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[Article]

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Abstract.—We tested the overwintering capability of young-of-the-year (age-0) windowpanes *Scophthalmus aquosus* to determine if there are cohort-specific differences in growth and mortality. We conducted a laboratory study at ambient estuarine winter temperatures from 9 November 1995 to 22 April 1996 with two cohorts (spring-spawned cohort: 83–140 mm total length [TL]; fall-spawned cohort: 15–37 mm TL). We hypothesized that (1) among individuals within both cohorts, winter growth rates would be low compared with summer growth rates; and (2) overwinter mortality rates of the smaller, fall-spawned fish would be higher than those of larger, spring-spawned fish due to size-selective mortality. Under ambient winter temperatures (-2.0 to $14.0°C$) with daily, ad libitum feeding in the laboratory, growth rates were low but positive for the fall- and spring-spawned fish. Overwinter mortality occurred in both cohorts but was higher for the fall cohort than for the spring cohort (75% and 31%, respectively). Within the fall cohort, mortality was size selective, with reduced survival of individuals smaller than 24 mm TL. Within the spring cohort, there was no evidence of size-selective mortality. We concluded that the first winter of life may be an important mortality bottleneck for both cohorts of age-0 windowpanes in the Middle Atlantic Bight but that mortality patterns are cohort specific and may be determined by different combinations of factors, such as fish size at the start of winter, the magnitude of water temperature decline between fall and winter, and the frequency and duration of extremely cold water temperatures. Thus, overwinter mortality during the first winter of life may influence the population dynamics of the windowpane and other multimodal spawners inhabiting the Middle Atlantic Bight.

Many investigators have focused on the early life history and ecology of marine organisms to understand patterns of variability in abundance and distribution of natural populations (e.g., Houde 1989; Bailey 1994; Eggleston and Armstrong 1995; Able and Fahay 1998). Hjort (1914) first suggested that the early life history of fish includes a series of "bottlenecks," or vulnerable periods. Since the time of Hjort's (1914) proposal, fish biologists have suggested that the identification of mechanisms that may influence survival during these vulnerable periods is crucial to understanding variability in year-class strength (Bailey and Houde 1989; Bailey 1994). Vulnerable periods for young fish may include significant seasonal shifts in the physical environment, such as the onset of cold, winter temperatures in temperate regions (Sogard 1997). During winter, not only are water temperatures low, but often food is scarce, energy reserves are depleted, and growth is slow or nonexistent (Hurst and Conover 1998).

Recent studies have revealed that for some species, overwinter mortality of young-of-the-year (age-0) fish may be size selective, whereby smaller individuals suffer higher mortality rates during extended periods of cold water temperatures compared with larger individuals (Sogard 1997; Fullerton et al. 2000; Hurst et al. 2000; Sogard and Olla 2000; Hales and Able 2001; Lankford and Targett 2001; Hurst 2007). Several mechanisms have been invoked to explain higher overwinter mortality rates of smaller age-0 fish, including (1) starvation due to the joint effect of the positive allometry between fish size and energy reserves and the negative allometry between fish size and metabolic rate (Thompson et al. 1991; Schultz and Conover 1999); (2) size-selective predation throughout the winter (Garvey et al. 1998); (3) differential effects of high population densities (Bernard and Fox 1997; Matthews et al. 2001); and (4) physiological stress due to cold water temperatures (e.g., osmoregulatory failure, Johnson and Evans 1996; exposure to lethal

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temperatures, Adams et al. 1982). How size-selective mortality resulting from these mechanisms affects the population dynamics of a species may become even more difficult to interpret when multiple cohorts of small fish occur at several times of the year as a result of multiple spawning events, a frequent occurrence in the Middle Atlantic Bight (Able and Fahay 1998).

