Abstract.–We sampled inner shelf habitat in the northeast Gulf of Mexico, for age-0 red snapper, *Lutjanus campechanus*, to estimate growth rates and seasonality, as well as to identify nursery habitats. We collected 7507 age-0 red snapper in 1994 and 1995, from 536 10-min trawl tows. Red snapper first settled to benthic habitat in June after reaching 17.4 mm standard length (age=26 d). In both years, catch per unit of effort (CPUE=number/10-min tow) peaked July through September, then declined in the fall as fish were leaving the habitat before winter. Most fish (80–81%) were caught at one location, 13 km south of Mobile Bay, Alabama. At this location in 1995, the August CPUE ±SE (712 ±243) far exceeded all previous estimates. Based on otolith microincrements, hatching-date frequencies showed distinct cohorts in June and July 1994 and May and June 1995. Growth rates for the June (0.77 mm/d) and July (0.71 mm/d) cohorts in 1994 were significantly faster compared with growth rates for May (0.51 mm/d) and June (0.67 mm/d) cohorts in 1995. Density-dependent mechanisms may be operating with faster growth rates and lower CPUEs in 1994, compared with slower growth rates and higher CPUEs in 1995. However, environmental constraints may also be operating, as indicated by the slow growth rate of the May 1995 cohort that probably resulted from colder temperatures. Newly settled red snapper were aggregated on the inner shelf, at a particular location and time period. These concentrations indicated an important nursery habitat just south of Mobile Bay, Alabama, from July through September.

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Nursery habitats, growth rates, and seasonality of age-0 red snapper, *Lutjanus campechanus*, in the northeast Gulf of Mexico*

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To enhance survival some fishes spawn many times within a given season (Lambert and Ware, 1984). This strategy may produce several distinct cohorts at the juvenile stage within that season (Szedlmayer et al., 1990), and individual cohorts may have an advantage over others owing to biotic and abiotic environmental factors (Miranda and Hubbard, 1994). For example, faster growth may increase survival because fish grow past size-specific predators more quickly than slower growing fish (Houde, 1987; Sogard, 1997).

Red snapper, *Lutjanus campechanus*, have an extended spawning season (Moseley, 1966; Collins et al., 1996) and within-year variations in early life stages might be expected, but information on the age-0 juvenile stage of red snapper is sparse, especially at first settlement. Baughman (1943) suggested that immature fish came close to shore, but this observation was based on only five juvenile red snapper. Ogren and Brusher (1977) indicated inshore nursery areas for age-0 red snapper in the deeper portions of St. Andrew's Bay, Florida, but catch rates were low—a total of 62 fish in 312 10-min trawl tows. Bradley and Bryan (1975) caught young red snapper during summer months and suggested that juvenile red snapper sought deeper water as they grew older, albeit their catch rates were also low, with a maximum of 10 fish/10-min tow. Holt and Arnold (1982) showed a bimodal size distribution in juvenile red snapper from June through December, but this pattern was derived from separate year classes, where red snapper reached 110–130 mm during their first year, 220–230 mm during their second year. Age-0 red snapper were conspicuously absent from that study in July, and only 26 age-0 red snapper were collected in three years of August samples. Szedlmayer and Shipp (1994) reported a catch rate for age-0 red snapper in July 1991 that exceeded all previous studies (130 fish/10-min tow), but their effort was low with only 17 trawl tows in July, August, and October.

Despite these previous efforts, no study has specifically targeted age-0 red snapper just after settlement. Thus, we suspected that the primary nursery habitats used by first settlers had not been adequately sampled. In the present study we examine the early life stage of red snapper just after settlement. We determine growth rates, distribution, seasonality, and

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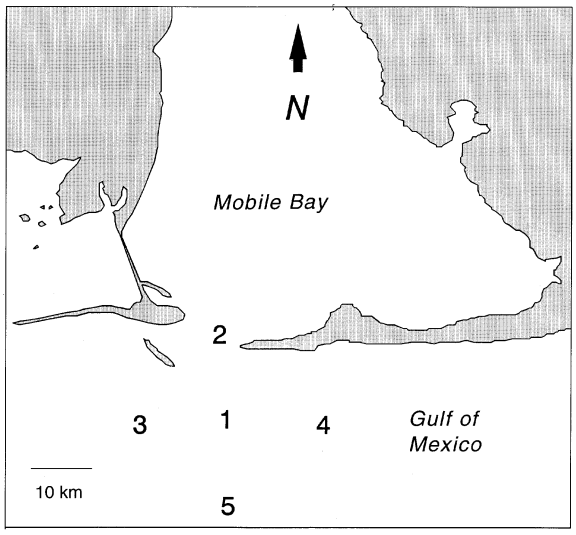

Figure 1
Map of station locations in the northeast Gulf of Mexico.

abundance; and identify multiple cohorts and primary nursery areas for this species.

Materials and methods

Age-0 red snapper were collected 0–26 km south of Mobile Bay, Alabama. Fish were sampled by trawl (7.62-m head rope, 2.54-cm mesh, 2-mm codend mesh). Five 10-min tows were taken every two weeks, at five fixed stations, from June 1994 through January 1995, and from June 1995 through January 1996 (Fig. 1). Sampling periods were sometimes longer owing to poor weather.

