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EARLY LIFE HISTORY OF THE BLACK DRUM *Pogonias cromis* (PISCES: SCIAENIDAE) IN TAMPA BAY, FLORIDA

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ABSTRACT: The distribution, relative abundance, habitat, age, growth, and feeding habits of larval and juvenile black drum (*Pogonias cromis*) from Tampa Bay, Florida, are described. Spawning took place in the lower bay or nearshore Gulf waters from November through May, with the majority of spawning occurring in March. Spawning peaks often coincided with, but were not dependent on, the new or full moon and were seemingly influenced by tidal period. Most spawning occurred during rising temperatures and occurred earlier in Tampa Bay than in northern latitudes. Most larvae were collected during March and April, and more were found in incidental surface dip-net collections in Bayboro Harbor than from regular plankton-net collections in the bay. Larvae collected in the middle and upper bay were larger (2.9-7.3 mm) than those collected in the lower bay (1.8-5.8 mm). Plankton-net collections from midwater depths at the single night station and from bottom depths at the three day stations contained the majority of larval black drum. Juveniles 30-60 mm SL were abundant in May and June in rivers and tidal creeks with low to moderate salinities and unvegetated mud bottoms. At lengths >100 mm SL, juveniles began dispersing throughout the bay. Ages determined from counting daily otolith rings agreed with ages determined by using length-frequency progressions and showed that black drum larvae had a growth rate of 0.2-0.3 mm/day, whereas juveniles 35 to 150 mm grew 0.8-0.9 mm/day. Forty-eight percent of the larval stomachs examined were empty; stomachs with food contained primarily copepods. Mollusks were the major food group in juvenile black drum stomachs; small (<60 mm) juveniles consumed mainly bivalve siphon tips, whereas larger (>75 mm) juveniles consumed more fish, bivalves, and gastropods.

Sciaenids make up a significant portion of the nearshore marine recreational and commercial fisheries in the southeastern United States. Black drum, *Pogonias cromis*, are the largest sciaenids in the southeastern United States (Silverman, 1979), and although adults occur both offshore and in bays, the young are dependent on estuaries for nursery habitat during early growth.

Black drum spawn in or near the estuaries where larval and juvenile development occurs. Eggs have been found in Laguna Madre, Texas (Breuer, 1960; Simmons and Breuer, 1962), and in Chesapeake Bay (Joseph *et al.*, 1964). Larvae have been collected from Texas bays and passes (Pearson, 1929; Breuer, 1963; Compton, 1964; King, 1971) and southwest Florida (Jannke, 1971). Previous studies of juvenile black drum primarily concerned inshore areas of Texas (Pearson, 1929; Breuer, 1962; Simmons and Breuer, 1962; Breuer, 1971) and the Chesapeake and Delaware Bay regions (Frisbie, 1961; Thomas and Smith, 1973). Limited data are available from Mississippi (Eztold and Christmas, 1979) and Florida (Kilby, 1955; Price and Schlueter, 1985). Price and Schlueter

(1985) provided most of the information on juvenile black drum from Tampa Bay, Florida. They collected 150 black drum from the littoral zone of upper Tampa Bay, mainly during spring and summer, and reported that mean lengths increased from 26.7 mm SL in May to 92.0 mm SL in August.

In the fall of 1981, we began surveying larval and juvenile sciaenids in Tampa Bay, Florida. This paper describes the distribution, relative abundance, habitat, age, growth, and feeding of larval and juvenile black drum in the Tampa Bay system.

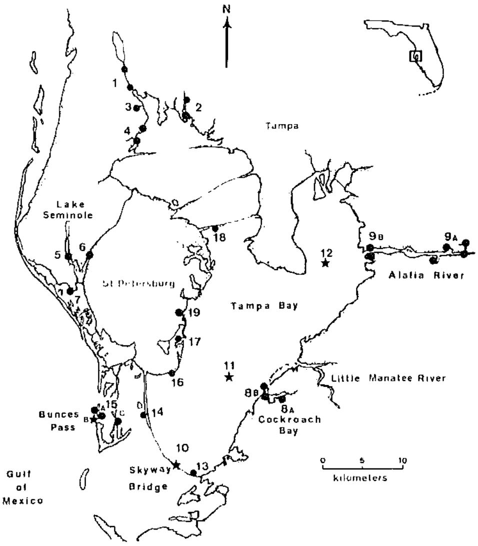

Figure 1. Map of Tampa Bay, Florida and vicinity. Solid dots represent sites for each seine station. Stars represent plankton stations. 1) Lake Tarpon, 2 sites. 2) Double Branch Creek, 2 sites. 3) Bishop Creek. 4) Alligator Lake spillway, 2 sites. 5) Lake Seminole spillway. 6) Cross Bayou. 7) Turtlecrawl Point. 8) Cockroach Bay: A, protected area; B, channel, 2 sites. 9) Alafia River: A, upstream, 4 sites; B, downstream, 2 sites. 10) Skyway Bridge (lower bay). 11) middle bay. 12) upper bay. 13) south Skyway causeway. 14) north Skyway causeway. 15) Bunces Pass: A, surf zone; B, channel, plankton and shore site; C, causeway. 16) Pinellas Point. 17) Big Bayou. 18) Gandy Bridge. 19) Bayboro Harbor (FMRI Laboratory).

MATERIALS AND METHODS

Sampling Stations, Gear, and Frequency: All collections were made in Tampa Bay, a relatively large, shallow, vertically mixed estuary on the west central Florida coast (Figure 1). This study began in the fall of 1981 as part of an early life history study of larval and juvenile red drum, *Sciaenops ocellatus*, in the Alafia River and other backwater areas of the bay (Stations 1-12, Tables 1 and 2, Figure 1). Originally, sampling stations were in rivers, tidal creeks, canals, and spillways and had freshwater discharge, sand or mud bottom, and little or no seagrass cover. Each station was sampled bi-weekly from September to December 1981. Beginning in January 1982, sampling was limited to once every three weeks in the Alafia River. In July 1982, we added six stations (13-18) that increased the diversity of habitats. These new stations had little freshwater influence and included habitats ranging from surf zones to protected and unprotected seagrass beds. The change in emphasis between years from sampling red drum in river and backwater habitats to a wide variety of habitats allowed us to sample more stations than would otherwise have been possible but limited information to a single year except at Alafia River seine stations and fall plankton samples at stations 10, 11, and 12.

Two bag seines (12.2 m × 1.2 m, 1.6 mm square mesh and 30.5 m × 2.4 m, 6.4 mm square mesh) were used at most sites to assure sampling the largest practical size range of juveniles found in each habitat. Collection methods at individual stations depended on water depth and characteristics of the shoreline. In muddy areas with steep banks or along open shores, the 30.5 m seine was set quickly in a semi-circle from the stern of the boat and slowly pulled ashore. The 12.2 m seine was then pulled parallel to shore for approximately 20 m in an adjacent area. In shallow grass flats, both seines were set parallel to shore at a depth of

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Table 1. Sampling dates, frequencies and physical parameters of juvenile *P. cromis* collections. Salinities and temperatures are mean surface water values with ranges in parenthesis. S, sand; M, mud; Sh, shell; Mod, moderate; + indicates vegetation was sparse.

