

Growth Variation, Settlement, and Spawning of Gray Snapper across a Latitudinal Gradient

KELLY DENIT* AND SU SPONAUGLE

*Division of Marine Biology and Fisheries,
University of Miami, Rosenstiel School of Marine and Atmospheric Science,
4600 Rickenbacker Causeway, Miami, Florida 33149, USA*

Abstract.—Newly recruited juvenile gray snapper *Lutjanus griseus* were collected each fall for two consecutive years (2000 and 2001) from sites in Florida and North Carolina. Spawning, settlement, and growth patterns were compared across sites based on otolith microstructure. Larval otolith growth trajectories were generally similar for larvae from different sites and years; however, the mean pelagic larval duration (PLD) was 1 d longer for fish from North Carolina than for fish from the more southern sites. As a result, fish were larger at settlement to North Carolina. Estimated juvenile growth rates ranged between 0.62 and 0.88 mm/d and differed across sites and years, growth being generally faster at the southern sites. Water temperature accounts for some of this variability; however, site-specific differences in other factors probably contributed to some of the observed differences in growth. Back-calculated spawning patterns showed a lunar association with the new and first-quarter moons at all sites except for North Carolina. Settlement patterns were lunar cyclic as well: settlement pulsed during the third-quarter and new moons at all sites, and in North Carolina an additional pulse associated with the full moon was present. Patterns of larval and juvenile growth coupled with recruitment dynamics across the latitudinal gradient are consistent with northward Gulf Stream transport of larvae from southern spawning sites.

A complete understanding of the population dynamics of a marine organism necessitates collection of data on all components of its life history. The complex life histories of benthic marine fish create difficulties in studying the pelagic larval phase. Consequently, we have relatively little knowledge of events occurring during larval life, including where larvae go and where successful settlers have come from.

Although the gray snapper *Lutjanus griseus* is ecologically and economically important and basic fishery data have been collected on adults (Manooch and Matheson 1984; Rutherford et al. 1983; Burton 2001), relatively little is known about larval life and the transition to settled juveniles. The geographic range for this species covers the western Atlantic from Florida through Brazil, including Bermuda, the Caribbean, and the northern Gulf of Mexico (Robins et al. 1986). Even though gray snapper do not survive the winter water temperatures of higher latitudes (Burton 2001), juveniles have been reported from as far north as Massachusetts (Sumner et al. 1911), and settlement stage larvae have been found in ichthyoplankton samples from North Carolina (Hettler and Barker 1993; Tzeng et al. 2003). The majority of gray snapper

landings from the southeast USA occur in Florida (Burton 2001).

As one of the top predators in sea grass beds and on coral reefs, gray snapper have an important ecological role in marine ecosystem communities. In sea grass beds, gray snapper have been shown to consume mainly shrimp, crabs, and fish—especially toadfish (Croker 1962; Starck and Schroeder 1971). Snapper removal from an ecosystem has been associated with significant changes in the food web on coral reefs in Cuba (Claro 1991) and the Florida Keys (Ault et al. 1998).

Adult gray snapper are associated with coral reefs, shipwrecks, rocky outcroppings, mangroves, and other natural live-bottom areas (Miller and Richards 1980; Claro et al. 2001; Ley and McIvor 2002). During new and full moons of summer months, adults aggregate on outer reef tracts in the Florida Keys for spawning (Starck and Schroeder 1971; Domeier et al. 1996; Lindeman et al. 2001; but see Allman and Grimes 2002). However, the geographic destination of eggs and larvae from these spawning events is unknown.

After a pelagic larval duration (PLD) of 22–42 d (Lindeman 1997; Allman and Grimes 2002; Tzeng et al. 2003), larvae settle into shallow estuarine sea grass and mangrove nursery areas (Laegdsgaard and Johnson 2001; Nagelkerken et al. 2001). With an intermediate PLD and the possibility of entrainment into the Gulf Stream, a

* Corresponding author: kdenit@rsmas.miami.edu

Received August 29, 2003; accepted April 23, 2004

broad geographical range of dispersal is possible for gray snapper. The question is whether these settlers are transported varying distances from a common spawning area or come from multiple sources.

Recruitment of juveniles into a population clearly influences population dynamics. However, variability in recruitment is difficult to predict without understanding the details of events occurring during the larval phase. This study was designed to measure the scope of variability in several early life history traits of gray snapper. Growth rates and survivorship are influenced by various physical and biological factors such as diet and environment (e.g., Boehlert and Yoklavich 1983; Miller et al. 1988; Buckel et al. 1995; Tupper and Boutilier 1995; Johnson and Evans 1996). Growth further influences larval duration (Searcy and Sponaugle 2000), which, in turn, theoretically constrains maximum dispersal distances. Fortunately, valuable information about the early life history phases can be obtained from otoliths (ear stones). Daily increment deposition in otoliths and changes in deposition (appearance) during life history transitions provide a measure of age, including PLD and postsettlement age at capture (Campana and Neilson 1985). These data can be used to back-calculate the timing of settlement and spawning, and the widths of increments provide a measure of relative growth at particular ages.

We used otoliths to investigate variation in early life history traits of gray snapper from Florida and North Carolina. Based on the collection of recruits (successful settlers), we compared the timing of settlement and spawning over this same spatial scale to examine the linkages between larval growth, PLD, and the timing of settlement. We analyzed larval otolith growth trajectories to investigate the relationship between growth and PLD, and we explored the possible effects of latitudinal differences in environmental conditions (i.e., temperature) by analyzing growth during the juvenile period. Larval and juvenile growth patterns combined with lunar settlement and spawning relationships provide a better understanding of the larval and juvenile life stages of gray snapper and insight into the possible source areas and transport of these fish.

Methods

Sample collections.—Early-stage (young-of-the-year) juvenile gray snapper were collected in 2000 and 2001 from four sites along the Florida coast (Sebastian Inlet, Jupiter, Biscayne Bay, and Florida

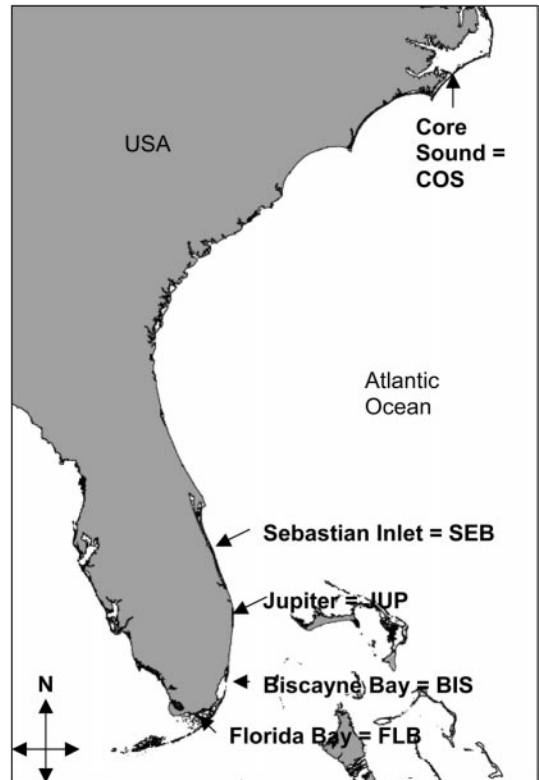


FIGURE 1.—Map of the southeastern United States indicating the five study sites by name and abbreviation.

Bay) and one site off the coast of North Carolina near Beaufort Inlet (Core Sound; Figure 1). A minimum of 15 fish were collected at each site each year in September and October (Table 1). Samples were collected with a 21.3-m push seine with 1-mm mesh at all sites except Core Sound and Florida Bay. In Core Sound and Florida Bay, a 3-m-long otter trawl with 6.4-mm mesh was used for collections. Florida Fisheries and Wildlife Commission and National Oceanic and Atmospheric Administration–National Marine Fisheries Service Beaufort laboratory personnel collected these samples as part of their routine sampling. During sampling, data collected included GPS position, bottom type, shore type, water temperature, salinity, and tidal stage. Florida Bay was not sampled in 2001 because of permit restrictions. Samples were frozen and transported to the University of Miami–Rosenstiel School of Marine and Atmospheric Science (RSMAS) for analysis.

Daily age estimation and growth.—All fish collected were used for otolith age estimation. Before dissection, each fish was weighed (wet weight, g)

TABLE 1.—Distribution of aged juvenile gray snapper at five different sites during 2000 and 2001. Fish were collected from mid-September to mid-October from Florida Bay (FLB), Biscayne Bay (BIS), Jupiter (JUP), Sebastian Inlet (SEB), and Core Sound (COS) and are shown by month of collection. The average monthly temperature ($^{\circ}\text{C}$) is also given.