All trawl tows were made with a 6:1 ratio of towing cable length to depth, and tow speeds of 40 to 80 m/min. Bottom dissolved oxygen, salinity, and temperature were recorded with a Hydrolab Surveyor II. We did not sample in May but were able to plot temperature data measured at 1 m depth, for May through December, from a NOAA buoy moored 70 km west of the sites. Sediment samples were collected by SCUBA divers and examined by grain size analysis (Holme and McIntyre, 1971).

All age-0 red snapper were stored on ice in the field and later frozen in the laboratory. Fish were thawed, weighed to the nearest 0.01 g with an Ohaus balance, and measured with a caliper to the nearest 0.1 mm standard length (SL).

Sagittal otoliths were removed from all age-0 red snapper and mounted in epoxy (Spurr, 1969). Left and right sagittal otoliths were assumed to be identical; only one otolith was used to estimate age from a particular fish. Otoliths mounted in epoxy were first cut with a Buehler diamond blade saw, then mounted on glass slides with Crystalbond thermoplastic cement, and ground on both sides in the transverse plane to the primordium, on 400 and 600 grit wet-dry sand paper. Type A alumina powder (0.3 µm) and Buehler polishing cloth were used for final otolith preparations (Secor et al., 1991).

Microincrements of otoliths were counted from the primordium to the margin, along the sulcus ridge, in the transverse plane. We made all counts at 750× magnification, using a Sony GVM video monitor, a Sony CCD video camera, and an Olympus BH2 light microscope.

Two independent blind counts were made on each otolith. If the two independent counts were within 10% of each other, their mean value was used to estimate age. If the two counts differed by >10%, a third blind count was made. The means of the two closest counts were then used to estimate ages. If counts still differed by >10 % after three counts, the otolith was rejected.

Age of each fish was subtracted from date of capture for hatching-date estimations. Hatching-date histograms were plotted after applying a three-day moving average for each year, and local minima were used to separate cohorts (Szedlmayer et al., 1991). A significance level of ≤0.05 was used for all statistical analysis. Catch per unit of effort (CPUE=mean number/10-min tow) was estimated for each sample date and station. Prior to analysis CPUEs were $\log(x+1)$ base-10 transformed. Two-way analysis of variance (ANOVA) was used to test for significant differences in mean CPUEs and mean SLs among dates and stations. Waller-Duncan's multiple comparison test was used to show specific differences detected by the ANOVAs.

Growth rates were estimated by linear regression of SL on collection date, and SL on age from otolith microincrement counts. Analysis of covariance (ANCOVA), Student's *t*-test, and Tukey's multiple comparison test were used to compare estimated growth rates (Zar, 1984).

Results

Salinity ranged from 30.5 to 35.4 ppt, dissolved oxygen from 3.7 to 7.9 ppm in 1994. Temperature increased from 22°C in June to a peak of 29°C in August, then decreased to 17°C by January 1995. The temperature (26°C) in early June 1995 was higher compared with the previous year, stayed near this level through July, increased to 30°C in September, then decreased in the fall (Fig. 2). Temperature data from the NOAA buoy indicated that temperatures

were probably colder in May of both years at the sample sites (Fig. 2). Temperature, salinity, and dissolved oxygen were similar among stations (Table 1). Visual observations of debris in trawl samples indicated shell deposits at station 1 that were not apparent at other stations. Grain size analysis indicated similar sediments between stations 1 and 5, and between stations 2 and 4, whereas station 3 had a significantly higher silt-clay fraction compared with all other stations (ANOVA, $P \leq 0.05$; Table 1).

From these nursery habitats, we collected 7507 age-0 red snapper from 536 10-min trawl tows in 1994 and 1995. Significantly more fish were collected in 1995 than in 1994 (ANOVA, $P \leq 0.05$; Fig. 3). Age-0 red snapper first settled to these habitats in late June, showed highest abundance July through September, then steadily declined in the fall of both years (ANOVA, $P \leq 0.05$; Fig. 3). Most fish, 80–81%, were collected at station 1 (ANOVA, $P \leq 0.05$; Fig. 4). At station 1, significantly higher peaks in CPUE ±SE for 1994, were 63.6 ±8.9 in July, 60.8 ±26.2 in August, and 40.3 ±13.4 in September (ANOVA, $P \leq 0.05$). In late August 1995 at station 1, we observed a CPUE (712 ±243) that far exceeded all previous estimates from this study or any previous study. Other significant peaks in CPUE for 1995 at station 1 were 76.2 ±21.4 in mid-August, and 81.4 5.0 in mid-September (ANOVA, $P \leq 0.05$).

Age-0 red snapper ranged from 17.8 to 124.4 mm SL. Fish first settled from the plankton after they reached 17.8 mm SL. The smallest (<20 mm SL) were present both years into mid-September, after which no new settlers were detected (Fig. 5). Significantly higher mean SLs were detected by late August in both years compared with earlier sample periods; size significantly increased with season (ANOVA, $P \leq 0.05$; Table 2; Fig. 5). Fish were significantly larger earlier in 1995, but fish from 1994 caught up in size by September, after which 1994 fish were significantly larger than 1995 fish (ANOVA, $P \leq 0.05$; Table 2; Fig. 5).

