Temporal and spatial dynamics of spawning, settlement, and growth of gray snapper (*Lutjanus griseus*) from the West Florida shelf as determined from otolith microstructures

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Abstract–The goal of our study was to understand the spatial and temporal variation in spawning and settlement of gray snapper (*Lutjanus griseus*) along the West Florida shelf (WFS). Juvenile gray snapper were collected over two consecutive years from seagrass meadows with a benthic scrape and otter trawl. Spawning, settlement, and growth patterns were compared across three sampling regions (Panhandle, Big bend, and Southwest) by using otolith microstructure. Histology of adult gonads was also used for an independent estimate of spawning time. Daily growth increments were visible in the lapilli of snapper 11–150 mm standard length; ages ranged from 38 to 229 days and estimated average planktonic larval duration was 25 days. Estimated growth rates ranged from 0.60 to 1.02 mm/d and did not differ among the three sampling regions, but did differ across sampling years. Back-calculated fertilization dates from otoliths indicated that juveniles in the Panhandle and Big Bend were mainly summer spawned fish, whereas Southwest juveniles had winter and summer fertilization dates. Settlement occurred during summer both years and in the winter of 1997 for the southern portion of the WFS. Moon phase did not appear to be strongly correlated with fertilization or settlement. Histological samples of gonads from adults collected near the juvenile sampling areas indicated a summer spawning period.

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A primary goal of fisheries ecology is to determine the causes of annual variation in recruitment and to predict the number of individuals that reach a harvestable size (Frank and Leggett, 1994). This variation can be substantial; recruitment to marine fish stocks can vary by one or two orders of magnitude (Shepherd and Cushing, 1990). An understanding of recruitment dynamics remains a critical, unresolved problem in fisheries science (Houde, 1987). Improved understanding is vital for better conservation of exploited marine fish populations for it would enable prediction of future harvests (Wooster and Bailey, 1987).

Gray snapper (*Lutjanus griseus*), also known as mangrove snapper, are found in the western Atlantic and Gulf of Mexico from North Carolina to Bermuda and south to Brazil. Rarely, individuals are recorded as far north as New England (Hoese and Moore, 1977). Adults generally occur offshore in areas associated with coral reefs or other hard bottom substrate. Spawning off Florida is thought to occur from June through September, and individual gray snapper probably spawn more than once during the spawning season (Starck, 1971). Larvae, which are planktonic up to about 10 mm standard length (SL) (Starck, 1971), have been reared in the laboratory and described by Richards and Saksena (1980). Juvenile gray snapper are associated with inshore *Thalassia* beds (Chester and Thayer, 1990). Young snapper remain in these *Thalassia* beds until approximately 80 mm SL when they begin to congregate around debris and channel edges. Sexual maturity occurs at 175–180 mm or three years of age (Starck, 1971).

Gray snapper support an important recreational and commercial fishery in the Gulf of Mexico. Commercial landings in the Gulf of Mexico, once over 900,000 lb in 1983 had declined to less than 430,000 lb by 1997 (Bennett[1]). Gray snapper are popular among sport fishermen; recreational landings in the Gulf of Mexico for 1997 were estimated at 877,000 lb (U.S. Dep. Commer.[2]).

The boundaries of the study area approximately represent the range of seagrass meadows along the West Florida shelf (WFS) (i.e. St. Andrew Bay is near the northwest extreme and Ft. Myers is near the southwest). The study area also experiences variation in climate, the north portion being warm-temper-

[1] Bennett, J. 1998. Automated landings assessment for responsive management. Gulf of Mexico Commercial landings for selected species, 87 p. Miami Laboratory, Southeast Fisheries Center, National Marine Fisheries Service, Miami, FL 33149.

[2] U.S. Department of Commerce. 1998. Fisheries of the United States. 1997. Current fishery statistics no. 9700, 156 p. Statistics Div, Rm 12340, 1315 East-West Highway, Silver Spring, MD 20910-3282.

ate and the southmost boundary being semitropical (Zieman and Zieman, 1989). This climate change results in latitudinal variation in the shallow water communities along the WFS: from a mainly West Indian fauna in the south to a Carolinian fauna in the north (Smith, 1976; Lyons, 1979).

The goal of our study was to improve our understanding of the recruitment dynamics of gray snapper by determining the spatial and temporal patterns in spawning and settlement along the WFS. The objectives of this study were 1) to establish spawning time through otolith back-calculation and the examination of adult gonads, 2) to determine settlement time (i.e. planktonic larval duration) from otolith microstructure, 3) to estimate growth rates for juvenile gray snapper, 4) to compare estimated spawning times, settlement times, and growth rates between sampling regions and years, and 5) to examine the potential influence of lunar phase on spawning and settlement events.

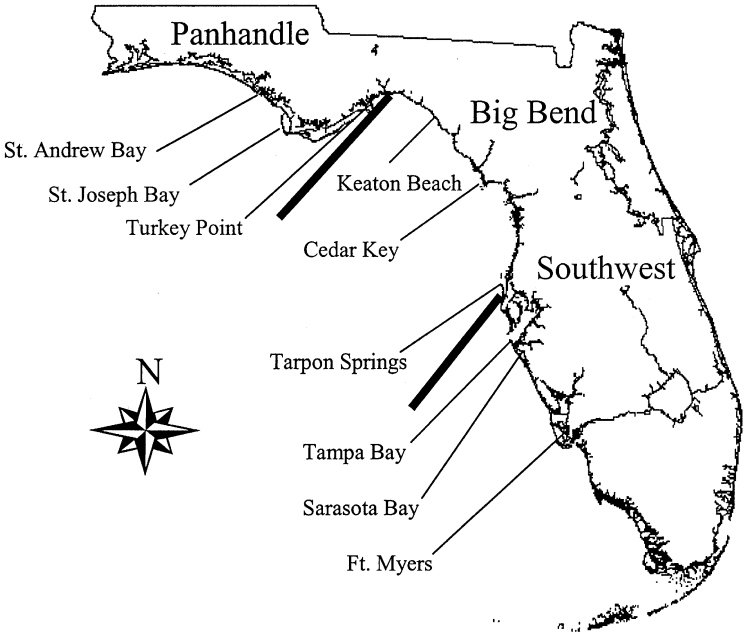

Figure 1

Sampling regions and station locations along the West Florida shelf (WFS). Thick black lines demarcate the three sampling regions: region 1, the Florida Panhandle; region 2, Big Bend; and region 3, Southwest Florida.