Station Number	No. of Sites	Sampling Dates	No. of Collections	Salinity (‰)	Temperature (°C)	Bottom Type	Vegetation Type	Water Clarity	Energy Level
1	2	9/24-12/21/81	13	15 (10-20)	24.0 (11.8-29.0)	S/M	none	1	low
2	2	9/24-11/19/81	9	18 (6-23)	23.7 (18.5-27.3)	S/M	mangrove	1	mod.
3	1	9/24-11/19/81	4	16 (12-21)	24.2 (20.5-29.9)	S/M	mangrove	1	low
4	2	10/8-12/21/81	17	11 (3-23)	21.6 (8.9-27.9)	M	*Spartina* +	1	low
5	1	10/27-12/18/81	7	17 (12-22)	21.5 (18.1-25.5)	M	mangrove	1	low
6	1	10/18-12/18/81	20	11 (4-26)	24.2 (18.3-29.8)	M	mangrove	1	low
7	1	10/15-12/18/81	11	32 (30-33)	20.8 (16.8-25.5)	S	*Juncus* +	2	mod.
8A	1	10/6-12/8/81	10	21 (14-25)	23.0 (16.5-26.1)	M	mangrove	1	low
8B	2	9/22/81-1/5/82	27	26 (23-29)	22.6 (16.7-30.0)	S/M	mangrove	2	mod.
9A	4	9/22/81-8/30/83	201	7 (0-25)	24.0 (12.5-31.6)	M	*Juncus* +	1	low
9B	2	11/10/81-8/30/83	90	14 (0-27)	24.9 (14.0-32.2)	S/M	mangrove	1	mod.
13	1	7/9/82-8/26/83	36	27 (16-30)	23.8 (13.0-31.7)	S/M	mixed seagrass	1	low-mod.
14	1	7/28/82-8/26/83	19	28 (22-31)	25.3 (15.8-33.0)	S/M	*Halodule*	1	low-mod.
15A	2	7/1/82-8/24/83	74	31 (27-35)	24.0 (15.0-31.6)	S	none	3	high
15C	1	7/1/82-8/24/83	56	30 (26-35)	23.8 (14.3-32.4)	S/M	mixed seagrass	2	mod.
16	1	7/9/82-8/26/83	36	26 (22-30)	25.1 (16.2-32.3)	S	*Thalassia*	2	high
17	1	7/9/82-8/26/83	20	23 (19-30)	26.3 (16.7-32.5)	S/M	mixed seagrass	1	low
18	1	7/9/82-8/26/83	34	20 (16-25)	25.4 (15.1-31.9)	S	mixed seagrass	2	mod.

about 1 m and then pulled to shore. Since collection methods at individual stations varied depending on water depth and characteristics of the shoreline, it was not possible to estimate fish densities using catch-per-unit-effort of a standard set.

Plankton net collections were taken at the surface and bottom at four stations located between the bay mouth and nursery areas in the Alafia River (Table 2, Figure 1). Station 10 collections were taken at night during a rising tide, but other plankton stations had to be sampled during the day and without regard to tidal stage. Ten-minute collections were made with a 1 m diameter conical net, 5 m long, with a 3-point wire bridle and 500-micron mesh. Collections from the lower bay were made with the net, passively "fishing" in the strong tidal current, tethered either to a bridge (Station 10) or to an anchored boat (Station 15B). At the middle and upper bay (Stations 11 and 12), nets were towed at 2-3 knots in an arc to avoid propwash. For surface collections, the net was buoyed by a large, styrofoam float. For bottom and mid-water samples, the net was taken to depth using a large weight (lower bay) or by fitting the net to an epibenthic sled (middle and upper bay). Contamination of bottom samples by organisms captured in the water column during the setting and retrieving of the gear was assumed to be minimal because the times required for the gear to reach depth and then to be brought to the surface were very short in comparison to the long (10 min) tow times.

Black drum larvae were also obtained by dip-netting from the seawall at Bayboro Harbor (Station 19) during 1983-85. The two dip nets used were 17 mm × 25 mm with 0.5 mm mesh and 32 mm × 32 mm with 1.6 mm mesh. Dip-net samples were taken on an irregular basis as weather and time permitted;

Table 2. Sampling dates, frequencies and physical parameters of larval *P. cromis* plankton and dipnet collections. Salinities and temperatures are mean surface water values with ranges in parenthesis. F, flood; M, mud; Mod, moderate; S, sand; Sh, shell; Var, variable.

Station Number	Sampling Dates	Time of Day	Sampling Frequency	No. of Collections	Tidal Stage	Salinity (⁰/₀₀)	Temperature (°C)	Bottom Type	Water Clarity	Energy Level
10	9/24-11/24/81 7/22/82-11/7/83	Night	2 wk	130	F	29 (25-32)	24.6 (15.3-31.4)	S	2-3	high
11	10/6-12/8/81 8/13/82-10/20/83	Day	3 wk	53	Var	25 (15-30)	23.0 (15.5-30.7)	S/Sh	1-2	high
12	9/29-12/22/81 8/13/82-10/30/83	Day	3 wk	48	Var	21 (7-29)	24.3 (12.7-32.3)	M	1-2	mod.
15B	8/18/82-8/26/83	Day	3 wk	33	Var	31 (27-34)	23.7 (15.1-32.1)	S	3	high
19	4/21-5/5/83 1/17-7/4/84 3/25-6/4/85	Day	1 day-1 wk	50	Var	25 (10-30)	21.9 (16.8-29.2)	S/M	2	var. (wind dependent)

although the dip net is not comparable to other gear, these samples contributed large numbers of larvae to the database. Individual samples were defined as ½ h to 1 h of effort during a single day. One hundred fifty-eight larvae were kept alive and used in tetracycline-marking experiments for validation of aging methods (see below). The remainder (n = 1742) were preserved and measured for length-frequency analysis and estimation of spawning dates.

Data Collection and Analysis: At each station, we recorded surface water salinity (⁰/₀₀, refractometer) and temperature (°C, mercury thermometer), tidal stage, bottom type, and vegetation and cover type. We also made subjective estimates of relative water clarity and energy level (current speed and wave energy). Water clarity was ranked as 1 (turbid), 2 (moderately turbid), or 3 (clear) and was estimated to be equivalent to secchi disc measurements of <1 m, 1 m to 2 m, and >3 m, respectively. Energy levels were characterized as low, moderate, or high. Low energy indicated low current and wave height, moderate energy indicated moderate current and/or wave height, high energy indicated high current and/or wave height.

Black drum larvae and juveniles used in age analyses were preserved in 95% ethanol. Other samples were preserved in 5% buffered formalin. Larvae were identified, counted, and measured to the nearest 0.1 mm using a dissecting microscope and optical micrometer. Juveniles used in analysis of age or diet were measured to the nearest 0.1 mm using dial calipers; others were measured to the nearest 1.0 mm. Reported lengths are notochord lengths (NL) for preflexion larvae or standard lengths (SL) for older specimens. We defined larvae as those fish <9 mm SL because the largest pelagic larva in plankton and dip-net collections was 9.2 mm SL. Total length measurements from the literature were converted to standard lengths using the regression equation given by Hein *et al.* (1980).

Growth of young-of-the-year black drum was estimated by following length-frequency progressions and by counting daily rings on sagittae. Larval otoliths were mounted whole on glass slides, and growth increments were counted at 630 × magnification. Juvenile otoliths were mounted in Spurr's plastic and sectioned to 0.125 mm using a low-speed Isomet saw (Haake *et al.*, 1982). Sections were cleared in glycerin for 1-4 weeks, then mounted on glass slides and examined at 200 × -630 × . Our otolith ring counts were made with the assumption that the rings are deposited beginning on the first day after hatch, as was the case with red drum (Peters and McMichael, 1987). Because counting the central rings on many juvenile otoliths was difficult, we measured the distance from the center to the tenth ring on ten larval otoliths and used the average distance (37 micrometers) to equal ten central rings for all juvenile otoliths. The accuracy of this method (variation no more than one ring) was verified by counting the central rings of ten exceptionally clear juvenile otoliths.

Daily ring formation in black drum otoliths was verified by marking hard parts of live fish with tetracycline. Wild-caught larvae (4-9 mm) were collected and placed in 38-l aquaria with a tetracycline hydrochloride solution of 10-15 mg/l for six hours and then maintained in clean water for 14 days. Juveniles (50-150 mm) were injected intraperitoneally with 0.1 mg/g body weight of tetracycline hydrochloride, reared for 10 days, re-injected, and reared for seven more days. Artificial light cycles were kept similar to natural cycles. Larvae were fed on newly hatched brine shrimp; juveniles were fed frozen adult brine shrimp twice daily. Otoliths were then removed, sectioned, and viewed with ultra-violet light at 200 × -630 × . Otoliths marked with tetracycline contained the same number of rings between the two marks and between the second mark and the otolith edge as the number of days elapsed between the two tetracycline treatments and between the second treatment and the termination of the experiment, respectively.

We randomly selected otoliths for age determination by size interval for 42 larvae and juveniles <50 mm (8-10 per 10 mm size class) and 98 larvae and juveniles 2-160 mm (10 per 15-mm size class) to describe early growth and growth during the first six months, respectively. Although subsampling by size may have biased the age-at-size equations (Snedecor and Cochran, 1967, p. 150), aging all fish and then subsampling by age was not practical.

The range of spawning dates and times of peak spawning were estimated in three ways: 1) date of capture in plankton collections, 2) subtraction of estimated larval age from date of capture, and 3) subtraction of estimated early juvenile (9-50 mm) age from date of capture. Ages for spawning date calculations were determined from the <50 mm growth equation.

