Spawning, growth, and overwintering size of searobins (Triglidae: *Prionotus carolinus* and *P. evolans*)*

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The northern searobin, *Prionotus carolinus*, and striped searobin, *P. evolans*, are among the most common benthic fishes of continental shelf waters between Cape Cod and Cape Hatteras, and both species have contributed occasionally to landings of the U.S. middle Atlantic states. Although several life history studies of these species have been published (Marshall, 1946; Wong, 1968; McEachran and Davis, 1970; Richards et al., 1979; McBride et al., 1998), their early life history has been poorly documented until recently (McBride and Able, 1994; Able and Fahay, 1998; McBride et al., 2002). Obstacles to early life history studies of these searobins include the following: 1) eggs and preflexion larvae are difficult to identify; 2) spawning occurs concurrently for several months; 3) slow growth rates confound analysis of size frequencies for determining cohort structure, and 4) conventional sampling methods have provided few late-stage larvae and early juveniles. I set out to avoid these problems by collecting juvenile specimens from the field and analyzing their otolith microincrements to determine spawning periodicity and growth rates. This approach has not previously been applied to any triglid (Secor et al., 1992).

This study demonstrates both interspecific and intraspecific differences in size during the first year. A literature review also suggests that age-0 *P. carolinus* are smaller than age-0 *P. evolans* and that conspecifics at northern latitudes are larger than conspecifics at southern latitudes (Table 1). In this study, daily sagittal micro-increments were validated and used to test whether interspecific spawning date differences, growth rate differences, or both, are responsible for size differences at first winter. Size at first annulus formation was also examined as an independent measure of age and growth rate. The results of this study improve our understanding of the continental shelf as a nursery ground and the geographic variation in life history traits for these two species.

Materials and methods

Otolith micro-increment validation

Otolith ontogeny was examined by using cultured embryos and yolksac larvae. *Prionotus carolinus* eggs were collected from ripe adults in August 1992 in coastal waters and fertilized in the laboratory. Embryos were raised in 10-liter aquaria under a 12:12 hour light:dark cycle, at 31 ppt salinity, and 26°C. Cultured *P. carolinus* embryos began to hatch after 48 hours and nearly all fish had hatched by 56 hours. Laboratory temperatures unintentionally dropped to 22°C after hatching, but no mortality was observed. Embryos and larvae were preserved in 95% ETOH at 8–16 hour intervals for the first three days and 22–26 hours for the following three days. No fish survived beyond six days. No water was exchanged, but constant aeration kept the aquaria well mixed during the experiment. Newly hatched *Artemia* sp. nauplii were supplied to yolksac larvae, but no feeding was observed. All mortalities appeared to be caused by starvation.

Embryos or larvae were placed on a slide under a cover slip or set in immersion oil (Secor et al., 1992) to examine otolith ontogeny. Otolith presence, size, and development were noted with both a binocular scope (≤50×) and a compound microscope (40–1000×) with polarized light. Notochord length (NL) was measured with an ocular micrometer to the nearest 0.1 mm. Otoliths were measured from a digitized video image through a compound microscope to the nearest 0.001 mm.

Field-collected *P. carolinus* juveniles were chemically marked with tetracycline, held in the laboratory under controlled conditions, and the relationship between "days captive" and "rings after the tetracycline mark" was tested against a 1:1 ratio. Newly settled *P. carolinus* (10–15 mm standard length [SL]) were collected near Beach Haven Ridge (New Jersey) by using a 1- or 2-m beam trawl on five different dates in October 1992 (see McBride et al. [2002] for sampling locations). These fish were divided into four replicate groups; each group was marked separately with a solution of oxytetracycline (dihydrate) and ambient seawater (a concentration of 500 mg/L; 26–28 ppt; 20–22°C) for 24 hours.

One 40-liter aquarium per replicate group was maintained as a flow-through (about 1–10 mL/s) system. Daily water temperature averaged 20.6°C (±2.7 SD), salinity averaged 28.5 ppt (±1.4) and the photoperiod was 12:12 hours of light:dark. Tetracycline-marked fish were fed thawed *Artemia* sp. 2–4 times daily, and a sup-

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Table 1

Standard length (mm) at age for *Prionotus carolinus* and *P. evolans* from two different geographic regions. Fishes older than age 6 are not included because they were typically represented by only individual fishes. nd = no data.