The windowpane *Scophthalmus aquosus* is a temperate flatfish that ranges from the Gulf of Saint Lawrence south to Florida but is most abundant from Georges Bank to Chesapeake Bay (Bigelow and Schroeder 1953; Grosslein and Azarovitz 1982). The species occurs primarily in the lower portion of estuaries, inlets, and the adjacent coastal ocean during the first year of life (Morse and Able 1995; Neuman and Able 2003). The timing of spawning along the northeastern United States has been determined from gonadal development of adults (Wilk et al. 1990), collection of eggs (Berrien and Sibunka 1999), and collection of recently hatched larvae (2–4 mm; Morse and Able 1995). Spawning is unimodal on Georges Bank, but a split spawning season is evident from southern New Jersey southward to Cape Hatteras, North Carolina (Morse and Able 1995). Off the coast of southern New Jersey, a spring-spawning event occurs in April to May and a fall-spawning event occurs in October to November (Wilk et al. 1990; Morse and Able 1995; Neuman and Able 2003). Thus, the two cohorts experience changing—though distinctly different—thermal regimes during the first year of life. The approximate 5-month difference in spawning time between these two cohorts results in a fall cohort composed of much smaller individuals compared with spring-spawned individuals by the time winter temperatures arrive (Neuman et al. 2001).

The purpose of this study was to determine the influence of winter temperatures on survival of age-0 individuals belonging to two cohorts of windowpanes. More specifically, the goals of this study were to (1) compare overwinter mortality and growth rates of spring- and fall-spawned individuals held under ambient winter conditions with food, (2) determine if patterns of overwinter mortality suggest size dependency such that fall-spawned windowpanes suffer higher overwinter mortality rates than spring-spawned fish, and (3) make predictions about the ability of fall- and spring-spawned fish to survive their first winter under natural conditions.

Materials and Methods

Experimental design.—Spring and fall-spawned age-0 windowpanes were collected in the lower portion of Great Bay, in Little Egg Inlet, and on the adjacent inner continental shelf in southern New Jersey from October to November 1995 by using demersal sampling gears (1- and 2-m beam trawls, 6-mm mesh; 6.1-m seine net, 6-mm mesh). All were held in sediment-free containers for approximately 1 week and were fed daily ad libitum rations of brine shrimp *Artemia* spp. nauplii and Atlantic silversides *Menidia menidia* before the start of the experiment. Two days prior to the start of the experiment, daily feeding ceased, fish were measured to the nearest millimeter (total length [TL]), and fish were marked by immersion in an aerated solution of oxytetracycline dihydrate and ambient seawater (concentration 0.9 g/L) for 24 h. Fish were monitored for an additional 24 h prior to being transferred to circular aquaria (66 cm in diameter; 26 cm high) containing elutriated sand (<1% silt/clay, 1.0–1.5 cm deep) and filtered, ultraviolet radiation-treated, flow-through seawater from Great Bay. At this time, the previous feeding schedule was resumed. Fish were assigned to their respective cohorts based on their initial sizes, which differed significantly between the cohorts (mean [± SD] initial size: fall cohort, 24.1 ± 1.05 mm TL; spring cohort, 111.4 ± 3.95 mm TL; $P < 0.001$) and corresponded well with sizes of field-captured spring- and fall-spawned windowpanes collected in other years (Neuman and Able 2003). Four fall-spawned fish ($n = 28$; 15–54 mm TL) of different sizes (e.g., 15, 24, 32, and 42 mm TL) were placed in each of seven aquaria, and two spring-spawned fish ($n = 16$; 83–160 mm TL) of different sizes (e.g., 85 and 120 mm TL) were placed in each of eight aquaria. The size differences among windowpanes in the same aquarium were apparent enough that with daily monitoring, we were able to identify individuals throughout the course of the experiment. Windowpanes were held at ambient temperatures (−1.1 to 13.9°C) and photoperiod (9 h light : 15 h dark to 14 h light : 10 h dark) from 9 November 1995 to 22 April 1996.

Mean daily temperatures (°C) were computed from multiple readings taken manually by a hand-held thermometer in the laboratory and in the estuary at the Rutgers University Marine Field Station (RUMFS) or from readings taken automatically every half-hour by a temperature recorder (Ryan Instruments Tempmentor) throughout the experiment. Mortality was assessed each day, and dead fish were removed and measured (TL). Survivors were measured in March and then again at the end of the experiment on 22 April, by which time ambient temperatures remained consistently above 9°C.

Water temperature analysis.—Mean daily laboratory temperatures recorded during the winter of 1995–1996 were compared to estuarine water temperatures extracted from a long-term data set (1976–1998; K. W. Able, unpublished data) in order to assess whether the

winter of 1995–1996 deviated from average winter temperatures. Mean daily laboratory temperatures were recorded as described above, and estuarine temperatures were recorded at the RUMFS boat basin near the intake for the laboratory flow-through system by using a hand-held thermometer.

