Abstract–This study reports new information about searobin (*Prionotus* spp.) early life history from samples collected with a Tucker trawl (for planktonic stages) and a beam trawl (for newly settled fish) from the coastal waters of New Jersey. Northern searobin, *Prionotus carolinus*, were much more numerous than striped searobin, *P. evolans*, often by an order of magnitude. Larval *Prionotus* were collected during the period July–October and their densities peaked during September. For both species, notochord flexion was complete at 6–7 mm standard length (SL) and individuals settled at 8–9 mm SL. Flexion occurred as early as 13 days after hatching and settlement occurred as late as 25 days after hatching, according to ages estimated from sagittal microincrements. Both species settled directly in continental shelf habitats without evidence of delayed metamorphosis. Spawning, larval dispersal, or settlement may have occurred within certain estuaries, particularly for *P. evolans*; thus collections from shelf areas alone do not permit estimates of total larval production or settlement rates. Reproductive seasonality of *P. carolinus* and *P. evolans* may vary with respect to latitude and coastal depth. In this study, hatching dates and sizes of age-0 *P. carolinus* varied with respect to depth or distance from the New Jersey shore. Older and larger age-0 individuals were found in deeper waters. These variations in searobin age and size appear to be the combined result of intraspecific variations in searobin reproductive seasonality and the limited capability of searobin eggs and larvae to disperse.

Larval and settlement periods of the northern searobin (*Prionotus carolinus*) and the striped searobin (*P. evolans*)*

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Although adult fish assemblages offshore of the middle Atlantic states are fairly well known (e.g. Edwards, 1976; Colvocoresses and Musick, 1984; Gabriel, 1992), the early life history of many of these same species and the function of shelf habitats as nursery grounds are poorly understood (e.g. Fahay, 1983, 1993; Able and Fahay, 1998). Because year-class strength is believed to stabilize prior to the early juvenile stage, information about the transition from the plankton to benthic (i.e. settlement) habitats should contribute to our understanding of the population processes of benthic fishes (Cushing and Harris, 1973; Campana et al., 1989; Myers and Cadigan, 1993). Settlement is regarded as a dynamic period of early development because mortality rates can differ between pre- and postsettlement life stages (Sale and Ferrell, 1988), dramatic morphological and physiological transformations occur (Youson, 1988; Markle et al., 1992; McCormick, 1993), and behaviors become evident that allow for delaying settlement until suitable juvenile habitat is found (Cowen, 1991; Sponaugle and Cowen, 1994). Ultimately, an understanding of the life cycle of any benthic species is constrained if the settlement period is not viewed as an integral transition from the planktonic to the adult period.

Our study contributes to an understanding of how fishes use continental shelf habitats as nurseries with an examination of the early life history of the northern searobin, *Prionotus carolinus*, and the striped searobin, *P. evolans*. Both are common species in the coastal region between Cape Cod and Cape Hatteras, but relatively little is known about their early life history owing largely to their low economic importance in relation to the heavily exploited fisheries of this region (McBride et

al., 1998). Both species are known to begin spawning as early as May and to continue spawning into October as determined by maturity indices (e.g. Richards et al., 1979; Wilk et al., 1990). *Prionotus* spp. eggs and larvae are known to be seasonally abundant above the continental shelf and within some estuaries (e.g. Richards et al., 1979; McBride and Able, 1994) but eggs and larvae are difficult to identify to species on a routine basis. Therefore we took advantage of recently reported morphological information (Able and Fahay, 1998) to examine ichthyoplankton collections.

Our study was designed to examine how spawning patterns varied between two congeners, but intraspecific spawning variation also became evident. A second goal of our study was to examine settlement—to date not reported for either species. Both species undergo flexion and complete fin-ray development at about 6–8 mm SL (Yuschak and Lund, 1984; Yuschak, 1985; Able and Fahay, 1998). Separation of prehensile rays on the pectoral fin, a major adaptation for benthic feeding (Morrill, 1895; Bardach and Case, 1965; Finger and Kakil, 1985), occurs in fish as small as 12 mm SL (Yuschak, 1985). Yet settled juveniles <25 mm SL are rare (Lux and Nichy, 1971; Richards et al., 1979; McBride and Able, 1994), which raises the question of whether *Prionotus* spp. are competent to settle after completing fin-ray development or whether they commonly delay settlement. Using a novel combination of sampling gears, we collected a continuum of late larval and early juvenile *Prionotus* spp. to examine settlement directly. We report for the first time species-specific larval abundances, distributions, ages, sizes, growth rates, and descriptions of early benthic existence.

Materials and methods

Collections were made in coastal waters of New Jersey, specifically near Beach Haven Ridge (Fig. 1, Table 1), a prominent sand ridge formation that rises to about 8 m depth and is surrounded by depths of 14–16 m (Stahl et al., 1974). Sampling frequency at two stations, one landward and the other seaward of the ridge, was every two to six weeks from July 1991 to November 1992. Two tows of a Tucker trawl (1 m²) were made at each station in a double, stepped-oblique fashion. One tow was made from the surface to the bottom (three minutes duration) and the other tow was fished from the bottom back to the surface (six minutes). Newly settled juveniles and older fishes were sampled with a 2-m beam trawl in Great Bay estuary, near Beach Haven Ridge, as well as in other habitats (Fig. 1). The data from these stations were arranged in the following groups: 1) the two principal ridge stations (described above); 2) miscellaneous stations scattered on top of and around the ridge; 3) stations along a transect leading directly offshore from the ridge; and 4) a cluster of stations within nearby Great Bay. Generally, three tows were completed at stations immediately landward and seaward of the ridge, but only two tows were completed at other stations. Beam trawl tows offshore of Little Egg Inlet took
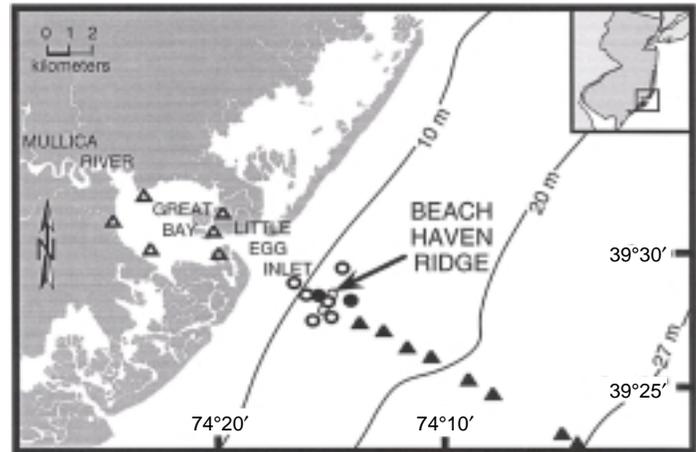

