Abstract—Life history aspects of larval and, mainly, juvenile spotted seatrout (*Cynoscion nebulosus*) were studied in Florida Bay, Everglades National Park, Florida. Collections were made in 1994–97, although the majority of juveniles were collected in 1995. The main objective was to obtain life history data to eventually develop a spatially explicit model and provide baseline data to understand how Everglades restoration plans (i.e. increased freshwater flows) could influence spotted seatrout vital rates. Growth of larvae and juveniles (<80 mm SL) was best described by the equation $\log_e standard\ length = -1.31 + 1.2162\ (\log_e age)$. Growth in length of juveniles (12–80 mm SL) was best described by the equation $standard\ length = -7.50 + 0.8417\ (age)$. Growth in wet weight of juveniles (15–69 mm SL) was best described by the equation $\log_e wet\text{-}weight = -4.44 + 0.0748\ (age)$. There were no significant differences in juvenile growth in length of spotted seatrout in 1995 between three geographical subdivisions of Florida Bay: central, western, and waters adjacent to the Gulf of Mexico. We found a significant difference in wet-weight for one of six cohorts categorized by month of hatchdate in 1995, and a significant difference in length for another cohort. Juveniles (i.e. survivors) used to calculate weekly hatchdate distributions during 1995 had estimated spawning times that were cyclical and protracted, and there was no correlation between spawning and moon phase. Temperature influenced otolith increment widths during certain growth periods in 1995. There was no evidence of a relationship between otolith growth rate and temperature for the first 21 increments. For increments 22–60, otolith growth rates decreased with increasing age and the extent of the decrease depended strongly in a quadratic fashion on the temperature to which the fish was exposed. For temperatures at the lower and higher range, increment growth rates were highest. We suggest that this quadratic relationship might be influenced by an environmental factor other than temperature. There was insufficient information to obtain reliable inferences on the relationship of increment growth rate to salinity.

Growth, mortality, and hatchdate distributions of larval and juvenile spotted seatrout (*Cynoscion nebulosus*) in Florida Bay, Everglades National Park

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The spotted seatrout (*Cynoscion nebulosus*) is an important recreational fish in Florida Bay and spends its entire life history within Florida Bay (Rutherford et al.,1989). The biology of adult spotted seatrout in Florida Bay is well known (Rutherford et al., 1982, 1989), as are the distribution and abundance of juveniles in the bay, including a description of the juvenile habitats and their diets (Hettler, 1989; Chester and Thayer, 1990; Thayer et al., 1999; Florida Department of Environmental Protection[1]). The temporal and spatial distribution and abundance of larval spotted seatrout in Florida Bay and adjacent waters, and the spatial and temporal spawning habits of these larvae also have been determined (Powell et al., 1989; Rutherford et al., 1989; Powell, 2003).

The early life history of spotted seatrout in other south Florida estuaries also has been well documented. Peebles and Tolley (1988) described the distribution, growth, and mortality of larval spotted seatrout in Naples and

Fakahatchee Bays, and McMichael and Peters (1989) described the size distribution, growth, spawning, and diet of spotted seatrout in Tampa Bay.

Information on growth and mortality of larval and juvenile spotted seatrout in Florida Bay is lacking. Research on these topics would enhance our understanding of the entire life history of this valuable species, and in particular aid in eventually developing a spatially explicit model for spotted seatrout that is highly desired by the Program Management Committee for the South Florida Ecosystem Restoration Prediction and Modeling Program. In addition, these life history studies could help clarify juvenile growth and survival and provide needed information for the restoration

[1] Florida Department of Environmental Protection. 1996. Fisheries-independent-monitoring program, 1995 annual report, 58 p. Florida Department of Environmental Protection, Florida Marine Research Institute, 100 8th Avenue SE, St. Petersburg, FL 33701.
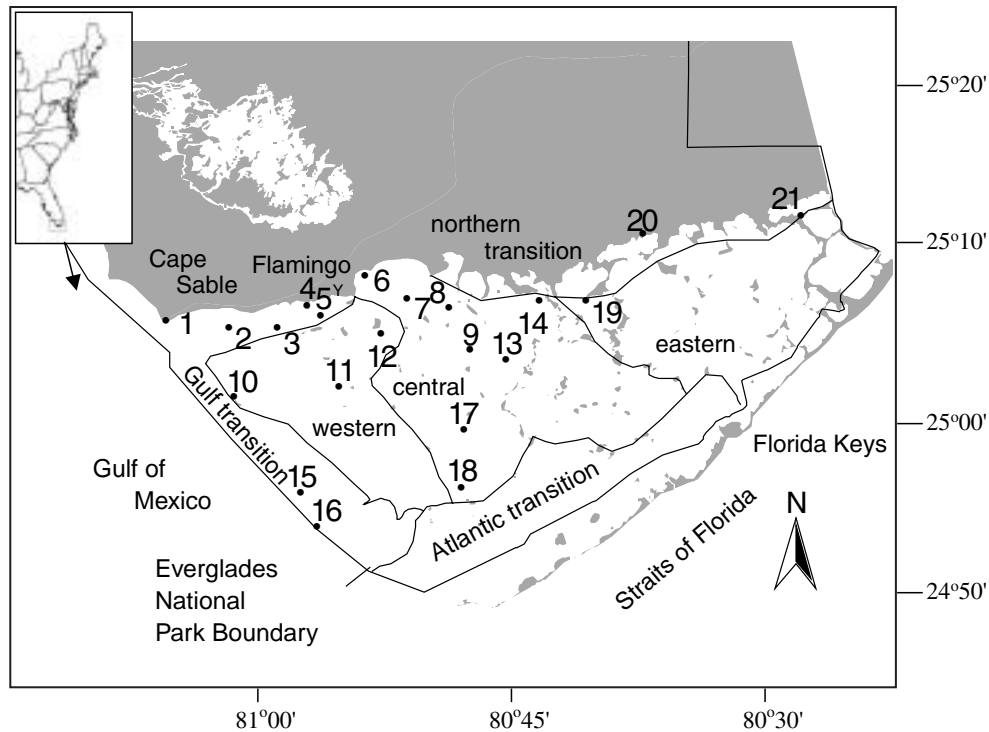
Figure 1

Location of sampling sites for spotted seatrout (*Cynoscion nebulosus*) in Florida Bay,
Everglades National Park, Florida, including Florida Bay Subdivisions.

of the Everglades, including a return of historic freshwater flows into Florida Bay.

Two conceptual frameworks have been advanced to couple the role of growth and mortality in influencing cohort dynamics. Anderson (1988), in a review of hypotheses relating survival of prerecruits to recruitment, advocated a growth-mortality hypothesis as a rational framework for early life history studies that address recruitment variability. This concept predicts that survival of a cohort is directly related to growth rates during the early life stages. The growth-mortality framework, which includes several important integrated components and is based on bioenergetic principles of growth and ecological theory that predict growth rate, is directly related to survival. If it can be demonstrated that survival is a function of growth during the early life stage, then a valuable tool becomes available for examining mechanisms influencing recruitment of marine fishes.

Another framework suggests that the mortality rate does not operate alone in determining stage-specific survival, but it is the mortality:growth (M:G) ratio (mortality per unit of growth) that determines stage-specific survival (see citations in Houde, 1997). Houde (1997) advanced the idea of using the M:G ratio as an estimator of production and potential survivorship especially in early life stages when both mortality and growth are high and variable. This concept was partly based on the strong coupling of growth and mortality demonstrated by Ware (1975) who argued that when growth rate is poorer than average, larvae would be exposed to sources of mortality over a longer period and hence their mortality rate would increase. Growth and

mortality values for successive cohorts would tend to form a cluster of points around a regression of mortality on growth based on average values for a particular species.

Our intent is not to test the growth-mortality hypothesis (*sensu* Hare and Cowen, 1997) as outlined by Anderson (1988), nor fully to develop the M:G ratio concept (Houde, 1997), but rather to use these concepts as a framework for our study. The major goal is to provide information on growth and survival of larval and, mainly, juvenile spotted seatrout that can ultimately be used to develop a spatially explicit model that can be linked to Everglades restoration activities. Therefore, the major objectives of this paper are 1) to determine overall growth rates of larval and juvenile spotted seatrout in Florida Bay; 2) to determine and compare juvenile growth rates geographically; 3) to estimate natural mortality rates of juveniles; 4) to estimate hatch-date distributions; 5) to compare cohort growth and mortality rates and G:M ratios for juveniles; and 6) to evaluate the effects of salinity and temperature on otolith growth—a surrogate for somatic growth.

Methods and materials

Field collections

Larval fish used for otolith microstructure analysis were collected from September 1994 through July 1997, mainly in the Gulf transition, western, and central subdivisions (Table 1, Fig. 1). These subdivisions designated by the

Table 1

Florida Bay sampling stations where otoliths from spotted seatrout were collected. Included are numbers (*n*) of larvae and juveniles used in the otolith microstructure analysis, and subdivisions as defined by the South Florida Ecosystem Restoration Prediction and Modeling Program, Program Management Committee.