Black drum diets were described from contents of the entire alimentary tract in larvae and the stomach (that portion of the alimentary tract between the esophagus and pylorus) in juveniles. The alimentary tract of larvae is hereafter referred to as the stomach. Contents were identified to the lowest possible taxon. Fullness was estimated subjectively on a scale of 0 (empty) to 5 (full). Volumes were measured by displacement or, for items <0.05 cm^3, by a squash method (modified from Hellawell and Abel [1971] by Ross [1974]). Specimens with empty stomachs were not used in dietary computations. Dietary comparisons among size classes and sampling locations were made using Schoener's Index of proportional overlap (Schoener, 1968) based on mean food volume following recommendations of Wallace (1981) and Linton *et al.* (1981). As a criterion for sample size in dietary analyses, we plotted the cumulative total number of new prey taxa against the cumulative total number of stomachs examined. A minimum sample size sufficient for description of prey taxa was indicated by the curve's asymptote. Unless otherwise noted, all dietary comparisons met this criterion for adequate sample size.

All statistics were done using the Statistical Analysis System (SAS Institute

Inc., 1982).

RESULTS

Distribution

Larvae—Regular Collections—Tampa Bay: We collected 112 black drum larvae (1.8-7.3 mm, $\overline{x} = 4.3$ mm) only during the plankton collections made between early January and mid-April 1983 (Table 3). Larvae were collected at four plankton net stations in Tampa Bay. Larvae were most abundant in samples taken from March 16-29 when 102 (91%) of the total number of larvae were collected. The highest recorded density was 125 larvae/1000 m^3 at the lower bay night station, although densities of 60-80 larvae/1000 m^3 occurred at each station in late March. Ninety percent of the larvae in daylight collections were from bottom samples, whereas 90% of the larvae in night collections came from midwater samples. Surface water temperatures for collections containing black drum larvae ranged from 15.5°-22.0°C; surface salinities ranged from 0-32$^0/_{00}$.

The largest larvae from regular collections were found in the middle and upper bay near the bottom. Mean larval lengths in bottom samples were significantly larger (Studentized Maximum Modulus or GT2-test, SAS 1982, $p<0.05$) at stations 11 and 12 than at station 15B. Larvae at station 10 were smaller on average than at stations 11 and 12, although the differences could not be tested statistically. Mean size of larvae was significantly larger ($p<0.05$) at the bottom than at the surface at both the middle bay and upper bay day stations (surface and bottom means 3.2 mm vs. 5.3 mm, and 3.5 mm vs. 5.1 mm, respectively). There were no significant differences ($p>0.05$) between the mean lengths of larvae in surface, midwater, and bottom samples at the lower bay night station, and larvae were collected only at the bottom at the lower bay day station.

Larvae—Incidental Collections—Bayboro Harbor: Approximately 1900 black drum larvae and juveniles were collected in 50 dip-net samples in Bayboro Harbor (Station 19) from 1983 to 1985. These fish averaged 6.4 mm (range 4.0-9.2 mm) and were collected from January to May. All larvae were collected near the surface from one area; therefore, no depth or areal comparisons could be made. Catch-per-unit effort of these larvae (number per hour) peaked between late March and mid-April. Unusually high concentrations of larvae (estimated at >100 larvae/m^3) were occasionally observed at an inside corner where two perpendicular cement seawalls join. Surface water temperatures for collections containing larvae ranged from 19.0°-22.8°C; surface salinities ranged from 22-30$^0/_{00}$.

Juveniles: Eighty-six percent of the 597 juvenile black drum collected were <90mm in length (range 10-210 mm), and 98% (585 fish) were collected in the Alafia River (Stations 9A and 9B). Recruitment to our sampling stations varied considerably between the two years. We collected 471 juveniles from February to June 1982, but only 31 were collected during those same months in 1983 even though the number of seine hauls made during that period in 1983 ($n=70$) was greater than in 1982 ($n=56$). No information was available for 1984 and 1985, but juveniles were again abundant in the Alafia River in 1986 and 1987 (personal observation). Juveniles 16 to 90 mm were found in a range of salinities but occurred most often in low to moderate salinity areas with unvegetated mud bottoms. In the Alafia River, juveniles 16 to 120 mm were collected at both the river mouth (9B) and upstream (9A) stations; larger juveniles (120-150 mm) came only from collections near the river mouth. Statistical comparisons of juvenile lengths showed that the means were not significantly different

($p>0.05$) between a protected upstream canal and a protected tidal creek near the river mouth (pooled mean = 46 mm, n = 411), although the exposed shore across from the tidal creek contained significantly larger juveniles ($\bar{x}$ = 58 mm, n = 154, $p<0.05$). Much larger juveniles were collected at the middle bay causeway station (18, $\bar{x}$ = 155 mm, n = 18). Overall, the largest juveniles taken during the study (140-210 mm) came from moderate- to high-salinity stations throughout the bay, including river mouth (9B), middle bay (18), and lower bay (13, 15) stations. Large juveniles were also observed (but not measured) in hook-and-line catches from the river mouth and bay-gulf passes.

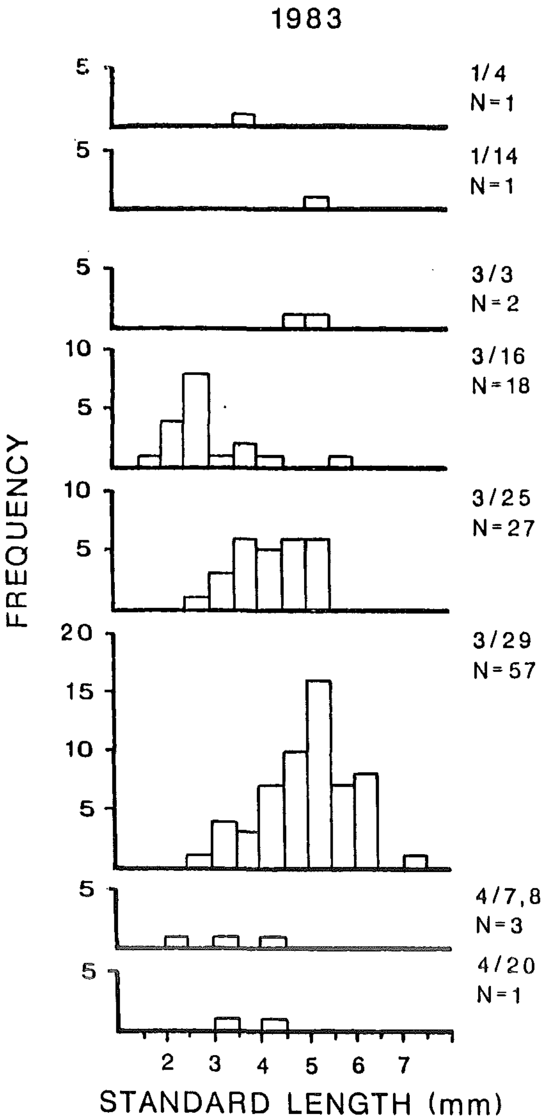

Figure 2. Length-frequency distributions of larval *P. cromis* from plankton collections in Tampa Bay during 1983, arranged by collection date.

Growth

Black drum growth rates determined from length-frequency plots ranged from 0.2 mm/day to 0.9 mm/day. Length-frequency progressions of larval black drum from the regular (open bay) plankton stations show an apparent modal increase in length from 2.5 mm on 16 March to 5.0 mm on 29 March, for a growth rate of 0.2 mm/day (Figure 2). Dipnet collections of larvae from the harbor showed almost no modal increases in length, even though collections were made on eight of eleven consecutive days between 25 March and 4 April 1985 (Figure 3). Monthly length-frequencies of juvenile black drum (Figure 4) contained few older fish but appeared to show cohort growth in 1982 from 35 mm in May to about 150 mm in September, and from 35 mm in June to 110 mm in September, for growth rates of 0.9 mm/day and 0.8 mm/day, respectively.