Materials and methods

Sampling and collection

We collected juvenile reef fish from the seagrass beds of the WFS from St. Andrew Bay in northwest Florida to Ft. Myers in southwest Florida. For spatial comparison of the results, we divided the study area into three sampling regions chosen on the basis of the differences in faunal composition (Lyons and Collard, 1974; Smith, 1976; Hoese and Moore, 1977) and type of coastal environment (Price, 1954) (Fig. 1). Region 1, the Florida Panhandle, embraces St. Andrew Bay to the St. Marks River, an area of sand beaches and barrier islands. Region 2, the Big Bend, spans the area from the St. Marks River south to Tarpon Springs. The Big Bend is unlike the other regions in that it has no barrier islands and is considered a zero-energy coastline (Murali, 1982). Region 3, Southwest Florida, includes the area from Tarpon Springs south to Ft. Myers. This region is similar to region 1 in that it is composed largely of sand beaches and barrier islands (Zieman and Zieman, 1989).

Station locations within these regions were chosen according to abundance of economically important fin fish species (Koenig and Coleman[3]). The 20 stations were located where there were large dense areas of seagrass in close proximity to the open gulf. The dominant species of seagrass in the study area is turtle-grass, *Thalassia testudinum,* followed by manatee-grass, *Syringodium filiforme,* and shoal-grass, *Halodule wrightii* (Zieman and Zieman, 1989). Station depth generally ranged from 1 to 3 meters.

We collected juvenile fish for this study every other month in 1996 and 1997, beginning in late February of 1996 and early March of 1997. At each station we made five replicate tows of 150 meters (m) in approximately 5 minutes (1.8 km/hour) using two different types of trawls. To collect the smallest postsettlement juveniles, a 1-m by 0.40-m benthic scrape constructed of a stainless steel frame with a 2-mm nylon mesh tail bag was used. This trawl was used from the beginning of the year until the fall. We used a 5-m by 3-m otter trawl with a 3-mm nylon mesh tail bag to collect larger individuals year round. The contents of each trawl were sorted and all juvenile fish of commercial value were removed, bagged, and stored on ice. At the end of a sampling trip, all juvenile fish collected were frozen. In the laboratory juvenile gray snapper were removed from samples, thawed, measured (standard length [SL] to the nearest 0.1 mm), and weighed to the nearest 0.1 g.

Otolith preparation and interpretation

Both the sagittae and lapilli were extracted from each snapper under a dissecting microscope by the "open-the-hatch method" (Secor et al., 1992). One lapillus was chosen at random from each fish for measurement. Whole lapilli were viewed with a compound microscope at 50× magnification with a video camera and monitor and the image was digitized on a microcomputer with image analysis software (BioScan, 1990). A measurement (nearest μm)

[3] Koenig, C. C., and F. C. Coleman. 1998. Recruitment indices and seagrass habitat relationships of the early juvenile stages of gag, gray snapper, and other economically important reef fishes in the eastern Gulf of Mexico. Final report (MARFIN award no. NA57FF0055) to Florida State University, 66 p. Department of Biological Sciences, The Florida State Univ., Tallahassee, FL 32306-2043.

was made from the anterior edge to the posterior edge along the longest axis.

We computed the linear regression of standard length on lapillus length to determine if otolith growth and somatic growth were proportional. To prepare lapilli for age determination, both lateral surfaces of the otolith were ground and polished on glass plates covered with a 3600- and 6000-grit polishing cloth. After being polished, the lapillus was mounted on a microscope slide with Pro-texx® mounting medium. Thirteen sagittae were also prepared to determine if sagittal section counts were consistent with lapilli counts. Because of the concave-convex shape of the sagittae, the technique used for examining the lapillus was not possible. Therefore, the more labor intensive process of embedding and sectioning the whole sagittae had to be used (Secor et al., 1992).

Growth in mm/day was estimated as the slope of the linear regression of standard length on the number of daily increments in the lapillus. Analysis of variance (ANOVA) and analysis of covariance (ANCOVA) were used to determine if estimated growth rates varied significantly among sampling regions and years.

Increment counts were made from sections of the lapilli and sagittae by using a compound microscope at 400–1000× magnification. Oil immersion was used at the 1000× magnification. Daily increments were distinguished from subdaily increments with the method of Campana (1992). Increments were counted twice by the same reader and counts that were different by no greater than 5% were averaged. Increment counts that differed by more than 5% were counted a third time, and if the third count differed by more than 5% of the previous counts, the otolith was rejected. An increment correction (3 days) was added to the total number counted based on the assumption that the first increment was not formed until after first feeding (i.e. approximately 3 days after fertilization) (Lindeman, 1997; Lindeman et al., 2000). This corrected increment count was subtracted from capture date to determine the fertilization date.

We interpreted the settlement mark in the lapillus to be where the pattern in the increment widths changed markedly (Wellington and Victor, 1989). Increments were counted from the primordium to the settlement mark and a correction of three increments was added to estimate the number of days before settlement or the planktonic larval duration. Those lapilli that did not have an obvious settlement mark were excluded from the analysis. Settlement dates were calculated by subtracting the number of post-settlement increments from the date of capture. ANOVA was used to compare the age at settlement (i.e. planktonic larval duration) with region, year, and region-year interaction. After converting lunar day of fertilization or settlement to a circular scale (Zar, 1984), we used a chi-square test to determine if fertilization and settlement dates were uniformly distributed across the lunar month.

To validate the periodicity of increment formation in lapilli we conducted an otolith marking experiment. Lapilli of live fish were marked with alizarin complexone, which has been shown to produce a well-defined mark in the otoliths of juvenile fish without producing high mortality (Tsukamoto et al., 1989; Lang and Buxton, 1993). Approximately 30 juveniles were captured with a benthic trawl and held in an 800-gallon flow-through seawater system for several days so that they might acclimate to captivity. Juveniles were fed once daily *ad libitum*. Because of the photosensitivity of alizarin complexone, juveniles were immersed in 20 L of an aerated 200 mg/L solution of alizarin complexone for 24 h in the dark. Juveniles were removed from the solution and returned to the flow-through seawater tank. Juveniles were sacrificed 7, 14, 21, or 28 days after marking and their lapilli were removed and prepared as previously described. Increments deposited after the alizarin complexone mark were counted as previously described, except that transmitted ultraviolet light was used to read increments. Linear regression was used to compare number of increments counted after the alizarin-complexone mark in the lapillus to the number of days the juveniles were held after marking. A *t*-test was used to determine if the slope of this regression was significantly different from 1.0.