Station number	Latitude (degrees and minutes)	Longitude (degrees and minutes)	Florida Bay subdivisions	Location	Juveniles (*n*)	Larvae (*n*)
1	25 06.81	81 05.27	Gulf transition	Cape Sable	—	4
2	25 06.37	81 01.42	Gulf transition	Middle Ground	1	10
3	25 06.40	80 58.58	Gulf transition	Conchie Channel	—	4
4	25 07.70	80 56.90	Gulf transition	Bradley Key	119	—
5	25 07.12	80 56.07	western	Murray Key	4	8
6	25 08.11	80 50.95	central	Snake Bight	3	—
7	25 09.45	80 53.42	central	Snake Bight	4	—
8	25 07.50	80 48.51	central	Rankin Lake	12	—
9	25 05.06	80 47.30	central	Roscoe Key	20	—
10	25 02.30	81 .1.12	Gulf transition	Sandy Key	49	—
11	25 02.90	80 55.00	western	Johnson Key Basin	125	—
12	25 06.00	80 52.50	western	Palm Key Basin	110	—
13	25 04.50	80 45.15	central	Whipray Basin	2	62
14	25 08.00	80 43.20	central	Crocodile Point	9	—
15	24 56.70	80 57.20	Gulf transition	Schooner Bank	2	—
16	24 54.70	80 56.31	Gulf Transition	Sprigger Bank	—	8
17	25 00.40	80 47.68	central	Sid Key Bank	6	—
18	24 57.03	80 47.52	central	Twin Key Basin	6	—
19	25 07.98	80 40.48	eastern	Madeira Point	1	—
20	25 11.85	80 37.15	northern	Little Madeira Bay	8	—
21	25 13.00	80 27.80	eastern	Shell Key	5	—

South Florida Ecosystem Restoration Prediction and Modeling Program, Program Management Committee, were based on modifications of the benthic mollusc community (Turney and Perkins, 1972). In 1994 and 1995, we used 60-cm bongo nets fitted with 0.333-mm mesh fished from the port side of a 5.4-m boat. Beginning in 1996, we used a paired 60-cm bow-mounted push net with 0.333-mm mesh nets similar to that described by Hettler and Chester (1990).
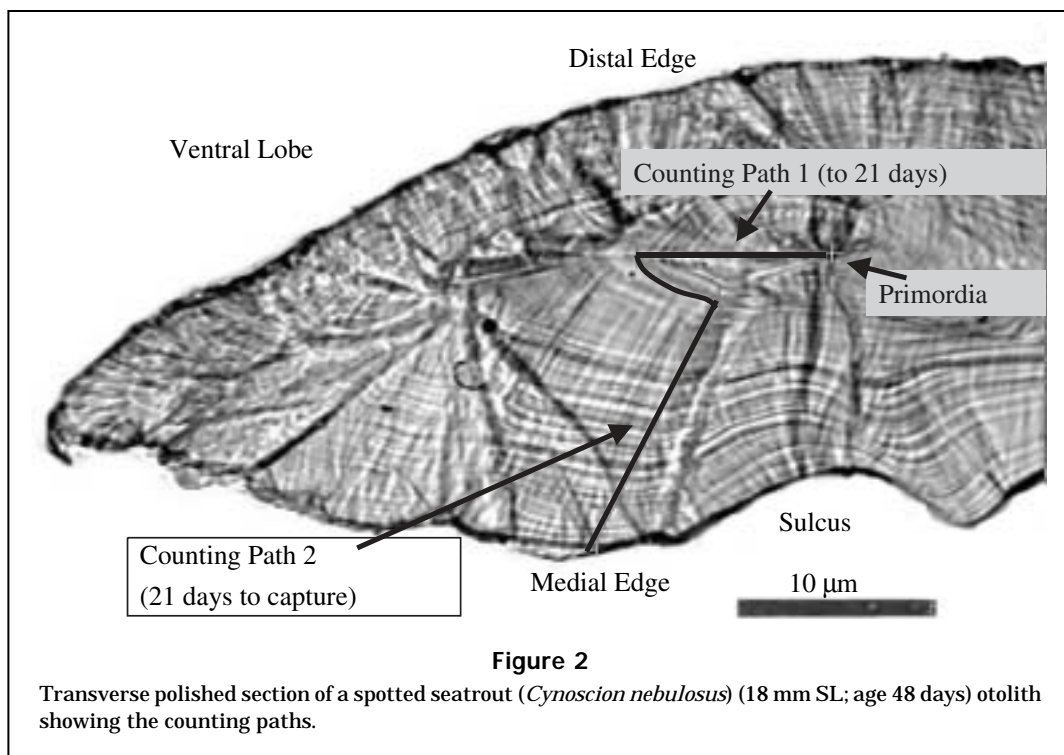
Juvenile spotted seatrout were obtained from monitoring programs established by the NOAA Center for Coastal Fisheries and Habitat Research (NOAA) and Florida Marine Research Institute (FMRI). NOAA collections were made from May 1995 through September 1997. Juveniles were collected with an otter trawl towed between two 5-m boats. The otter trawl measured 3.4 m (headrope) and was fitted with a 3.2-mm mesh tailbag with 6-mm mesh. FMRI collections were made in 1995 with a seine and a trawl. The 21.4-m center-bag drag seine was fitted with a 1.8 m × 1.8 m × 1.8 m bag of 3.2-mm mesh. The 6.1-m (headrope) otter trawl was fitted with a body of 38.1-mm stretch mesh and a 3.2-mm mesh tailbag. The majority of juveniles (86%) from NOAA and FMRI collections were collected in 1995.

Otolith microstructure analysis

Otolith processing Otolith removal and preparation generally followed the methods of Secor et al. (1991). All oto-liths, except for the right sagitta, were mounted on a slide with mounting media and archived. The right sagittal otolith was embedded for transverse sectioning or polishing (or both). The left sagitta was embedded for transverse sectioning if the right was damaged. Sagittae were read with a light microscope at 1000× magnification under oil immersion. The first increment was determined as that following the core increment; which was defined as a well-defined dark increment surrounding the core (Powell et al., 2000). Two blind counts of increments were made by one reader and if the counts differed by more than 5, then the otolith was read again. If the counts were within the acceptable range, the two counts were averaged. Based on a previous validation study (Powell et al., 2000), 2.5 days were added to the increment counts to obtain the daily age. A total of 582 sagittal otoliths were aged. This total included 96 from larval collections from September 1994 through July 1997, 139 juveniles from NOAA collections from June 1995 through September 1997, and 347 from FMRI collections from June 1995 through December 1995.

Increment widths were measured on 347 otoliths from FMRI collections (1995) by using image analysis. The measuring path consisted of two segments: a ventral path from the core to the 21st increment and a ventral-medial path along the sulcus, from the 21st increment to the edge (Fig. 2). The 21st increment was selected as the transition point in these measuring paths by test reading 30 otolith sections representing the entire range of sample fish

Figure 2

Transverse polished section of a spotted seatrout (*Cynoscion nebulosus*) (18 mm SL; age 48 days) otolith showing the counting paths.

lengths. In all samples, the 21st increment could easily be traced in both measuring paths and in all samples the first 21 increments could be measured within the same image. Increment widths were averaged over a 7-day period. Age estimates were also obtained and we eliminated any otolith used to measure increment widths if the difference in total increment count between the two methods (counts obtained directly from the microscope versus those attained by image analysis) was greater than 7 days or 10%. On this basis, 117 otoliths were removed from the increment width analysis.

We believed counts obtained directly from the microscope were more accurate than those obtained by summing the number of increments measured on the computer monitor with the image analysis system. Counting increments directly through the microscope lens allows the reader to optically section the otolith (by varying the focus), which helps in detecting daily increments. "Frozen" multiple images are a result of using the image analysis; hence optical sectioning is not possible.