For two size groups, growth rates determined by otolith counts were comparable to rates estimated from length-frequency modes. Equations for fish <50 mm detailed early growth and provided a means to estimate spawning dates from lengths (see Spawning section). A second set of equations depicted growth for juveniles over the entire size range used in otolith analysis (2-160 mm). Equations best describing growth of 42 black drum <50 mm for size-at-age and age-at-size from otolith data were:

$$L = -3.977 + 0.589A, \; r^2 = 0.96 \qquad (1)$$

$$\text{and } A = 2.412L - 0.016L^2, \; r^2 = 0.97, \qquad (2)$$

where L is notochord or standard length in millimeters and A is the age in days. Using Equation 2, we estimate that a fish

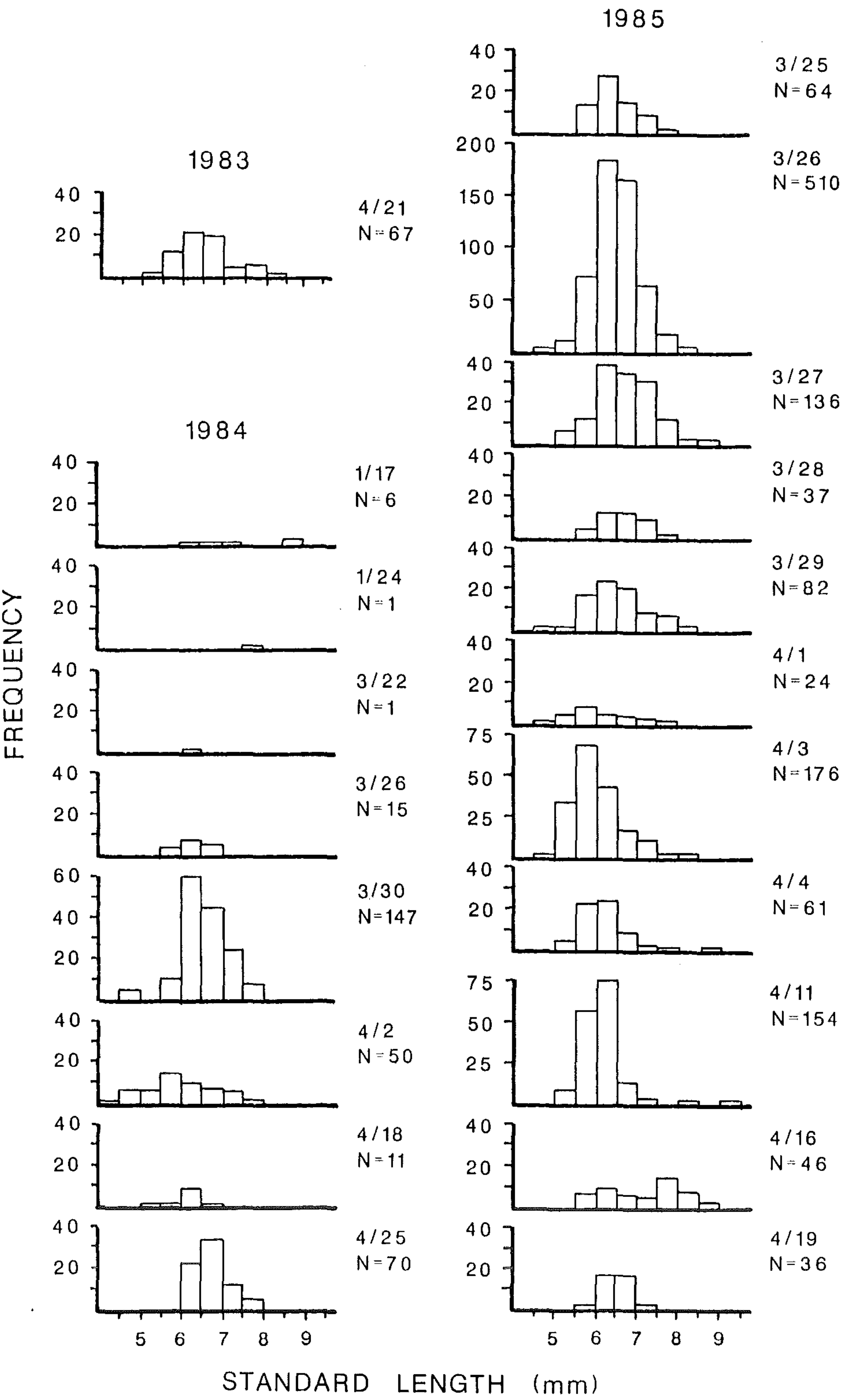

Figure 3. Length-frequency distributions of larval *P. cromis* from dipnet collections in Bayboro Harbor during 1983, 1984, and 1985, arranged by collection date.

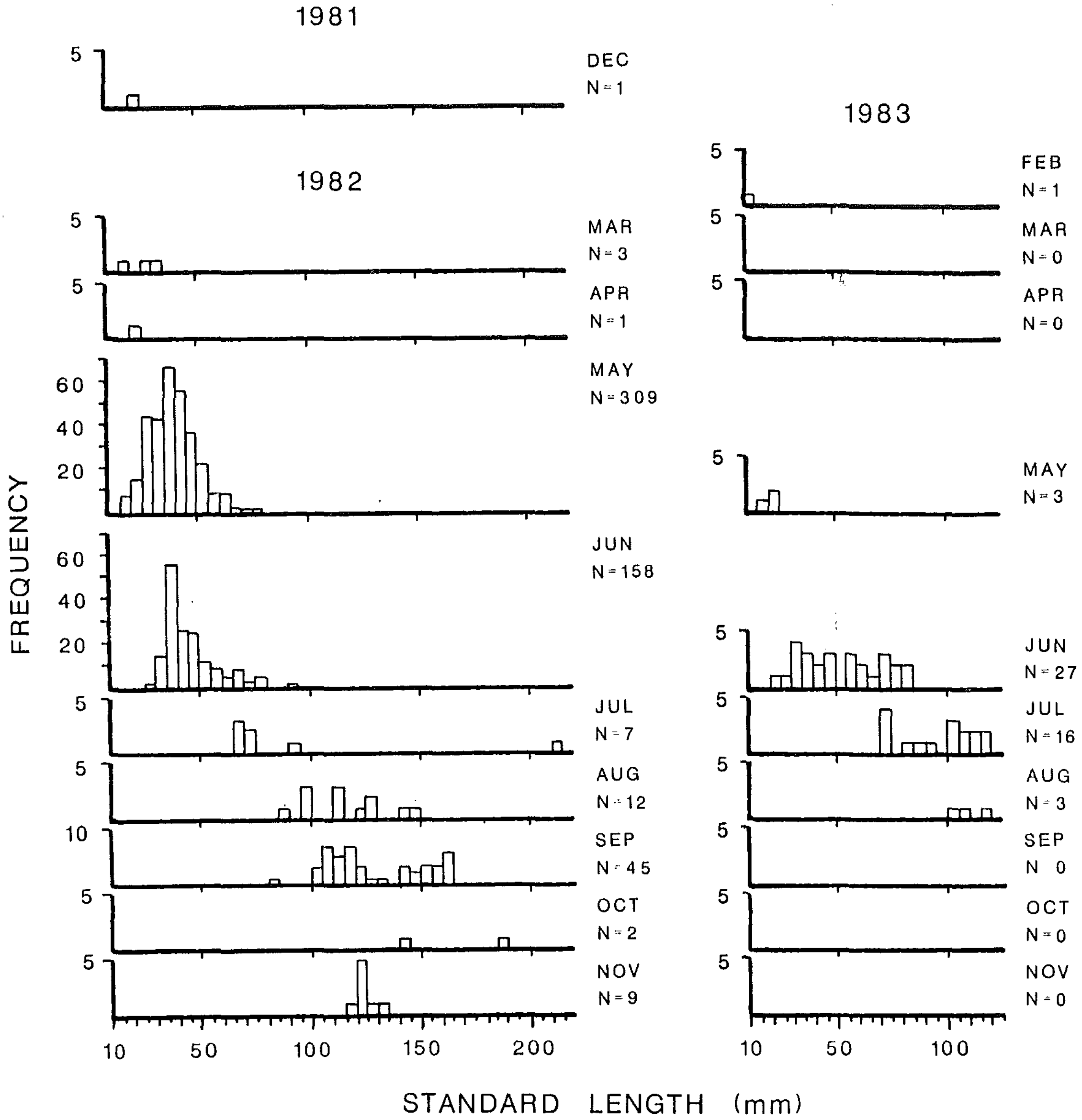

Figure 4. Length-frequency distributions of juvenile *P. cromis* from seine collections in Tampa Bay during 1981, 1982, and 1983, arranged by month.