	Chesapeake		New England	
Age (yr)	*P. carolinus*[1]	*P. evolans*[2]	*P. carolinus*[3]	*P. evolans*[3]
0	nd	nd	75	90
1	126	132	130	160
2	163	186	195	210
3	180	207	220	235
4	197	224	245	260
5	204	245	255	290
6	211	270	270	305

[1] Average length values converted from fork length using equations in Wong (1968; Tables 2 and 3).
[2] Values are medians converted from fork lengths as reported in McEachran and Davis (1970, p. 347–348).
[3] Values estimated as a median from Richards et al. (1979; Fig. 7).

plemental feed with vitamins and oils was given at least once each week. Their ration was approximately 10% of their body weight/day; this ration was adjusted 1–3 times weekly to reflect the changes in weight during the experiment. Uneaten food was removed daily. Three to seven fish were removed from each replicate aquarium after 16, 26, 36, 46 days (total n=75), measured to the nearest 0.1 mm SL, and preserved in 95% ETOH. Growth rates between the replicate tanks varied from 0.21 to 0.44 mm/d according to least squares, linear regression of standard length on date of removal. Eleven of 86 fish initially placed in the aquaria died during the experiment and were not used for validating microincrement deposition rate.

After preservation, both sagittae were extracted from each fish, mounted on a coded glass slide in nail polish, sanded along the sagittal plane, and swabbed with immersion oil. After a fluorescing increment was located in the ocular crosshairs using a ultraviolet light source, the light was turned off and I counted the microincrements from the crosshair to the otolith margin on three separate dates. An average of these three counts was used to estimate increment number from the tetracycline mark to the peripheral edge.

Daily age and growth

Sagittal microincrements were examined from other postsettlement *P. carolinus* and *P. evolans* juveniles collected during August–October 1991 at locations in Great Bay (New Jersey), Delaware Bay, and continental shelf sites between Chesapeake Bay and Long Island Sound. Fishes were collected with bottom trawls and seine nets and either preserved in 95% ETOH or frozen. Specimens for aging were subsampled in a stratified (1-mm length category) random manner to proportionally represent the complete size range of each independent sample.

Otoliths were mounted on coded slides in nail polish and sanded to the core along one side of the sagittal plane or embedded in an epoxy resin and sectioned to the core (Secor et al., 1992). I counted microincrements through a compound microscope, typically at 400× by using polarized light, on three separate occasions. If the range of all three counts was >20% of the mean count, then the specimen was excluded from further analyses; this criterium resulted in 14 of 137 specimens being rejected. The mean increment count for sagittae was used to estimate "otolith age" in days. Daily age included four additional days—an estimate of the time between hatching and the date of first ring deposition. Hatching dates were calculated by subtracting daily age from date of capture.

Annual age and growth

Size attained by the end of the first growing season was estimated from *P. carolinus* and *P. evolans* juveniles collected during later winter and early spring cruises by the National Oceanic and Atmospheric Administration's National Marine Fisheries Service (see also McBride et al., 1998). Fishes were sampled with bottom trawls during two consecutive cruises (February 1993 and March–April 1993), which included a total of 447 stations (Fig. 1). The effective period of sampling for searobins was actually February–March (only one searobin was caught in 160 tows made during April).

At sea, only fishes ≤120 mm SL were saved because larger fishes were presumed to be older than 1 year (see Richards et al., 1979). Fishes were kept frozen to preserve the otolith structure. Specimens were subsampled from each independent sample (i.e. tow) in a stratified (5-mm length intervals), random manner. This subsampling approach was chosen again to moderate the resulting sample size while proportionally representing the complete size range of each independent sample; this approach also exaggerates the size range by dampening the modes of resulting size-frequency data. Sagittae were mounted in nail polish on a coded glass slide, sanded, and polished along