Data analysis   Data from all years and sources were used for 1) overall growth (i.e. larval and juvenile); 2) juvenile growth; and 3) estimates of juvenile mortality. Data from NOAA larval and juvenile collections were used to estimate a body-length–otolith-radius relationship. Data from 1995 FMRI and NOAA collections, which was the most complete data set, were used for growth comparisons between cohorts, and hatchdate distributions. Data from 1995 FMRI collections were used for 1) growth comparisons between geographical subdivisions; 2) estimating a wet-weight–age relationship to compute the ratio of wet-weight specific-

growth to mortality (G:M ratios), which assesses the relative recruitment potential of individual cohorts (Houde, 1996; Rilling and Houde, 1999; Rooker et al., 1999); and 3) determining the influence of temperature on otolith increment width. We used the FMRI data set exclusively for the above analyzes because collections were spatially more localized and wet weights were available.
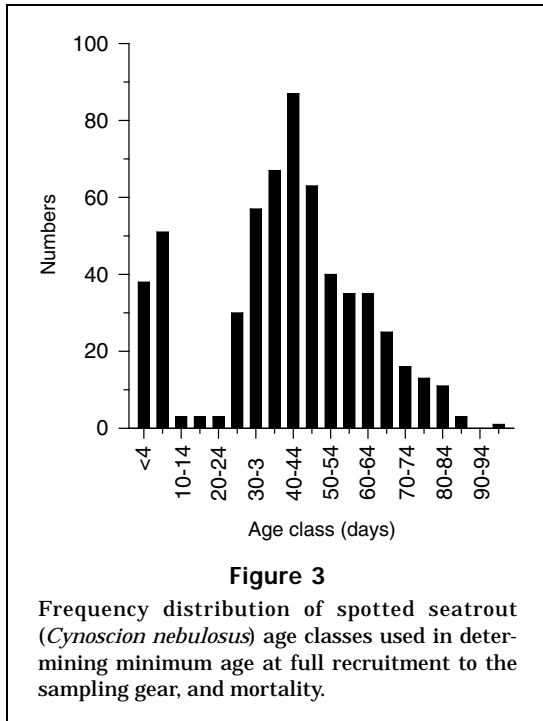
Natural mortality (*M*) estimates were derived by regressing $\log_e$ unadjusted numbers on age classes (5-day bins); the resulting slope provided an estimate of total mortality (Ricker, 1975). However, on the basis of the age-frequency distributions (Fig. 3), we considered juveniles ≥40 days old fully recruited to our gear and juveniles ≥90 days old appeared to avoid our gear. Hence, only juveniles between 40 and 90 days old were used to calculate mortality.

Hatchdate distributions were computed on a weekly basis and adjustments for mortality were made on individual juveniles by the equation

$$N_o = N_t / e^{-Zt},$$

where N_0 = estimated number at hatching;
   N_t = number at time t (N_t=1 because N_0 was calculated for each individual fish);
   Z = instantaneous daily mortality coefficient; and
   t = age in days.

Spotted seatrout cohorts were divided into weekly units, but comparisons between cohort growth was done on a monthly basis because of inadequate numbers for weekly comparisons. A test of heterogeneity of slopes was imple-

Figure 3

Frequency distribution of spotted seatrout (*Cynoscion nebulosus*) age classes used in determining minimum age at full recruitment to the sampling gear, and mortality.

Figure 4

Mean and ranges of temperature and salinity data by station used in the otolith microstructure longitudinal analysis (relationship between increment width and temperature and salinity). For station locations relative to subdivisions, see Table 1 and Figure 1.
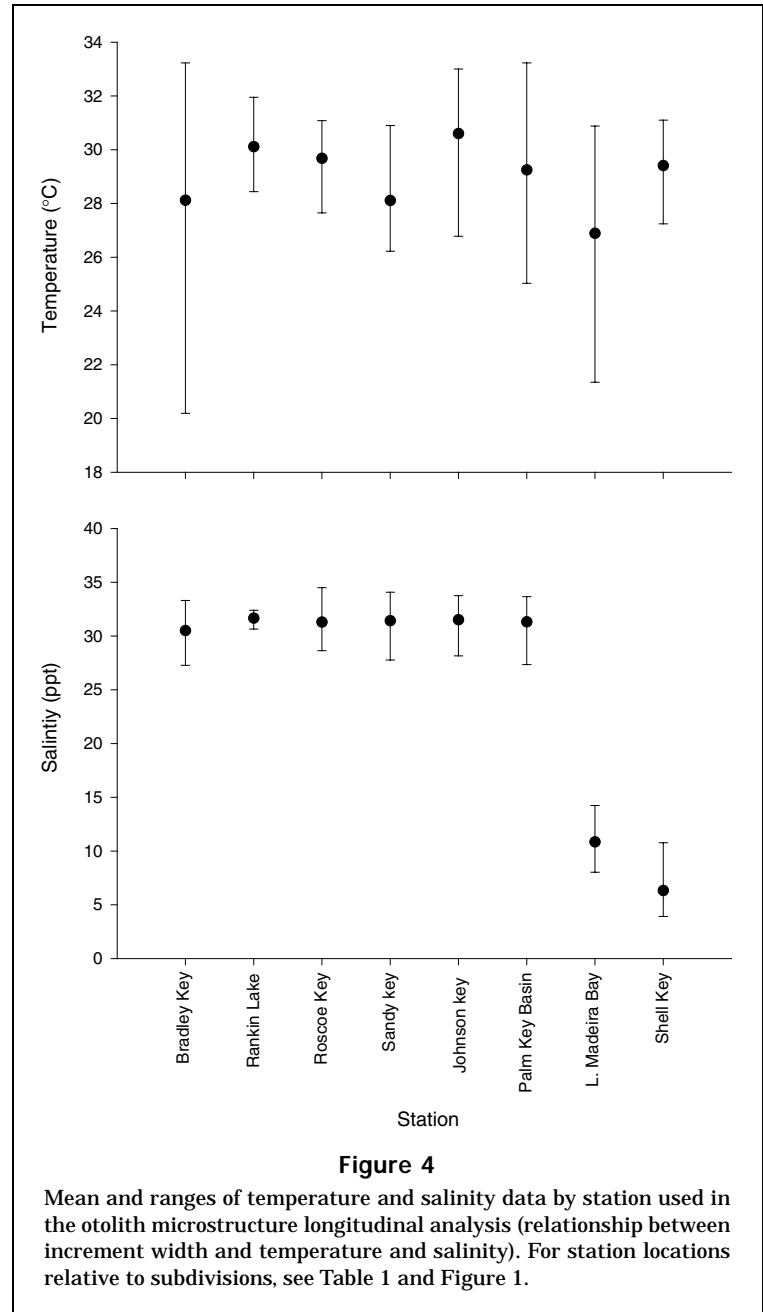
mented by using a generalized linear model (SAS/STAT software, version 6.12, SAS Institute, Cary, NC) to test if growth differed among cohorts. A general linear test (Neter et al., 1983) was used to compare growth between three geographical subdivisions (Gulf transition, western, and central). This test is a function of the error sum of squares of the reduced model minus the error sum of squares of the full model. Adequate numbers of juveniles were not available to compare growth in eastern and northern subdivisions (Table 1). Circular statistics (Batschelet, 1981) were used to determine if spawning, as determined from hatchdate distributions, was uniform over the lunar month. The phase of the moon for 1995 was identified by the fraction illuminated (U. S. Naval Observatory Applications Department, 1997). A 3-point moving average was used to test if spawning was cyclical.

Cohorts (1995) were categorized according to the following hatchdates: cohort A, 29 March–2 May ("April"); cohort B, 3 May–6 June ("May"); cohort C, 7 June–4 July ("June"); cohort D, 5 July–1 August ("July"); cohort E, 2 August–5 September ("August"); cohort F, 6 September–3 October ("September").

Comparisons of the relative recruitment potential of individual cohorts (G:M ratios) between all cohorts were unresolved. Although cohort mortality estimates could be generated, they were appropriate (by analyzing r^2 and *P*-values from regression analysis) for only three cohorts (cohorts B, D, and F).

A random coefficient model was used to investigate the relationship between growth rate of otoliths with age and temperature from juveniles collected in 1995. Most fish were exposed to salinities in a narrow range between 28 and 34 ppt; only 9 fish were exposed to salinities in the 5–13 ppt range (Fig. 4). Consequently, there was insufficient information to obtain reliable inferences on the relationship of growth rate to salinity or the relationship to salinity and temperature for growth information obtained by using either otolith measuring path. This was a disappointment because growth responses to salinity were considered an important objective in relation to proposed Everglades water management activities. Thus, investigation was restricted to the relationship of growth with temperature. A separate model was fitted for the first (1–21 increments)

and second (22–60 increments) measuring paths because otolith increment width changed at a constant (age-independent) rate for each path. We did not include fish with >60 increments because the relationship past this number was determined for only 10% of the fish and included obvious outliers. Letting Y_{ij} be the otolith width measurement for fish i at age α_{ij}, where j indexes time, the model for each path was

$$Y_{ij} = \alpha_{0i} + \alpha_{1i}\alpha_{ij} + e_{ij},$$

where α_{0i} and α_{1i} are the fish-specific intercept and slope describing the relationship between increment width and age for fish i, and e_{ij} is a normally distributed error term; thus, α_{1i} is the growth rate for fish i over the measuring path. Temperature exhibited only negligible change for any given fish over the measuring path; thus, temperature for fish i was summarized as t_i, the average temperature over the path for that fish. To determine an appropriate model for the relationship between intercept and growth rate and temperature, a preliminary analysis was performed in which ordinary least squares estimates of α_{0i} and α_{1i} were obtained separately for each fish i and plotted against temperature. For the first measuring path (1–21 increments), the appropriate model was

$$\alpha_{0i} = \beta_{00} + \beta_{0i}t_i + b_{0i}, \ \alpha_{1i} = \beta_{10} + \beta_{11}t_i + \beta_{12}t_i^2 + b_{1i},$$

where b_{0i} and b_{1i} are normally distributed random effects, allowing growth rates for fish at the same temperature to vary across fish. For the second measuring path (22–60 increments), the appropriate model was,

$$\alpha_{0i} = \beta_{00} + \beta_{01}t_i + \beta_{02}t_i^2 + b_{0i}, \ \alpha_{1i} = \beta_{10} + \beta_{11}t_i + \beta_{12}t_i^2 + b_{1i},$$