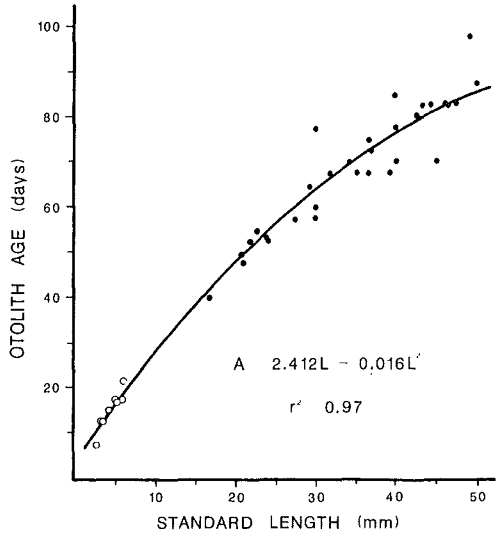

Figure 5. Growth rate of 8 larval (open circles) and 34 juvenile (solid circles) *P. cromis* from Tampa Bay. Ages were determined by counting daily increments on sagittae of specimens <50 mm SL.

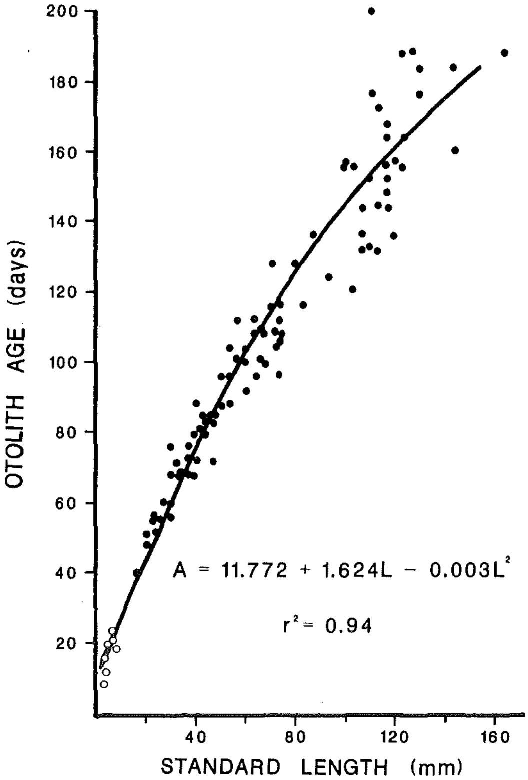

Figure 6. Growth rate of 7 larval (open circles) and 91 juvenile (solid circles) *P. cromis* from Tampa Bay. Ages were determined by counting daily increments on sagittae of specimens up to 160 mm SL.

would be an average of 23 days old at 10 mm, 58 days old at 30 mm, and 81 days old at 50 mm (Figure 5). In terms of growth per day, larvae were calculated to have grown from about 2 mm at hatching to 10 mm at age 23 days or at a rate of 0.3 mm/day. Growth from 10-50 mm was estimated to take 58 days or 0.7 mm/day.

Equations best describing growth of 98 black drum 2-160 mm for size-at-age and age-at-size were:

$$L = -15.231 + 0.823A,\ r^2 = 0.93 \quad (3)$$

and $$A = 11.772 + 1.624L - 0.003L^2,\ r^2 = 0.94. \quad (4)$$

Using Equation 4, we estimate that a fish would be an average of 28 days old at 10 mm, 58 days old at 30 mm, and 86 days old at 50 mm, or about 5 days older than the ages predicted by the <50 mm equation for fish both 10 mm and 50 mm (Figure 6). We estimate that juveniles 100 mm and 150 mm would be an average of 144 days old and 188 days old, respectively. In terms of growth per day, the overall growth rate from hatching to 150 mm would average 0.8 mm/day, and fish growing from 35-150 mm would average 0.9 mm/day.

Spawning

Black drum spawn from November to April or May in the Tampa Bay area. Larval collection data indicated that spawning may occur from late December or early January through mid-April, with peak spawning occurring during mid-March (Figures 2, 3, and 7). Juvenile collection data showed a similar peak in spawning activity (Figures 4 and 8). In addition, a 20 mm individual from December 1981 indicated that some spawning occurred prior to December, whereas a mode at 120 mm in November 1982 indicated spawning might continue until May.

Spawning dates estimated from larval data (Figure 7) indicated that only a minor amount of spawning occurred in late December and early January, 1983

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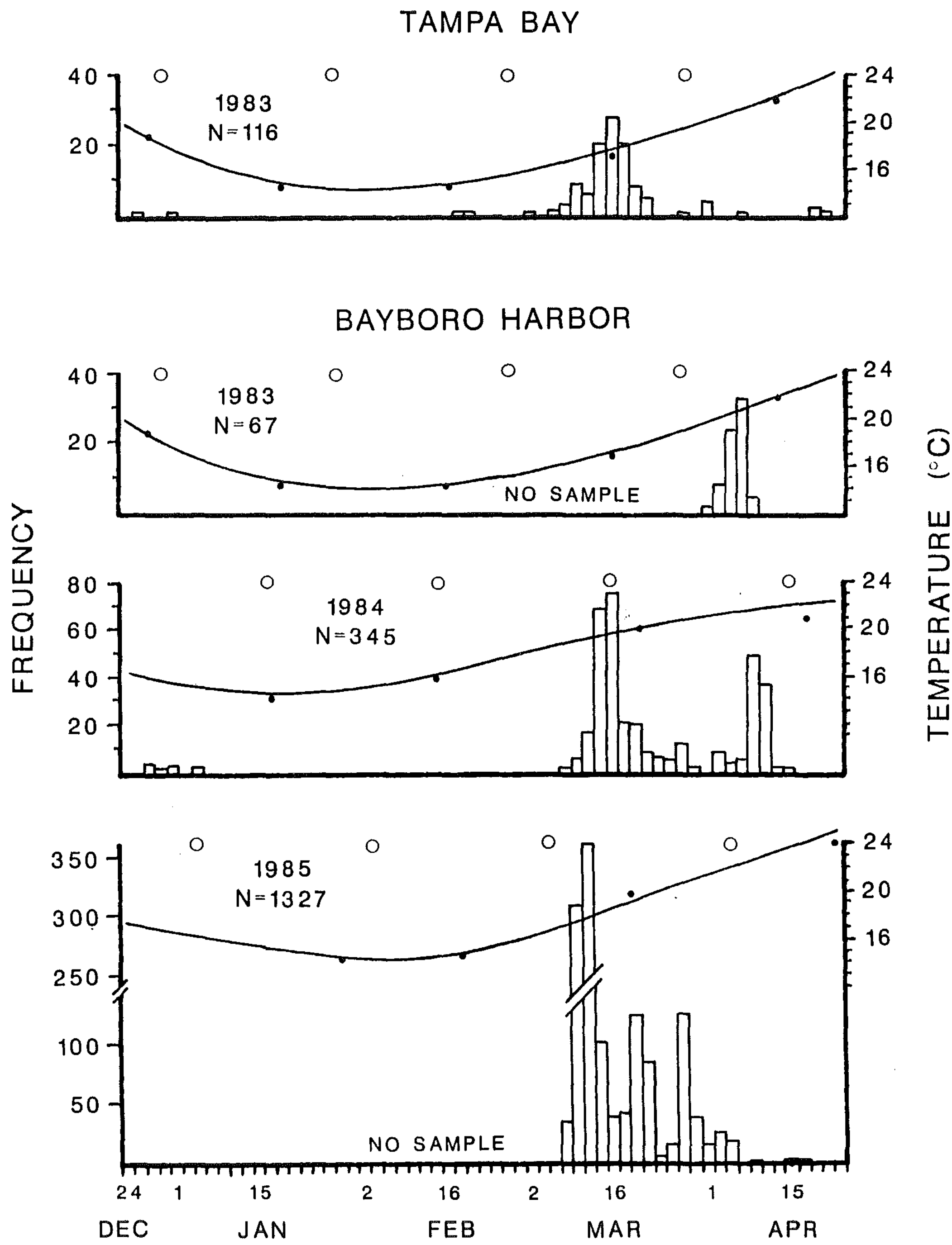

Figure 7. Spawning dates calculated for 1,855 larval *P. cromis* from Tampa Bay plankton and dipnet collections during 1983, 1984, and 1985. Spawning date was determined by subtracting the calculated age from the collection date. Equation used to calculate age was: $A = 2.412L - 0.016L^2$. Open circles indicate a full moon. Curved line with solid circles indicates water temperatures at bay mouth.

and 1984, and that no spawning occurred during the remainder of January and February in those years. Most spawning took place between early March and mid-April, with spawning peaks present in mid-March of all three years. In addition, an early April peak occurred in both 1983 and 1984.