Figure 1

Map of sampling station locations in southern New Jersey, including the main stations at Beach Haven Ridge (landward and seaward: filled circles), other ridge stations (open circles), continental shelf transect stations (filled triangles), and estuarine stations (open triangles). The state of New Jersey, and the study location, are shown in the inset.

one minute to complete, but estuarine tows were reduced to 20 or 30 seconds to avoid collecting large volumes of macroalgae, detritus, shell, etc. Sampling occurred during daylight unless otherwise stated. Details of sampling procedures are provided by Hales et al.[1] Volume or area sampled was calculated by using a flow-meter for ichthyoplankton collections or a meter wheel for beam trawl collections. Larval density is presented as the geometric mean number of fish/m³ for Tucker trawl collections. Juvenile density is presented as the geometric mean number of fish/m² of sea bottom. Calculations of geometric means follow Sokal and Rohlf (1981).

The standard length (SL) of all, or at least 20 fish per tow, was measured after the fish were preserved in 95% ETOH. The term "larva" was used in reference to individuals collected in Tucker trawl tows. Preflexion larvae were distinguished from flexion larvae by the absence or presence, respectively, of cartilaginous urals on the ventral edge of the notochord tip; the development of these urals accompanied flexion of the notochord tip (Kendall et al., 1984). Larvae were characterized as postflexion stage once the notochord tip moved anterior to the posterior edge of the hypurals.

Daily age was estimated from counts of sagittal otolith microincrements, which were validated as daily by McBride.[2] Otoliths with a maximum length less than about

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[1] Hales, L. S., Jr., R. S. McBride, E. A. Bender, R. L. Hoden, and K. W. Able. 1995. Characterization of non-target invertebrates and substrates from trawl collections during 1991–1992 at Beach Haven Ridge (LEO-15) and adjacent sites in Great Bay and on the inner continental shelf off New Jersey. Technical report (contribution 95-09), 34 p. Institute of Marine and Coastal Sciences, Rutgers, The State University of New Jersey, New Brunswick, NJ.

[2] McBride, R. S. In review. Spawning, growth, and overwintering size of searobins (Triglidae: *Prionotus carolinus* and *P. evolans*).

500 µm were removed and mounted whole on glass slides in immersion oil. Otoliths longer than about 500 µm were mounted in nail polish on a glass slide, sanded with 1500 grit sandpaper along the sagittal plane, and polished with 0.3-µm grinding powder. Immersion oil was used liberally to enhance the clarity of all otoliths, and polarized light aided the viewing of microincrement structure. Microincrement counts were made with a compound microscope, typically at 400×. Slides were coded and microincrements were counted by one reader on three separate occasions. A constant of 4 days, representing the period between hatching and deposition of the first ring, was added to the mean microincrement count to estimate age since hatching (McBride[2]). Preserved (95% ETOH) *P. carolinus* and *P. evolans* were selected in a stratified (0.5-mm intervals), random manner to compare ages and lengths. Microincrement counts from this comparative material ranged, based on all individuals, between 0% and 32% of the mean microincrement count for each otolith (mean=12.0%; *n*=41).

Prionotus carolinus were collected in far greater numbers than *P. evolans* and they were examined in greater detail. Size and age distributions were initially defined from collections made during the period of peak seasonal abundance (i.e. late September 1991), when a random sample of 34 larvae was selected from a Tucker trawl sample for 23 September. Another sample of juvenile *P. carolinus* was selected from a 2-m beam trawl tow on 23 September 1991 at a station near the above plankton tow (Table 2). Four final samples were selected from 2-m beam trawl tows set one month later (21–22 October) at four stations along a transect of varying depths. Otoliths from all juveniles collected at these stations were analyzed (i.e. only fish that were mutilated or that had cracked otoliths or otoliths sectioned beyond the core were excluded). General methods of measuring and staging individual fish, and preparing otoliths, followed that described above. Sagittal microincrements were counted on two (for larvae) or three (for juveniles) separate dates by one reader. The range of these microincrement counts, for all individuals, was from 0.0% to 25.0% (mean=9.6%; *n*=127) of each mean count.

Results

Interspecific comparisons

Prionotus carolinus were more numerous and occurred more frequently than *P. evolans* in nearly all collections, typically by an order of magnitude (Table 1). Spawning by both species occurred from at least July to October offshore of southern New Jersey (Fig. 2). Modal size of larvae generally increased with time, but there were exceptions that indicated a pattern of multiple spawning events. For example in August 1991, modal size for *Prionotus* spp. and *P. carolinus* was notably smaller (3–4 mm) than the previous month (5–6 mm) (Fig. 3). Peak larval abundances varied somewhat between years but were highest from July to September.

Prionotus carolinus was the smaller but older congener at each developmental stage. Size and stage were com-

Table 1

Details of plankton and beam trawling data examined in our study. Larvae reported as *Prionotus* spp. were nearly all preflexion stages that did not exhibit diagnostic characters for separating these two congeners. For beam trawl collections, total number of fish are shown at left and the number of age-0 fish are shown to the right (in parentheses). See Figure 1 for general sampling areas.

Sampling area	Tow depth (m)	Net type	Year	Months	Number of cruises	Number of tows	Number of fish collected		
							P. carolinus	P. evolans	Prionotus spp.
Beach Haven Ridge (landward and seaward only)	0–15	1×1-m Tucker trawl (505-µm mesh)	1991	Jul – Dec	5	21	1274	48	84
			1992	Jan – Nov	14	56	17	0	17
	12–16	2-m beam trawl (6-mm mesh)	1991	Jul – Dec	6	61	459 (403)	40 (32)	0
			1992	Jan – Nov	14	89	122 (79)	26 (18)	0
Other ridge stations	6.1–17	2-m beam trawl (6-mm mesh)	1991	Aug – Oct	4	22	286 (284)	11 (8)	0
			1992	Jan – Nov	13	46	38 (35)	2 (1)	0
Ridge-transect stations	17–24	2-m beam trawl (6-mm mesh)	1991	Oct	1	7	73 (73)	0	0
			1992	Apr – Nov	4	28	114 (111)	0	0
Great Bay	1.4–8	2-m beam trawl (6-mm mesh)	1992	Aug – Oct	3	38	0	1 (1)	0