Gonad histology and analysis

To obtain an estimate of the spawning time that was independent of otolith-based spawning dates, adult gray snapper gonads were examined. All adult gray snapper were collected as part of an ongoing study by the National Marine Fisheries Service on reef fish reproduction. Fish were collected from commercial and recreational landings from Panama City, Florida, to Ft. Myers, Florida, from January to December in 1996 and from April to November in 1997. Each fish was weighed whole (i.e. ungutted [g]) and total length (TL) and fork length were measured (mm). All fish collected were at least 252 mm TL (minimum legal size) and were assumed to be sexually mature (Domeier et al., 1996).

Gonads were removed and stored on ice and then processed by the methods of Collins et al. (1996). A small sample of each gonad was examined with a dissecting microscope (250×) to measure the maximum oocyte diameter (nearest 0.1 mm). The developmental stage of ovarian sections was determined by using the methods of Wallace and Selman (1981). Ovarian stages were assigned on the basis of the most advanced ovarian stage or follicle stage present: 1—primary growth (early oocytes); 2—cortical alveolar (previtellogenic); 3—vitellogenic; 4—hydrated; and 5—spent (i.e. presence of postovulatory follicles). Sections of testes were staged according to the methods of Moe (1969): 1—spermatogonia; 2—primary spermatocytes; 3—secondary spermatocytes; 4—spermatids; and 5—spermatozoans. The timing and duration of spawning were determined by plotting oocyte diameter and histological development stage by sampling date.

Results

Sampling and collection

Juvenile gray snapper were found in seagrass meadows along the west Florida shelf from June to November in the two most northern sampling regions, and from April

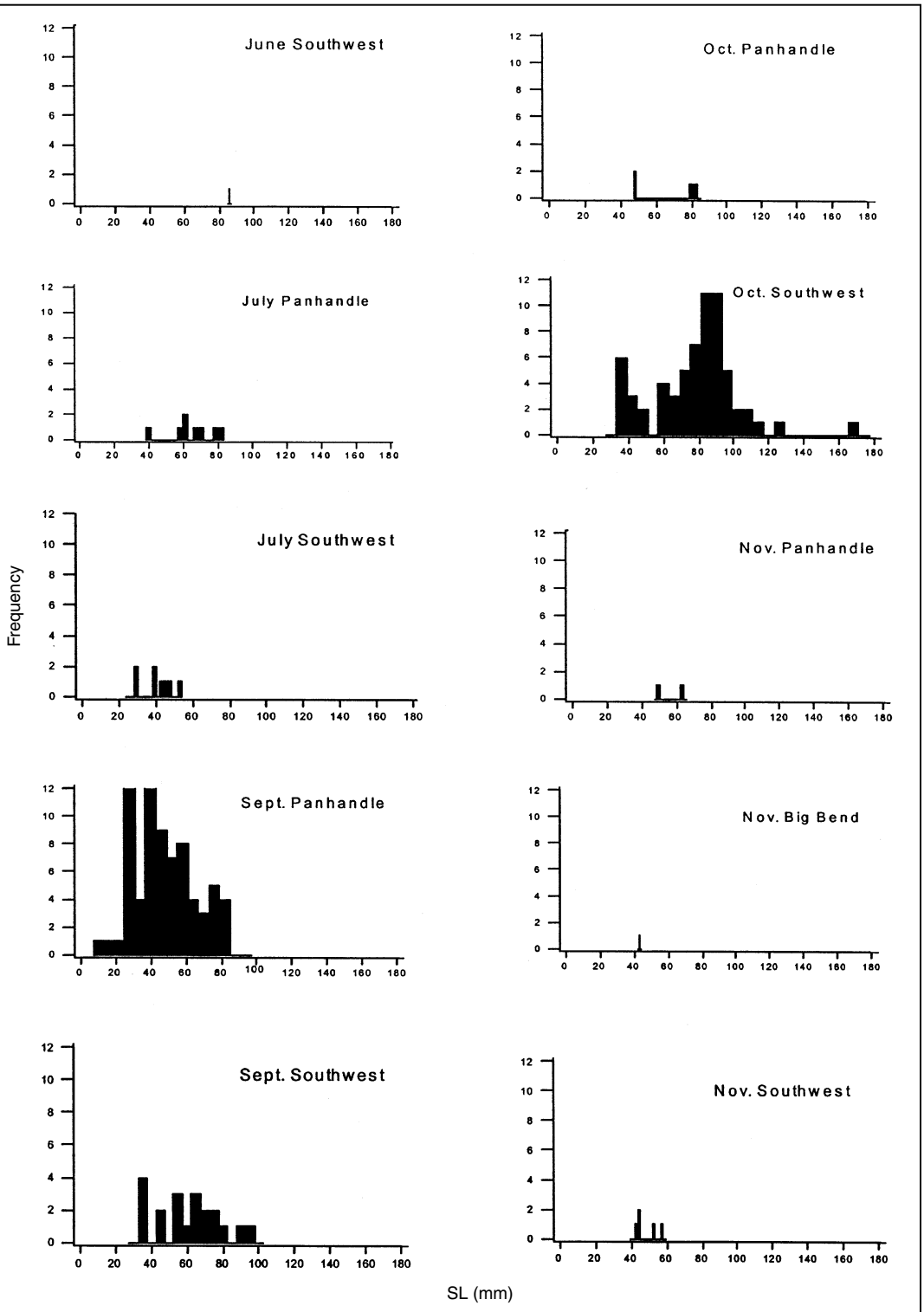

Figure 2

Length (SL, mm) frequency distribution of gray snapper juveniles by region and sampling month in 1996.

to November in the most southern area. The first juvenile was collected in the otter trawl in June 1996 from the Southwest (Fig. 2). In July we collected 14 fish in the benthic scrape and only one in the otter trawl along the entire WFS. The largest numbers were collected in September and October from the Panhandle and Southwest. The fol-