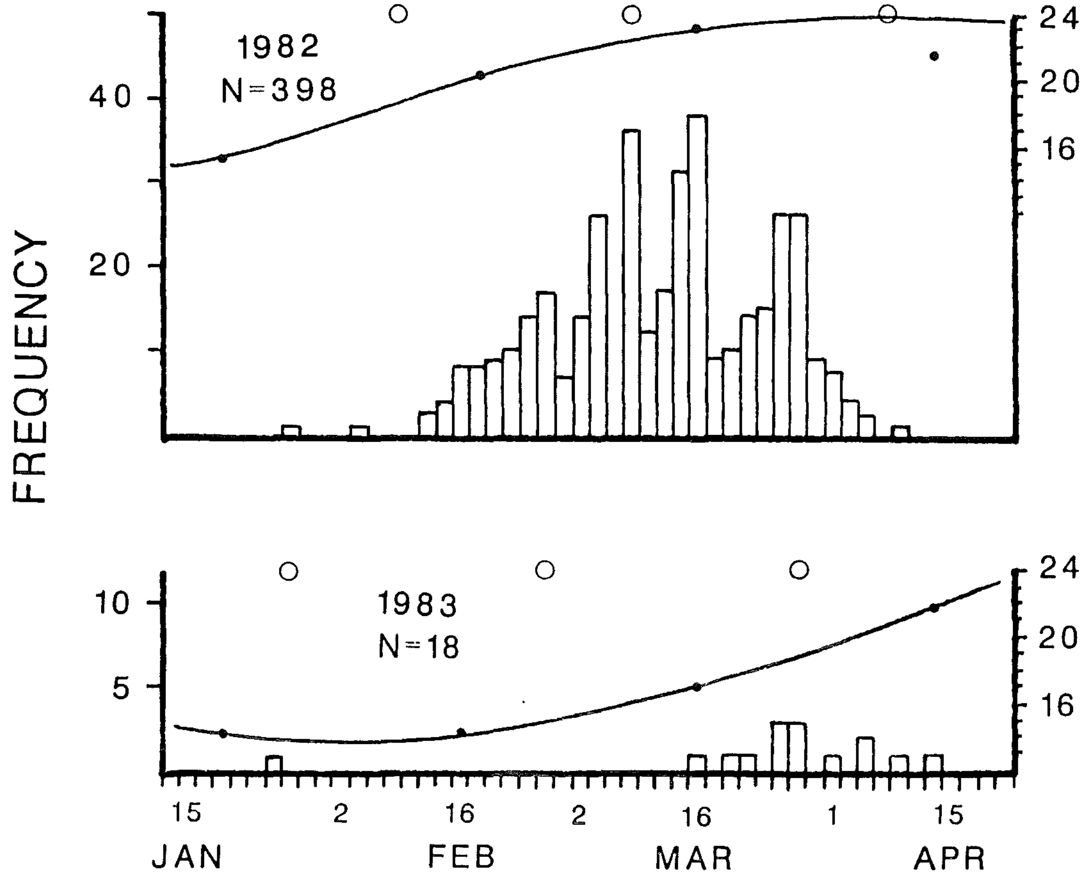

Figure 8. Spawning dates calculated for 417 juvenile *P. cromis* (8-50 mm) from Tampa Bay seine collections during 1981, 1982, and 1983. Spawning date was determined by subtracting the calculated age from the collection date. Equation used to calculate age was: $A = 2.412L - 0.016L^2$. Open circles indicate a full moon. Curved line with solid circles indicates water temperatures at bay mouth. The single individual for 1981 was estimated to have spawned on 4 November and is not shown.

Juvenile black drum data (Figure 8) from 1982 indicated peak spawning from early to mid-March. The two-month spawning period (mid-February to mid-April) generally falls within the range of dates estimated from plankton samples for 1983.

Peak spawning occurred during the period of rising water temperatures in the spring (Figures 7 and 8). Peak spawning also occurred at the time of the full moon in 1982 (juvenile data), 1984, and 1985 (larval data). However, in 1983, spawning peaks (both sets of larval data) occurred at the time of the new moon, which suggests that tidal influence, and not the specific moon phase, may determine the amount of spawning activity or successful recruitment.

Spawning, as determined by larval size, probably occurred in both the bay and nearshore Gulf waters because the smallest larva and the smallest mean larval length both occurred at the lower bay day station (Table 3). However, the presence of larvae as small as 3.1 mm at the upper bay station suggests spawning may also occur within the bay.

Feeding Habits

We examined 341 stomachs, 16.4% of which were empty. The highest per-

Table 3. Numbers and mean standard lengths of black drum larvae collected during 1983 at four plankton net stations in Tampa Bay and from 1983 to 1985 at one dipnet station in Bayboro Harbor. Sample depths are followed in parentheses by the number of collections examined.

Station		Number of Larvae	Mean SL (mm)	Length Range (mm)
PLANKTON NET COLLECTIONS				
Lower Bay				
10	Surface (6)	2	4.0	2.8-5.1
	Midwater (4)	28	4.2	3.0-5.3
	Bottom (6)	1	3.8	3.8
	Total (16)	31	4.2	2.8-5.3
15B	Surface (5)	-	-	-
	Bottom (5)	20	2.9	1.8-5.8
	Total (10)	20	2.9	1.8-5.8
Middle Bay				
11	Surface (4)	4	3.2	2.9-6.3
	Bottom (3)	24	5.3	4.2-6.3
	Total (7)	28	5.0	2.9-6.3
Upper Bay				
12	Surface (3)	4	3.5	3.1-3.8
	Bottom (3)	29	5.1	4.1-7.3
	Total (6)	33	4.9	3.1-7.3
DIPNET COLLECTIONS				
Middle Bay				
19	Surface (50)	1742	6.4	4.0-9.2

centage of empty stomachs (48%) occurred in larval fish and in fish 15-30 mm. Most other size classes had fewer than 10% empty stomachs. Overall mean fullness (excluding fish with empty stomachs) was 3.4 on a scale of 1-5. Mean fullness values for individual size classes ranged from 2.8 to 3.8. Our day-collected larvae had higher incidences of feeding and higher mean fullness values than did the night-collected larvae.

We identified over 28 different prey items from black drum stomachs (Table 4). Copepods were the predominant prey items in larval stomachs, occurring in 75% of the larvae, making up 95% of the numeric portion, and making up 58% of the mean volume (Figure 9). The numeric and volumetric importance of copepods was reduced with increasing fish size. Copepods were rarely found in 30-60 mm fish and were not evident in any fish >60 mm.

Mollusks, or mollusk body parts, were the predominant food groups in most juvenile size classes in terms of number and volume. In fish <60 mm, mollusks were represented mainly as bivalve siphon tips. In larger fish, bivalves and gastropods were the predominant food items, although shells or shell fragments of these animals were rarely found. Sand was found in 68% of juvenile stomachs, probably as an incidental result of their benthic feeding habits.

Polychaetes, shrimp, and crabs also occurred in most size classes >15 mm, but they never made up a large percentage of the diet in any size class. Amphipods (primarily *Ampelisca vadorium*) and insects also occurred in many size classes. The largest mean volume percentage (18%) of insects occurred in 75-90 mm fish (n = 6). The stomachs of fish in all other size classes contained less than 10% insects by volume.

Fish scales and other fish remains were found in stomachs of fish in all size classes >30 mm. Although fish remains were found in many stomachs, the reported volume in each stomach was low because the most numerous items (fish scales) were not measured volumetrically.

We found that larval fish had low (<37%) dietary overlap with all other size classes (Table 5). The highest overlap in juveniles usually occurred between adjacent size classes, with the least similarity occurring between distant size classes.

We compared the diets of black drum collected in the two areas of primary abundance in the Alafia River. Fish <75 mm from the up-river site (9A) had high numbers of mollusks (primarily siphon tips), whereas fish <75 mm from the lower river (9B) fed primarily on amphipods and fish and contained very few mollusks. Black drum >75 mm were available mainly from the lower river site and fed on fish, bivalves, and gastropods.