Month	Number or temperature	2000					2001				
		FLB	BIS	JUP	SEB	COS	FLB	BIS	JUP	SEB	COS
Sep	Number	0	32	22	0	28	0	0	25	0	17
	Temperature	28.7	29.7	32.0	28.7	25.6	28.6	28.9	28.5	28.2	25.4
Oct	Number	15	20	12	49	18	0	31	10	40	13
	Temperature	26.9	27.4	30.5	26.8	21.0	27.3	27.4	26.5	26.8	20.4

and its standard length (SL) was measured to the nearest 0.1 mm by digital calipers. Standard techniques were used to dissect each fish to remove the sagittal otoliths (Brothers 1987). One sagitta was used for aging. A randomly selected otolith from each fish was mounted in epoxy, sectioned, polished, and read according to standard protocols (Secor et al. 1991). Otoliths were examined under a Leica transmitted-light microscope at $400\times$. The microscope image was captured with a frame grabber and displayed on a computer screen. Using Image-Pro image analysis software (Media Cybernetics 1998), we enumerated increments along the anterior dorsal section of the otolith from the core to the outer edge. A consistent reading axis was selected that was not the longest axis of either larval or juvenile otolith growth, but one along which increments were visible to the edge. Otolith

radius (μm)-at-age was recorded for every day of the larval and juvenile periods. The timing of settlement was determined by examining otoliths for optical marks associated with settlement (Figure 2). Using these data, we could determine the larval duration and juvenile age (including a 3 d correction for time to first ring formation; Lindeman 1997), as well as daily growth rates (increment widths) during larval and juvenile periods. Age-specific otolith growth rates were obtained for several periods during the larval stage. Somatic growth rates were estimated by linear regression of SL on age, based on otolith microincrement counts (Szedlmayer and Conti 1999).

Based on age validation studies by Allman (1999) and Ahrenholz (2000), each increment was assumed to reflect 1 d of growth. We followed a standard protocol for reading and interpreting the

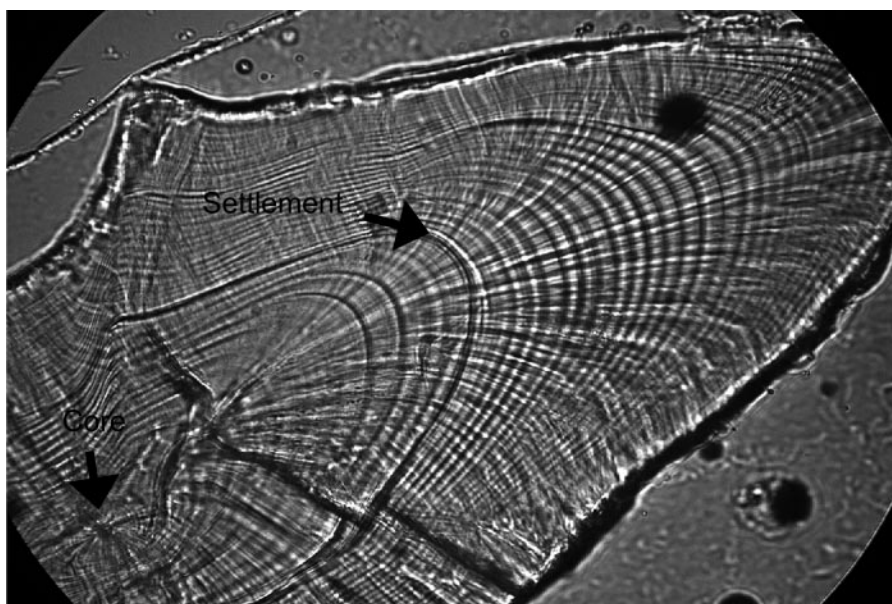


FIGURE 2.—The transverse section of a sagittal otolith from a Core Sound gray snapper, the core and settlement areas being indicated by arrows. All readings were made along the anterior dorsal area of the otolith from the core to the outer edge. The otolith was taken from a 31.73-mm (SL) juvenile that was 53 d old.

otoliths. First, all unclear, abnormally shaped (nonlinear growth axis) sagittae were discarded. A sagitta from each specimen was read twice independently by the same reader. If the increment counts were within 5% of each other, one measurement was randomly selected for analysis (Searcy and Sponaugle 2000). If the increment counts differed by more than 5%, the otolith was read again. If the increment counts from the third reading differed from the other readings by more than 5%, the otolith was discarded. If the difference on the third count was less than 5% of one of the former readings, then one of these two measurements was randomly selected for analysis.

Data analysis.—The larval increment width data (growth trajectories) were analyzed by using repeated-measures analysis of variance (MANOVA). This technique allows comparisons to be made at the resolution of an individual fish (Chambers and Miller 1995; Meekan and Fortier 1996) and is needed for longitudinal data where data points are not independent (i.e., more than one measurement from each fish). MANOVA comparisons were made among groups with the null hypothesis of no differences among groups. The interaction term used was Wilk's λ , which is based on sample size, number of groups in the comparison, and number of intervals being analyzed. Separate one-way analyses of variance (ANOVAs) were used to compare PLDs and otolith size at settlement within each year because Florida Bay was not sampled in the second year (Underwood 1997). Where applicable, Tukey's multiple comparison test was used to identify site-specific differences (Zar 1984).

Analysis of covariance (ANCOVA) was used to compare the slopes (growth rates) of the regressions of standard length on days postsettlement (Sokal and Rohlf 2000). In 2001, no small (SL < 25 mm) juvenile fish were collected at Core Sound, which created a problem. The length–age regression line for the fish from Core Sound produced a *y*-intercept of 4.0 mm. Because settlement at a size of 4 mm is not biologically realistic, this result is most likely an artifact of the lack of younger fish. The regressions for fish from all the other sites in both years, including Core Sound fish from 2000, had a *y*-intercept of 7–11 mm (see Results). In North Carolina, Tzeng et al. (2003) found ingressing gray snapper to have a size range of 11–16 mm. We estimated size at settlement for the Core Sound fish from the otolith radius at settlement. Relationships of SL to otolith radius by site for all of the fish collected were calculated and

compared by ANCOVA. The resulting statistics showed that in the year 2000 the SL–otolith radius for Florida Bay fish was significantly different from all the other sites (ANCOVA, $P < 0.01$; Tukey's test, $P < 0.01$). For the fish collected in 2001 there was no significant difference among sites in the relationship between SL and otolith radius (ANCOVA, $P = 0.74$). When fish from Florida Bay in 2000 were excluded, there was no significant difference between years (ANCOVA, $P = 0.32$). Combining all of the SL–otolith radius data (except Florida Bay) generated a regression equation of $y = 0.1017x - 9.7$ ($R^2 = 0.86$). From this equation, the mean otolith radius at settlement for fish from Core Sound in 2001 (199.82 μm) was equivalent to a size at settlement of 10.62 mm. Given this more realistic size at settlement, we forced the regression for the Core Sound fish from 2001 through this *y*-intercept. All statistical comparisons were made by using this adjusted regression line.

To determine whether settlement peaked during a particular time of the lunar month, day of settlement was assigned a lunar day, from 1 (new moon) to 29 and the distribution of settlement over the lunar cycle was analyzed by using Rayleigh circular statistics (Zar 1984). The same technique was used to analyze back-calculated spawning patterns.

Results

We collected a total of 514 juvenile gray snapper over all sites, 382 (74%) of which had readable otoliths. Of those, 342 (90%) had increment counts that were within 5% of each other and therefore were included in the final analysis. The wet weights of collected fish ranged from 0.05 to 8.49 g, the size range from 11.6 to 65.1 mm, SL, and postsettlement age from 2 to 60 d. In 2000, Florida Bay fish had the highest mean size and postsettlement age, followed by Core Sound (Figure 3). In 2001, Core Sound fish had the greatest mean size and postsettlement age (Florida Bay was not sampled).

The larval otolith growth trajectories for year 2000 fish were not significantly different among sites (Table 2; Figure 4). In 2001, the only significant difference was between Jupiter and Sebastian Inlet fish, the Jupiter fish having significantly faster growth in the week before settlement. Larval otolith growth trajectories for fish at a given site did not differ between years (Table 2).