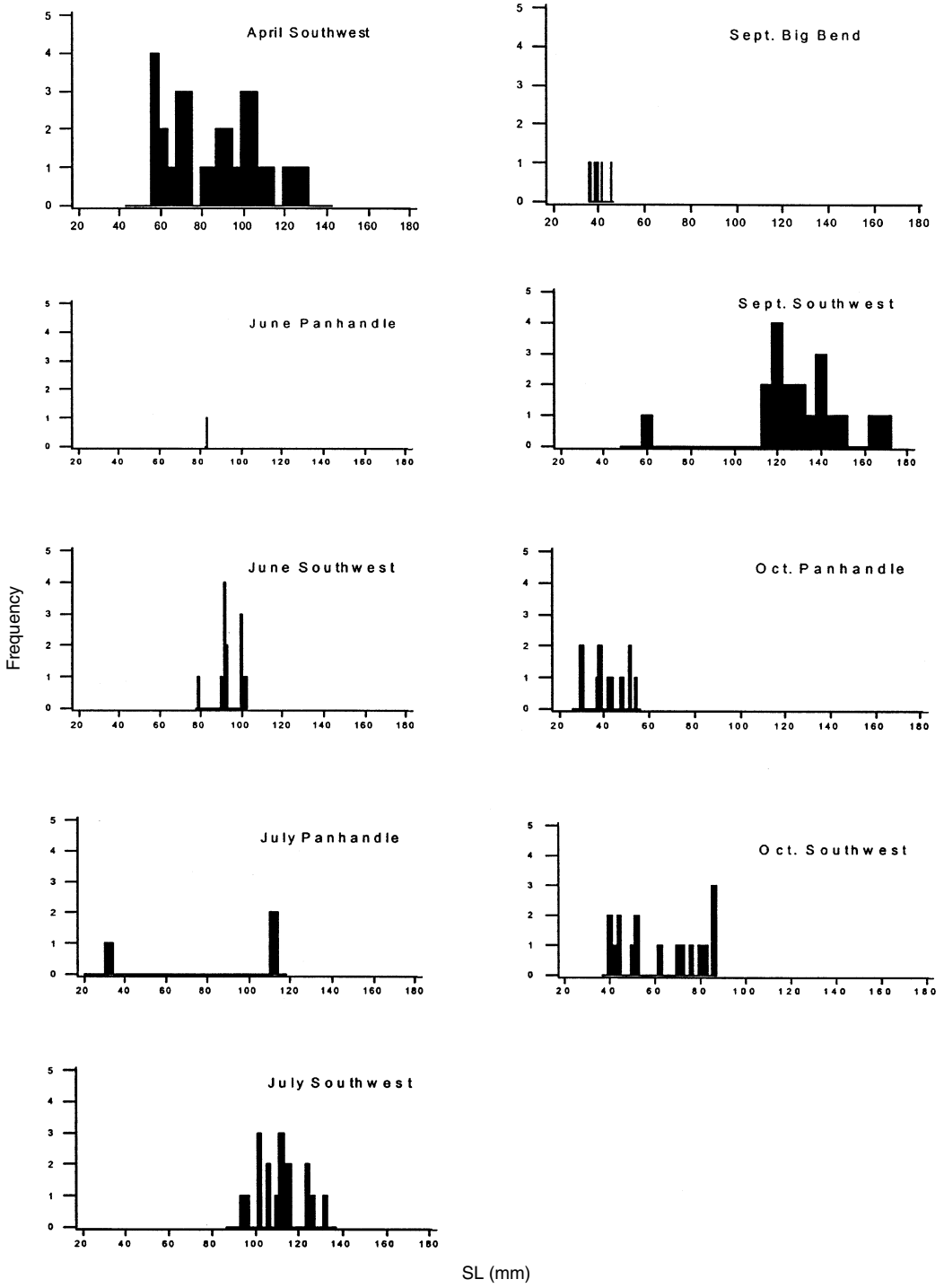

Figure 3

Length (SL, mm) frequency distribution of gray snapper juveniles by region and sampling month in 1997.

lowing year (1997), juveniles were initially collected in April in the otter trawl in the most southerly part of the Southwest sampling area (i.e. near Sanibel Island) (Fig. 3). The catch rate decreased in June, then increased during late summer, and peaked in September. Only two fish were collected in the benthic scrape, both in June.

There was evidence of multiple cohorts in the Southwest in October 1996 and in April 1997. Juveniles collected in 1997 (mean=88.3 mm SL) were, on average, about 50% larger than those collected in 1996 (mean=59.9 mm SL). Fish collected from the Southwest were also larger on average than those from the Panhandle both years.

Age and growth

Increments in the lapillus occurred at regular intervals and a consistent width and marked contrast was evident between each one. More closely spaced increments occurred at irregular intervals with less contrast between them. Usually we counted fewer increments in sagittae than in lapilli. Lapilli were thinner and flatter than sagittae and therefore required less grinding and could be examined whole, whereas sagittae had to be sectioned first. Increments near the edge of the lapilli were also clearer and easier to distinguish compared with those from sagittal sections. Increment counts were successfully assigned to 137 (71%) of the juveniles collected in 1996 and 97 (82%) of the 1997 collection. Uncorrected increment counts ranged from 35–128 (mean=75) in 1996 and 50–226 (mean=125) in 1997.

Several lines of evidence suggested that increments were deposited daily. The linear regression of SL (mm) on lapillus length (μm) indicated a highly significant relationship between body size and otolith size for fish collected in 1996 (P<0.000, r^2=0.97) and 1997 (P<0.000, r^2 = 0.96). Juveniles selected for the otolith marking experiment ranged from 31.4 to 44.6 mm SL (mean=38.4 mm, standard error=0.63 mm). Only 21 out of 30 surviving alizarin-complexone–marked juveniles had otoliths with visible marks and no fish harvested on day 21 had readable marks. Mean growth rate for survivors was estimated at 0.33 mm/d. The slope (b=0.87) of the regression of the number of increments counted after the alizarin mark on the number of days juveniles were held after marking was not significantly different from 1.0 (Fig. 4) (t-test, P<0.05); therefore we did not reject the hypothesis that increments were deposited daily.

Instantaneous daily growth of juvenile snapper was 1.02 mm/d in 1996 compared with 0.60 mm/d in 1997 (Fig. 5). ANOVA indicated a significant difference in slopes (i.e. growth rates) between years (P<0.001). However, ANCOVA indicated that there was no significant difference in growth rate among regions. Because there was a significant difference in standard lengths between years and regions, only those size ranges that overlapped between the two regions (i.e. Panhandle and Southwest, 1996: 29–83 mm SL, 1997: 39–112 mm SL) and between years (i.e. 32–110 mm SL) were included in the analysis.