To better interpret laboratory findings, we wanted to identify potential differences in winter water temperatures from shallow, estuarine habitat (similar to that near the intake for the flow-through laboratory) compared with deeper, inner shelf habitats. To estimate temperatures on the inner continental shelf during the course of the laboratory study, we accessed bottom temperatures from November to April of 1997–1998 and 1998–1999 at a location inside the estuary at 3-m depth (Buoy 126; Kennish and O'Donnell 2002) and a Rutgers University Underwater Research Observatory station on the inner continental shelf at 15-m depth (39°27.40′N, 74°14.75′W; www.marine.rutgers.edu/mrs). Daily means for these locations were computed from data collected every half-hour inside the estuary with a YSI data logger and every 1.3 s on the inner shelf with a Sea-Bird Electronics temperature sensor.

Growth analysis.—Differences in mean individual growth rates (mm/d) of fish that survived were compared within and between cohorts by using single classification analyses of variance (ANOVAs) for two different time intervals: (1) from 9 November 1995 to 19 March 1996; and (2) from 19 March to 22 April 1996. Growth analyses were not conducted for those individuals that died because death dates varied among individuals and therefore growth comparisons for the same time interval and temperature regime were not possible.

Overwinter Mortality Analysis

Event analysis was used to assess the occurrence and timing of mortality among age-0 windowpanes and to estimate predictive models where the effect of cohort (spring versus fall) upon the risk of death was assessed. For these analyses, the observed data were fit to an accelerated failure time model based upon the Weibull distribution using cohort as the covariate (see equation [11] of Chambers and Leggett 1989). The parameters of the accelerated failure time model were estimated by using maximum likelihood analysis (SAS Institute 1995). Parameters were incorporated into two conditional functions used to describe the distribution of overwinter deaths: (1) the conditional cumulative frequency function,

$$F(t; v) = 1 - \exp\left[-(t/\alpha)^{\gamma} e^{v'\beta}\right];$$

and (2) the hazard function,

$$h(t; v) = (\gamma/\alpha)(t/\alpha)^{(\gamma-1)}\exp(v'\beta),$$

where t is time, α is the scale parameter in units of the mortality observations (d), γ is the shape parameter and is dimensionless, v is the cohort (0 = spring, 1 = fall), and β is the magnitude of the effect of cohort. The cumulative frequency function measures the probability that an individual has died by a particular date. The hazard function measures the probability that an individual will die on a particular date given that it has survived until that date. In other words, the cumulative frequency function is measuring the cumulative probability of death while the hazard function is measuring the instantaneous probability of death.

Size-selective mortality analysis.—To examine the possibility of size-selective mortality within the spring and fall cohorts, we used single classification ANOVAs to compare mean initial sizes of fish that died versus those that survived the experiment. In addition, we examined the possibility of size-selective mortality within and between cohorts by plotting the initial size of fish against their death date (for those that died) or against the final day of the experiment (for those that survived).

Results

Overwinter Temperature

Water temperatures during the winter of 1995 to 1996 fell below average temperatures (computed from 22 years of estuarine temperature data; K. W. Able, unpublished data) on a number of occasions. The months of November and December were colder than average and were characterized by numerous dramatic temperature declines, while January was warmer than average (Figure 1A). Temperatures during February, March, and April vacillated above and below average temperatures. Water temperature decreased gradually from the start of the experiment on 9 November until 5 December and then declined precipitously until 14 December. From that point on, temperatures remained below 7°C until the end of February. In March, temperatures increased steadily until the end of the experiment on 22 April (Figure 1A).