Table 2
Daily age, size, and hatching dates for planktonic (flexion and postflexion stages) larvae and benthic (settled stage) juveniles of *P. carolinus* collected in September and October 1991, offshore of southern New Jersey (see Fig. 8 for station locations). Data are presented as means (±1 standard error), and the range of values is given in parentheses. Larvae were collected with a 1×1-m Tucker trawl (0.505-mm mesh) and juveniles with a 2-m beam trawl (6-mm mesh).

| Date	Stage	Station	*n*	Age (days)	Length (mm)	Hatching date
23 Sep	flexion	OT5	9	15.4 ±0.73 (12–17.5)	5.3 ±0.20 (4.1–6.2)	8 Sep ±0.73 (6 Sep–11 Sep)
23 Sep	postflexion	OT5	25	17.7 ±0.53 (12–23.0)	7.0 ±0.20 (5.7–9.5)	5 Sep ±0.53 (31 Aug–11 Sep)
23 Sep	settled	OT5	23	37.4 ±1.91 24–61.3)	12.2 ±0.44 (8.5–15.8)	17 Aug ±1.91 (24 Jul–30 Aug)
21 Oct	settled	OT2	15	60.9 ±3.06 (46–94.7)	17.5 ±1.42 (12.8–30.4)	19 Aug ±3.06 (18 Jul–5 Sep)
21 Oct	settled	OT5	13	62.2 ±2.81 (52–90.7)	16.8 ±1.58 (12.8–35.3)	20 Aug ±2.81 (22 Jul–30 Aug)
22 Oct	settled	Sta. C	29	75.1 ±2.71 (54–134.0)	21.9 ±1.44 (13.1–59.4)	8 Aug ±2.71 (10 Jun–29 Aug)
22 Oct	settled	Sta. E	13	90.0 ±3.20 (69.3–105.3)	26.3 ±0.96 (20.2–33.7)	24 Jul ±3.20 (8 Jul–13 Aug)
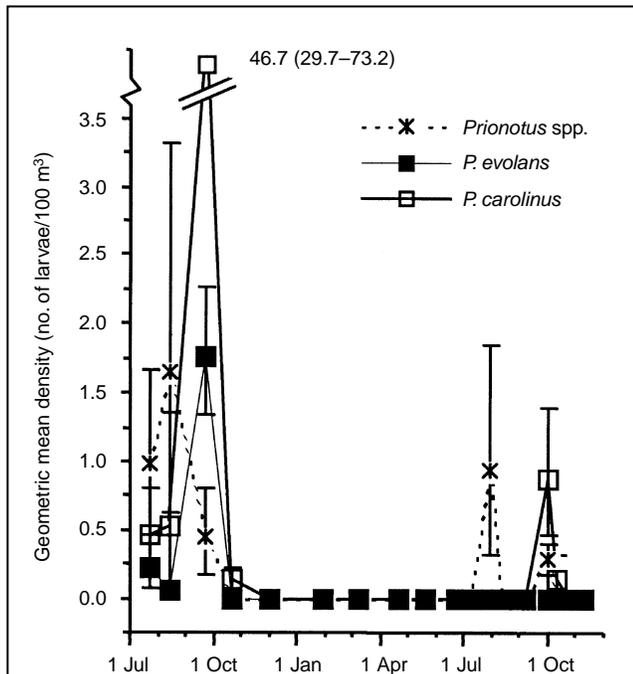
Figure 2
Density (geometric mean number of larvae per 100 m³ [±1 standard error, SE]) of *Prionotus* spp., *P. carolinus*, and *P. evolans* larvae for each cruise near Beach Haven Ridge, based on daylight tows of a Tucker trawl at the landward and seaward stations (see Fig. 1). Note break in scale (range of SE bars are given in parentheses).
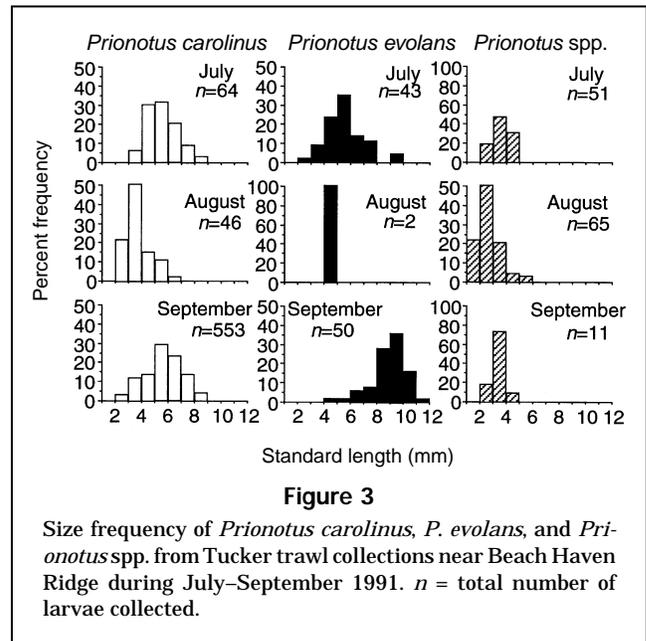

Figure 3
Size frequency of *Prionotus carolinus*, *P. evolans*, and *Prionotus* spp. from Tucker trawl collections near Beach Haven Ridge during July–September 1991. *n* = total number of larvae collected.

pared for 534 *P. carolinus* and 81 *P. evolans* collected with the Tucker trawl during both day and night. Flexion was complete at a larger size for *P. evolans* than for *P. carolinus* (range: 6.7–7.5 mm versus 5.4–6.8 mm SL), and planktonic postflexion *P. evolans* larvae were captured at larger sizes than postflexion *P. carolinus* (range: 6.7–11.9 versus 5.4–9.8 mm SL). *Prionotus evolans* completed flexion at a younger age than *P. carolinus* (approximately 13

versus 18 days after hatching) (Fig. 4). Both species settled as early as 18–19 days after hatching, but this was more characteristic of *P. evolans*; most *P. carolinus* did not settle until 24–25 days old.