In 1994, age-0 red snapper were first abundant (CPUE=63.6) at station 1 and had limited settlement (CPUE=2.0) at station 3 (Fig. 6). Also, fish were significantly larger (ANOVA, $P \leq 0.05$), less abundant, and showed up later at all other stations compared with fish at station 1 in 1994. We did not detect patterns in inshore-offshore movement from fish size, location, and seasonality; we did determine that after first settlement at station 1, fish showed expansion in all directions (Fig. 6). In 1995, new recruits were most abundant in July at station 3 (CPUE=78). After July, patterns were similar to 1994, and most fish were observed at station 1 and fewer larger fish were observed at other stations later in the season (Fig. 7).

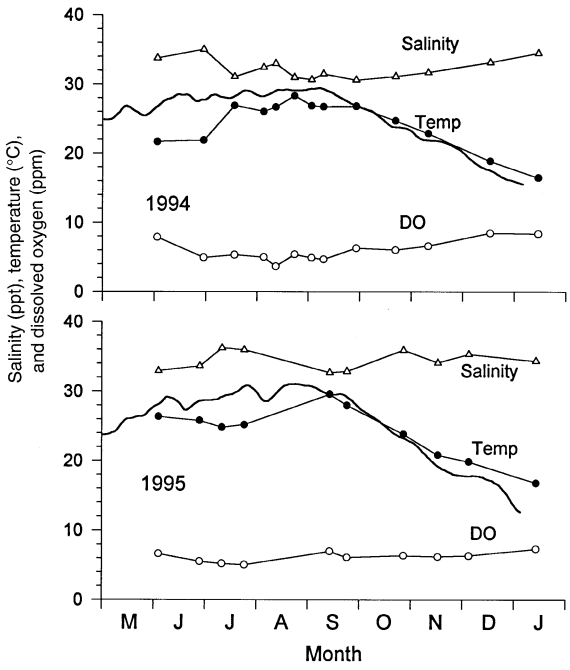

Figure 2

Bottom water temperature (°C), salinity (ppt), and dissolved oxygen (ppm) pooled by stations, in the northeast Gulf of Mexico, from June 1994 to January 1995, and June 1995 to January 1996. Lines without symbols are mean daily surface temperatures based on 10-d moving averages, obtained from a NOAA moored buoy.

The required precision (≤10%), was shown for 57% of all otolith counts (Table 3). Age of red snapper was 26 to 144 days; thus fish may spend up to four months in these habitats. We detected separate late May–June and July cohorts in 1994, and May and June cohorts in 1995, from hatching-date frequencies (Fig. 8).

Growth rates were significantly different among cohorts (ANCOVA, $P \leq 0.05$). The fastest growth rates were observed for June (0.77 mm/d) and July (0.71 mm/d) cohorts in 1994. Growth rates for May (0.51 mm/d) and June (0.67 mm/d) cohorts in 1995 were significantly less than the previous year and significantly different from each other (ANCOVA, $P \leq 0.05$; Fig. 9). Growth rate estimates from SL on varying dates (0.52 mm/d in 1994; 0.62 mm/d in 1995; Fig. 5) were significantly lower than most cohort growth estimates, with the exception of the slow growing May 1995 cohort (ANCOVA, $P \leq 0.05$). In station comparisons for 1995, fish from station 2 had a significantly faster growth rate (0.86 mm/d), followed by fish from station 1 (0.71 mm/d), whereas slower growth rates were observed for station 3 (0.54 mm/d) and station 5 (0.60 mm/d; ANCOVA, $P \leq 0.05$; Table

Table 1

Mean temperatures, mean salinities, mean dissolved oxygen (DO), depths, and +SEs substrate types for trawl stations from the northeast Gulf of Mexico. See Figure 1, for station locations.

Station	Mean temperature (°C)	Mean salinity (ppt)	Mean DO (ppm)	Depth (m)	Substrate type
1994					
1	24.5+1.0	32.7+0.5	5.4+0.4	18.7+0.6	fine sand-shell
2	24.6+1.3	29.9+0.9	6.1+0.5	15.6+0.6	coarse sand
3	24.3+1.4	31.7+0.7	6.1+0.5	13.4+0.6	silt, clay, sand
4	24.9+1.3	32.3+0.5	6.3+0.4	15.0+0.4	coarse sand
5	24.6+1.2	32.7+0.5	6.3+0.4	20.7+0.6	fine sand
1995					
1	24.0+1.2	35.5+0.7	6.3+0.4	19.5+0.1	fine sand-shell
2	25.3+1.2	32.6+0.4	6.2+0.2	16.1+0.7	coarse sand
3	22.6+1.3	33.6+1.3	5.5+0.5	12.7+0.2	silt, clay, sand
4	23.6+1.2	35.6+0.4	6.1+0.2	14.8+0.2	coarse sand
5	23.8+1.3	34.8+0.9	6.5+0.3	20.8+0.2	fine sand

4). Station 4 growth rates were not estimated because of low catch rates.