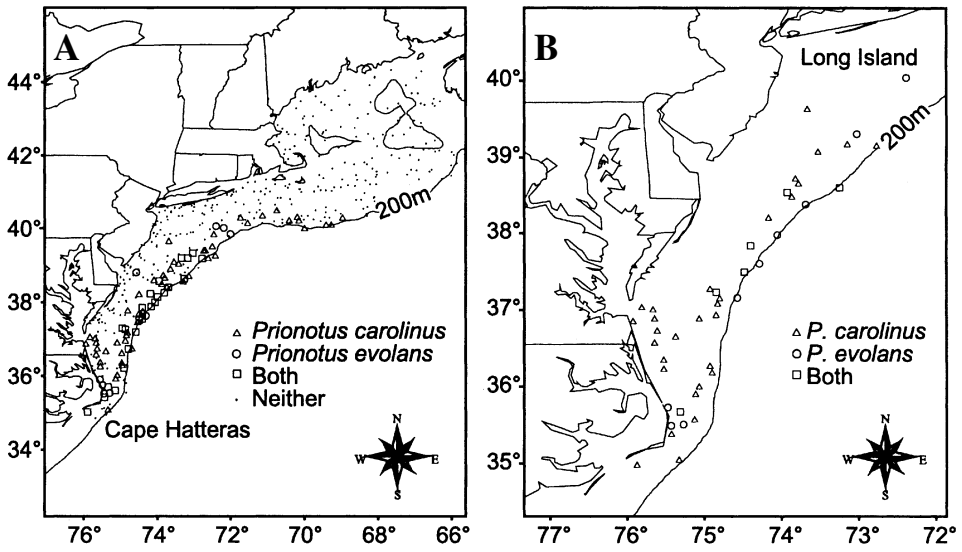

Figure 1

(**A**) Locations of all sampling during February–April 1993. Locations are indicated where searobins were and were not collected in tows. (**B**) Sample locations for age-0 searobins used for estimating overwintering size. Locations are for cruise dates during February–March 1993. No age-0 *Prionotus* spp. were collected during April 1993, and sampling areas covered during April (north of 40°N) are not shown.

the sagittal plane, and viewed under a binocular scope (typically at 20×) to check for the presence (e.g. age-1) or absence (e.g. age-0) of an annulus. Annulus formation occurs in March for both species (Wong, 1968; McEachran and Davis, 1970), and an annulus on the otolith margin was not counted.

Results and discussion

Otolith microstructure

Two pairs of otoliths (the sagittae and lapilli) were present prior to hatching in cultured embryos, having formed at the same time as the optic vesicles. No asterisci were observed in cultured yolksac larvae and, from personal observations of field-caught specimens, the asterisci form after flexion of the notochord. First ring deposition in sagittae was contemporaneous with eye pigmentation and yolksac absorption, although this process was not observed directly. Instead, it was observed that the diameter of the sagittal core (=primordium) steadily increased during yolksac absorption but that no microincrements were evident. I conclude that the laboratory specimens would have laid down their first ring at yolk absorption had they survived because the diameters of their sagittae were similar to the sagittal core diameters of wild fish (i.e. the diameter of the first microincrement). The maximum sagittal diameter of laboratory-cultured *P. carolinus* larvae was 26.3 µm and the mean sagittal core diameter of field-caught fish was 27.0 or 26.8 µm (n=8 flexion stage and n=6 postflexion specimens, respectively).

Yolksac absorption occurred approximately six days after fertilization and four days after hatching at 22–26°C; therefore four days were added to the average number of microincrements counted for both species, although this developmental pattern was observed only for *P. carolinus*. The rate of larval development observed in the present study is consistent with other reports of *P. carolinus* cultured at 15–22°C. Yuschak and Lund (1984) observed yolksac absorption by *P. carolinus* larvae at 3.4 mm NL and first feeding at 3.5–5 days after hatching. Kuntz and Radcliffe (1917) reported *P. carolinus* hatching at about 60 hours (2.5 days) and starvation 5–6 days after hatching.

Sagittal microincrement deposition occurred daily in chemically marked *P. carolinus* juveniles cultured in the laboratory. Data from four replicate aquaria (75 fish) were pooled because an ANCOVA did not indicate a significant difference by either the interaction of treatments (slope–replicate interaction: P=0.48) or the covariate (replicate: P=0.12). The resulting relationship was

$$Y = 1.23 + 0.94\ (X),$$

where Y = the number of microincrements after the tetracycline mark; and
X = the number of days following marking.