Both species grew relatively slowly, and approximately linearly, during the larval and early juvenile period (i.e. ≤0.3 mm/d; Fig. 4, and next subsection). These slow growth rates, combined with the late peak in spawning (i.e. around August), resulted in small body sizes by the onset of winter. These smaller body sizes were particularly true for *P. carolinus*, for which the most pronounced size mode was 10–15 mm SL in autumn 1991 and 1992 (Fig. 5). At this time (i.e. September–December), individuals <50 mm SL constituted 85% of *P. carolinus* and 52% of *P. evolans* from all beam trawl tows combined; during autumn a majority of *Prionotus* spp. were <25 mm SL.

At beam trawl stations, densities of *P. carolinus* were consistently higher than those for *P. evolans* in both 1991 and 1992 (Fig. 6). Geometric mean densities of age-0 *P. carolinus* during the peak period of settlement (September–October) were much higher in 1991 (8.98 fish 100/m²) than in 1992 (1.56 fish 100/m²). Geometric mean densities of age-0 *P. evolans* during September–October were also higher in 1991 (0.32 fish 100/m²) than in 1992 (0.09 fish 100/m²). These interannual differences were consistent with higher larval densities of both species in 1991 versus 1992 (Fig. 2). Maximum densities of age-0 searobins at a single station reached 28.9 *P. carolinus* 100/m² and 3.2 *P. evolans* 100/m², both in September 1991. Searobins larger than 150 mm SL were collected infrequently from June to October; occasionally they were found together with age-0 conspecifics in the same beam trawl tows. Age-0 searobins of both species were collected primarily in continental shelf versus estuarine habitats during July–December (Fig. 7).

Settlement of *Prionotus carolinus*

The seasonality of settlement by *P. carolinus*, although lasting from at least July to October, 1991, was punctuated by a 2–3 week period in September when the vast majority of larvae appeared to settle near Beach Haven Ridge (Fig. 8). Densities of age-0 *P. carolinus* near Beach Haven Ridge were very low during both July and August (geometric means ranging from 0.0 to 1.1 fish 100/m²). During September, densities increased dramatically (range: 0.8–7.3 and 0.8–28.9 fish 100/m² on September 12 and 23–24, respectively). Individuals were collected at all stations along a depth transect, from 6 to 16 m, in late September. Settled, age-0 *P. carolinus* were still widespread and abundant in late October (0.0–13.3 fish 100/m²), but they were not collected on 2 December 1991, and on 28 January and 10 March 1992.

Collections for 23 September 1991 demonstrate a wide range of *P. carolinus* developmental stages and ages present at Beach Haven Ridge (Fig. 9A). All flexion stages were present (6.5% preflexion, 26.0% flexion, and 67.4% postflexion; *n*=169). Planktonic larvae subsampled randomly from a Tucker trawl tow (*n*=34; Table 2) had hatched during a two-week period from
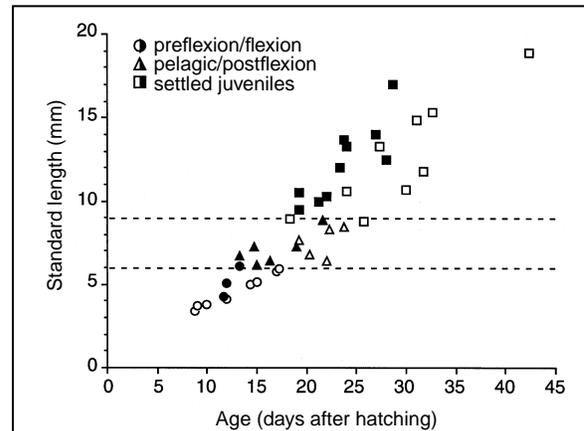

Figure 4

Relationship between daily age and length for *Prionotus carolinus* (open symbols) and *P. evolans* (filled symbols) for preflexion and flexion stages collected with a Tucker trawl (circles), postflexion stages collected with a Tucker trawl (triangles), and settled juveniles collected with a beam trawl (squares). The upper dashed line indicates the approximate size at settlement, and the lower dashed line indicates size at completion of flexion for both species.
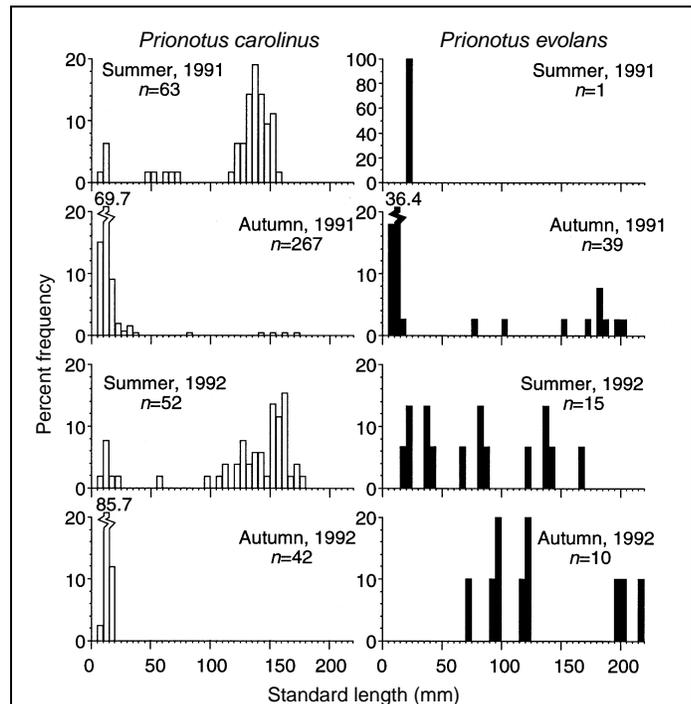

Figure 5

Size frequency of *Prionotus carolinus* and *P. evolans* for beam trawl collections near Beach Haven Ridge (daylight tows at the landward and seaward stations [Fig. 1]). Data were pooled by season: summer (May–August) and autumn (September–December). *n* = total number of fish collected. No data for January–April 1992 are shown because only a single fish (*P. carolinus*; 45 mm SL) was collected at these stations during this period.

August 31 to September 11. Individuals collected by beam trawl on the same day (23 September 1991) had hatched about 2 weeks earlier (from 24 July to 30 August) than the above larvae (Fig. 9). These juveniles appeared to settle as young as 24 days after hatching and at sizes as small as 8.5 mm SL (Table 2). The total hatching date distribution for both larvae and newly settled juveniles collected on September 23 reflected a spawning period that ranged from late July to early September and that peaked in late August and early September.