Bottom water temperatures inside the estuary (3-m depth) were cooler and more variable than temperatures recorded in the coastal ocean (15-m depth) from November through February of 1997–1998 and 1998–1999 (Figure 1). From February through the end of March, estuarine temperatures were still more variable than those recorded on the inner shelf, but estuarine temperatures fluctuated both above and below inner shelf temperatures. Through the month of April, estuarine water temperatures were consistently warmer,
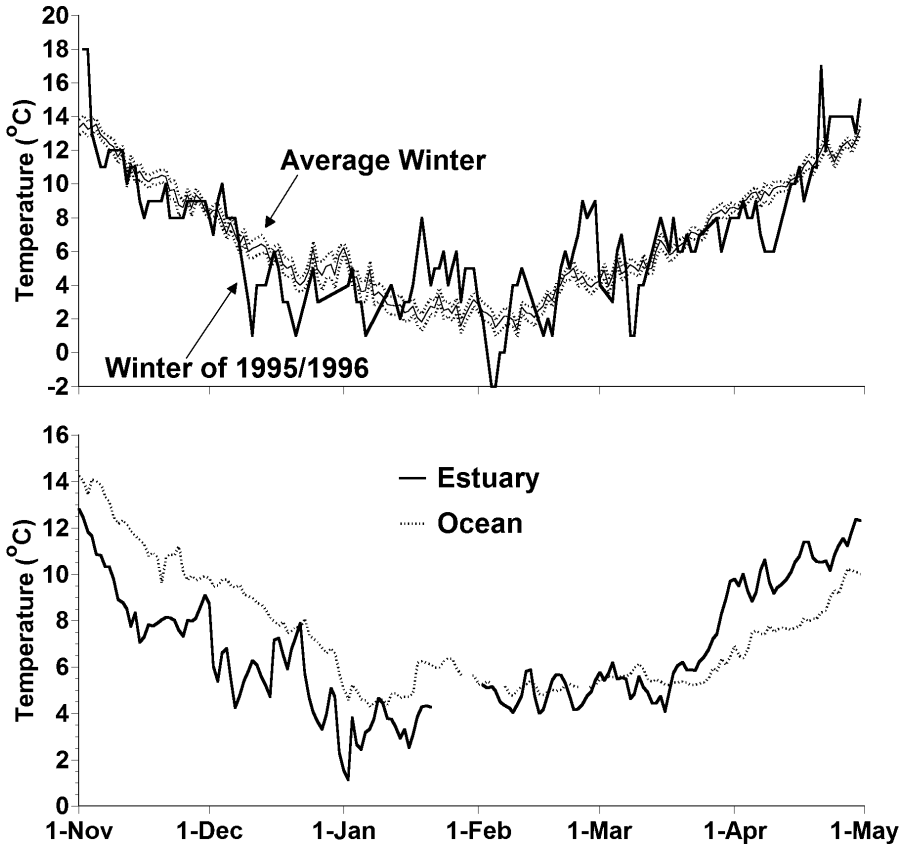
FIGURE 1.—(**Upper**) Mean daily estuarine water temperatures computed from daily readings taken at the Rutgers University Marine Field Station from November to April 1976–1998 (solid line; K. W. Able, unpublished data). Upper and lower confidence limits ($\alpha = 0.05$) around daily means are also shown (broken lines). Mean daily temperatures recorded during the study period from November 1995 to April 1996 are represented by the bold solid line. (**Lower**) Mean daily estuarine water temperatures computed from readings taken every half-hour at buoy marker 126 at 3-m depth and mean daily ocean water temperatures computed from 1.3-s readings taken at a Rutgers University Underwater Research Observatory station on the inner continental shelf at 15-m depth (39°27.40′N, 74°14.75′W; www.marine.rutgers.edu/mrs) from November to April 1997–1998 and 1998–1999 are presented.

but were again more variable, than coastal ocean water temperatures (Figure 1).

Overwinter Growth

Under ambient winter temperatures (−2.0 to 14.0°C) with daily feeding in the laboratory, mean (± SD) overall growth rates of survivors from the spring and fall cohorts were not statistically different (0.16 ± 0.015 and 0.14 ± 0.009 mm/d, respectively; Table 1). A more detailed examination of the survivors during different time intervals revealed that while there were no differences in mean growth rates between cohorts, within each cohort growth was significantly slower during the cold winter months (9 November to 19 March) than during the period when temperatures began warming (19 March to 22 April; 0.12 ± 0.014 versus 0.48 ± 0.056 mm/d for the spring cohort; 0.12 ± 0.010 versus 0.45 ± 0.038 mm/d for the fall cohort; $P < 0.05$; Table 1).