Discussion

Age-0 red snapper used inner shelf habitat at first settlement, and an area 13 km south of Mobile Bay (station 1) held particularly high numbers. No other study has reported such high CPUEs of age-0 red snapper. Many factors could contribute to this important nursery habitat at station 1. Temperature, dissolved oxygen, salinity, and depths, showed little difference among stations, but one potential aspect that may provide avenues for future studies is substrate type. The substrate in this area may be highly suitable, e.g. relic shell beds (Schroeder et al., 1995) with fine sand sediments, and there is a general shift from shell-sand-mud to "clean" sand east of Mobile Bay,[1] where few fish were collected. Age-0 red snapper may be selecting such shell habitats. For example, age-0 red snapper showed a preference for shell over sand substrata in laboratory studies (Szedlmayer and Howe, 1997)and a preference for almost any small relief structure (e.g. shells) in relation to flat sand substrata in natural habitats (Workman and Foster, 1994). Shells were observed in trawl collections at station 1 and not apparent in trawl samples at other stations. However, we were un-

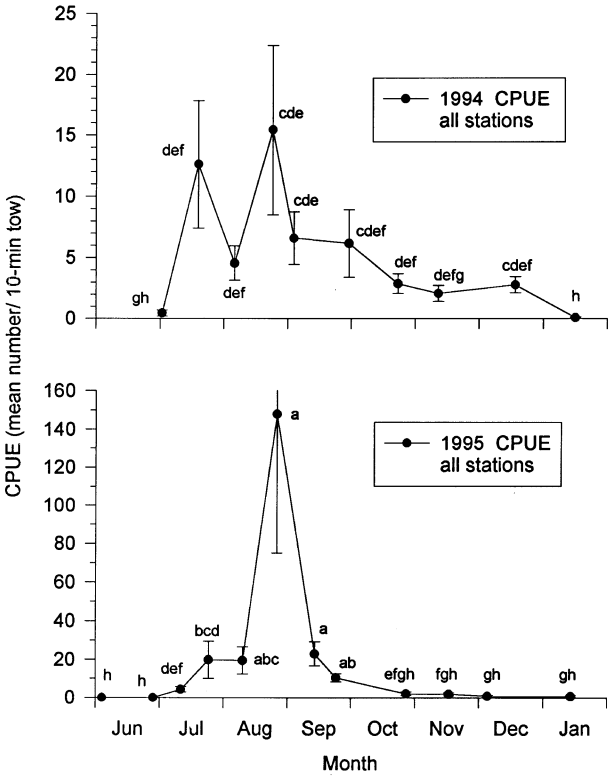

Figure 3

Mean CPUE (number/10-min tow) of age-0 red snapper, *Lutjanus campechanus*, by date from the northeast Gulf of Mexico. Each point represents mean CPUE for that date. Error bars are standard errors. Different letters show significant differences both within and between years (ANOVA; Waller-Duncan test; $P \leq 0.05$).

[1] Hummell, R. L. 1998. Geological survey of Alabama, Tuscaloosa, AL. Personal commun.

able to confirm the presence of shell deposits from sediments collected by SCUBA divers.

Red snapper first settled in June, showed peaks in July, August, and September, then quickly declined in numbers from the habitat. There is evidence that this decline of age-0 red snapper from open relatively flat habitats in the fall results from larger age-0 fish migrating to reef structure. In a study of fish recruitment to 1-m^3 concrete artificial reefs, 20 km south of Mobile Bay, age-0 red snapper showed large (up to 89 fish/reef) influxes to these reefs in September and October.[2] This seasonal pattern was similar to the pattern suggested by Holt and Arnold (1982). They found that recruitment of small red snapper to benthic substrate occurred primarily from June through September, and in the fall a few larger age-0 fish were collected by trap near a sunken ship.[3]

Metamorphosis from larva to juvenile is ecologically important in the early life history of fish. In

Table 2

Mean SL (mm) of age-0 red snapper, *Lutjanus campechanus*, for each sample date in 1994 and 1995, from the northeast Gulf of Mexico. Means with different letters show significant differences (ANOVA, Waller-Duncan's test; $P<0.05$).

Date	*n*	Mean SL (mm)	SE
30 June 94	5	25.0[a]	2.01
11 July 94	328	24.1[a]	0.19
1 August 94	121	36.1[c]	0.64
11 August 94	137	26.6[a]	0.72
17 August 94	401	36.1[c]	0.66
30 August 94	165	41.6[d]	1.22
8 September 94	322	42.9[d]	0.46
26 September 94	154	70.5[hg]	1.88
13 October 94	72	75.4[i]	1.59
31 October 94	54	85.9[j]	1.28
14 December 94	42	99.2[k]	3.12
10 January 94	2	116.1[l]	8.35
11 July 95	108	33.2[bc]	0.62
24 July 95	454	31.8[b]	0.40
9 August 95	485	35.5[bc]	0.35
25 August 95	3696	41.1[d]	0.08
12 September 95	572	57.1[e]	0.38
22 September 95	259	66.5[fg]	0.66
25 October 95	53	60.8[e]	2.36
14 November 95	44	72.7[hi]	2.52
2 December 95	18	65.3[f]	4.83
10 January 96	15	89.4[j]	4.67

Table 3

Comparison of otoliths prepared and percent accepted for estimation of age in age-0 red snapper, *Lutjanus campechanus*.