Pelagic larval duration is related to larval growth in that faster-growing larvae often settle

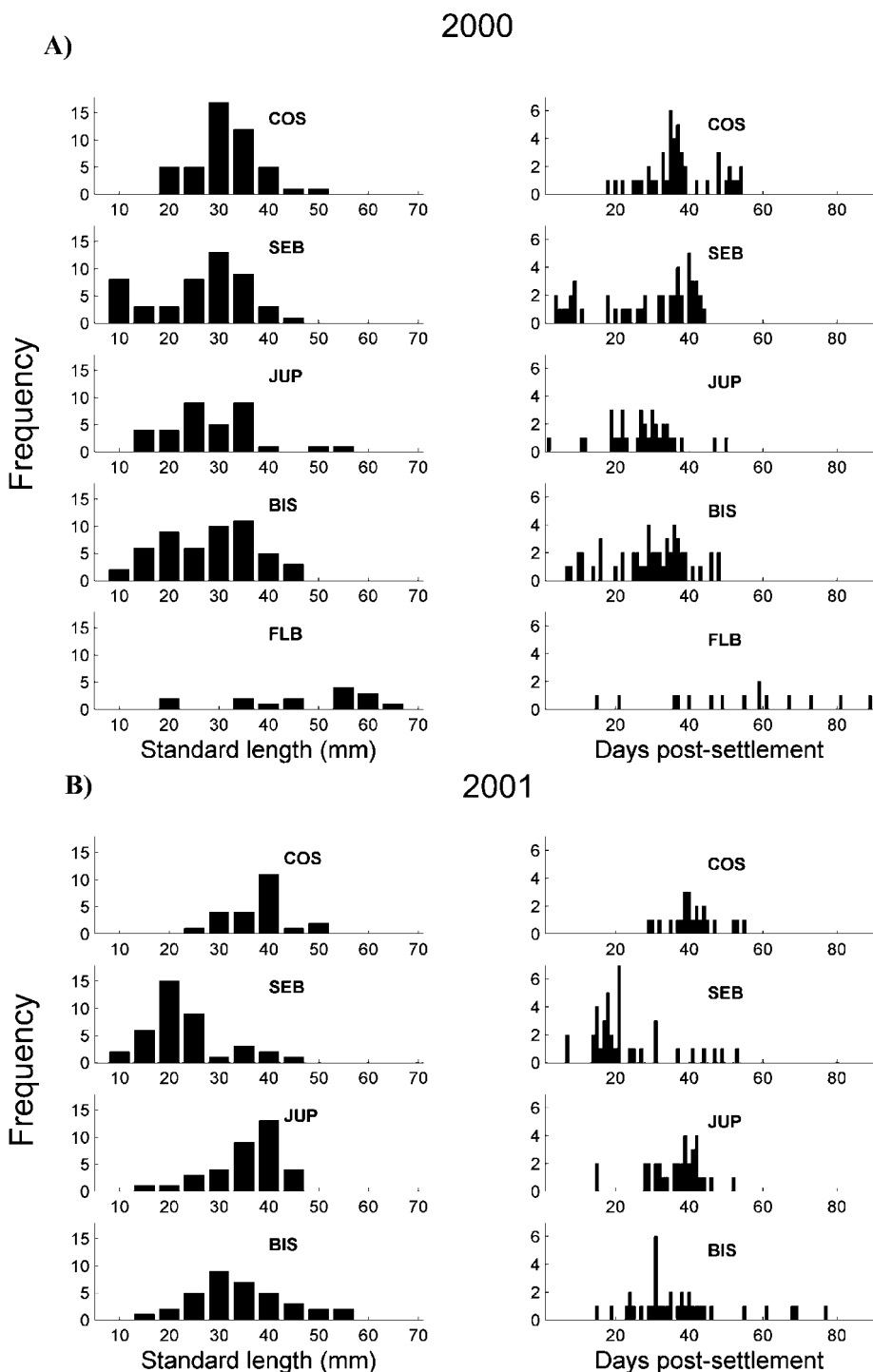


FIGURE 3.—Standard length and age histograms for juvenile gray snapper captured in (A) 2000 and (B) 2001. The study sites are plotted from top to bottom in order of their latitudinal location (north at the top, south at the bottom). See Figure 1 for site abbreviations.

TABLE 2.—Results of repeated-measures MANOVA of larval otolith growth increments of gray snapper collected from the sites identified in Table 1. *P*-values are provided for the interaction terms; asterisks indicate significant differences at *P* < 0.05.

Years(s)	Site	Site			
		BIS	JUP	SEB	COS
2000	FLB	0.450	0.496	0.246	0.155
	BIS		0.790	0.407	0.329
	JUP			0.052	0.581
	SEB				0.269
2001	BIS		0.213	0.359	0.223
	JUP			0.032*	0.575
	SEB				0.590
2000–2001		0.597	0.200	0.534	0.391

earlier (Searcy and Sponaugle 2000). Despite similar larval growth trajectories, PLDs of fishes differed significantly among sites (ANOVA; *P* = 0.001 for year 2000, *P* = 0.014 for year 2001, *P* = 0.037 between years). The PLDs of fish from the most northern location were longer than those from southern locations in both years. In 2000, Core Sound fish had significantly longer PLDs than fish from Biscayne Bay and Jupiter (Table 3; Figure 5). In 2001, Core Sound and Sebastian Inlet fish had significantly longer PLDs than fish from Jupiter. Within sites, fish from Biscayne Bay and Sebastian Inlet had significantly longer PLDs in 2001 than in 2000.

Size at settlement (as reflected in the otolith settlement radius) is a function of larval growth rates and PLD. During both years, snapper from the more northern sites had larger otolith radii at settlement than did those from the more southern sites (ANOVA; *P* < 0.01 for year 2000, *P* = 0.009 for year 2001; Table 4). In 2000, Core Sound fish had a significantly larger otolith radius at settlement than did fish from all of the other sites. In addition, Sebastian Inlet juveniles had a significantly larger otolith radius at settlement than Biscayne Bay juveniles. This trend of larger size at settlement for the northern sites compared to the southern sites also was evident in 2001, but differences were only significant between Core Sound and Jupiter, and between Sebastian Inlet and Jupiter (Table 4). Within sites, only fishes settling to Biscayne Bay had a larger mean otolith size at settlement in 2001 (ANOVA; *P* = 0.006; Table 4).

To examine juvenile growth, we calculated growth rates for each site by regressing standard length on juvenile (postsettlement) age (Table 5; Figure 6). Growth rates ranged from 0.62 to 0.88 mm/d. In 2000, juvenile growth rates differed sig-

nificantly across sites (ANCOVA; *P* = 0.002); Florida Bay fish grew significantly faster than the Core Sound and Sebastian Inlet fish (Table 5). In 2001 (ANCOVA; *P* = 0.001), the only significant difference in growth rates occurred between Jupiter and Sebastian Inlet, with Jupiter fish having faster growth rates than fish from Sebastian Inlet (Table 5). There also were differences within sites between years (ANCOVA; *P* = 0.006); at Core Sound, snapper growth rates during 2001 were significantly faster than in 2000 (Table 5). There was a significant positive relationship between juvenile growth rate and mean temperature, indicating that temperature contributed to some variation in growth rate (Figure 7).

To examine the relationship between PLD and the timing of settlement (whether differences in PLD resulted in differences in the timing of settlement), we examined the timing of settlement to each site over a lunar cycle (Figure 8). In 2000, the distribution of gray snapper settlement to Sebastian Inlet and Biscayne Bay was not uniformly distributed over the lunar cycle. Peaks in settlement occurred at days 29.7 and 23.4, corresponding to the third-quarter and new moons, respectively. In 2001, fish from Core Sound and Sebastian Inlet had nonuniform settlement distributions, settling in peaks associated with the first-quarter moon (day 5.3) and new moon (day 27.8), respectively. Overall, settlement occurred frequently around the third-quarter and new moons, except at Core Sound where additional fish settled between the first-quarter and full moons, leading to an overall statistically uniform distribution in 2000.

In both years, back-calculated spawning dates ranged from late June to early October, peaking in July and August. In 2000, spawning dates ranged from late June to early October. In 2001, spawning dates covered a slightly narrower window from early July to late September. When the data were collapsed into a single lunar cycle, fish that settled to Biscayne Bay and Sebastian Inlet in 2000 were spawned nonuniformly over the lunar cycle (Figure 9). Biscayne Bay fish were spawned primarily during the new moon (day 2.5), whereas Sebastian Inlet fish were spawned during the first-quarter moon (day 8.0). In 2001, fishes from Biscayne Bay and Sebastian Inlet had nonuniform spawning distributions with peaks associated with the new moon (days 26.8 and 2.8, respectively), and gray snapper from Core Sound were spawned mainly during the first-quarter moon (day 9.7). Overall, in both years, spawn dates were clustered around