By substitution, these considerations yielded models 1 and 2 for the first and second paths, respectively:

$$Y_{ij} = (\beta_{00} + \beta_{01}t_i) + (\beta_{10} + \beta_{11}t_i + \beta_{12}t_i^2)\,a_{ij} + b_{0i} + b_{1i}a_{ij} + e_{ij} \tag{1}$$

$$Y_{ij} = (\beta_{00} + \beta_{01}t_i + \beta_{02}t_i^2) + (\beta_{10} + \beta_{11}t_i + \beta_{12}t_i^2)\,a_{ij} + b_{0i} + b_{1i}a_{ij} + e_{ij} \tag{2}$$

thus representing otolith increment width in each case as having a straight line relationship with age, where the slope (age-independent growth rate) depends on average temperature according to a quadratic relationship. The random effects allow observations on the same fish to be correlated, whereas observations across fish are independent. Models 1 and 2 were implemented in SAS Proc Mixed (SAS/STAT software, version 6.12, SAS Institute, Cary, NC).

Daily temperature records were obtained from the United States Department of Interior's National Park Service, Florida Bay monitoring stations and averaged over a 7-day period. In 1995, temperature records were available only for Johnson Key Basin (JKB), Whipray Basin (WB), Little Blackwater Sound (LBS), and Little Madeira Bay (LMB), but spotted seatrout were also collected at other sites

(Table 1). Daily temperatures were estimated for Sandy Key (SK) and Roscoe Keys (RK) from values recorded during sampling trips because both these stations are not in close proximity to National Park Service monitoring sites. Sandy Key values were regressed on JKB values (same dates). Sandy Key temperatures were collected from January 1994 through August 1996. The regression model for temperature was $SK = 0.76 + 0.9536\ JKB$ [$r^2=0.89$; $n=25$]. Roscoe Key values were regressed on WB values (same dates). Roscoe Key temperatures were collected from January 1994 through August 1996. The regression model for temperature was $RK = 5.60 + 0.7976\ WB$ [$r^2=0.87$; $n=31$]. Temperature values were available at Murray Key (MK) in 1997. To attain values for our 1995 analysis we regressed MK on JKB (same dates). The temperature regression model was $MK = 0.77 + 0.9680\ JKB$ [$r^2=0.99$; $n=342$].

We reported measurements in standard length (SL). For preflexion and flexion larvae, standard length was measured from the tip of the snout to the tip of the notochord. For postflexion larvae and juveniles, standard length was measured from the tip of the snout to the base of the hypural plate.

Results

Overall growth of larvae and juveniles (<80 mm SL) was best described by the equation $\log_e$ *standard length* = $-1.31 + 1.2162$ ($\log_e$ *age)* [$n=582$; $r^2=0.97$]. Growth in body length of juveniles (12–80 mm SL) was best described by the linear equation *standard length* = $-7.50 + 0.8417$ (*age*) [$n=486$; $r^2=0.84$]; hence, juveniles between approximately age 20–100 days grew on average 0.84 mm/d. There were no significant differences in juvenile growth in body length among three geographical subdivisions [$F^4_{327}=0.756$; $n=333$] (Table 2), but there was a significant growth difference in length for one of six 1995 cohorts (Table 3, Fig. 5). Growth in wet weight of juveniles (15–69 mm SL) was best described by the equation $\log_e$ *wet weight* = $-4.44 + 0.0748$ (*age*) [$n=347$, $r^2=0.84$]. There was a significant growth difference in wet weight for one cohort (Table 4, Fig. 6).

Weekly 1995 hatchdate distributions, determined by using daily instantaneous mortality (0.0585, Fig. 7), indicated juveniles in collections (i.e. survivors) were from spawning that was cyclical and protracted (Fig. 8). The most intense successful spawning occurred during 21–27 June (9.2% of total). Using a 3-point moving average, we observed three similar cycles (Fig. 8). From data on survivors, ~25% of juveniles were spawned by late May, 50% by early July, and 75% by late August and from data on cohorts, three cohorts (cohorts C, D, and E; early June–late August) comprised 55% of the total estimated spawn of spotted seatrout. There was no correlation between spawning and moon phase (periodic regression $r^2=0.019$, $P=0.754$) (Fig. 8).

The relative recruitment potential (G:M ratio) of the 1995 year class estimated from the wet-weight specific growth coefficient (0.0748) and the instantaneous daily mortality rate (0.0585, Fig. 7) was 1.28. The G:M ratio for three cohorts (B, May; D, July; and F, September) was greater than the ratio for the total 1995 year class because mortal-

Table 2

Summary of growth data used to compare growth in length of spotted seatrout among three Florida Bay subdivisions. Growth was best described by the linear equation: *standard length = a + b* (age in days).

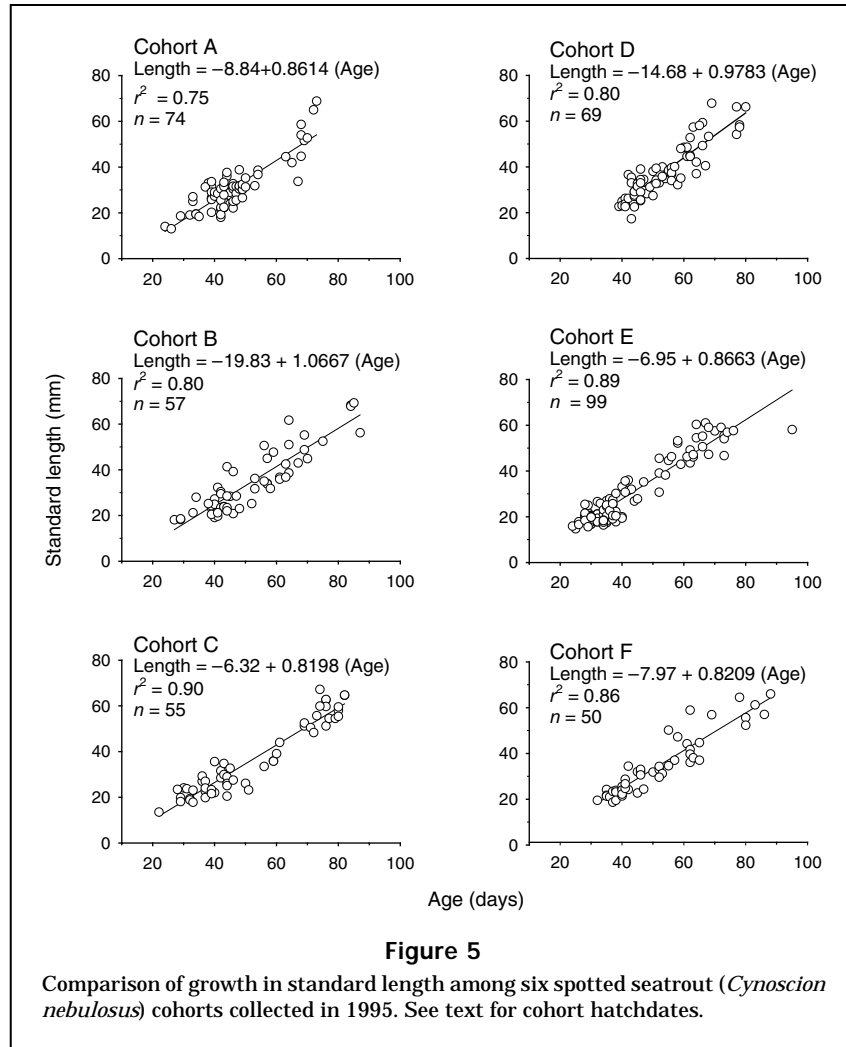| Subdivision	Intercept	Slope	*n*	*r²*	Size range (mm SL)
Gulf transition	−11.07	0.8914	139	0.86	16–69
Central	−12.23	0.9298	49	0.80	15–63
Western	−10.56	0.8834	145	0.85	17–69

Table 3

Summary of statistics for a test for heterogeneity of slopes for cohort somatic growth rates of spotted seatrout. Cohorts were categorized according to month of hatchdate (see text). The base parameter is cohort F and all parameter estimates are deviations from the base cohort. For growth equations, see Figure 5.