Settled juveniles with a similar hatching date distribution were identifiable one month later at stations near Beach Haven Ridge, but not at stations farther offshore (Fig. 9, B and C). Fish collected near Beach Haven Ridge on 21 October 1991 had a hatching date distribution with a mode from late August through early September and the overall distribution was skewed to the left. This period was similar to the hatching date distributions for larvae and newly settled fish collected on 23 September 1991. In contrast, fish collected from offshore stations (i.e. stations C and E) on 22 October 1991 were 2–4 weeks older and 5–10 mm larger on average (Table 2, Fig. 9).
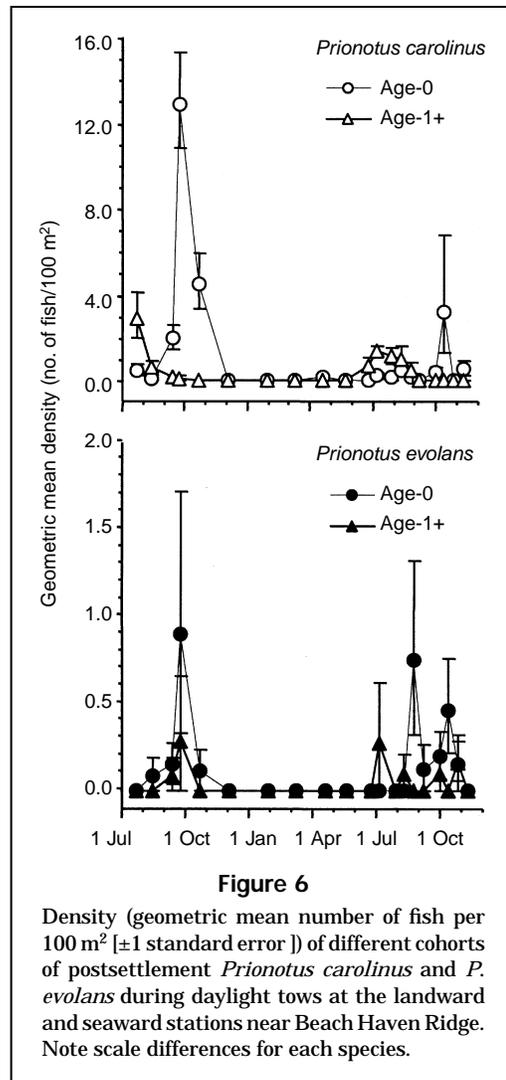
Plots of *P. carolinus* size versus age did not indicate any abrupt change at settlement, specifically for postflexion larvae and settled juveniles collected on 23 September 1991 (Fig. 10). Growth rates for this September collection fitted a linear model (SL=3.24+0.229[age]; r^2=0.77). Because *Prionotus* larvae hatch at about 3 mm SL (Yuschak, 1985), this model's y-intercept is biologically realistic. Growth rates of fish collected in October did not differ significantly between stations (ANCOVA: $prob._{slopes}$=0.13, $prob._{intercept}$=0.51); therefore the data were pooled. Linear, least squares regression of all data produced an unrealistic y-intercept (SL=−7.01+0.382[age]; SE_a=2.0; r^2=0.74). This model was rerun after restricting the y-intercept to 3 mm and the resulting equation indicated that age-0 *P. carolinus* continued to grow at about 1 mm every 4 days (SL=3 +0.251[age]; r^2=0.65) as they had during the larval and settlement period.

Size and age of *P. carolinus* juveniles varied significantly along a 12-km transect (12–20 m depths; Fig. 1). The linear relationship: *Hatching age* = 17.8 + 3.43 × *depth*; r^2=0.35, P<0.01; n=69) showed that for every two meters change in depth offshore the fish collected were about one week older on average (Fig. 11). Sampling in both 1991 and 1992 showed a consistent trend for larger (and presumably older) fish to be collected in deeper water in October and November (Fig. 12). After accounting for the effects of depth, or possibly the distance from shore, it appeared that fish reached a larger size in October of 1991 than in 1992 or that larger fish in 1992 were not found in the sampling area.

Discussion

Spawning grounds and seasonality of spawning

Prionotus carolinus are more abundant than *P. evolans* in continental shelf habitats whether they are measured as eggs, larvae, juveniles, or adults (Keirans et al., 1986;

Figure 6

Density (geometric mean number of fish per 100 m² [±1 standard error]) of different cohorts of postsettlement *Prionotus carolinus* and *P. evolans* during daylight tows at the landward and seaward stations near Beach Haven Ridge. Note scale differences for each species.

McBride and Able, 1994; Able and Fahay, 1998; McBride et al., 1998; our present study). The low numbers of *P. evolans* observed in our study may be biased somewhat by our focused effort to sample the continental shelf rather than estuaries. *Prionotus evolans* reside in shallower, warmer habitats than do *P. carolinus* during the spawning season (McBride and Able, 1994). If *P. evolans* spawn to some degree in shallower waters or estuarine habitats, then this would at least partly explain the generally low abundance of *P. evolans* early life stages in our collections.