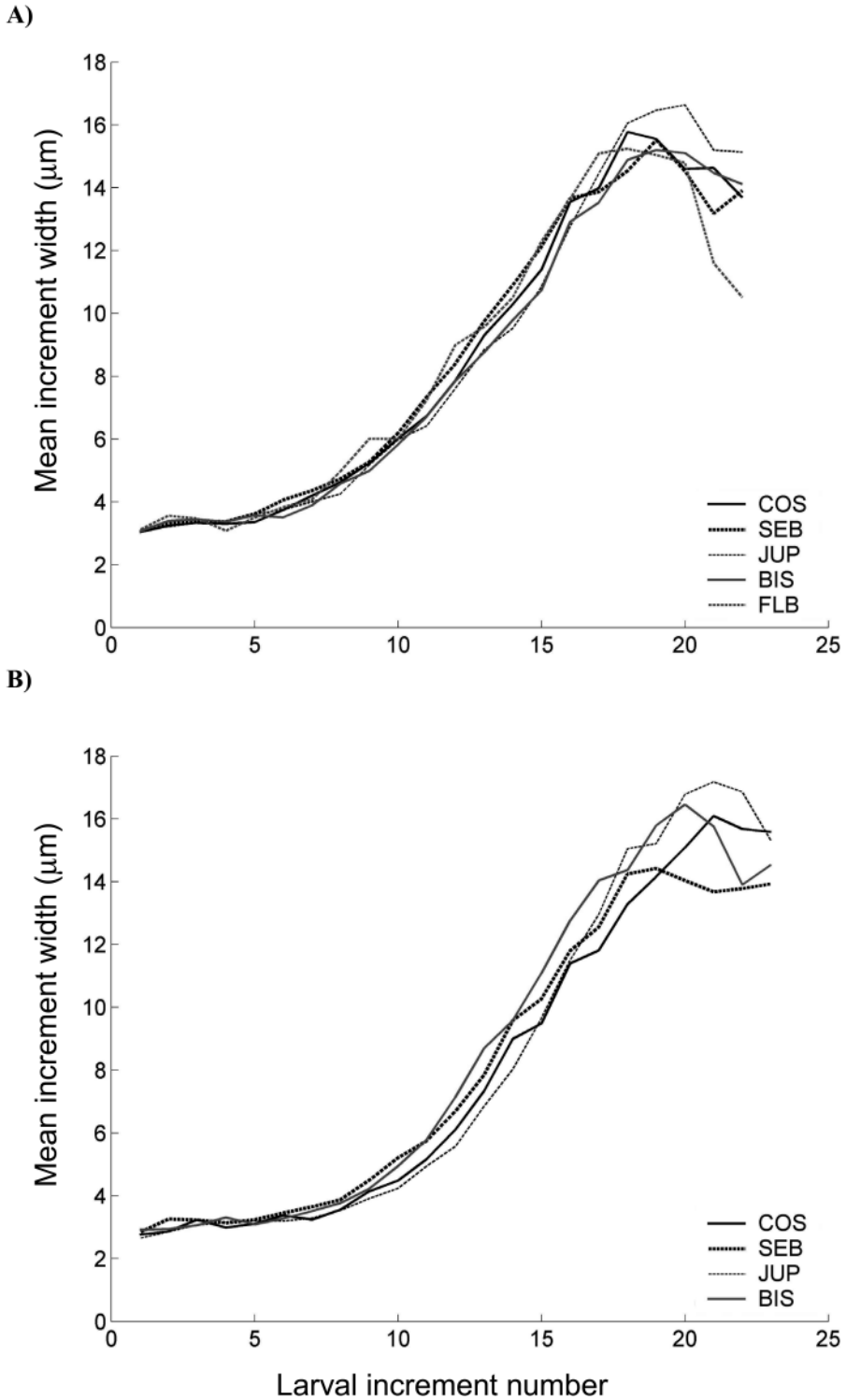


FIGURE 4.—Mean increment width as a function of larval increment number plotted to the mean pelagic larval duration for each year (without 3-d correction) for fish captured in (A) 2000 and (B) 2001 at the sites identified in Figure 1.

TABLE 3.—Mean pelagic larval durations (PLD; d) by site and year for gray snapper collected from the sites identified in Table 1. *P*-values are for Tukey pairwise tests comparing pelagic larval duration between sites for 2000 and 2001 and within sites between years; asterisks indicate significant differences at *P* < 0.05.

Year and statistic	Site				
	FLB	BIS	JUP	SEB	COS
2000					
Mean PLD	24.4	24.5	24.7	24.9	26.1
<i>n</i>	15	52	47	48	46
<i>P</i>					
FLB		1.000	1.000	0.931	0.059
BIS			0.992	0.880	0.002*
JUP				0.699	0.002*
SEB					0.054
2001					
Mean PLD		25.6	25.3	26.7	26.9
<i>n</i>		36	35	39	23
<i>P</i>					
BIS			0.901	0.233	0.170
JUP				0.048*	0.040*
SEB					0.973
2000–2001					
<i>P</i>		0.037*	0.066	0.001*	0.102

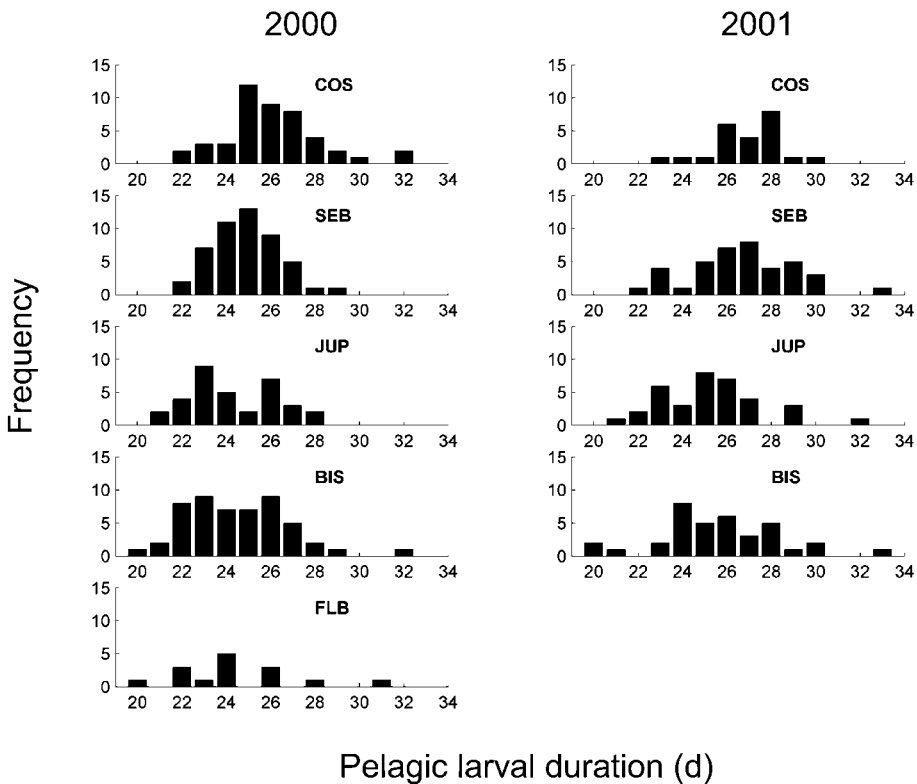


FIGURE 5.—Pelagic larval durations of gray snapper collected in 2000 and 2001 from five sites. The histograms are plotted from top to bottom in latitudinal order (north at the top, south at the bottom); sites are identified in Figure 1.

TABLE 4.—Mean otolith radius at settlement (μm) as a proxy for size at settlement by site and year for gray snapper collected from the sites identified in Table 1. *P*-values are for Tukey pairwise tests comparing radius at settlement between sites for 2000 and 2001 and within sites between years; asterisks indicate significant differences at $P < 0.05$.

Year and statistic	Site				
	FLB	BIS	JUP	SEB	COS
2000					
Mean otolith radius	180.92	179.09	182.17	190.80	204.97
<i>n</i>	15	52	47	48	46
<i>P</i>					
FLB		0.998	1.000	0.402	0.000*
BIS			0.948	0.018*	0.000*
JUP				0.248	0.000*
SEB					0.003*
2001					
Mean otolith radius		192.77	179.38	195.86	199.82
<i>n</i>		36	35	39	23
<i>P</i>					
BIS			0.108	0.95	0.715
JUP				0.024*	0.012*
SEB					0.931
2000–2001					
<i>P</i>		0.006*	0.632	0.274	0.277

TABLE 5.—Juvenile growth rates (mm/d) of gray snapper collected from the sites identified in Table 1 by site and year based on least-squares regression of standard length on days postsettlement. The *P*-values from an ANCOVA comparing the growth rates from each site for 2000 and 2001 and within sites between years are provided for each comparison; asterisks indicate significant differences at $P < 0.05$.