Overwinter Mortality

Overwinter mortality occurred for both the fall and spring cohorts but was much higher for fall-spawned windowpanes (75% and 31%, respectively; Figure 2A, B). The observed cumulative mortality of fall-spawned individuals increased throughout the first 2 months of the experiment, increasing most dramatically during the steep decline in temperature (from 8.8°C to 0.5°C) that occurred from 5 to 14 December. At that point, 71% of the individuals had died. For the remaining 112 d of the experiment, one additional fall-spawned windowpane died. The estimated Weibull (cumulative

Table 1.—Mean ($\pm$SE) initial and final fish sizes (total length [TL]) of age-0 windowpanes by cohort (spring or fall) and overwinter mortality status (mortalities or survivors) during the winter of 1995 to 1996, and growth rates of age-0 fish that survived the winter (NA = not applicable). Mean growth rates (mm/d) of windowpane survivors from 9 November 1995 to 19 March 1996, from 19 March to 22 April 1996, and overall were compared within and between cohorts. For initial sizes, different letters within the same cohort and column indicate significant differences in initial sizes between fish that died versus those that survived the winter ($P < 0.05$). For growth rates of survivors, different letters within the same column or same row indicate significant differences over different time intervals between cohorts or within cohorts, respectively ($P < 0.05$).

| Cohort | Overwinter mortality status | n | Initial TL (mm) | Final TL (mm) | Fish growth (mm/d) | | |
					9 Nov–19 Mar	19 Mar–22 Apr	Overall
Spring spawned	Mortalities	5	116.6 $\pm$ 6.22 z	132.5 $\pm$ 6.15	NA	NA	NA
	Survivors	11	109.1 $\pm$ 5.03 z	135.6 $\pm$ 4.40	0.12 $\pm$ 0.014 z	0.48 $\pm$ 0.056 y	0.16 $\pm$ 0.015 z
Fall spawned	Mortalities	21	22.6 $\pm$ 1.12 z	25.4 $\pm$ 1.57	NA	NA	NA
	Survivors	7	28.7 $\pm$ 1.67 y	52.6 $\pm$ 2.88	0.12 $\pm$ 0.010 z	0.45 $\pm$ 0.038 y	0.14 $\pm$ 0.009 z

mortality frequency) distribution for fall-spawned fish provided a good fit to the observed date-at-death overwinter mortality data (Figure 2A).

The spring-spawned fish suffered less mortality (31%) than fall-spawned individuals. The five overwinter deaths of spring-spawned fish occurred on 6 February, when the lowest mean daily temperature was recorded ($-2.0°C$; Figure 2A, B). The estimated Weibull (cumulative frequency) distribution provided a poorer fit to observed overwinter mortality data for spring-spawned windowpanes than for fall-spawned windowpanes (Figure 2A).

The hazard functions (Figure 2B) estimated the probability that a fall- or spring-spawned fish would die on a particular date given that it had survived until that date (date-specific mortality). For example, on day 3 of the experiment, a fall-spawned fish had about a 5% chance of dying on that day given that it had survived until day 3. This probability decreased rapidly for fall-spawned windowpanes throughout the first 2 months of the experiment, encompassing the time period when temperatures dropped steadily. Date-specific mortality leveled off in January, and the probability of a fall-spawned fish dying after January given that it survived until January was very low (1%) and changed little through the remainder of the winter. Date-specific mortality for the spring cohort was very low (0.05%) throughout the experiment. Cohort had a significant effect on the probability of survival as estimated by the accelerated failure time model ($\chi^2 = 9.26$, $P < 0.01$).

Size-selective Overwinter Mortality

Overwinter mortality differed between cohorts because it was size selective. More of the small individuals (15–37 mm TL) belonging to the fall cohort died during the experiment than larger, spring-spawned individuals (83–140 mm TL; Figure 3). There was size-selective mortality within the fall cohort as well. Fifty percent of the individuals that entered the experiment at

a TL greater than or equal to 24 mm did not die, while 94% of the individuals that entered the experiment at less than 24 mm experienced mortality ($\chi^2 = 7.81$, $P < 0.01$; Figure 3). Most of the fall-spawned fish that did expire died within the first 2 months of the experiment as temperatures declined steadily (Figure 3). In addition, fall-spawned survivors were larger at the start of the experiment than fall-spawned fish that experienced overwinter mortality (28.7 $\pm$ 1.67 versus 22.6 $\pm$ 1.12 mm, respectively; $P < 0.05$; Table 1).