In general, we expect that larval distributions are good predictors of spawning locations for both *Prionotus* species because of the short (i.e. about three weeks) larval dispersal periods of these species (e.g. Houde and Zastrow [1993] reported several shelf species with planktonic duration >100 days). In some coastal areas, the distribution of *Prionotus* spp. eggs and larvae indicates that spawning may be limited to estuaries; however, the abundance of *Prionotus* larvae offshore of New Jersey suggests that spawning by these species occurs outside estuaries as well. For example, Merriman and Sclar (1952) did not find *Prionotus*
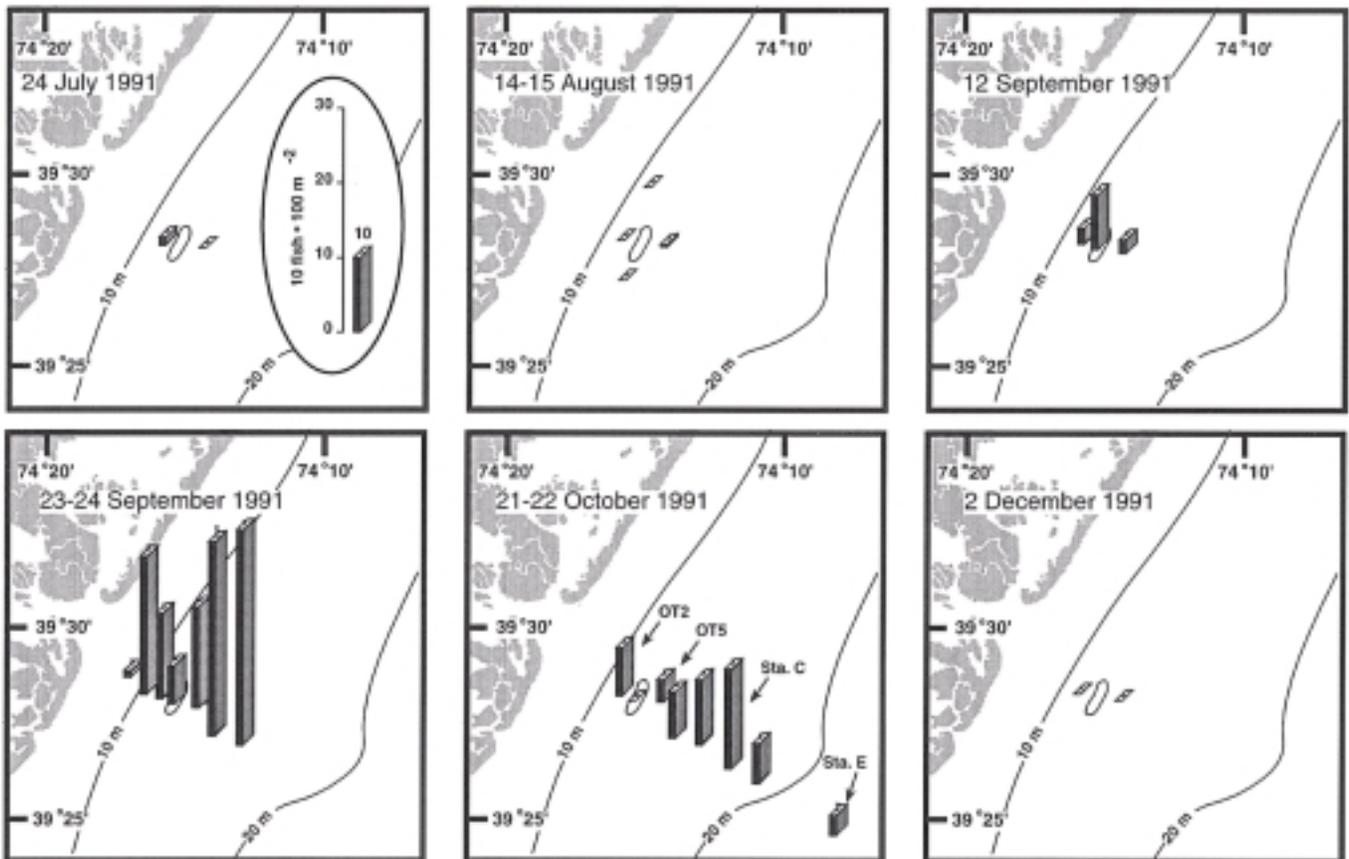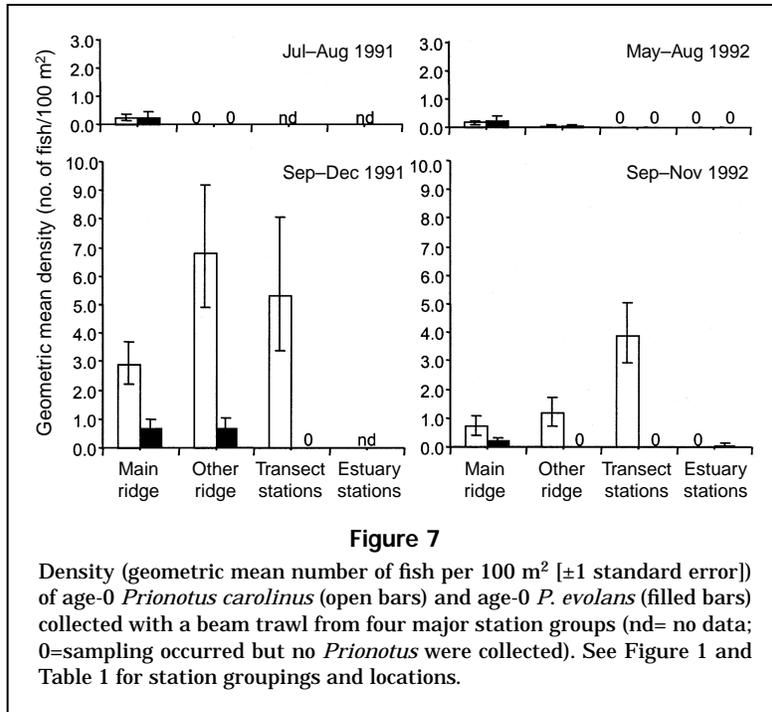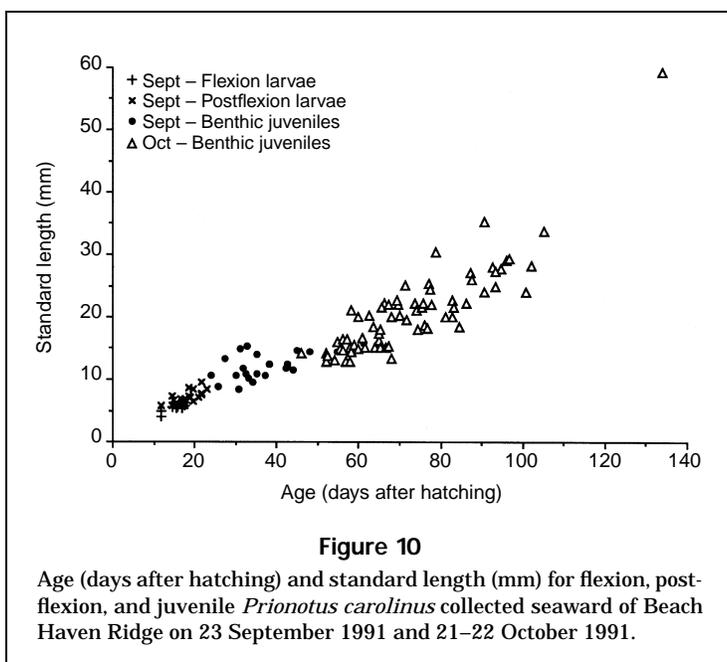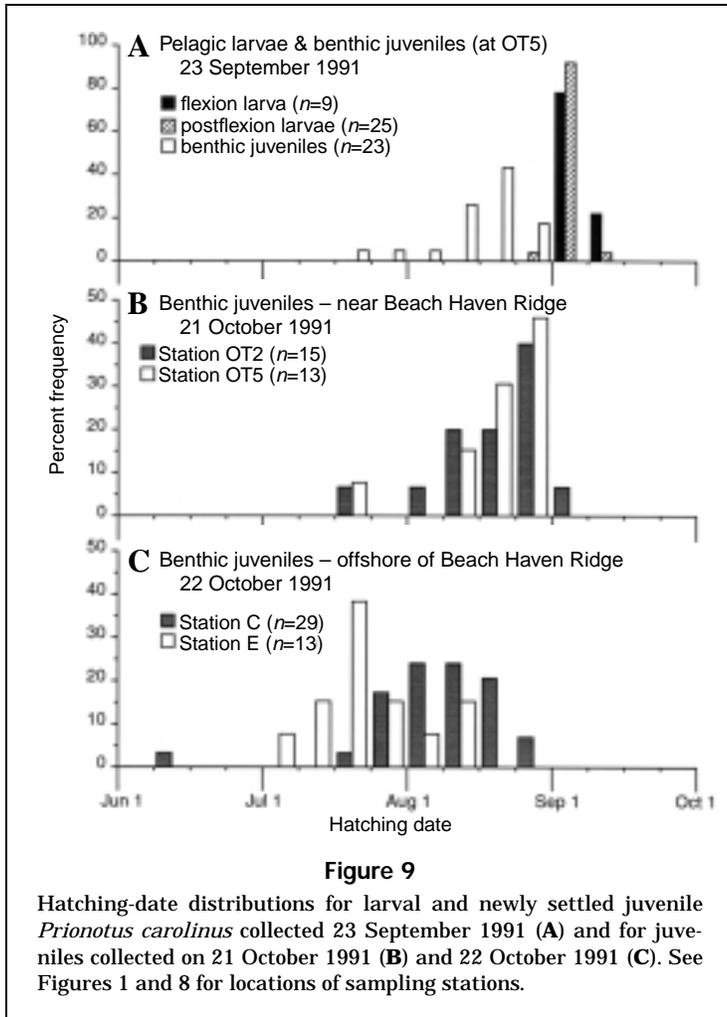
Figure 7