Year and statistic	Site				
	FLB	BIS	JUP	SEB	COS
2000					
Slope	0.8736	0.7953	0.8848	0.6865	0.6172
Intercept	8.230	7.214	6.590	9.113	10.949
R^2	0.86	0.83	0.82	0.90	0.74
<i>n</i>	15	52	34	48	46
<i>P</i>					
FLB		0.141	0.858	0.013*	0.001*
BIS			0.343	0.582	0.175
JUP				0.009*	0.000*
SEB					0.937
2001					
Slope		0.8060	0.8023	0.6757	0.7187
Intercept		8.080	9.242	10.071	10.620
R^2		0.78	0.74	0.92	0.76
<i>n</i>		36	35	39	23
<i>P</i>					
BIS			0.071	0.203	0.990
JUP				0.000*	0.260
SEB					0.209
2000–2001					
<i>P</i>		0.321	0.962	0.245	0.000*

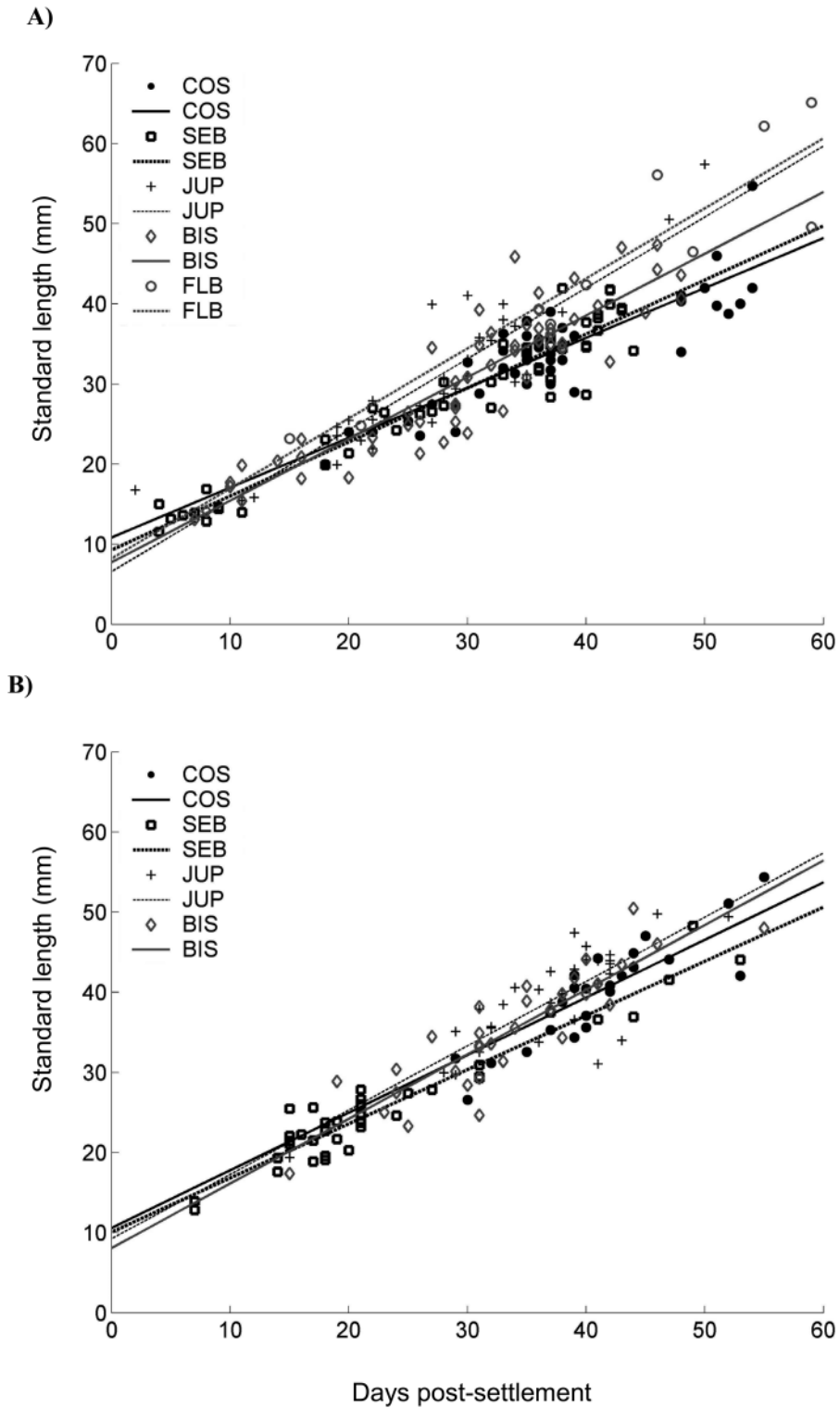


FIGURE 6.—Regression of standard length on days postsettlement for gray snapper captured in (A) 2000, and (B) 2001 from the sites identified in Figure 1. Slopes and intercepts are given in Table 5.

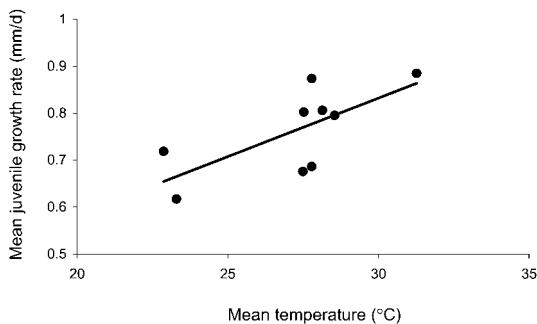


FIGURE 7.—Regression of mean juvenile growth rate on mean temperature (September and October) for gray snapper juveniles captured in 2000 and 2001 from the five collection sites. See Table 1 for site-specific temperatures. A least-squares regression line was fit to the data from both years ($y = 0.0249x + 0.0849$; $R^2 = 0.49$, $P < 0.001$).

the new and first-quarter moons. The exception was in 2000, where additional spawning was associated with the full and third-quarter moons at Core Sound, which led to an overall statistically uniform distribution (Figure 9).

Discussion

Larval Growth Trajectories

Larval otolith growth trajectories for juvenile gray snapper were similar across sites in both years except that in 2001 fish from Jupiter grew significantly faster than fish from Sebastian Inlet. The significant difference in growth occurred only during the last week before settlement as the larval growth trajectories of Sebastian Inlet fish leveled off before settlement relative to fish from the other sites. Latitudinal differences in water temperature are unlikely to be the cause of this difference because Sebastian Inlet and Jupiter are geographically close and had similar water temperatures. Further, larval growth rates of Core Sound fish did not differ from those at Sebastian Inlet, which

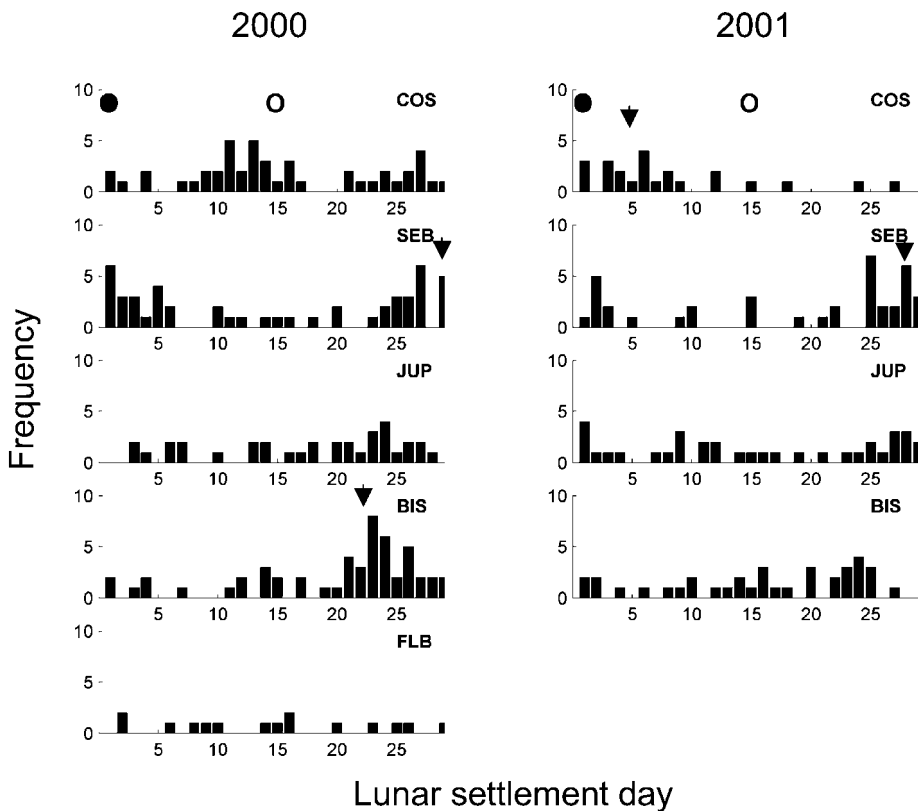


FIGURE 8.—Back-calculated settlement pattern, by site and year, of juvenile gray snapper plotted over a single lunar cycle. Rayleigh circular tests (Z -statistic) were used to test uniformity; where settlement was nonuniform, arrows indicate the mean lunar day of settlement. Day 1 = new moon; day 15 = full moon. Site codes as in Figure 1.