Date	Otoliths prepared	Otoliths with >10% precision	Percent accepted
11 Jul 94	318	172	54
17 Aug 94	316	149	47
8 Sep 94	322	118	37
10–13 Jul 95	108	78	72
9–10 Aug 95	245	180	73
11–13 Sep 95	279	160	57
Total	1588	857	57

[2] Szedlmayer, S. T. 1994. Production or attraction: an evaluation of artificial reefs in coastal Alabama. Alabama Universities Tennessee Valley Research Consortium Final Report, Auburn University, Auburn, AL, 48 p.

[3] Holt, S. A. 1997. Marine Science Institute, Univ. Texas, Port Aransas, TX. Personal commun.

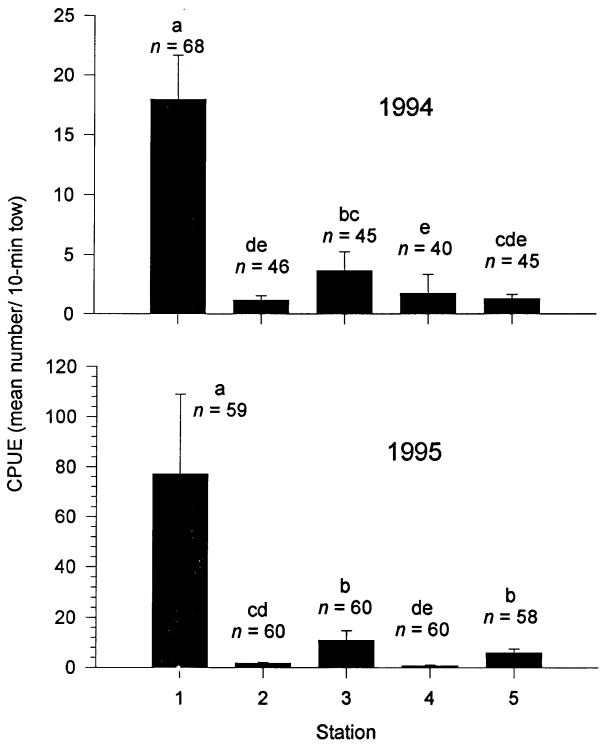

Figure 4

Mean CPUE (number/10-min tow) of age-0 red snapper, *Lutjanus campechanus*, by station from the northeast Gulf of Mexico. Error bars are standard errors, and *n*'s are number of trawl tows. Different letters show significant differences both within and between years (ANOVA; Waller-Duncan test; $P \leq 0.05$).

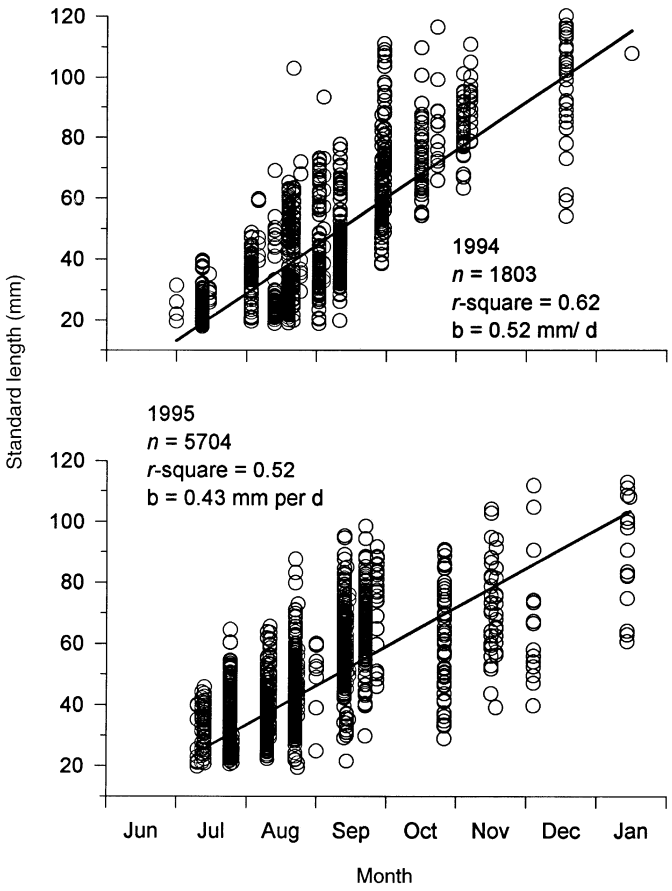

Figure 5

Linear regression of age-0 red snapper, *Lutjanus campechanus*, SL on date for 1994 and 1995, for all fish collected from the northeast Gulf of Mexico. Data points are individual fish. Growth rates were significantly different between years (*t*-test; $P \leq 0.05$).

many fish species this transition occurs simultaneously with habitat change, i.e. from pelagic larvae to benthic juveniles. On the basis of smallest fish collected during this study, larval red snapper metamorphose near 26 d and at 18 mm in length. Collins et al. (1980) suggested similar settlement sizes (12.4 to 22.4 mm SL) from plankton net samples.