Parameter	Estimate	Standard error	*t*-value	*P*-value
Intercept	−7.97270	3.02829	−2.63	0.0088
Cohort A	−0.86811	4.31970	−0.20	0.8408
Cohort B	−11.85849	3.91387	−3.03	0.0026
Cohort C	1.65094	3.86470	0.43	0.6695
Cohort D	−6.70820	4.74936	−1.41	0.1586
Cohort E	1.02077	3.50931	0.29	0.7713
Slope	0.82088	0.05613	14.62	<0.001
Cohort A	0.04054	0.08604	0.47	0.6378
Cohort B	0.24578	0.07106	3.46	0.0006
Cohort C	−0.00113	0.07091	−0.02	0.9873
Cohort D	0.15741	0.08730	1.80	0.0721
Cohort E	0.04544	0.06821	0.67	0.5058

Table 4

Summary of statistics for a test for heterogeneity of slopes for cohort wet-weight growth rate of spotted seatrout. Cohorts were categorized according to month of hatch date (see text). The base parameter is cohort F and all parameter estimates are deviations from the base cohort. For growth equations, see Figure 6.

Parameter	Estimate	Standard error	*t*-value	*P*-value
Intercept	−4.27384	0.23763	−17.99	<0.0001
Cohort A	0.10201	0.37014	0.28	0.7830
Cohort B	−0.46348	0.34092	−1.36	0.1749
Cohort C	−0.27866	0.32116	−0.87	0.3862
Cohort D	−0.19540	0.38352	−0.51	0.6108
Cohort E	−0.38260	0.29853	−1.28	0.2009
Slope	0.06974	0.00439	15.88	<0.0001
Cohort A	0.00195	0.00729	0.27	0.7889
Cohort B	0.00679	0.00622	1.09	0.2754
Cohort C	0.00502	0.00575	0.87	0.3835
Cohort D	0.00759	0.00702	1.08	0.2808
Cohort E	0.01188	0.00564	2.11	0.0359

Figure 5

Comparison of growth in standard length among six spotted seatrout (*Cynoscion nebulosus*) cohorts collected in 1995. See text for cohort hatchdates.

Table 5

Daily growth (wet weight in grams) rates and daily mortality rates for three cohorts in Florida Bay in 1995. Cohorts were categorized according to month of hatchdate (see text). The G:M ratio derived from the growth and mortality rates is also presented. For growth equations and associated r^2 values, see Figure 6.
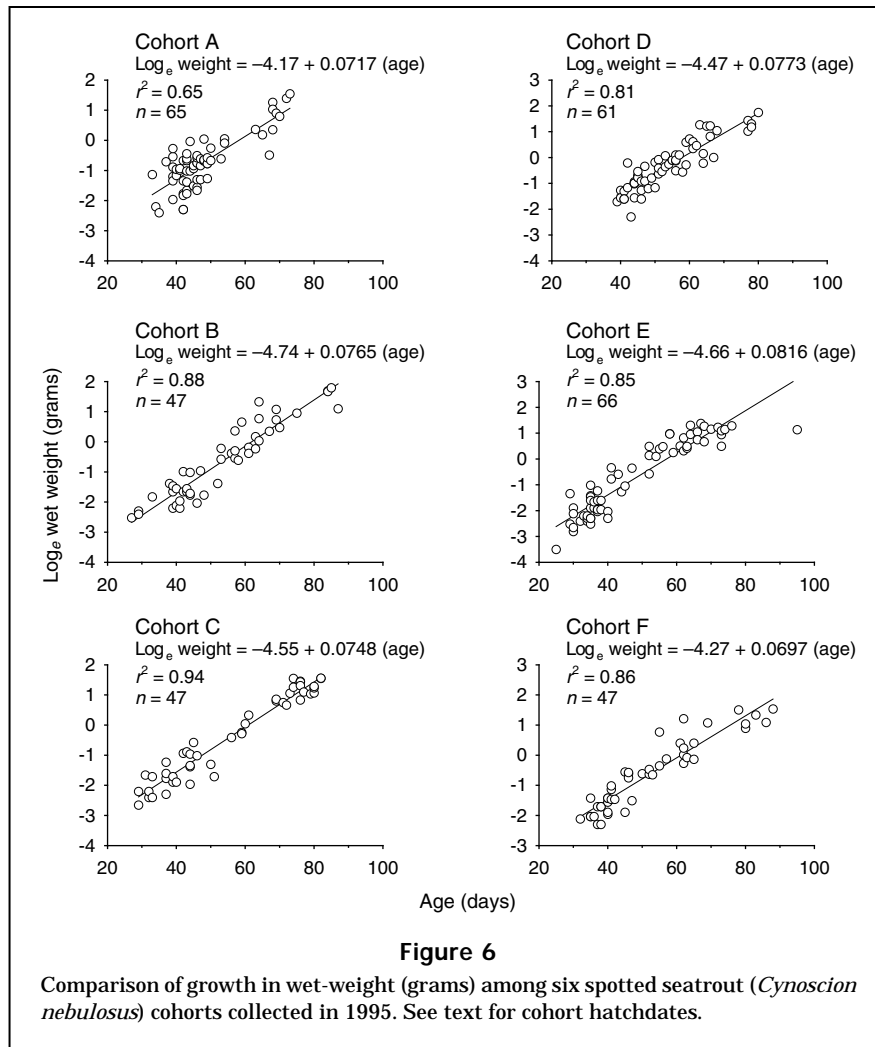
Cohort	Hatchdate month	Growth rate	Mortality rate	r^2	G:M ratio	Size range (mm SL)
B	May	0.0765	0.0445	0.54	1.72	28–62
D	July	0.0773	0.0565	0.82	1.37	37–68
F	September	0.0697	0.0354	0.67	1.97	37–66

ity rates appeared relatively low compared to the overall mortality rate (0.0585) for juveniles (Table 5). However, differences in mortality rates among these three cohorts were not significant (F^4_{21}=1.414). There were no significant differences in weight-specific coefficients among the three cohorts (B, D, and F) (Table 4), but a significant difference in length-specific coefficients among the three cohorts was found (Table 3). Cohort B (May) had a significantly higher growth rate than the other two cohorts.

There was a close relationship between otolith radius and body length (Fig. 9). A linear equation with the sagittal ventral radius, had a similar r^2 as a curvilinear equation with the sagittal dorsal radius. However, we were unable to measure increment widths along this plane and instead used a combination of a ventral path and a ventral medial path.

As an initial demonstration that otolith increment width increased with age along the 1–21 increment measuring path and decreased along the 22–60 increment path, simpli-

Figure 6

Comparison of growth in wet-weight (grams) among six spotted seatrout (*Cynoscion nebulosus*) cohorts collected in 1995. See text for cohort hatchdates.
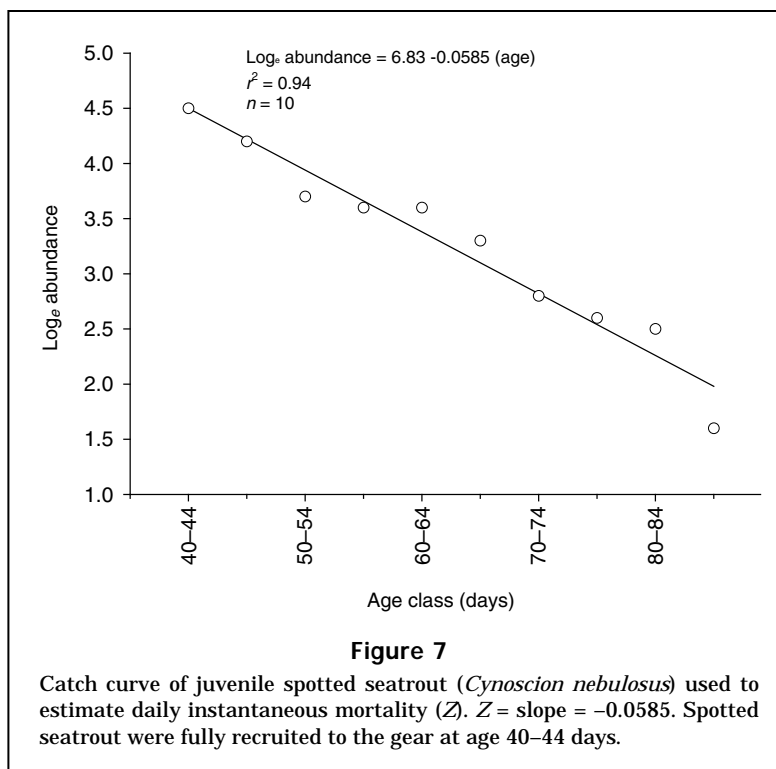
fied versions of Equations 1 and 2 (see above) were fitted, in which all coefficients of temperature were set equal to zero, so that Equations 1 and 2 represent simple linear relationships with age. For the first path, the estimate of slope was 0.153 μm/d ($P<0.0001$); that for the second path was −0.065 μm/d ($P<0.0001$). Addition of quadratic terms to each model was not supported ($P=0.81$ and 0.12, respectively). For the first path, whether intercept or growth rate were associated with temperature was determined by testing whether the parameters β_{01}, β_{11}, and β_{12} were equal to zero. There was no evidence that any of these parameters were different from zero ($P=0.45$, 0.35, and 0.42, respectively); the latter two may indicate that the data do not support the contention that growth rate depends on temperature in this range (1–21 d). For the second path, tests of $\beta_{02}=0$ and $\beta_{12}=0$ offered strong evidence that these parameters are different from zero ($P<0.001$ in each case). In particular, these results suggested for the age range 22–60 d, otolith growth rates decrease. The extent of the decrease is strongly associated with average temperature according to a quadratic relationship such that growth rates were more steeply decreasing with age for lower temperatures

and then became shallower at higher temperatures. In summary, for temperatures at the lower and higher end of the observed temperature range, otolith growth rates for the age range 22–60 d were higher than they were in the middle of the observed temperature range.