A test of statistical power (i.e. 1 – beta, as in Dixon and Massey [1951] and Cohen and Cohen [1975]) indicated a 99.9% confidence that microincrement deposition did not deviate from unity by more than 0.02 rings/d. McBride (1994) presented preliminary evidence of daily sagittal microincrements in *P. evolans*.

Reproductive seasonality The reproductive period for both species was prolonged and overlapping (Fig. 2). The range of *P. carolinus* hatching dates was from 19 May to 5 September and *P. evolans* hatching dates extended from 2 June to 3 September. Median hatching dates for *P. carolinus* were significantly later than *P. evolans* (13 August versus 26 July; Wilcoxon 2-sample test: P=0.011). Both species spawned for at least three months but *P. carolinus* hatching dates were dramatically skewed to the left (i.e. most individuals hatched late in the season). Previous studies independently demonstrated that both species spawn contemporaneously in the New York Bight: Keirans et al. (1986) calculated egg densities, Wilk et al. (1990) examined gonadosomatic indices, McBride and Able (1994) used length-frequency analysis, and McBride et al. (2002) examined larval densities. All demonstrated an extended spawning season for both species from about May to September; furthermore, a bimodal pattern of spawning output was reported for *Prionotus* spp. by Keirans et al. (1986) and McBride and Able (1994). My sampling procedure (i.e. a stratified, random design with respect to length intervals) would flatten frequency peaks and emphasize the range of hatching dates, a method not well suited for identifying multiple spawning peaks. Moreover, McBride et al. (2002) identified notable geographic variation in spawning seasonality, which could not be separated out in the present study and should be accounted for in future research. Intra-annual reproductive periodicity of *Prionotus* should also be evaluated by examining gonads for cyclic, group-synchronous oocyte development, which could be an underlying process leading to a protracted spawning period with regularly spaced peaks in production.

I conclude that interspecific size differences are at least partly the result of interspecific differences in reproductive seasonality (Table 1; i.e. the smaller congener was spawned later in the year). However, Able and Fahay (1998) noted that *P. evolans* eggs are larger than *P. carolinus* eggs; thus size differences exist among embryos. In addition, McBride et al. (2002) showed that interspecific size-at-age differences are evident throughout the larval period.

Age and growth Age-0 *P. evolans* were larger at a common age than *P. carolinus* (Fig. 3). On the basis of all individuals examined, *P. evolans* did not grow at a significantly higher rate (ANCOVA interaction of slopes; P=0.099), but this species was significantly larger than *P. carolinus* in general (ANCOVA test of intercepts; P=0.0001). The regression slopes, based on all data, were significantly different from zero (P<0.001) for both *P. carolinus* (SL=0.12+0.323×*age*; r^2=0.62; n=70) and *P. evolans* (SL=3.52+0.429×*age*; r^2=0.53; n=53). The intercepts for these linear growth models were biologically meaningful, particularly that for *P. evolans* because the intercept was roughly equal to the known size at hatching (3 mm; Able and Fahay, 1998). *Prionotus evolans* collected at four different stations in Delaware Bay during October 1991 deviated strongly from the average growth rates for this species (Fig. 3). Such small, slow-growing fish demonstrated the degree of intraspecific variation possible for *P. evolans* growth rates.

Age-0 *P. carolinus* were also much smaller on average than *P. evolans* during winter (Fig. 4). By February–March, age-0 *P. carolinus* ranged from 27 to at least 117 mm SL, but this size distribution was strongly bimodal with modes at 42.5 mm and 87.5 mm SL. The age-0 *P. evolans* were all larger than 75 mm SL and appeared to grow even larger than 120 mm SL, which was the cutoff size for collections, so that the interspecific size difference is even greater than that indicated in Figure 4. Apparently all age-1 *P. evolans* are larger than this cutoff value because none were observed in the samples, whereas age-1 *P. carolinus* ranged from 56 to at least 118 mm. Although age-1 *P. carolinus* were generally larger than age-0 conspecifics, the sizes of both age classes overlapped in a manner that would confound length–frequency analyses of this species.