Discussion

Overwinter Growth

The sizes and growth rates of windowpanes held under ambient winter conditions in the laboratory corresponded well with estimates based on field collections, suggesting that laboratory observations reflect natural growth conditions to some degree (Morse and Able 1995; Neuman 1999). Despite laboratory observations that fall-spawned fish ate much more consistently (usually daily unless temperatures dropped below 2°C) than spring-spawned fish (M. J. Neuman, personal observation), there were no intercohort differences in mean overall growth rates of overwinter survivors. In addition, overwinter growth rates of survivors from both cohorts were an order of magnitude lower than summer growth rates (1.1 mm/d) estimated from length frequency distributions and length-at-capture data (Morse and Able 1995; Neuman 1999; Table 1). Most of the positive growth for both cohorts began when temperatures rose in March (Table 1; Figure 1).

We were not able to identify a temperature below which windowpane growth ceased. Our laboratory data suggest that fall-spawned windowpane survivors should be able to ingest food, if it is encountered in nature at temperatures as low as 2°C; however, spring-spawned survivors stopped feeding at temperatures of approximately 6–7°C (M. J. Neuman, personal obser-
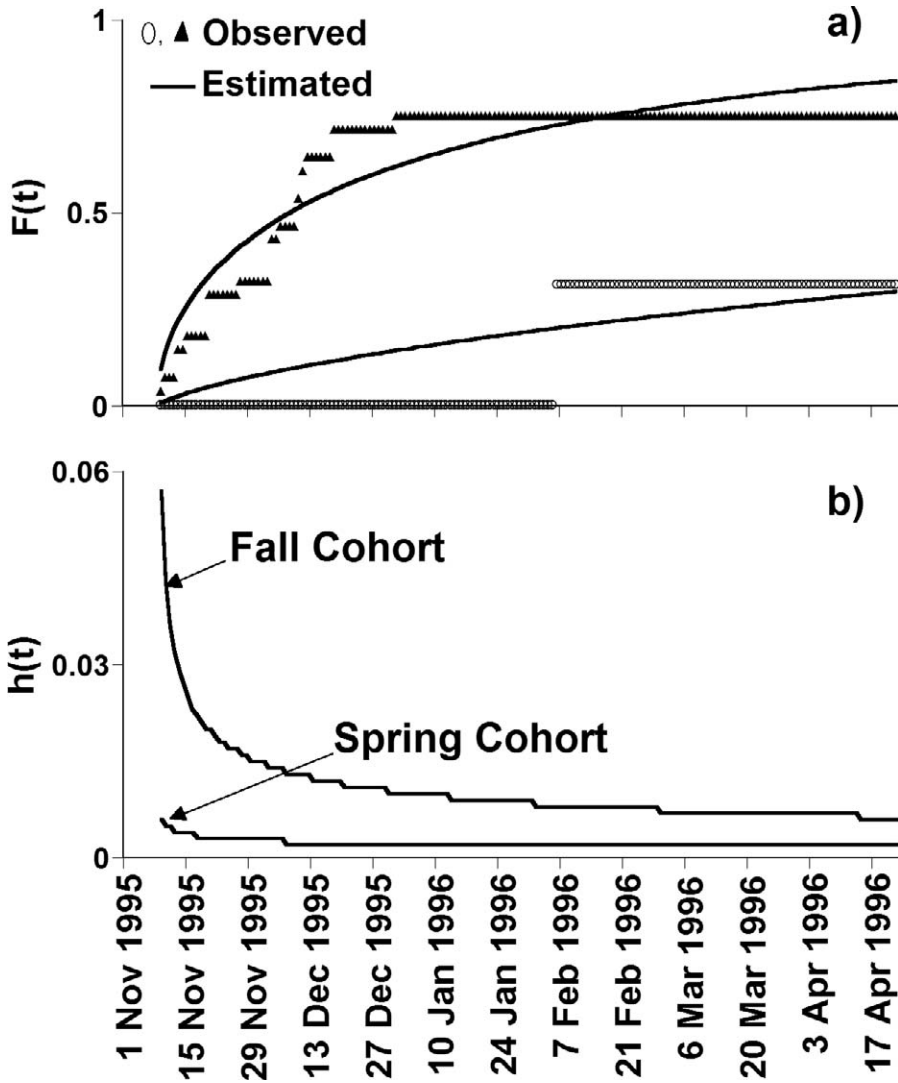
FIGURE 2.—(a) Observed overwinter mortality functions ($F[t]$) and estimated cumulative mortality distributions (solid lines) for spring (circles) and fall (triangles) spawned windowpanes held at ambient winter temperatures from November 1995 to April 1996. (b) Date-specific (instantaneous) mortality rates (solid lines) represented by the hazard function ($h[t]$) for cumulative mortality distributions in (a) are shown.