Discussion

Growth in body length of juvenile spotted seatrout in Florida Bay was faster than growth of juveniles from Tampa Bay (Table 6, McMichael and Peters, 1989). Florida Bay is generally considered an oligotrophic system (Fourqurean and Robblee, 1999). Nevertheless, seagrass beds in western Florida Bay, where juvenile spotted seatrout are most common (Chester and Thayer, 1990), are significantly more dense than beds in northwestern Florida waters, slightly north of Tampa Bay (Iverson and Bittaker, 1986). Increased growth of juveniles in Florida Bay could be attributed to the dense seagrass beds that provide habitat for epifaunal crustaceans (Holmquist et al., 1989; Matheson et al., 1999), which are important in the diet of juve-

Figure 7

Catch curve of juvenile spotted seatrout (*Cynoscion nebulosus*) used to estimate daily instantaneous mortality (*Z*). *Z* = slope = −0.0585. Spotted seatrout were fully recruited to the gear at age 40–44 days.

Table 6

Comparison of spotted seatrout growth (size in mm SL at age) between Tampa Bay, Florida (McMichaels and Peters, 1989) and Florida Bay, Florida (this study).

Area	Age (days)								
	10	20	30	40	50	60	70	80	90
Tampa Bay	5.1	10.2	15.3	20.3	25.4	30.5	35.6	40.7	45.8
Florida Bay	4.4	10.3	16.9	23.3	31.4	39.2	47.2	55.6	64.1

nile spotted seatrout (Hettler, 1989; McMichael and Peters, 1989). Additionally, warmer water temperatures have been observed in Florida Bay (Boyer et al., 1999) compared to Tampa Bay (McMichael and Peters, 1989); these warmer temperatures could enhance growth if adequate food is available (Warren, 1971). However, our study and that of McMichael and Peters (1989) were quite a few years apart; hence differences that we observed could also be accounted for by interannual variability. In addition, differences in growth could also be attributed to differences in sampling gear between the two studies.

Florida Bay is a heterogenous ecosystem and consists of ecologically distinct regions (Phlips and Badylak, 1996; Fourqurean and Robblee, 1999); however, we did not detect any differences in growth of juvenile spotted seatrout among our three subdivisions. In general, juvenile collections from the central subdivision were from stations that were spatially dispersed; whereas, juvenile collections in the western and Gulf transition subdivisions were from relatively few stations (Table 1). Normally, the central subdivision is characterized by the highest salinities in the bay and the western and the Gulf transition are characterized by high salinities (Orlando et al., 1997). However, in our study, salinities in the three subdivisions were moderate and similar (Fig 4), and growth rates estimated for the three subdivisions could be useful as baseline rates, particularly in the central subdivision where salinities are commonly hyperhaline (Orlando et al., 1997).
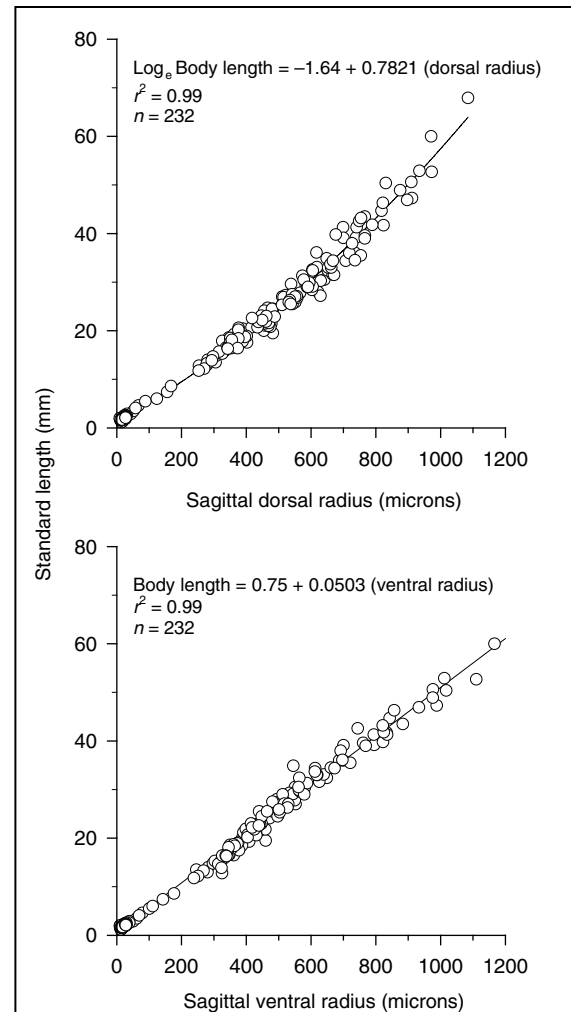
The spawning habits of spotted seatrout throughout their entire range are generally similar. They have a protracted spawning season, are multiple spawners, and reach sexual maturity at an early age. Initiation of spawning might be temperature dependent, with water temperatures between 20° and 23°C necessary to initiate reproductive development (Brown-Peterson and Warren, 2001). Hatchdate distributions calculated for spotted seatrout in
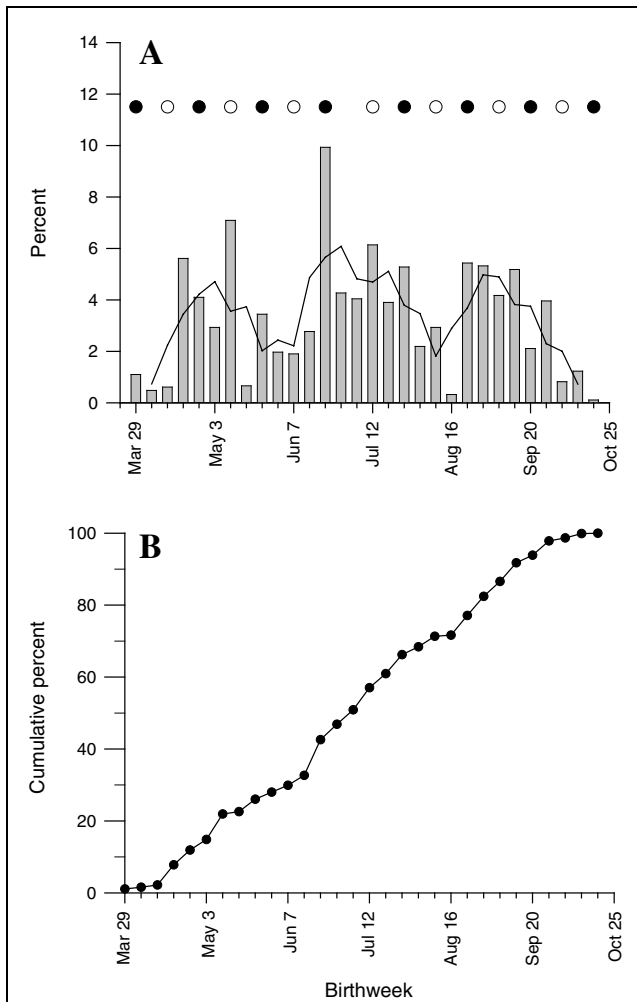
Figure 8

(**A**) Spotted seatrout (*Cynoscion nebulosus*) (*n*=417) weekly hatchdate distributions adjusted for mortality, including moon phases (●=new moon; ○=full moon), and 3-point moving average (solid line) of hatchdate distributions. (**B**) Cumulative frequency of spotted seatrout (*n*=417) hatchdate distributions.

Figure 9

The relationship between sagittal otolith radius and standard length (top), and sagittal ventral radius and standard length (bottom) for spotted seatrout (*Cynoscion nebulosus*).

Florida Bay in this study along with early stage larval collections (Powell, 2003) indicate that spotted seatrout spawn between March and October (based on hatchdate distributions) and that the majority of spawning occurs between 27° and 35°C , with very little spawning between 20º and 26°C (based on early stage larval collections). Spawning peaks, based on larval collections in 1994–96, occurred in June, August, and September (Powell, 2003), and early May, late June, and late August through early September based on 1995 hatchdate distributions (this study). However, Stewart (1961) reported that spotted seatrout in Florida Bay spawned throughout the year and that spawning peaked in spring and fall. Another larval fish study in Florida Bay indicated that some spawning occurs as early as February and continues into December (Rutherford et al., 1989).