Age-0 red snapper otoliths had daily microincrements when growth rates were >0.3 mm/d (Szedlmayer, 1998). In the present study, the nursery period was in the warmer summer months, when food should be abundant; and by all indications, growth rate far exceeded the 0.3 mm/d threshold rate. Thus, back calculation of first increment formation accurately estimated hatching date for age-0 red snapper. One difficulty with the otolith ageing methods was the low (57%) percentage of otoliths that met the required predetermined precision. However, this low percentage was due to personnel skill in otolith preparation. For example, an inexperienced technician would typically over polish several otoliths, that were subsequently rejected when counting. This same technician, after gaining experience and in-

Table 4

Comparison of growth rates among selected stations in 1995. Means with different letters show significant differences (ANCOVA, Tukey's test; $P \leq 0.05$).

Station	Growth rate mm/d	*n*	r^2
1	0.71[a]	227	0.86
2	0.86[b]	25	0.89
3	0.54[c]	115	0.80
5	0.60[c]	49	0.76

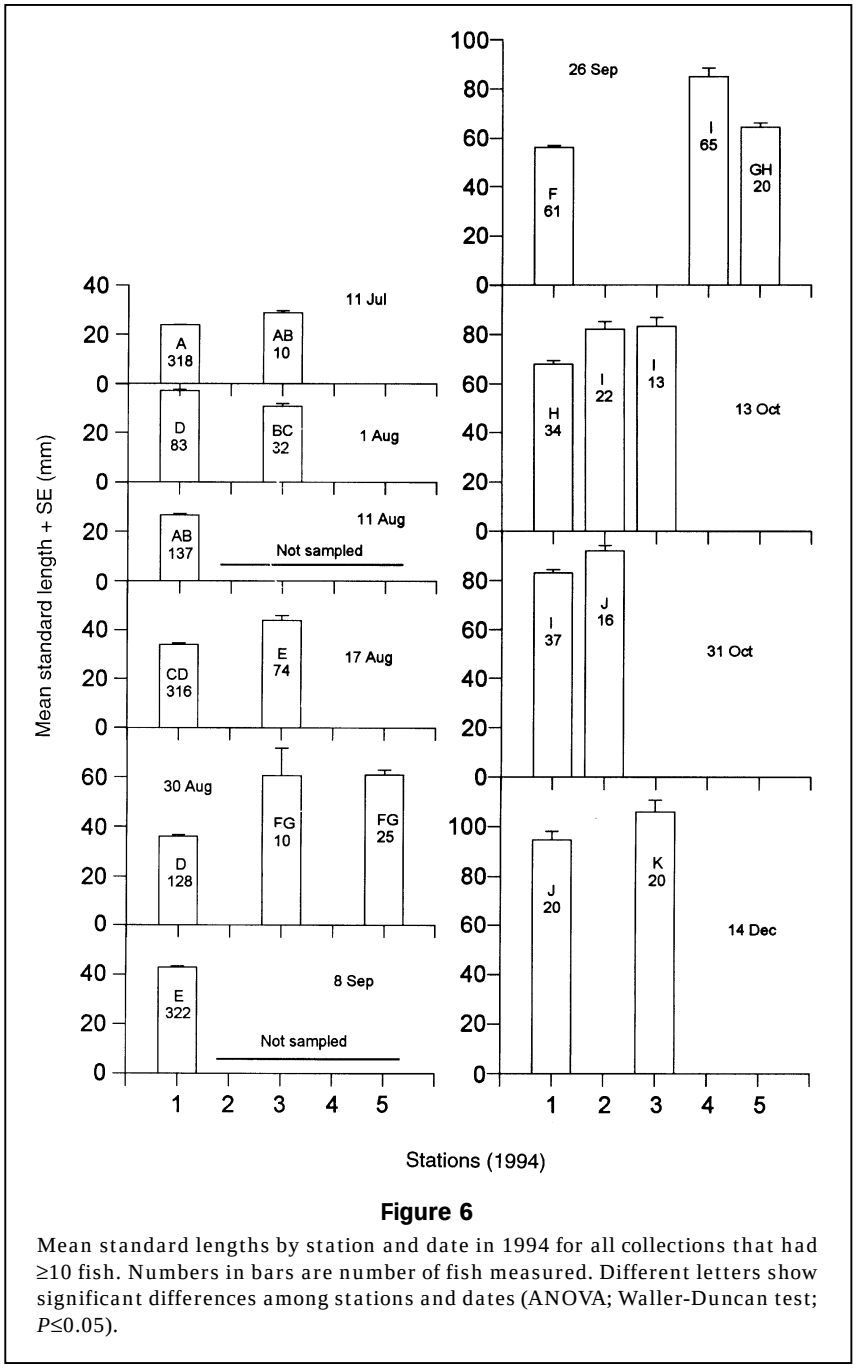

Figure 6

Mean standard lengths by station and date in 1994 for all collections that had ≥10 fish. Numbers in bars are number of fish measured. Different letters show significant differences among stations and dates (ANOVA; Waller-Duncan test; $P \leq 0.05$).

creased skill, would make an acceptable preparation of the second otolith from the same fish.