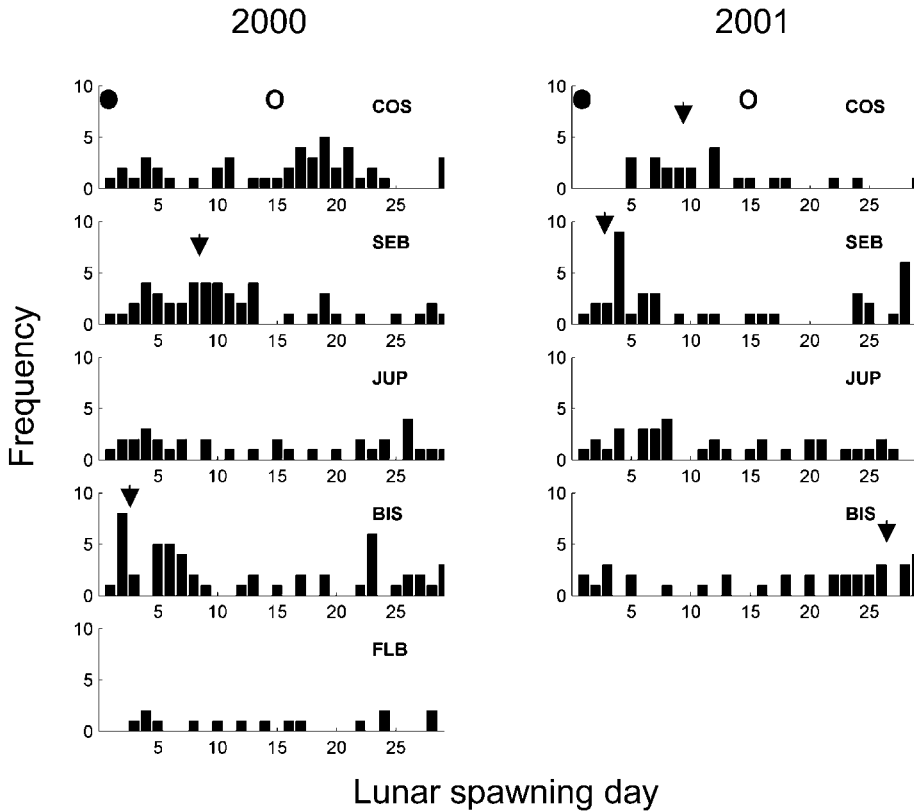


FIGURE 9.—Back-calculated spawning pattern, by site and year, of juvenile gray snapper plotted over a single lunar cycle. Rayleigh circular tests (Z-statistic) were used to test uniformity; where settlement was nonuniform, arrows indicate the mean lunar day of settlement. Day 1 = new moon; day 15 = full moon. Site codes as in Figure 1.

would be expected if differences in water temperature were significantly influencing the last portion of larval growth. A site-specific difference such as decreased primary production near Sebastian Inlet may have contributed to reduced larval growth before settlement as well as lower juvenile growth rates (see below). Overall, however, the trends of larval growth were similar among sites and years, suggesting that fish settling to different sites may have occupied a similar water mass during their larval phase and may have been transported from spawning sites by analogous paths.

Pelagic Larval Duration

Settlement marks on the otoliths of gray snapper appeared similar to those of several other reef fish species (Brothers and McFarland 1981; Victor 1982; Sponaugle and Cowen 1994): a darker ring followed by narrower and more regular growth rings during juvenile life. The PLDs measured for juvenile gray snapper in this study were very similar to those calculated for juvenile gray snapper

along the west coast of Florida (25 d; Allman and Grimes 2002), in Florida and Cuba (25–40 d; Lindeman 1997), and for newly settled juveniles collected along the coast of North Carolina (30 d; Tzeng et al. 2003; for consistency with this study, we added to Tzeng et al.'s increment counts a 3-d correction factor for time to first ring formation). The higher range in PLDs for snapper in Lindeman's (1997) study may result from inclusion of snapper from Cuba. Cuban fish may be spawned from an island source population (C. Paris, UM-RSMAS, personal communication) and thus may have different PLDs than do fish spawned along the southeastern United States. Despite the overall similarity in larval growth trajectories for fish in the present study, the PLDs of these fish were significantly different between the northern site and the southern sites. In both years, Core Sound fish had longer PLDs than fish from more southern sites. Although differences among sites were not always significant, there was a consistent trend in both years for longer PLDs at more northern sites.

The difference in PLDs, despite similar larval growth trajectories, suggests that habitat availability, rather than growth, determined the timing of settlement. Other reef species have been shown to delay settlement until suitable habitat is found (Victor 1986; Cowen 1991; Sponaugle and Cowen 1994).

Similar larval growth trajectories and slightly longer northern PLDs suggest that snapper larvae occupied the same or similar water masses originating south of North Carolina. If fish were transported north from Florida by the Gulf Stream, a small time lag may have been associated with finding suitable settlement habitat. Rough calculations indicate that PLDs are sufficient for larvae to be transported from known spawning aggregation sites around the Dry Tortugas (Domeier et al. 1996; Lindeman et al. 2001) 2,790 km to Cape Lookout, North Carolina (close to Core Sound). Based on an average Gulf Stream speed of 1.25 m/s (Hare and Cowen 1996), a planktonic organism could travel 2,808 km in 26 d, which places gray snapper larvae at approximately the right location by the time of their mean PLD. The interaction of active larval behavior and real Gulf Stream currents would result in variation around this estimate. Gray snapper larvae may be transported by way of the Gulf Stream to North Carolina and then across the continental shelf (Govoni and Pietrafesa 1994) into nearshore estuarine habitats, as are other larval fishes that utilize estuaries (Hare et al. 1999). Although analysis of juvenile gray snapper from Georgia and South Carolina would allow for greater spatial resolution, low numbers of juveniles precluded collections from these areas (J. Hare, NMFS Beaufort, personal communication).

Size at Settlement

Otolith size (radius) at settlement (reflecting somatic size at settlement) is related to larval growth rates and PLD. Although faster growing larvae typically have larger sizes-at-age, they are often smaller at settlement because they spend a shorter period in the plankton (Searcy and Sponaugle 2000). As a result of the longer time spent in the larval stage (i.e., longer PLD), Core Sound fish were significantly larger at settlement than fish from many of the other sites in both years. Fish from Sebastian Inlet also were larger at settlement than fish from Jupiter (2001) and Biscayne Bay (2000). Given that the mean increment width for snapper just before settlement was approximately 15 μm , one additional day in the larval period for

Core Sound fish led to a significant increase in otolith radius. Such PLD-induced differences in otolith radius are apparent among years as well: 2001 Biscayne Bay fish had a significantly larger otolith radius at settlement than those in 2000 because the PLD was significantly longer in 2001. Thus, despite generally similar larval growth trajectories, longer PLDs of fish settling to the northern site led to additional somatic and otolith growth and an increased size at settlement for those fish. Calculated size at settlement based on the regression of standard length on postsettlement age for fish from Core Sound in this study is consistent with settlement sizes found in a study of ingressing gray snapper in North Carolina (Tzeng et al. 2003).

Juvenile Growth Rates

The characteristics of water masses occupied by larval gray snapper collected in this study are not known; however, juveniles were collected from distinct locations characterized by different environmental conditions. A trend of faster juvenile growth for fish from the more southern sites was evident in the growth rates calculated by regressing standard length on postsettlement age. In both years growth rates were significantly different among sites. Juvenile growth rates tracked the latitudinal gradient in both years, but these differences were most apparent in 2000 when fishes from the southern sites, Florida Bay and Jupiter, grew the fastest, and fishes from the northernmost site, Core Sound, grew the slowest. In 2000 the mean water temperature in September–October ranged from 28.7°C to 27.4°C in Florida Bay and from 25.6°C to 21.0°C at Core Sound. Water temperature was highest in Jupiter (32–30.5°C), where fish had the highest growth rate. Latitudinal variation in water temperature is a probable explanation, given that growth is directly related to water temperature for many species (e.g., Lang et al. 1994; Nixon and Jones 1997). However, changes in other environmental factors cannot be ruled out. For example, in 2001, fish from Sebastian Inlet grew more slowly than fish from Jupiter despite rather similar water temperatures in that year. The broader shelf of Sebastian Inlet likely results in a different oceanographic regime, which could, for example, influence prey availability.

In general, temperature differences among sites accounted for at least half of the variability in juvenile growth rates. Clearly, other factors must have contributed to this variability. We have no data on prey availability or consumption differ-

ences among sites. All of the juveniles were collected in sea grass beds, the fish in Florida being collected in sea grass beds near mangroves. No doubt there are differences in species of sea grass and other community parameters, but no comparable work is available on habitat-specific differences in growth, so robust habitat differences cannot be evaluated in this study.