Density (geometric mean number of fish per 100 m² [±1 standard error]) of age-0 *Prionotus carolinus* (open bars) and age-0 *P. evolans* (filled bars) collected with a beam trawl from four major station groups (nd= no data; 0=sampling occurred but no *Prionotus* were collected). See Figure 1 and Table 1 for station groupings and locations.

Figure 8

Densities (geometric mean [±1 standard error]) of age-0 *Prionotus carolinus* collected with a beam trawl during six consecutive cruises (July–December 1991). Number of stations varied between cruises. The scale bar indicates 10 fish/100 m².

Figure 9

Hatching-date distributions for larval and newly settled juvenile *Prionotus carolinus* collected 23 September 1991 (**A**) and for juveniles collected on 21 October 1991 (**B**) and 22 October 1991 (**C**). See Figures 1 and 8 for locations of sampling stations.

Figure 10

Age (days after hatching) and standard length (mm) for flexion, postflexion, and juvenile *Prionotus carolinus* collected seaward of Beach Haven Ridge on 23 September 1991 and 21–22 October 1991.

spp. eggs or larvae in Block Island Sound, and Able and Fahay (1998) did not observe *Prionotus* larvae above the continental shelf north or east of Hudson Canyon, New York. Instead there are many reports of *Prionotus* eggs, larvae, and juveniles in southern New England estuaries, specifically in Long Island Sound (Wheatland, 1956; Richards, 1959; Williams, 1968; Richards et al., 1979) and Narragansett Bay (Herman, 1963; Bourne and Govoni, 1988; Keller et al., 1999). Thus, the relative importance of estuaries versus shelf habitats as spawning grounds for *Prionotus* may vary in other regions compared with our results for New Jersey. Nonetheless, *Prionotus* spawning seasonality appears to follow a pattern similar to that of other species with a wide latitudinal range that have a shorter spawning season at higher latitudes (e.g. Conover, 1992) and that spawn later in the south (e.g. Barbieri et al., 1994). An important departure from this general trend is that *Prionotus* reproductive seasonality may vary not only with respect to latitude but along an estuary-shelf gradient as well. Because adults of both *Prionotus* species enter estuaries early in the spring and migrate back out to the shelf in summer (McBride and Able, 1994), we postulate that spawning occurs first in estuaries at a given latitude. In support of this hypothesis are the collective results from our study and other published reports. After the summer spawning peak within estuaries such as Chesapeake Bay and Long Island Sound, *Prionotus* spawn during August and September offshore of Chesapeake Bay and New Jersey. In contrast, spawning does not continue into late summer offshore of southern New England (Pearson, 1941; Richards et al., 1979; Able and Fahay, 1998).

To explain this potentially novel spawning pattern does not require any new controlling mechanism other than that used to explain spawning by other coastal fishes of the region. Temperature and photoperiod are known to influence spawning activity in fishes (Burger, 1939) and may influence spawning seasonality of searobins. Water temperatures offshore of the middle Atlantic seaboard are known to fluctuate widely both temporally and spatially (Colvocoresses and Musick, 1984) and this fluctuation affects the spawning pattern of many species. For example, a simple south to north progression of spawning activity above the shelf is evident for *Centropristis striata* (Able et al., 1995) and *Scophthalmus aquosus* (Morse and Able, 1995). For *Prionotus*, however, we propose that spawning seasonality is controlled by an interaction between latitudinal and estuarine gradients of temperature (i.e. earlier spawning in estuaries occurs because of earlier warming of these shallow embayments). Temperature has already been shown to affect the distribution of *Prionotus* adults along both latitudinal and estuarine gradients (McBride and Able, 1994;

McBride et al., 1998). Because few other species use both estuarine and shelf habitats for spawning, such patterns are not commonly observed.

Linking metamorphosis and settlement

Prionotus carolinus are often ranked as among the most abundant species in regional trawling surveys for adult fish or plankton surveys for larval fish (McBride and Able, 1994). The results from the small-mesh beam trawl used in our experiment demonstrate that the juvenile stages of *P. carolinus* are also very abundant offshore. Age-0 *Prionotus* spp. are found in estuaries, as discussed above for the southern New England region, but our observation of high densities of juvenile *Prionotus* in shelf habitats offshore of New Jersey suggest that neither species requires estuarine nursery habitats during their life cycle. Most searobins complete their life cycle in continental shelf habitats (Hoff, 1992), with the notable exception of *P. scitulus* whose young are concentrated in lower salinity, estuarine habitats (Ross, 1978).