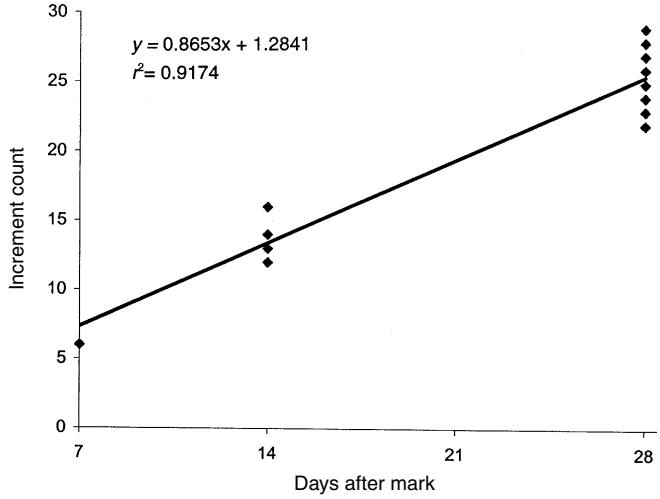

Figure 4

Linear regression of increment count on number of days after alizarin marking of the lapillus.

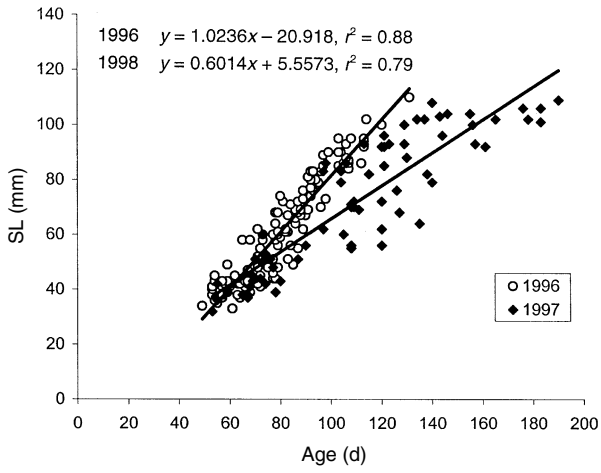

Figure 5

Linear regression of SL (mm) on age (d) for 1996 and 1997.

Fertilization-date distribution

There were distinct patterns in the temporal and spatial distribution of fertilization dates. Our results however provided little support for lunar periodicity in spawning. Back-calculated fertilization dates indicated that surviving juveniles in the Panhandle and Big Bend were mainly summer spawned fish, whereas Southwest juveniles had winter and summer fertilization dates. In 1996, the earliest back-calculated birth date was 25 February from a fish from the Southwest, although a few (i.e. six fish) were recorded from late April and early May from the Panhandle and a few more by mid-May from the Southwest (Fig. 6). Most fish spawned beginning in mid-June and a peak in fertilization dates occurred during mid-July for both regions. Frequency of spawning then declined and the latest fertilization date of the year was recorded in mid-September from the Southwest. A chi-

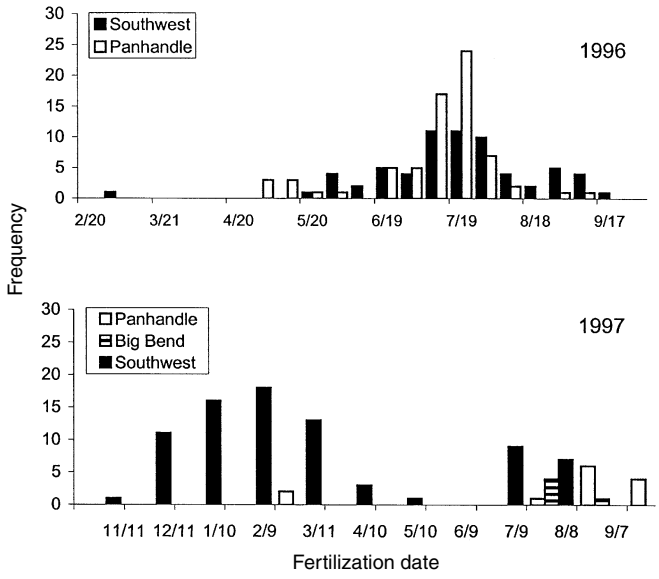

Figure 6

Fertilization-date distribution for 1996 and 1997.

square test revealed only a marginal difference ($P<0.10$) from a uniform distribution in fertilization dates across lunar month.

As in 1996, fertilization in 1997 began in mid-June, peaked in early August, and included birth dates from all three regions; however, the distribution for 1997 was bimodal. Spawning began in November of 1996 and peaked in late January of 1997, then declined into April. With the exception of two individuals collected in late February from the Panhandle, all individuals from the first fertilization-date peak were from the Southwest. The last back-calculated fertilization date for the year was in early September from the Panhandle. Fertilization dates for 1997 did not conform to a lunar cycle because a chi-square test indicated no significant difference from a uniform fertilization-date distribution across lunar month.

Results from the reproductive condition of adult gonads were compared with results from back-calculated fertilization dates from otoliths to determine if surviving juveniles were derived from a subset of the original propagules. We compared otolith data with oocyte diameters because large ova are indicative of ripe females (i.e. >0.59 mm maximum oocyte diameter) (Davis and West, 1993). In 1996, the maximum oocyte diameter distribution indicated that females were in spawning condition from May to September and that a peak in spawning activity occurred in mid-July (Fig. 7). Spawning activity, signified by the presence of hydrated oocytes, also occurred from May through mid-September. Only one female with postovulatory follicles was found in 1996, collected in mid-July. Male spawning times (i.e. May–September) mirrored those of females; however, only five males contained ripening spermatids, and none contained spermatazoa in 1996. All gonads collected in 1996 were from the Panhandle.