Overall, the mean juvenile growth rates calculated in this study (0.62–0.88 mm/d) were similar to the growth rates calculated for juvenile gray snapper by other workers. Lindeman's (1997) calculated growth rate of 0.92 mm/d may be slightly higher because of the inclusion of Cuban gray snapper, which may be experiencing different environmental conditions. Tzeng et al. (2003) used newly settled (11–16 mm) snapper to calculate a lower mean growth rate of 0.50 mm/d for snappers from North Carolina. The difference between our Core Sound growth rate and Tzeng et al.'s (2003) may be due to the larger size range (20–55 mm SL) of fish used in our study. Selective mortality of slower growers over time (see review by Sogard 1997) may skew the growth trajectories of older survivors toward faster growth. This also may have contributed to differences in growth rates between years at Core Sound in our study. Allman and Grimes (2002) sampled juveniles from the entire west coast of Florida and found growth rates of 1.0 mm/d in 1996 and 0.6 mm/d in 1997. In contrast to the present study, they found no significant difference in growth rates among fish across a latitudinal gradient from the panhandle to the southwestern tip of Florida.

Settlement and Spawning

The timing of settlement was generally coherent among most sites in Florida. In 2000, settlement of gray snapper to Biscayne Bay and Sebastian Inlet pulsed with the third-quarter and new moons. Settlement to Florida sites was less distinct in 2001 (only Sebastian Inlet fish had a significant pulse during the third-quarter to new moon), but the patterns were roughly similar to those seen in 2000. Settlement to Core Sound during 2000 occurred during the same period, but another pulse occurred during the first-quarter to full moon, 15 d later. Settlement of 2001 fish to Core Sound was entirely different, pulsing during the first-quarter moon. In general, fish at all of the sites except Core Sound settled in pulses associated with the third-quarter and new moons. These results differ somewhat from previous studies on the settlement pattern of gray snapper. Tzeng et al. (2003) found that major

pulses of ingressing snapper in North Carolina occurred during the new moon, with smaller numbers arriving around the full moon over the course of a 2-year study. Tzeng et al.'s (2003) study used settlement-stage gray snapper to analyze settlement patterns, whereas in this study we focused on early juveniles. Therefore, the slight difference in lunar settlement patterns might be the result of selective mortality. Allman and Grimes (2002) found settlement along the west coast of Florida to be marginally associated with the new moon in one of the years of their sampling but not in the other. Contrary to Smith (1995), who found no correlation between settlement and the lunar cycle in Sebastian Inlet, during both years of this study gray snapper settlement to Sebastian Inlet was significantly associated with the third-quarter to new moon. Settlement during this time of the lunar cycle may reflect both light levels and tidal amplitude cycles. Predation risk is thought to be lower during the waning moon because of reduced light levels (Johannes 1978), which may increase the likelihood of survival for larvae settling during the third-quarter and new moons. Core Sound snapper exhibited the greatest variability in the timing of settlement, which may reflect longer transport times to Core Sound. If snapper are transported from distant sources, larvae may have fewer options and be less able to synchronize their settlement to environmental cues. The trade-off between remaining in the plankton and settling during optimum conditions probably shifts as larvae get older (Sponaugle and Pinkard 2004a, 2004b).

Back-calculated successful spawning dates were also more similar among Florida sites. In the year 2000, recruits from Biscayne Bay and Sebastian Inlet were spawned primarily during the new and first-quarter moons. A similar pattern was apparent in 2001. In contrast, successful spawning of Core Sound fish was associated with the first-quarter moon in 2001 but was not significantly different from uniform timing in 2000 because of a strong peak associated with the full to third-quarter moon and a weaker peak at the new first-quarter moon. Spawning pulses during the new moon agree with previously published data. Tzeng et al. (2003) found that juvenile gray snapper collected from North Carolina had back-calculated spawning dates associated with the new moon. Domeier et al. (1996) concluded that adult spawning peaked during the new and full moons. Allman and Grimes (2002) found a marginal association of spawning with the lunar cycle in 1 year of sampling but no association in the second year. The difference in

successful spawning patterns between Core Sound fish and the other sites may be related to the constraints associated with long-distance transport.

The differences in the settlement patterns of gray snapper from the Florida sites and Core Sound despite similar larval growth rates are consistent with transport of larvae up the southeastern U.S. coast. Similar larval otolith growth trajectories suggest that larvae occupy the same or similar water masses, such as the Gulf Stream. Slightly longer PLDs for fish settling to North Carolina are not due to differences in larval growth rates but more likely are the result of lack of access to suitable settlement habitat. Our findings are consistent with the idea that these larvae are Gulf Stream exports (Burton 2001); however, future studies will combine these age and growth data with otolith microchemistry data to gain a better understanding of the population connectivity for this species.

Acknowledgments

This study was conducted as part of a larger study on snapper population connectivity in collaboration with S. Thorrold (WHOI), J. Hare (NMFS, Beaufort), R. Cowen (UM-RSMAS), and L. Barbieri (FFWCC). This work is a result of research sponsored in part by NOAA Office of Sea Grant, U.S. Department of Commerce, under Grant No. NA96RG00025 to the Virginia Graduate Marine Science Consortium and Virginia Sea Grant College Program. The U.S. Government is authorized to produce and distribute reprints for governmental purposes, notwithstanding any copyright notation that may appear hereon. We thank J. Hare, NMFS Beaufort Laboratory, and L. Barbieri and E. McDevitt, Florida Fish and Wildlife Conservation Commission, for sample collection. J. Fortuna (UM-RSMAS) and E. Laban (NMFS Beaufort) provided guidance in the techniques of preparing otolith sections. The manuscript benefited from conversations with or comments of S. Thorrold, J. Hare, R. Cowen, J. Serafy, D. Benetti, C. Paris, K. Lindeman, K. Grorud-Colvert, and three anonymous reviewers.

References

- Ahrenholz, D. W. 2000. Periodicity of growth increment formation in otoliths of juvenile gray snapper (*Lutjanus griseus*) and lane snapper (*Lutjanus synagris*). *Journal of the Elisha Mitchell Scientific Society* 116:251–259.
- Allman, R. J. 1999. The temporal and spatial dynamics of spawning, settlement, and growth of gray snapper (*Lutjanus griseus*) determined using otolith microstructure. Master's thesis. Florida State University, Tallahassee.
- Allman, R. J., and C. B. Grimes. 2002. Temporal and spatial dynamics of spawning, settlement, and growth of gray snapper (*Lutjanus griseus*) from the West Florida shelf as determined from otolith microstructures. *Fishery Bulletin* 100:391–403.
- Ault, J. S., J. A. Bohnsack, and G. A. Meester. 1998. A retrospective (1979–1996) multispecies assessment of coral reef fish stocks in the Florida Keys. *Fishery Bulletin* 96:395–414.
- Boehlert, G. A., and M. M. Yoklavich. 1983. Effects of temperature, ration, and fish size on growth of juvenile black rockfish, *Sebastes melanops*. *Environmental Biology of Fishes* 8:17–28.
- Brothers, E. B. 1987. Methodological approaches to the examination of otoliths in aging studies. Pages 319–330 in G. E. Hall, editor. *Age and growth of fish*. Iowa State University Press, Des Moines.
- Brothers, E. B., and W. N. McFarland. 1981. Correlations between otolith microstructure, growth, and life history transitions in newly recruited French grunts (*Haemulon flavolineatum*, Haemulidae). *Rapports et Proces-Verbaux des Reunions, Conseil International pour l'Exploration de la Mer* 178:369–372.
- Buckel, J. A., N. D. Steinberg, and D. O. Conover. 1995. Effects of temperature, salinity, and fish size on growth and consumption of juvenile bluefish. *Journal of Fish Biology* 47:696–706.
- Burton, M. L. 2001. Age, growth, and mortality of gray snapper, *Lutjanus griseus*, from the east coast of Florida. *Fishery Bulletin* 99:254–265.
- Campana, S. E., and J. D. Neilson. 1985. Microstructure of fish otoliths. *Canadian Journal of Fisheries and Aquatic Sciences* 42:1014–1032.
- Chambers, R. C., and T. J. Miller. 1995. Evaluating fish growth by means of otolith increment analysis: special properties of individual-level longitudinal data. Pages 155–174 in D. Secor, J. Dean, and S. Campana, editors. *Recent developments in fish otolith research*. University of South Carolina Press, Columbia.
- Claro, R. 1991. Changes in fish assemblages structure by the effect of intense fisheries activity. *Tropical Ecology* 32:36–46.
- Claro, R., K. C. Lindeman, and L. R. Parenti, editors. 2001. *Ecology of the marine fishes of Cuba*. Smithsonian Institution Press, Washington, D.C.
- Cowen, R. K. 1991. Variation in the planktonic larval duration of the temperate wrasse *Semicossyphus pulcher*. *Marine Ecology Progress Series* 69:9–15.
- Crocker, R. A. 1962. Growth and food of the gray snapper, *Lutjanus griseus*, in Everglades National Park. *Transactions of the American Fisheries Society* 91:379–383.
- Domeier, M. L., C. C. Koenig, and F. C. Coleman. 1996. Reproductive biology of gray snapper (*Lutjanus griseus*), with notes on spawning for other Western Atlantic snappers (Lutjanidae). Pages 189–201 in F. Arreguin-Sanchez, J. L. Munro, M. C. Balgos, and D. Pauly, editors. *Biology and culture of tropical*