Hatching-date distributions clearly indicated separate hatching cohorts with peaks approximately one month apart. The multiple spawnings within a given year in red snapper may be an adaptation to increase survival. By spreading reproductive efforts over time, a species may increase the probability of matching the correct biotic and abiotic conditions for enhanced survival and subsequent recruitment.

Two differences were apparent when hatching-date estimates were compared with estimated spawning periods from gonadosomatic index (GSI) maxima (Collins et al., 1996). First, GSI estimates showed little indication of May spawning, as suggested by May hatching dates in the present study; and second, present estimates showed little indication of August spawning, as indicated by high GSIs for red snapper in August (Collins et al. 1996). These differences between hatch dates and GSIs were probably

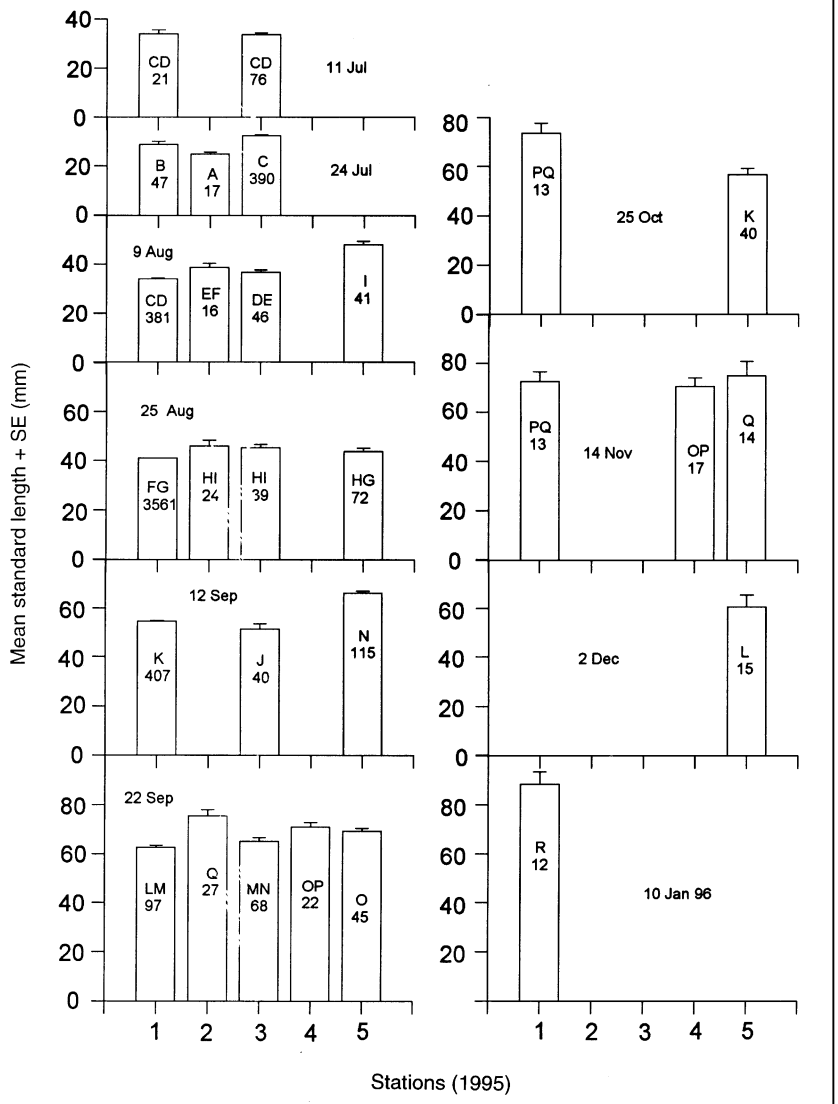

Figure 7

Mean standard lengths by station and date in 1995 for all collections that had ≥10 fish. Numbers in bars are number of fish measured. Different letters show significant differences among stations and dates (ANOVA; Waller-Duncan test; $P \leq 0.05$).

due to yearly variation. Collins et al. (1996) sampled from 1991 to 1993. Lack of evidence for August spawning in our study may also have resulted from low survival of later spawned fish or from new recruits having settled to different habitats not sampled in the present study.