DISCUSSION

Distribution

King (1971) collected most of his 5,172 larval black drum ($\bar{x}$ = 5 mm TL, 4.4 mm SL) at surface and midwater depths and reported that this distribution did not change with the time of day. Plankton samples from our lower bay night station indicated that most larvae

Table 4. Volumes (cm³ × 10³) of all food items identified from *P. cromis* collected in Tampa Bay.

	SIZE CLASS									
	<8	8-15	15-30	30-45	45-60	60-75	75-90	90-105	105-120	>120
Number examined	23	-	44	104	62	32	9	12	32	24
Number with food	12	-	23	94	60	31	6	11	30	21
ITEM										
POLYCHAETA										
Polychaete setae	-	-	-	-	-	0.1	-	-	-	-
Polychaete remains	-	-	3.1	48.6	22.4	37.5	2.0	20.0	30.9	131.5
MOLLUSCA										
Siphon tips	-	-	23.9	168.6	57.6	23.4	0.9	-	28.0	-
Bivalve remains	-	-	-	-	-	-	-	-	196.0	18.0
Gastropod remains	-	-	-	-	-	5.0	-	-	87.5	36.0
Mollusk remains	-	-	-	3.4	-	-	-	-	164.0	674.0
COPEPODA										
Harpacticoid copepodite	0.1	-	2.7	-	-	-	-	-	-	-
Harpacticoid nauplii	0.1	-	-	0.1	0.3	-	-	-	-	-
Calanoid copepodite	1.0	-	-	-	-	-	-	-	-	-
Copepod nauplii	0.1	-	-	-	-	-	-	-	-	-
AMPHIPODA										
Ampelisca vadorum	-	-	-	69.3	114.8	41.3	-	-	-	-
Microdeutopsus sp.	-	-	-	-	7.5	-	-	-	-	-
Corophium sp.	-	-	-	-	-	-	-	-	-	1.8
Amphipod remains	3.0	-	9.7	60.8	1000.0	12.9	10.0	-	-	2.0
MYSIDACEA										
Taphromysis sp.	-	-	4.0	-	-	-	-	-	-	-
DECAPODA										
Shrimp remains	-	-	-	-	13.0	23.0	5.0	-	52.0	7.5
Crab remains	-	-	-	3.6	3.0	4.3	-	30.0	32.0	-
INSECTA										
Chironomid larvae	-	-	4.9	3.6	2.9	-	40.0	-	-	-
Notonectid parts	-	-	-	-	-	1.8	1.8	7.5	48.0	53.2
Insect remains	-	-	-	2.4	-	1.8	-	-	-	-
OSTEICHTHYES										
Fish scales*	-	-	-	8	19	14	2	6	8	7
Fish remains	-	-	-	8000.0	0.1	-	10.0	-	42.0	0.1
MISCELLANEOUS										
Sand*	-	-	9	64	42	25	4	9	22	12
Plant remains	-	-	-	0.9	2.7	0.9	0.6	0.4	5.4	3.9
Leptocheilus rapax	-	-	3.6	5.4	0.5	2.7	-	-	-	-
Foraminifera	-	-	-	0.1	-	-	-	-	-	-
Nematodes	-	-	0.5	-	-	-	-	-	-	-
Limulus polyphemus	-	-	-	-	-	2.0	-	-	-	-
Erichsonella sp.	-	-	-	-	-	-	-	-	30.0	-
Ostracods	-	-	-	0.5	-	-	-	-	-	-
Shell fragments*	-	-	-	-	-	-	-	1	-	-
Fecal pellets	-	-	-	-	-	-	-	-	-	0.9
Pollen grains	0.1	-	-	-	-	-	-	-	-	-
Crustacean remains	-	-	-	6.9	0.6	-	1.8	-	20.0	-
Unidentified remains	0.2	-	17.3	123.1	67.6	179.7	34.0	69.5	85.8	110.3

* Indicates occurrence instead of volume.

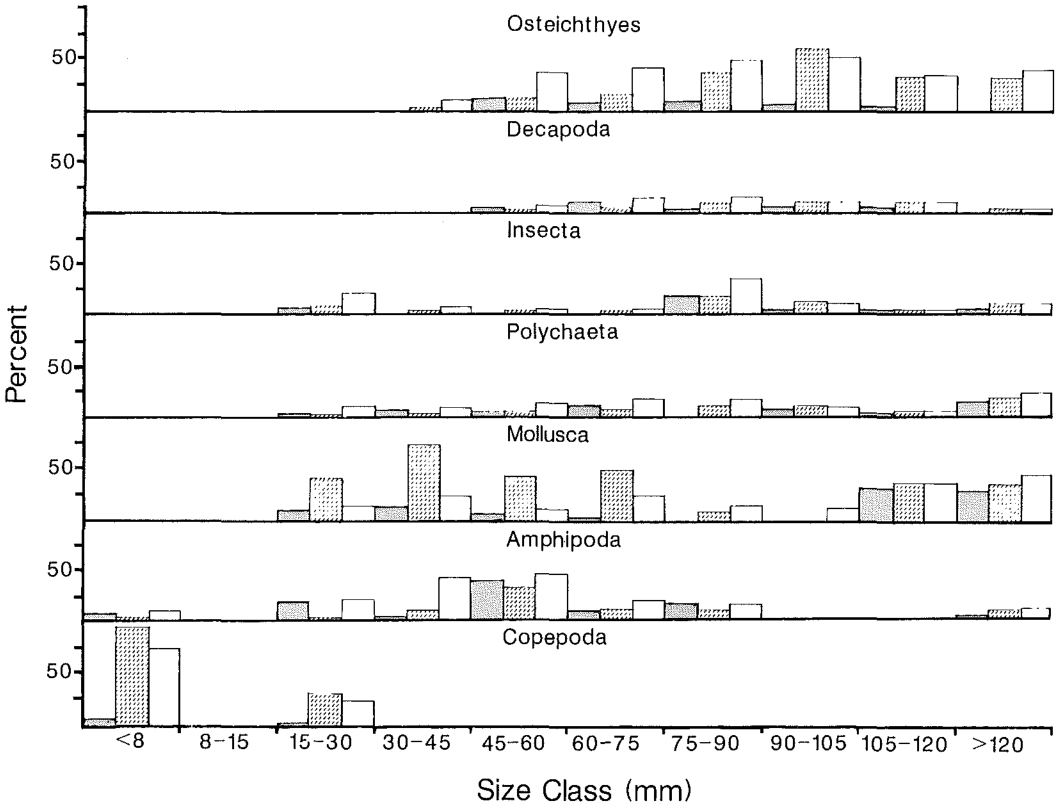

Figure 9. Percent volume (striped), number (stippled), and occurrence (open) of major prey items from 15 mm size classes of *P. cromis* collected in Tampa Bay.

were at midwater depths in lower Tampa Bay at night. Our three regular day stations contained few larvae at the surface; however, at the harbor station, hundreds of larvae were collected from the surface during the day. This may indicate a distinct difference in depth distribution between areas or a high degree of net avoidance by larvae during the day. Delayed settling also may have contributed to the number of large larvae along the harbor bulkhead, indicating that lack of an adequate shallow transition zone may result in an extended pelagic stage. Data on mullet also suggests that shallow-water areas are important during the

Table 5. Dietary overlap based on average proportional volume of prey items for 15 mm size classes of *Pogonias cromis*. Values approaching 1 indicate diet similarity and values approaching 0 indicate no similarity. Numbers in parentheses indicate number of fish with food. Size classes which did not meet our criterion of minimum sample size are indicated by an *.

	15-30 (23)	30-45 (94)	45-60 (60)	60-75 (31)	75-90 (6*)	90-105 (11)	105-120 (30)	>120 (21)
<8 (12)	.34	.31	.37	.37	.37	.28	.27	.23
15-30 (23)		.81	.62	.64	.69	.54	.54	.58
30-45 (94)			.77	.69	.69	.56	.57	.55
45-60 (60)				.64	.64	.51	.48	.41
60-75 (31)					.73	.78	.68	.62
75-90 (6*)						.66	.64	.56
90-105 (11)							.67	.57
105-120 (30)								.82

transition phase from planktonic to benthic feeding (Blaber, 1987).