Our findings of age and size at settlement largely agree with Yuschak and Lund's (1984) and Yuschak's (1985) descriptions of early development of cultured specimens. The developmental rate of cultured specimens of *P. carolinus* and *P. evolans*[3] did not differ notably from our observations of field-collected individuals, which further supports our conclusion that neither species delays settlement. *Prionotus evolans*, cultured at 20°C, were all at preflexion and flexion stages after 11–13 days; they were at flexion and newly postflexion stages after 18–20 days; and all were at the postflexion stage at 25 days. All available *P. carolinus* specimens, cultured at 15°C, were less than 20 days old; they followed a similar, if slightly slower, rate of development compared with *P. evolans*. Fin-ray development, which greatly facilitates locomotion, is complete in postflexion individuals. Prehensile, chemosensory pectoral rays, which would facilitate benthic feeding, are completely separated by 11.5 mm SL. Thus, on the basis of cultured and field-caught specimens, both species are well developed (i.e. are similar to adults) and well-suited for a bottom-feeding and swimming life style as they complete flexion. Other species delay metamorphosis to settle during favorable lunar phases (Sponaugle and Cowen, 1994), but settlement by *Prionotus* was so concentrated in a single month (i.e. September) that we could not test spawning or settlement cycles in more than one month. Nevertheless, because larvae of *Prionotus* species commonly bury themselves in loose substrate (Bardach and Case, 1965), and this material was common to all our sampling stations (Hales et al.[1]), competent larvae are likely not habitat limited (one mechanism identified with the delay of settlement).

The variation of *P. carolinus* sizes and ages along a depth gradient could be caused by one or a combination of three processes. There could be differential larval survivorship, juvenile movements, or adult reproduction rates
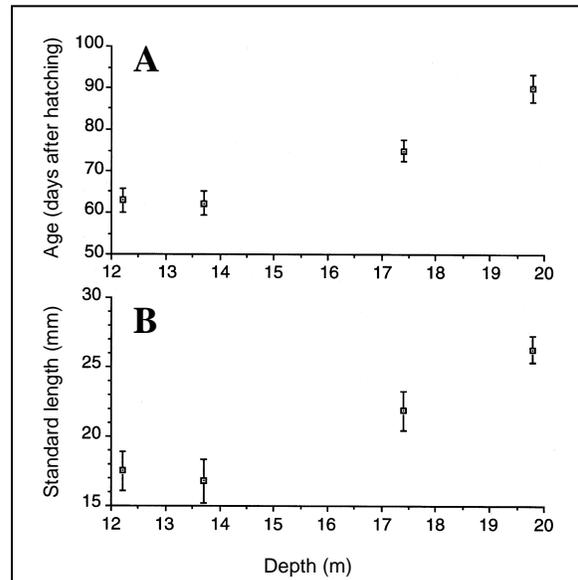

Figure 11

Age (**A**) and size (mean ±1 standard error) (**B**) of juvenile *Prionotus carolinus* plotted in relation to depth. Data are for fish collected on 21–22 October 1991 (near and offshore of Beach Haven Ridge: stations OT2, OT5, C, and E) and aged by using sagittal microincrements (see Table 2 and Fig. 9 for sample sizes).
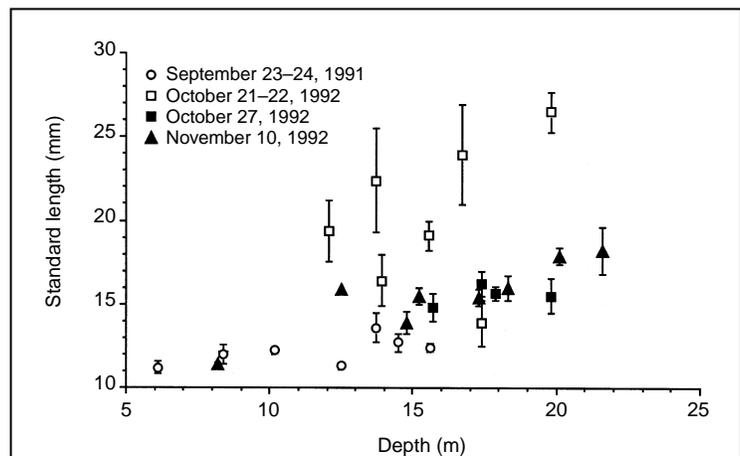

Figure 12

Standard length (mm; mean [±1 standard error]) of juvenile *Prionotus carolinus* in relation to depth for four separate cruises in 1991 (open symbols) and 1992 (filled symbols). All benthic juveniles collected were included in these calculations.

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[3] This material was cultured by P. Yuschak (see Yuschak and Lund [1984] and Yuschak [1985]) and has been examined by R.S.M.

across the shelf to account for this spatial pattern of older and larger juveniles farther offshore. The last process was identified earlier as potentially important. Testing and eliminating these hypotheses, however, requires spatially explicit larval distribution data, in addition to the benthic data that we collected, which would allow a comparison of pre-and postsettlement distributions with abundance of *Prionotus* propagules. Spatially explicit environmental data would also be useful because we observed dynamic changes in the physical parameters in our sampling area, and we suspect that these could affect *Prionotus* survival. Vertical stratification of the water column was noted near Beach Haven Ridge on 14 August 1991, but not during cruises in September or October 1991. Low dissolved oxygen levels near the bottom of the ridge, at about 3 ppm (in contrast to >8 ppm in the upper water column) could have negatively affected settlement rates near the ridge in 1991. Stratification near the ridge was also noted in 1992 with similarly depressed levels of dissolved oxygen (Hales et al.[1]). Low dissolved oxygen offshore of New Jersey is not uncommon (Falkowski et al., 1980; Glenn et al., 1996) and may be another process that can contribute to geographic variations in size and age of *Prionotus* species offshore of the middle Atlantic states. We postulate that spatially explicit patterns of reproductive seasonality and age-0 fish size for *P. carolinus* and *P. evolans* within coastal waters offshore of the middle Atlantic states are related to each other because the short planktonic larval durations for both species limit larval dispersal. Interannual variations in water temperature or vertical stratification of oxygen concentrations may be proximate causes for these geographic variations of reproductive seasonality and age-0 size. These patterns could be somewhat unique to searobins, compared with other regional fishes, because searobins use both estuarine and shelf habitats for spawning.

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