The intraspecific size variation of age-0 fishes, of both *Prionotus* species, was spatially correlated. Individually,

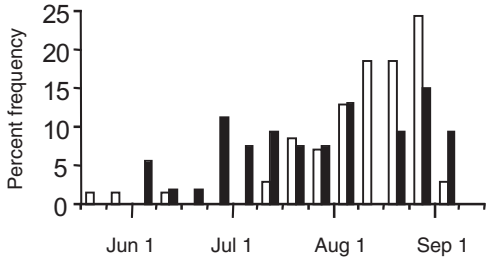

Figure 2

Backcalculated hatching dates (*date of capture* – [*otolith age* + 4]) for age-0 *Prionotus carolinus* (open bars; n=70) and *P. evolans* (filled bars; n=53) collected in estuarine and continental shelf habitats during 1991.

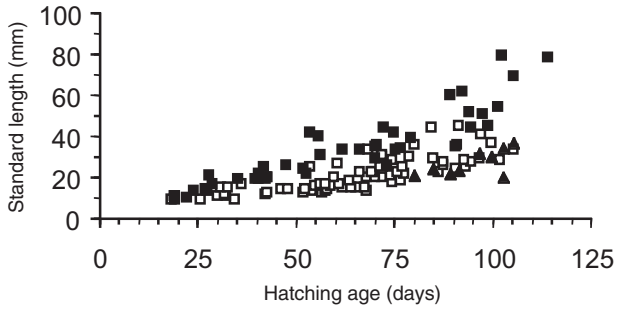

Figure 3

Length-at-age relationships for *Prionotus carolinus* (open symbols) and *P. evolans* (filled symbols). *Prionotus evolans* from Delaware Bay are depicted separately (triangles) from all other *P. evolans* (squares). Sample sizes are identical to those in Figure 2.

depth and latitude explained a significant ($r^2 \geq 0.30$; $P < 0.01$) amount of the variability of the mean size of age-0 *P. carolinus* during winter (Fig. 5). Each variable also contributed significantly ($P \leq 0.02$) to a multiple regression; nearly half ($r^2 = 0.47$) of the variance of the mean age-0 *P. carolinus* size between individual trawl tows was explained by the linear, least-squares equation

$$mean\ SL = -158 + 0.37 \times (depth[\text{m}]) + 5.7 \times (latitude[^\circ\text{N}]).$$

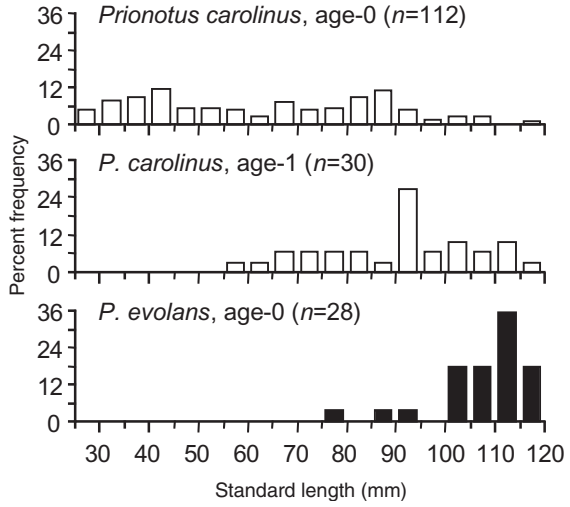

Figure 4

Size frequency of *Prionotus carolinus* (open bars) and *P. evolans* (filled bars) based on collections from continental shelf habitats in February–March 1993 (see Figure 1B). The upper boundary (120 mm SL) represents the size cutoff used during field collecting and does not necessarily define the maximum size attained for any age class. *n* = number of fish in sample.