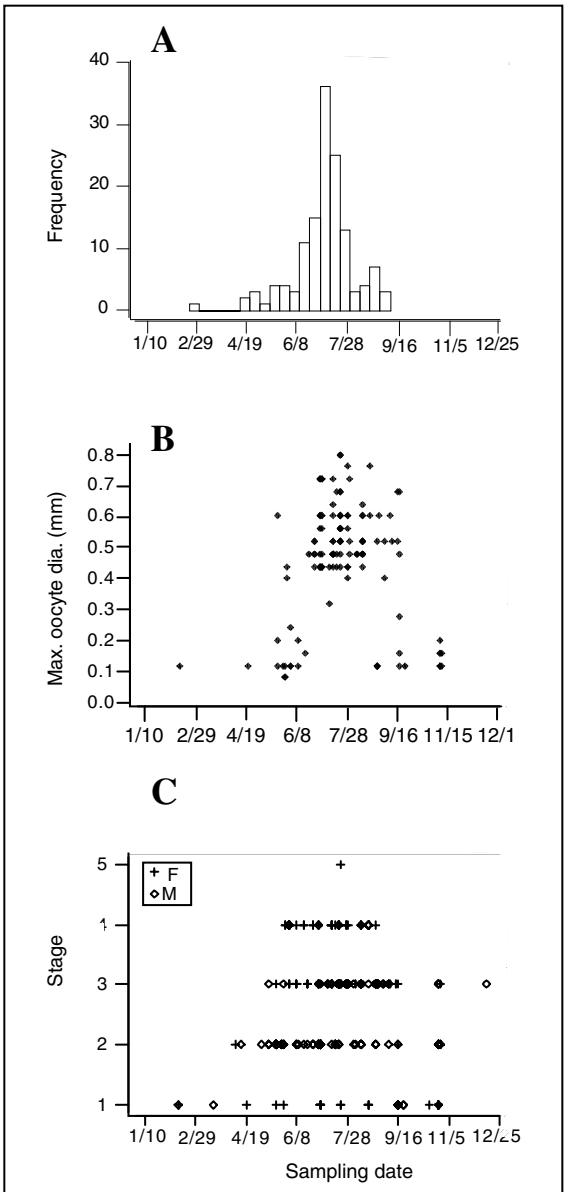

Figure 7

Comparison of spawning time as determined by back-calculation from otoliths (**A**), maximum oocyte diameter (**B**) and histological stage (**C**) for 1996. All fish were collected from the Panhandle.

In 1997 gonad data were available from all three regions and the results of comparisons of gonads from the three regions may indicate the presence of juveniles that were not derived from local spawning. Gonad data for all regions indicated peak spawning during mid-July (Fig. 8). Gonad data from the Panhandle suggested spawning times similar to those for the otolith data, i.e. a May through September spawning period and a summer peak. However, the back-calculated fertilization dates from late February and early March did not correspond to oocyte diameter or histological-stage data. Very few juveniles

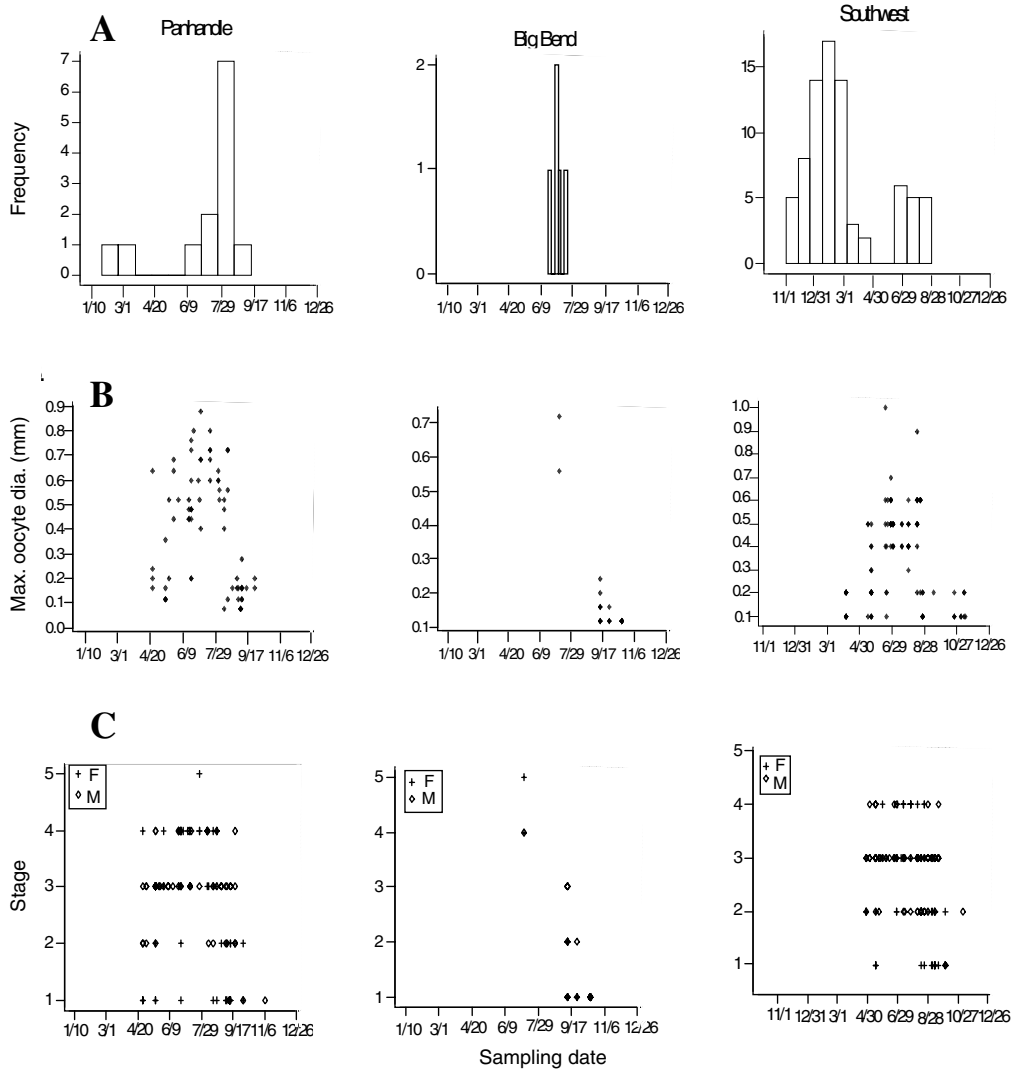

Figure 8

Comparison of spawning time as determined by back-calculation from otoliths (**A**), maximum oocyte diameter (**B**) and histological stage (**C**) for 1997.

or adult fish were collected from the Big Bend; however, these data also suggested a mid-summer spawning period. Oocyte diameter and developmental stage data from the Southwest indicated summer spawning (May to September) but because no adult gonads were collected earlier in the year, a winter fertilization-date mode (as back-calculated from otoliths) could not be determined.