- groupers and snappers. ICLARM Publishing, Philippines.
- Govoni, J. J., and L. J. Pietrafesa. 1994. Eulerian views of layered water currents, vertical distribution of some larval fishes, and inferred advective transport over the continental shelf off North Carolina, USA, in winter. *Fisheries Oceanography* 3:120–132.
- Hare, J. A., and R. K. Cowen. 1996. Transport mechanisms of larval and pelagic juvenile bluefish (*Pomatomus saltatrix*) from South Atlantic Bight spawning grounds to Middle Atlantic Bight nursery habitats. *Limnology and Oceanography* 41:1264–1280.
- Hare, J. A., J. A. Quinlan, F. E. Werner, B. O. Blanton, J. J. Govoni, R. B. Forward, L. R. Settle, and D. E. Hoss. 1999. Larval transport during winter in the SABRE study area: results of a coupled vertical larval behaviour-three-dimensional circulation model. *Fisheries Oceanography* 8(Supplement 2): 57–76.
- Hettler, W. F., and D. L. Barker. 1993. Distribution and abundance of larval fishes at two North Carolina inlets. *Estuarine, Coastal, and Shelf Science* 37: 161–173.
- Johannes, R. E. 1978. Reproductive strategies of coastal marine fishes in the tropics. *Environmental Biology of Fishes* 3:65–84.
- Johnson, T. B., and D. O. Evans. 1996. Temperature constraints on overwinter survival of age-0 white perch. *Transactions of the American Fisheries Society* 125:466–471.
- Laegdsgaard, P., and C. Johnson. 2001. Why do juvenile fish utilise mangrove habitats? *Journal of Experimental Marine Biology and Ecology* 257:229–253.
- Lang, K. L., C. B. Grimes, and R. F. Shaw. 1994. Variation in the age and growth of yellowfin tuna larvae, *Thunnus albacares*, collected about the Mississippi River plume. *Environmental Biology of Fishes* 39:259–270.
- Ley, J. A., and C. C. McIvor. 2002. Linkages between estuarine and reef fish assemblages: enhancement by the presence of well-developed mangrove shorelines. Pages 539–562 in J. W. Porter and K. G. Porter, editors. *The Everglades, Florida Bay, and coral reefs of the Florida Keys: an ecosystem sourcebook*. CRC Press, Boca Raton, Florida.
- Lindeman, K. C. 1997. Development of grunts and snappers of southeast Florida: cross-shelf distributions and effects of beach management alternatives. Doctoral dissertation. University of Miami, Coral Gables, Florida.
- Lindeman, K. C., T. N. Lee, W. D. Wilson, R. Claro, and J. S. Ault. 2001. Transport of larvae originating in southwest Cuba and the Dry Tortugas: evidence for partial retention in grunts and snappers. *Proceedings of the Gulf and Caribbean Fisheries Institute* 52:732–747.
- Manooch, C. S., III, and R. H. Matheson III. 1984. Age, growth, and mortality of gray snapper collected from Florida waters. *Proceedings of the Annual Conference Southeastern Association of Fisheries and Wildlife Agencies* 35(1981):331–344.
- Media Cybernetics. 1998. *Image-Pro Plus: the proven solution for image analysis*. Media Cybernetics, Silver Spring, Maryland.
- Meekan, M. G., and L. Fortier. 1996. Selection for faster growth during the larval life of Atlantic cod, *Gadus morhua*, on the Scotian shelf. *Marine Ecology Progress Series* 137:25–37.
- Miller, G. C., and W. J. Richards. 1980. Reef fish habitat, faunal assemblages, and factors determining distributions in the South Atlantic Bight. *Proceedings of the Gulf and Caribbean Fisheries Institute* 32:114–130.
- Miller, T. J., L. B. Crowder, J. A. Rice, and E. A. Marschall. 1988. Larval size and recruitment mechanisms in fishes: toward a conceptual framework. *Canadian Journal of Fisheries and Aquatic Sciences* 45:1657–1670.
- Nagelkerken, I., T. Kleijnen, R. A. Klop, C. J. van den Brand, E. Cocheret de la Moriniere, and G. van der Velde. 2001. Dependence of Caribbean reef fishes on mangroves and sea grass beds as nursery habitats: a comparison of fish faunas between bays with and without mangroves/sea grass beds. *Marine Ecology Progress Series* 214:225–235.
- Nixon, S. W., and C. M. Jones. 1997. Age and growth of larval and juvenile Atlantic croaker, *Micropogonias undulatus*, from the Middle Atlantic Bight and estuarine waters of Virginia. *Fishery Bulletin* 95:773–784.
- Robins, C. R., G. C. Ray, J. Douglas, and R. Freud. 1986. *A field guide to Atlantic coast fishes*. Houghton Mifflin, Boston.
- Rutherford, E. S., E. B. Thue, and D. G. Buker. 1983. Population structure, food habits, and spawning activity of gray snapper, *Lutjanus griseus*, in Everglades National Park. National Park Service, South Florida Research Center Report SFRC-83/02, Homestead, Florida.
- Searcy, S., and S. Sponaugle. 2000. Variable larval growth in a coral reef fish. *Marine Ecology Progress Series* 206:213–226.
- Secor, D. H., J. M. Dean, and E. H. Laban. 1991. *Manual for otolith removal and preparation for microstructural examination*. Electric Power Research Institute and Belle W. Baruch Institute for Marine Biology and Coastal Research, Palo Alto, California.
- Smith, S. L. 1995. Recruitment of larval snappers (Family Lutjanidae) through Sebastian Inlet, Florida. Master's thesis. Florida Institute of Technology, Melbourne, Florida.
- Sogard, S. 1997. Size-selective mortality in the juvenile stage of teleost fishes: a review. *Bulletin of Marine Science* 60:1129–1157.
- Sokal, R. R., and F. J. Rohlf. 2000. *Biometry*. Freeman, New York.
- Sponaugle, S., and R. K. Cowen. 1994. Larval durations and recruitment patterns of two Caribbean gobies (Gobiidae): contrasting early life histories in demersal spawners. *Marine Biology* 120:133–143.
- Sponaugle, S., and D. Pinkard. 2004a. Impact of variable pelagic environments on natural larval growth

- and recruitment of a reef fish. *Journal of Fish Biology* 64:34–54.
- Sponaugle, S., and D. Pinkard. 2004b. Lunar cyclic population replenishment of a coral reef fish: shifting patterns following oceanic events. *Marine Ecology Progress Series* 267:267–280.
- Starck, W. A., II, and R. E. Schroeder. 1971. Investigations on the gray snapper, *Lutjanus griseus*. University of Miami Press, Coral Gables, Florida.
- Sumner, F. B., R. C. Osburn, and L. J. Cole. 1911. A biological survey of the waters of Woods Hole. U.S. Bureau of Fisheries Bulletin 31:549–794.
- Szedlmayer, S. T., and J. Conti. 1999. Nursery habitats, growth rates, and seasonality of age-0 red snapper, *Lutjanus campechanus*, in the northeast Gulf of Mexico. *Fishery Bulletin* 97:626–635.
- Tupper, M., and R. G. Boutilier. 1995. Effects of habitat on settlement, growth, and postsettlement survival of Atlantic cod (*Gadus morhua*). *Canadian Journal of Fisheries and Aquatic Sciences* 52:1834–1841.
- Tzeng, M. W., J. A. Hare, and D. G. Lindquist. 2003. Ingress of transformation stage gray snapper, *Lutjanus griseus* (Pisces: Lutjanidae) through Beaufort Inlet, North Carolina. *Bulletin of Marine Science* 72:891–908.
- Underwood, A. J. 1997. *Experiments in ecology: their logical design and interpretation using analysis of variance*. Cambridge University Press, Cambridge, UK.
- Victor, B. C. 1982. Daily otolith increments and recruitment in two coral reef wrasses, *Thalassoma bifasciatum* and *Halichoeres bivittatus*. *Marine Biology* 90:317–326.
- Victor, B. C. 1986. Delayed metamorphosis with reduced larval growth in a coral reef fish (*Thalassoma bifasciatum*). *Canadian Journal of Fisheries and Aquatic Sciences* 43:1208–1213.
- Zar, J. H. 1984. *Biostatistical analysis*. Prentice-Hall, Englewood Cliffs, New Jersey.