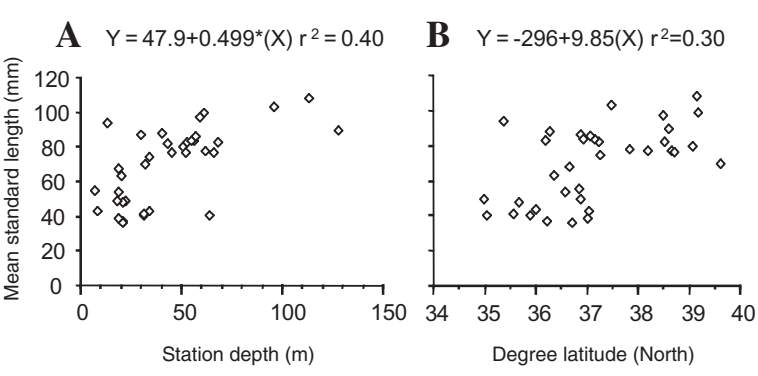

Figure 5

Linear relationships between mean size (standard length [mm]) of age-0 *Prionotus carolinus* and depth (**A**) or latitude (**B**) of sampling location. All fish were collected during February–March 1993 with bottom trawls in continental shelf waters (see Fig. 1B). See text for further details of multivariate analysis and results.

Similar analyses for *P. evolans* suggested that depth, but not latitude, was correlated with age-0 size variations. However, samples sizes of *P. evolans* were smaller than those for *P. carolinus* and age-0 *P. evolans* grow larger than the maximum size saved in field collections; therefore it is possible that age-0 *P. evolans* have a similar response to depth and latitude as age-0 *P. carolinus*.

Life history consequences

Late-summer spawning by *Prionotus* is not unique among fishes in waters offshore of the middle Atlantic states: *Scophthalmus aquosus* spawn late in the summer (Morse and Able, 1995) and three hake species (*Urophycis bilinearis*, *U. chuss*, and *U. regia*) have peaks in spawning during July–September (Wilk et al., 1990). Late spawning is not even evident for all *Prionotus* throughout their range. McBride et al. (2002) noted that the reproductive season for *Prionotus* varies with respect to latitude and coastal depth, and their observation that late spawning was common only offshore of the southern middle Atlantic states is consistent with the data presented in the present study for larger (i.e. presumably older) *P. carolinus* found during winter at higher latitudes. Sherman et al. (1984) noted a close association between *Prionotus* spawning cycles and zooplankton abundance cycles in continental shelf waters, and they suggested that the *Prionotus* spawning season is adapted for larvae to experience optimal prey encounter rates. However advantageous this match between larvae and their prey may seem, late-spawned *Prionotus* have an apparent size disadvantage during winter compared to many other species because of a shorter growing season.

Generally, coastal fishes of temperate waters appear to spawn in a manner that maximizes growth rates and size of their progeny, particularly in response to size-selective mortality (Conover, 1992; Sogard, 1997). Overwintering sizes of age-0 *P. carolinus*, however, do not suggest that such a scenario is occurring. Age-0 *P. carolinus* are smaller than or about the same size as typical age-0 prey species on the continental shelf, such as *Menidia menidia* and *Anchoa mitchilli* (Conover and Murawski, 1982; Vouglitois et al., 1987). Despite their small size, reports of age-0 *Prionotus* in gut contents of predatory fishes are rare (Marshall, 1946; Richards et al., 1979; Maurer and Bowman[1]). Size-selective mortality, a process that would select for early spawning and fast growth rates, may not be important because *Prionotus* are capable of burying themselves in the substrate (Bardach and Case, 1965)—an antipredator tactic. If size-selective mortality is not important, then

[1] Maurer, R. O., Jr., and R. E. Bowman. 1975. Food habits of marine fishes of the northwest Atlantic–data report. Laboratory Reference 75-3, 90 p. Northeast Fisheries Science Center. Woods Hole, MA 02543.

it is possible that overwinter mortality rates are similar between small individuals spawned late in the growing season and larger conspecifics spawned early, and that late spawning is not selected against for *P. carolinus*.

In this study, I demonstrate that interspecific and clinal variations of overwintering size for *Prionotus* species exist and that these are consistent with previous age and growth studies. Ginsburg (1950) also noted clinal variation for some meristic characters of both congeners that is consistent with Jordan's rule (i.e. higher counts at higher latitudes). McBride et al. (2002) have demonstrated regional differences in spawning seasonality for *Prionotus* species and short larval durations that limit dispersal of *Prionotus* planktonic stages; these are the likely mechanisms maintaining regional differences in juvenile sizes and meristic characters. Researchers should be aware of this demonstrated clinal variation and the potential for further life history, phenotypic, and possibly genetic variation of *Prionotus* species in temperate waters of the western North Atlantic.

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