Peak spawning activity of spotted seatrout is highly variable (McMichael and Peters, 1989; Brown-Peterson and Warren, 2001). McMichael and Peters (1989) observed two spawning peaks: spring and summer. Older fish participate in two peak spawning periods (Tucker and Faulkner, 1987), and a portion of the larger spring-spawned fish (age-1+) enter the spawning population during their second summer, augmenting the number of summer spawning fish.

We found that spawning activity and moon phase were uncorrelated, which is not in concordance with observations of McMichael and Peters (1989). They found that distinct peaks in spawning (based on hatchdate distributions of larval spotted seatrout) occurred at monthly intervals, and this periodicity might coincide with moon phase. However, this monthly periodicity was not observed when their data for juvenile spotted seatrout were examined. Moreover, statistical tests were not performed on the data in their study.

Our inferences, from this study, in relation to spotted seatrout peak spawning are based on hatchdate distributions and should be viewed with caution because hatchdates are based on survivors. Differential survival for early life history stages can bias results. Hatchdate distributions are valuable when compared to egg or recently hatched larval densities and might suggest processes responsible for differential cohort survivorship. Because spotted seatrout undergo a protracted spawning period and because there is high variation associated with icthyoplankton samples (Cyr et al., 1992), intensive and extensive sampling of recently hatched larvae would be required over a long duration to answer these process-oriented mortality questions.

The daily instantaneous mortality rate of juvenile spotted seatrout was higher in Florida Bay than those reported from northwestern Florida systems (Nelson and Leffler, 2001). Mortality rates of juvenile spotted seatrout from Florida Bay were 5.7%/d; whereas, for the other systems, rates approximated 3%/d. In general, mortality rates might increase with increasing estuarine temperatures (Houde and Zastrow, 1993). Although we were unable to estimate instantaneous daily mortality rates for larval spotted seatrout, these data have been estimated for larvae (3.5–6.5 mm) in two southwestern Florida estuaries (Peebles and Tolly, 1988). Highly variable rates were reported between the two Florida estuaries (Naples Bay: 0.70 or 50%/d; and Fakahatchee area: 0.37 or 31%/d). Houde (1996) reported a generalized instantaneous daily mortality rate for marine fish larvae of 0.239 (21%/d). Estimating mortality rates for larval spotted seatrout in Florida Bay will be critical for calculating G:M ratios in order to evaluate stage-specific survival and to develop credible spatially explicit models.

Mortality rates of spotted seatrout cohorts could be calculated for only three of six cohorts (B, May; D, July; and F, September) because slopes were significantly different from zero for only these cohorts. Furthermore, mortality rates of two of the three cohorts (B and F) were associated with low r^2 values (Table 5); hence the G:M ratios along with the mortality rates for these three cohorts should be considered "rough" estimates. Attaining more accurate mortality estimates for spotted seatrout would be valuable in linking cohort variability with potential recruitment and stage-specific survival. For example, larval cohorts of bay anchovy (*Anchoa mitchilli*) from Chesapeake Bay, a temperate estuary, exhibit growth rates that are temporally variable and mortality rates that are spatially and temporally variable (Rilling and Houde, 1999). Temperature, zooplankton prey and gelatinous predators are believed to influence growth and mortality rates of the bay anchovy. For striped bass (*Morone saxatilis*) in a subestuary of Chesapeake Bay, cohorts exhibited highly variable seasonal G:M ratios that were strongly influenced by temperature (Houde, 1997). In a subtropical estuary, cohort-specific mortality rates for juvenile red drum varied temporally; early and late season cohorts exhibited the highest mortality rates, which coincided with highest growth rates and G:M ratios for midseason cohorts (Rooker et al., 1999). We agree with Houde (1997) that future research should focus on the variability and causes of variability in growth and mortality, both of which interact to determine stage-spe-

cific survival. The developmental stage or age where G:M variability is greatest, along with the relationship of this variability to recruitment, need to be determined for spotted seatrout in Florida Bay. No doubt a relationship exists between G:M ratios and recruitment. Future research should also determine if cohort G:M ratios and somatic growth rates are seasonally or spatially variable. If they are, then a limited spatial and temporal sampling program could be designed to annually evaluate G:M ratios at highly variable stages or ages as an index of year-class strength of spotted seatrout in Florida Bay. Such an index could be verified by examining year-class catch rates on an annual basis or by virtual population analysis.

In our study there was little temporal difference in growth of juvenile spotted seatrout cohorts. Larval growth and mortality, which was not treated adequately in our study, could be influenced by copepod prey—an important dietary component of larval spotted seatrout (McMichael and Peters, 1989). The copepod *Acartia tonsa* is dominant in Florida Bay, but egg production rates for this species are low in the bay compared to those in other systems (Kleppel et al., 1998). We suspect the "bottleneck" to recruitment of spotted seatrout could occur during the larval stage. Hence, future research should examine mortality and growth of larval and recently settled spotted seatrout; in particular the patterns of larval production potential (G:M ratios). Research in these areas should increase our understanding of the degree of variability in stage-specific survival and recruitment of spotted seatrout in Florida Bay (Houde, 1996).

For most species, especially those with protracted spawning habits, it is most informative to analyze cohort growth and mortality. For example, striped bass and bay anchovy cohorts in Chesapeake Bay exhibit highly variable growth rates, mortality rates, and stage durations (Rutherford and Houde, 1995; Rilling and Houde, 1999). This variability could cause differential survival for cohorts and result in frequency distributions of survivor hatchdates that do not resemble recently hatched larvae or egg-production frequency distributions (e.g. Crecco and Savoy, 1985; Rice et al., 1987).

We are unable to interpret the significance of the absolute value of the G:M ratio for juvenile spotted seatrout, because interannual comparisons were not made, but we presented the ratio for future comparisons. Generally, the G:M ratio is <1.0 during the early larval stage, indicating a decline in biomass. However, the G:M ratio of a cohort will eventually exceed 1.0 as a result of a relative decline in mortality as larvae grow (Houde and Zastrow, 1993). Clearly, stage specific analysis of the spotted seatrout from egg through juvenile stage would have been more informative in determining when the maximum G:M ratio occurs (when cohort biomass increases at a maximum rate) and in providing insight into stage-specific dynamics of spotted seatrout (Houde, 1997). A constraint of our study was our inability to estimate larval mortality rates; hence early life history stage dynamics could not be examined.

Size-selective mortality in the juvenile life history stages can have important consequences for recruitment. Sogard (1997) argued that "within-cohort size-selective mortality"

is more evident in the juvenile stage than during the egg and larval stages when random mortality independent of fish size is more likely to occur (e.g. dispersal of eggs and larvae away from suitable nursery areas). In addition, variation in size, which provides a "template" for size-selective processes, increases during the juvenile stage as larval size is constrained by egg size. Sogard (1997) cited a number of recent studies that suggest the early juvenile period plays a greater role in determining year-class strength than previously thought.

We were unable to determine if salinity influenced increment width (a surrogate for somatic growth) at early life stages. Understanding the relationship between salinity and growth is critical because Everglades restoration will most likely result in increased freshwater flows to Florida Bay, and during low rainfall periods, salinities in the north central portion of the bay can exceed 45 ppt (Orlando et al., 1997; Boyer et al., 1999). But, salinities were moderate and similar at most stations where juvenile trout were collected in the bay during 1995 (Fig. 4). Very few fish were collected at low salinities; in fact, juvenile spotted seatrout are not commonly collected at low-salinity stations (Table 1; Florida Department of Environmental Protection[1]), and hyperhaline conditions were not observed in 1995. Therefore, we were only able to determine if temperature could influence increment widths. The curvilinear relationship between otolith growth rate and temperature, although a statistically strong relationship, is difficult to explain biologically. Temperature could mask other factors, e.g. temporal variability in prey and predator availability, and optimal temperatures for growth (Rooker et al., 1999). We were able to demonstrate that one cohort grew faster than five other cohorts, possibly indicating differential prey availability in 1995. An individual-based bioenergetics model for spotted seatrout now in preparation (Wuenschel et al.[2]) should add to our understanding of the effects of salinity and temperature on larval and juvenile spotted seatrout

Acknowledgments

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[2] Wuenschel, M. J., R. G. Werner, D. E. Hoss, and A. B. Powell. 2001. Bioenergetics of larval spotted seatrout (*Cynoscion nebulosus*) in Florida Bay. Florida Bay Science Conference, April 23–26, 2001, p. 215–216. Westen Beach Resort, Key Largo, Florida. Abstract. Center for Coastal Fisheries and Habitat Research, Beaufort Laboratory, 101 Pivers Island Road, Beaufort, NC 28516.

Literature cited

Anderson, J. T.
  1988. A review of size dependent survival during pre-recruit stages of fishes in relation to recruitment. J. Northw. Atl. Fish. Sci. 8:55–66.

Batschelet, E.
  1981. Circular statistics in biology, 371 p. Academic Press, New York, NY.