The June and July 1994 cohorts had growth rates that were significantly faster in relation to 1995 cohort growth rates. Growth rates estimated from SL on varying dates were probably inaccurate owing to extended settlement of new recruits, but results showed the same pattern as SL on age estimates, i.e. 1994 growth rates were significantly faster compared with 1995 estimates (*t*-test, $P \leq 0.05$; Fig. 5). If growth rates were an indication of the probability of survival (Houde, 1989; Sogard, 1997), then 1994 cohorts may have had an advantage over the 1995 spawned cohorts. Growth rate typically decreases with decreasing temperature and may have resulted in the low growth rate observed for the May 1995 cohort. Thus, it appears that both density dependent and density independent mechanisms are operating

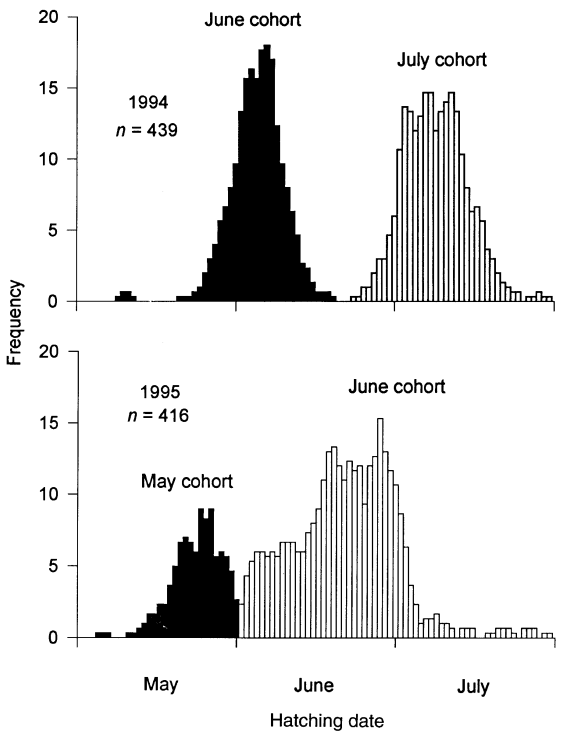

Figure 8

Hatch date frequencies of age-0 red snapper, *Lutjanus campechanus*, pooled over all dates from 1994 and 1995. A three day moving average was applied before plotting.

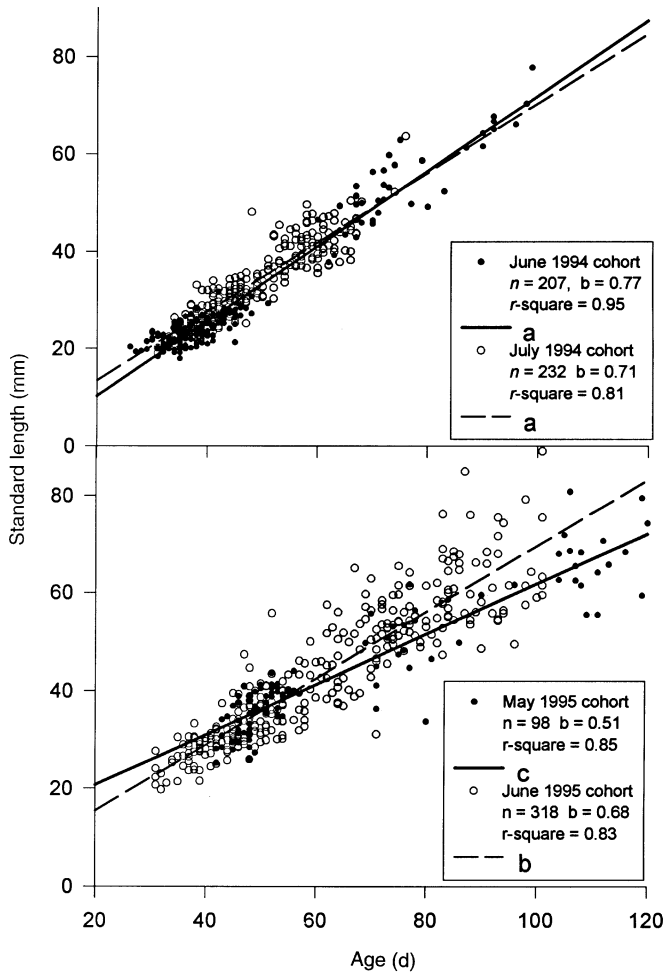

Figure 9

Growth rates of separate cohorts of age-0 red snapper, *Lutjanus campechanus*, from SL on age regressions from the northeast Gulf of Mexico. Data points are individual fish. Different letters show significant differences among cohorts both within and between years (ANCOVA; Tukey's test; $P \leq 0.05$).

(Bromley, 1989; Rijnsdorp and Vanleeuwen, 1992; Rogers, 1994). In 1994, there were fewer fish but faster growth rates than those in 1995, and in 1995 the early May cohort showed the slowest growth rates, probably from colder temperatures. This scenario suggests that if red snapper spawn early (May), temperature may play an important role. As the season progresses into July and August, temperature increases, settlement increases, and competition for food and shelter may become the limiting factors, such that later spawnings in August have lower survival.

The inner shelf habitat in the northeast Gulf of Mexico, particularly the location 13 km south of Mobile Bay, Alabama, should be considered an important nursery area for age-0 red snapper from July through September. Future research should address mechanisms that help to define this red snapper nursery habitat, and back calculation methods could be used to compare the relative contributions of various within-year cohorts to subsequent year classes.

Acknowledgments

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