Most previous studies report small black drum juveniles in habitats similar to ours — shallow, quiet, and muddy-bottomed tidal creeks, rivers, secondary bays, and lagoons (Pearson, 1929; Frisbie, 1961; Breuer, 1962; Simmons and Breuer, 1962; Breuer, 1971; Thomas and Smith, 1973; Price and Schlueter, 1985). These studies show that juveniles move out of these habitats as they grow, although the reported size at which they move out varies greatly. Thomas and Smith (1973) reported that juveniles first move from creeks to rivers when they measure from 25-40 mm, whereas Pearson (1929) noticed movement when juveniles measured 70-80 mm. In Tampa Bay, the study by Price and Schlueter (1985) and our study found the most noticeable movement out of creeks and secondary bays when the fish were about 100 mm. In our study, we also noticed that during the fall, as juveniles reached 150-200 mm, they moved into open waters of the river mouths, bays, passes, and nearshore Gulf.

Growth

Our larval growth rates, estimated from otolith analyses, agreed with rates estimated by the modal progressions in length-frequencies. The laboratory-reared specimens of Joseph *et al.* (1964) grew to 5 mm SL and 7.5 mm SL after one month at 21 °C (about 0.2 mm/day), a rate similar to our estimate (0.2-0.3 mm/day).

Juvenile growth rates estimated from otolith analyses also agreed with rates estimated by the modal progressions of length-frequencies (both 0.8-0.9 mm/day). Many studies reported juvenile growth rates similar to those found in our study (Pearson, 1929, Mar-Dec data only; Gunter, 1945; Abbe, 1967; Bryan, 1971; Thomas, 1971, Aug-Nov data only; Branch and Strawn, 1978, July data only; Garza *et al.*, 1978; Cornelius, 1984; Price and Schlueter, 1985; Murphy and Taylor [Pers. comm., Florida Marine Research Institute], approximately 250 mm SL at 1 yr). In addition, Breuer (1971) reported on a cohort with similar growth rates, but average sizes were larger in any given month, suggesting an early spawn (December or January) for that particular group. Studies in the Chesapeake and Delaware Bay regions (Joseph *et al.*, 1964; Thomas, 1971) indicated later spawning peaks than did Gulf of Mexico studies; however, average lengths for Delaware River specimens reported by Thomas (1971) for later in the year (Aug-Nov) were similar to those reported for specimens in Gulf studies.

Spawning

Each of the three methods used to estimate spawning dates in our study had its advantages and disadvantages. The first two methods estimated spawning dates from larval collection data and are good estimates of time of spawning. However, these methods do not measure the level of spawning before and after our plankton collections or indicate what is represented by the large number of larvae present in some collections. Large numbers could indicate increased spawning activity, a high density of larvae at a sampling site, or a change in the actual spawning site during the season, which would place larvae of a size susceptible to collection at our stations during only a portion of the year.

Spawning estimates from juvenile collection data were less precise than were estimates made using larval collection data because greater variation in growth rates may have occured during the relatively long period (>2 months) prior to capture. Juvenile samples were probably less affected by sampling bias because a large number of specimens were available (n = 416), and they were sampled on a finer time scale relative to their age

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than were the larvae (3 wk sampling cycles during 6 wks of growth from 8-50 mm, versus 2-3 wk sampling cycles taken during 3 wks of larval growth).

The distribution of larvae <3.5 mm recorded during this study indicated that spawning took place predominately in the lower bay or nearshore waters, which is similar to other reports of spawning in nearshore waters, passes, sounds, and bays (Pearson, 1929; Breuer, 1960; Simmons and Breuer, 1962; Joseph *et al.*, 1964; Eztold and Christmas, 1979; Mok and Gilmore, 1983). Spawning may occur further offshore in the northern Gulf of Mexico to fit conditions unique to that area (Cody *et al.*, 1984; Ditty, 1984).

Data from collections of black drum eggs and larvae and the back-calculation of spawning dates indicate that most spawning occurs in winter or spring. Gulf studies report peak spawning in February and March (Simmons and Breuer, 1962; Jannke, 1971; Eztold and Christmas, 1979; Cody *et al.*, 1984) or March and/or April (Pearson, 1929; Breuer, 1960; Compton, 1964; Fontenot and Rogillio, 1970; King, 1971; Ross *et al.*, 1983; Music and Pafford, 1984; present study). In Chesapeake Bay, spawning peaks in March, May, or June, which is somewhat later than in the Gulf (Frisbie, 1961; Joseph *et al.*, 1964; Thomas and Smith, 1973). Peak spawning may be somewhat temperature-dependent because peak spawning occurred during rising temperatures and appeared to occur earlier in Tampa Bay than in northern latitudes.

In addition to the peak spawning period, there are numerous reports of spawning in other seasons. Several studies from Florida and Texas have found evidence of limited spawning in December and January, a period of falling temperatures (Breuer, 1971; Jannke, 1971; present study). Also, many authors have reported a separate spawning in summer, a time when water temperatures would be quite high (Pearson, 1929; Breuer, 1963; Compton, 1964; Thomas and Smith, 1973; Ross *et al.*, 1983).

The stimuli for spawning are not completely understood. The majority of black-drum spawning in Tampa Bay occurred in mid-March regardless of absolute water temperature or of whether the moon phase was full or new. Music and Pafford (1984) reported increased spawning by black drum on the full moon; however, since we found peaks on new- and full-moon phases, we believe that tidal period may have more influence. Secondary spawning peaks were evident in our data less than a month after peak spawning in two of the four years (*e.g.*, late March and early April peaks in 1983 and 1984 harbor data). The existence of these multiple peaks in spring suggests either that all fish do not ripen at the same time or that some fish spawn more than once. Two studies (Arnold *et al.*, 1977; Roberts *et al.*, 1978) have indicated that some or all of the female red drum (*Sciaenops ocellatus*) held under laboratory conditions spawn during as many as 100 consecutive days. Tucker and Faulkner (1987) found that another sciaenid (*Cynoscion nebulosus*) was capable of spawning on several consecutive days and that spawning activity was concentrated seasonally, just after a full moon.

In general, black drum probably ripen in the spring as the water temperature rises above some minimum requirement of the local population. This would explain differences in peak spawning times between black drum in south Florida and those in Virginia, but it would not explain the stimulus for December spawning (while temperatures are falling) or July spawning (as temperatures peak). Pearson (1929) suggested that the youngest maturing fish (240-325 mm) might reach sexual maturity several months prior to, or after, older fish. The small size of ripe fish he found from July to October tends to support the hypothesis that Age I fish mature and spawn in July or August during their second summer; however, December spawning could be the result of a few fish ripening and spawning early, before they are limited by falling winter temperatures.

Feeding Habits

The majority of juvenile fish examined had food in their guts, but only about half of the larval fish stomachs examined contained food. The high percentage of empty larval stomachs may be attributed to long tow times and the numerous night samples (Peters and McMichael, 1987). The high percentage of juvenile stomachs with food and the high fullness values of these stomachs indicated that a significant amount of feeding occurred during the time of our collections (0900-1600). We had no night collections for juveniles; however, Thomas (1971) found that feeding occurred during both day and night and that it was least intensive during early morning hours. He found amphipods more abundant in gut contents at night and isopods, annelids, and insects more abundant during the day.

Our study, like others (Pearson, 1929; deSylva *et al.*, 1962; Simmons and Breuer, 1962; Thomas, 1971; Music and Pafford, 1984), found small (<60 mm SL) juveniles feeding on an assortment of items, including amphipods, mollusks, polychaetes, and small fish. The diet changed somewhat with size: larger black drum consumed larger quantities of crabs, shrimp, fish, and mollusks. Only our study found that small (<60 mm) juvenile black drum consumed pelecypod siphon tips. Siphon-nipping has been reported for other benthic-feeding fishes (Edwards and Steele, 1968; Modde and Ross, 1983; McMichael and Ross, 1987).

The guts of the juveniles we examined lacked shell or shell fragments, even when they contained bivalve or gastropod remains. Apparently, juveniles have the ability to break the shell and ingest just the animal, whereas adults have been reported with large quantities of shell in their guts (Pearson, 1929).

In juvenile black drum, feeding habits change with morphological development. The subterminal mouth and sensitive chin barbels develop early and are adapted to benthic feeding. Small juveniles feed on soft-bodied benthic animals until their pharyngeal teeth become developed and they can start consuming hard-bodied prey. Large juveniles (>200 mm) with well-developed pharyngeal teeth have diets similar to adult black drum, which prey mainly on mollusks and crabs (Pearson, 1929; Music and Pafford, 1984).

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