurus* (Soletchnik et al. 1989) and *L. campechanus* (Arnold et al. 1978) have been spawned in captivity without the aid of hormone injection, the time of spawning and spawning behavior were not reported. Davis and West (1993) report that *L. vittus* (Australia) spawns during the early afternoon. This conclusion was based on the presence of hydrated eggs between 1100 and 1500 hours, and a peak in the presence of early post-ovulatory follicles by 1700 hours. *Lutjanus vittus* is probably an unusual example of daytime spawning among a group of primarily dusk or nocturnal spawners.

Both snapper species observed spawning are group- rather than pair-spawners (Wicklund 1969; Suzuki and Hioki 1979). The behavior of *L. jocu* within a spawning aggregation reported here may also indicate group spawning. Some species of aggregating groupers are pair spawners (i.e., *Mycteroperca tigris*: Sadovy et al., in press) while at least one species is a group spawner (*E. striatus*: Colin 1992). It is possible that future studies will find that the lutjanids also have representative group and pair spawning species. The presence of group spawning among lutjanids may also play a role in the formation of spawning aggregations. It is not known whether or not group spawning species can successfully reproduce when populations are severely depleted.

Spawning aggregations of both lutjanids and serranids are often fished out of existence upon discovery by fishers. Although the United States is taking measures to protect the mutton snapper at Riley's Hump, Florida, the annual aggregation is already a tiny fraction of what it once was. Proactive rather than reactive management is called for where aggregation sites exist. As we have seen, specific aggregation sites are often used by more than one species of fish; protecting an aggregation site would serve to protect multiple species in many cases.

Acknowledgements

Captain Don DeMaria and Carl Cabral provided valuable information regarding the locations and habits of snappers that made this study possible. Chris Ninnis and the Fisheries Department of the Turks and Caicos provided their assistance and resources while studying mutton snapper at West Caicos. Grant money from the Florida

Department of Natural Resources and the Caribbean Marine Research Center supported various aspects of this research. Scott Harris provided valuable technical support regarding the manipulation of the large database.

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