Boyer, J. N., J. W. Fourqurean, and R. D. Jones.
  1999. Seasonal and long-term trends in the water quality of Florida Bay (1989–1997). Estuaries 22:417–430.

Brown-Peterson, N. J., and J. W. Warren.
  2001. The reproductive biology of spotted seatrout, *Cynoscion nebulosus*, along the Mississippi Gulf Coast. Gulf Mexico Sci. 2001:61–73.

Chester, A. J., and G. W. Thayer.
  1990. Distribution of spotted seatrout (*Cynoscion nebulosus*) and gray snapper (*Lutjanus griseus*) juveniles in seagrass habitats of western Florida Bay. Bull. Mar. Sci. 46:345–357.

Crecco, V., and T. Savoy.
  1985. Effects of biotic and abiotic factors on growth and relative survival of young American shad, *Alosa sapidissima*, in the Connecticut River. Can. J. Fish. Aquat. Sci. 42: 1640–1648.

Cyr, H., J. A. Downing, S. Lalonde, S. B. Baines, and M. L. Price.
  1992. Sampling larval fish: choice of sample number and size. Trans. Am. Fish. Soc. 121:356–368.

Fourqurean, J. W., and M. B. Robblee.
  1999. Florida Bay: a history of recent ecological changes. Estuaries 22:345–357.

Hare, J. A., and R. K. Cowen.
  1997. Size, growth, development, and survival of the planktonic larvae of *Pomatomus saltatrix* (Pisces: Pomatomidae). Ecology 78:2415–2431.

Hettler, W. F., Jr.
  1989. Food habits of juveniles of spotted seatrout and gray snapper in western Florida Bay. Bull. Mar. Sci. 44: 152–165.

Hettler, W. F., and A. J. Chester.
  1990. Temporal distribution of ichthyoplankton near Beaufort Inlet, North Carolina. Mar. Ecol. Prog. Ser. 68: 157–168.

Holmquist, J. G., G. V. N. Powell, and S. M. Sogard.
  1989. Decapod and stomatopod communities of seagrass-covered mud banks in Florida Bay: inter- and intra-bank heterogeneity with special reference to isolated subenvironments. Bull. Mar. Sci. 44:251–262.

Houde, E. D.
  1996. Evaluating stage-specific survival during the early life of fish. *In* Survival strategies in early life stages of marine resources (Y. Watanabe, Y. Yamashita, and Y. Oozeki, eds.), p. 51–66. Balkema, Brookfield, VT.
  1997. Patterns and consequences of selective processes in teleost early life histories. *In* Early life history and recruitment of fish populations (R. C. Chambers and E. A. Trippel, eds.), p. 173–196. Chapman and Hall, London.

Houde, E. D., and C. E. Zastrow.
  1993. Ecosystem-and taxon-specific dynamic and energetic properties of larval fish assemblages. Bull. Mar. Sci. 53: 290–335.

Iverson, R. L., and H. F. Bittaker.
  1986. Seagrass distributions and abundances in eastern Gulf of Mexico coastal waters. Estuar. Coast. Shelf Sci. 1986:577–602.

Kleppel, G. S., C. A. Burkart, L. Houchin, and C. Tomas.
1998. Egg production of the copepod *Acartia tonsa* in Florida Bay during summer. 1. The roles of food environment and diet. Estuaries 21:328–339.

Matheson, R. E., Jr., S. M. Sogard, and K. A. Bjorgo.
1999. Changes in seagrass-associated fish and crustacean communities on Florida Bay mud banks: the effects of recent ecosystem changes? Estuaries 22:534–551.

McMichael, R. H., Jr., and K. M. Peters.
1989. Early life history of spotted seatrout, *Cynoscion nebulosus* (Pisces: Sciaenidae), in Tampa Bay, Florida. Estuaries 12:98–110.

Nelson, G. A., and D. Leffler.
2001. Abundance, spatial distribution, and mortality of young-of-the-year spotted seatrout (*Cynoscion nebulosus*) along the Gulf Coast of Florida. Gulf Mex. Sci. 19:30–42.

Neter, J., W. Wasserman, and M. H. Kutner.
1983. Applied linear regression models, 547 p. Richard D. Irwin, Inc., Homewood, IL.

Orlando, S. P., Jr., M. B. Robblee, and C. J. Klein.
1997. Salinity characteristics of Florida Bay: a review of the archived data set (1955–1995), 33 p. Office of Ocean Resources Conservation and Assessments, NOAA, Silver Spring, MD.

Peebles, E. B., and S. G. Tolley.
1988. Distribution, growth and mortality of larval spotted seatrout, *Cynoscion nebulosus*: a comparison between two adjacent estuarine areas of southwest Florida. Bull. Mar. Sci. 42:397–410.

Phlips, E. J., and S. Badylak.
1996. Spatial variability in phytoplankton standing crop and composition in a shallow inner-shelf lagoon, Florida Bay, Florida. Bull. Mar. Sci. 58:203–216.

Powell, A. B.
2003. Larval abundance and distribution, and spawning habits of spotted seatrout, *Cynoscion nebulosus*, in Florida Bay, Everglades national Park, Florida. Fish. Bull. 101:704–711.

Powell, A. B., D. E. Hoss, W. F. Hettler, D. S. Peters, and S. Wagner.
1989. Abundance and distribution if ichthyoplankton in Florida Bay and adjacent waters. Bull. Mar. Sci. 44:35–48.

Powell, A. B., E. H. Laban, S. A. Holt, and G. J. Holt.
2000. Validation of age estimates from otoliths of larval and juvenile spotted seatrout, *Cynoscion nebulosus*. Fish. Bull. 98:650–654.

Rice, J. A., L. B. Crowder, and M. E. Holey.
1987. Exploration of mechanisms regulating larval survival in Lake Michigan bloater: a recruitment analysis based on characteristics of individual larvae. Trans. Am. Fish. Soc. 116:481–491.

Ricker, W. E.
1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board. Can. 191, 382 p.

Rilling, G. C., and E. D. Houde.
1999. Regional and temporal variability in growth and mor-tality of bay anchovy, *Anchoa mitchilli*, larvae in Chesapeake Bay. Fish. Bull. 97:555–569.

Rooker, J. R., S. A. Holt, G. J. Holt, and L. A. Fuiman.
1999. Spatial and temporal variability in growth, mortality, and recruitment potential of postsettlement red drum, *Sciaenops ocellatus*, in a subtropical estuary. Fish. Bull. 97:581–590.

Rutherford, E. S., and E. D. Houde.
1995. The influence of temperature on cohort-specific growth, survival, and recruitment of striped bass, *Morone saxatilis*, larvae in Chesapeake Bay. Fish. Bull. 93:315–332.

Rutherford, E. S., E. B. Thue, and D. G. Buker.
1982. Population characteristics, food habits and spawning activity of spotted seatrout, *Cynoscion nebulosus*, in Everglades National Park, 48 p. United States Park Service, South Florida Research Center Report T-668, Homestead, Florida.

Rutherford, E. S., T. W. Schmidt, and J. T. Tilmant.
1989. Early life history of spotted seatrout (*Cynoscion nebulosus*) and gray snapper (*Lutjanus griseus*) in Florida Bay, Everglades National Park, Florida. Bull. Mar. Sci. 44:49–64.

Secor, D. H., J. M. Dean, and E. H. Laban.
1991. Manual for otolith removal and preparation for microstructural analysis, 85 p. Belle W. Baruch Institute for Marine Biology and Coastal Research Technical Publication 1990-01.

Sogard, S. M.
1997. Size-selective mortality in the juvenile stage of teleost fishes: a review. Bull. Mar. Sci. 60:1129–1157.

Stewart, K. W.
1961. Contributions to the biology of the spotted seatrout (*Cynoscion nebulosus*) in the Everglades National Park, Florida. M.S thesis, 103 p. Univ. Miami, Coral Gables, FL.

Thayer, G. W., A. B. Powell, and D. E. Hoss.
1999. Composition of larval, juvenile and small adult fishes relative to change in environmental conditions in Florida Bay. Estuaries 22:518–533.

Tucker, J. W., Jr., and B. E Faulkner.
1987. Voluntary spawning patterns of captive spotted seatrout. Northeast Gulf Sci. 9:59–63.

Turney, W. J., and B. F. Perkins.
1972. Molluscan distribution in Florida Bay. Sedimenta III, 37 p. Rosenstiel School of Atmospheric Science, Univ. of Miami, FL.

U. S. Naval Observatory Applications Department.
1997. Fraction of the moon illuminated. [Available at http//aa.usno.navy.mil/data/docs/Moon Fraction.html.] Last accessed 17 December 2001.

Ware, D. M.
1975. Relation between egg size, growth, and natural mortality of larval fish. J. Fish. Res. Board Can. 32:2503–2512.

Warren, C. E.
1971. Biology and water pollution control, 434 p. W. B. Saunders Company, Philadelphia, PA.