Larval duration

Presumed settlement marks were distinguishable in some, but not all otoliths that were assigned ages. These marks were identified by a sharper contrast than preceding marks (Fig. 9). In addition, at this mark the increment pattern changed abruptly, postsettlement increment widths being consistently narrower than those laid down before settlement. Of the 135 otoliths collected during 1996 which were assigned ages, 80 (59%) had readily distinguishable settlement marks, whereas in 1997, 62 (64%) had distinguishable marks. The estimated age at settlement (planktonic larval duration) for 1996 and 1997 fish ranged from 20 to 32 days (mean=25 days) and from 20 to 33 days (mean=24.7 days), respectively. ANOVA indicated no significant sampling region or year effect or region-and-year interaction on the age at settlement (planktonic larval duration).

In 1996, settlement first began in mid May in the Panhandle and continued throughout the summer, peaking during the first week of August in the Panhandle and Southwest, and ending finally on 1 October in the Southwest (Fig. 10). Results for settlement date data showed no evidence for lunar periodicity in settlement, a chi-square

test indicating that the distribution of lunar settlement dates was not significantly different from a uniform distribution. The back-calculated settlement date distribution for 1997 indicated two distinct settlement events. Settlement of the first mode began in December of 1996, peaked in late winter, and then declined into late spring. All juveniles from the first event were from the Southwest. The second settlement mode was similar to that seen in the 1996 settlement date distribution, beginning in late June, peaking in early August, and finally ending in the early fall. The evidence for lunar periodicity in settlement in 1997 was weak; a chi-square test indicated only a marginally significant difference ($P<0.10$) from a uniform distribution across lunar month for 1997 settlement dates.

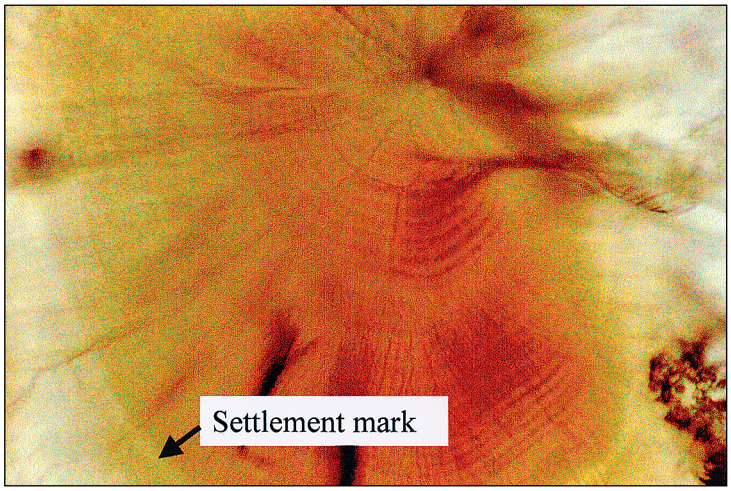

Figure 9
Photomicrograph (400×) of settlement mark in a lapillus of gray snapper.

Discussion

Sampling and collection

The collection of juvenile gray snapper from June to November in 1996 was consistent with a May–September spawning period found from previous studies in which the reproductive condition of adults collected off South Florida was used (Starck, 1971; Domeier et al., 1996). However, in 1997 juvenile gray snapper were initially collected in April from southwest Florida, indicating a much earlier spawning time. Differences in the timing of the first appearance of juvenile snapper for 1997 could be related to the seasonal cycle of seagrass dieback and regeneration. *Thalassia* experiences leaf die off with temperatures below 15°C (Zimmerman and Livingston, 1976). In the northern most part of the sampling region, greater leaf die off and slower growth during the spring would be expected compared with more southerly areas. This would most certainly limit the chances of survival of early settling larvae in the north because of greater predation risk and lower food availability.

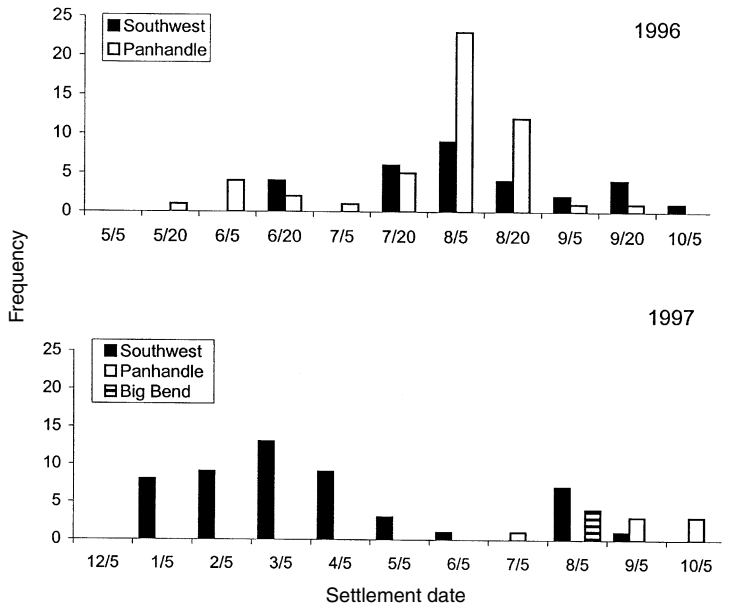

Figure 10
Settlement-date distribution for 1996 and 1997.

If gray snapper are truly recruitment-limited and if postsettlement mortality is relatively constant (Shulman and Ogden, 1987) and individuals do not migrate out of the area during the monitoring period (Robertson et al., 1988), juvenile abundance would be an effective predictor of adult abundance two to three years later when the adults are entering the fishery. Gag (*Mycteroperca microlepis*), a species with a similar early life history to that of the gray snapper, have a low rate of emigration from the seagrass nursery area during summer and a mortality rate of less than 1%/d (Koenig and Coleman, 1998). Johnson and Koenig (in press) found a strong correlation between juvenile gag abundance in seagrass meadows and year-class strength in the fishery several years later. Juvenile indices have been used successfully to document recruitment for a number of temperate fish species and invertebrates. For example, juvenile indices for striped bass were found to explain 83% of the variation in reported landings from 1963 to 1983 (Goodyear, 1985). These data for gray snapper could provide a fishery-independent method for forecasting size of year classes several years into the future. This would be a valuable addition to stock assessment which typically features age-based hind-casting methods such as

virtual population analysis from fishery-dependent data. However, before these data can be used reliably there must be a demonstrated relationship between juvenile abundance and year-class strength.

Age and growth

Because of the strong linear relationship between otolith size and fish size and the regression of increments deposited after alizarin marks on days after marking, we did not reject the hypothesis that one increment was deposited daily. In addition, Ahrenholz (2000) found no significant difference from 1 increment/d deposited from lapilli of alizarin-marked juvenile gray snapper. Juvenile congeneric red snapper (*Lutjanus campechanus*) have also been shown to deposit daily increments above a minimum growth rate (i.e. >0.3 mm/d FL) (Szedlmayer, 1998).

The daily growth rate for juveniles varied between sampling years (1 mm/d in 1996 and 0.6 mm/d in 1997) and was similar to growth rates for juvenile red snapper (0.54–0.86 mm/d, Szedlmayer and Conti, 1999). The difference in growth between years could be explained by the fact that most juveniles collected in 1997 were winter-spawned fish collected from SW Florida that may have experienced lower temperatures and that initially had a slower growth rate. Variability in the growth of larval and juvenile fish has been linked to water temperature in many species (Lang et al., 1994; Nixon and Jones, 1997). However, when the same size range of juveniles was compared between regions, there was no significant difference in growth rate. Similarly there was no difference in regional growth rate of co-occurring juvenile gag from the west Florida shelf (Fitzhugh[4]).

Fertilization-date distribution

All indicators of the temporal distribution of spawning (i.e. juvenile otoliths, oocyte diameter, and histological stage of gonads) indicated peaks in spawning from May until August and a dominant peak in mid-July. Very few gray snapper gonads were collected during the winter months in 1996 and none in 1997 because the majority of gray snapper are landed in July and August (U.S. Dep. Commer.[5]) when they aggregate on offshore reefs to spawn and are probably easier to catch (Starck, 1971; Domeier et al., 1996; Domeier and Colin, 1997). Spawning time has been related to both increasing water temperature and photoperiod for other lutjanids (Arnold et al., 1978; Grimes and Huntsman, 1980).

No obvious temporal differences were observed in reproductive development between regions from adult gonads; however, we determined winter back-calculated fertilization dates for the most southerly part of the sampling region in 1997. In contrast, Domeier et al. (1996) back-calculated spawning dates from June through September using the otoliths from juvenile gray snapper collected from south Florida. Gray snapper larvae have a relatively long pelagic stage of 25 days. The possibility exists that winter-spawned fish were produced from outside the Gulf of Mexico, perhaps from a nearby insular population, and transported from there to settle along the southwestern part of the Florida shelf. The view that winter-spawned fish were Gulf of Mexico expatriates is supported by Grimes's (1987) review of lutjanid reproduction. He found two patterns: 1) continental populations, with extended summer spawning periods; and 2) insular populations, which spawned year-round with pulses in the spring and fall. However, Domeier et al. (1996) suggested after field observations that snapper spawning patterns are species specific, as opposed to habitat dependent. We collected winter-spawned juveniles in only one of the two years of sampling; therefore it is unknown how frequently expatriate settlement events occur and what their importance to gray snapper recruitment might be.

We could not conclusively demonstrate that spawning occurs in association with lunar cycle peaks. Fertilization date hind-cast from otoliths in 1996 were only marginally associated with a lunar cycle and no relationship was evident in 1997 data. Similarly gonad stage data from adult gray snapper did not reveal any lunar pattern. However, the association of spawning with the lunar cycle has been reported for congeneric species, as well as other conspecific populations. Domeier et al. (1996) used a GSI to determine that gray snapper spawning peaked around the time of the new and full moon. Upon examination of adult gonads, Starck (1971) speculated that gray snapper spawned during or near the full moon. The congeneric species *Lutjanus vaigiensis* spawned about the time of the full moon (Randall and Brock, 1960) and *Lutjanus kasmira* spawned during both new and full moons in the laboratory (Suzuki and Hioki, 1979).

Larval duration

Presumed settlement marks were noted in many (60%) of the ageable otoliths, and they were similar in appearance to those observed for several other reef fish species (Brothers and McFarland, 1981; Victor, 1982 and 1986; Sponaugle and Cowen, 1994). Settlement marks are thought to be associated with morphological and ecophysiological changes which occur during the transition from a planktonic to a benthic life stage (Brothers and McFarland, 1981; Victor, 1982; Brothers, 1984). Several lines of evidence suggest that we correctly identified settlement marks. On average, planktonic duration, or length of the presettlement life history phase (i.e. difference between fertilization and settlement dates) was 25 days for both sampling years. Similarly, Koenig and Domeier[6] reported the planktonic

[4] Fitzhugh, G. F. 2000. Unpubl. data. National Marine Fisheries Service, 3500 Delwood Beach Road, Panama City, Florida 32408.

[5] U.S. Department of Commerce. 1998. Fisheries of the United States, 1997. Current fishery statistics no. 9700, 156 p. Statistics Division, Rm. 12340, 1315 East-West Highway, Silver Spring, MD 20910-3282.

[6] Koenig, C. C., and M. L. Domeier. 1993. Unpubl. data. Department of Biological Sciences, The Florida State Univ., Tallahassee, FL 32306-2043.

larval duration to be 24 days (21 d + 3d correction) from otoliths of wild juvenile fish collected off the Florida Keys. Richards and Saksena (1980) recorded settlement for three laboratory-reared gray snapper that were 26, 26, and 36 days old respectively. Thus, gray snapper appear to have a planktonic duration similar to the majority of reef fish (i.e. from 20 to 30 days [Victor, 1991]).

There was no obvious difference in the age at settlement among regions or years. For 1996 and 1997, the temporal distribution of settlement was about the same in the northern and southern parts of the west Florida shelf. In 1997, birth dates and corresponding settlement dates were recorded during the winter months for only the most southern sampling region. Settlement date was marginally associated with the new moon in 1997, possibly reflecting high transport into seagrass meadows at that time. Shenker et al. (1993) found a correlation between onshore transport of settlement-stage Nassau grouper (*Epinephelus striatus*) and the new moon. However, Smith (1995) found no significant association with recruitment of gray snapper through Sebastian Inlet, Florida, and lunar cycle.

Conclusions

This study established that there were differences in the timing of spawning and settlement of gray snapper across the West Florida shelf. Juveniles collected from southwest Florida indicated earlier spawning times than previously reported. Additional year-round sampling of juvenile gray snapper would help to identify the influence of early spawning events on recruitment. Further study of larval transport and genetic markers could aid in the identification of source populations.

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