vation). Throughout the range where windowpanes are most abundant (Georges Bank to Chesapeake Bay), temperatures during an average winter remain above 2°C and below 6°C (Figure 1; Able and Fahay 1998). This suggests that growth of fall-spawned survivors should be slow but positive during most years if food is available; however, patterns of overwinter growth for spring-spawned fish in nature are more difficult to predict. Although spring-spawned fish appeared to stop feeding at temperatures below 6–7°C, their growth rates were still positive (Table 1). A possible reason for this discrepancy could be that spring-spawned fish

utilize energy reserves to maintain somatic growth without overwinter feeding.

Other laboratory studies have revealed that over-winter growth rates in a variety of species may be low, even when fish are offered ad libitum rations (Thompson et al. 1991; Copeland and Carline 1998; Garvey et al. 1998; Hurst and Conover 1998; Hales and Able 2001; Curran and Able 2008). In some of these cases, low temperatures have been shown to affect growth rates independently of prey availability whereby growth has ceased below certain temperatures (<5°C to 10°C in striped bass *Morone saxatilis*: Hurst
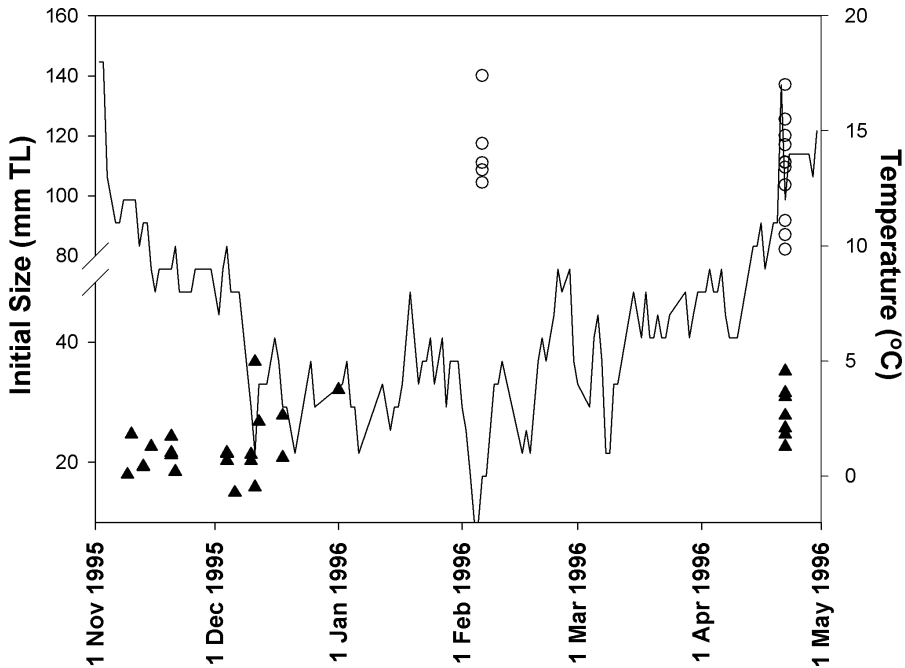
FIGURE 3.—Size-selective survivorship of spring (circles) and fall (triangles) spawned cohorts of windowpanes. Initial size (mm total length [TL]) of individuals from both cohorts is plotted against the date of death (for those fish that experienced overwinter mortality) or the last day of the experiment (for those fish that survived the winter). Mean daily temperatures recorded during the study period from November 1995 to April 1996 are represented by the solid line.

and Conover 1998; <6°C in largemouth bass *Micropterus salmoides*: Garvey et al. 1998). Field studies have offered conflicting evidence concerning overwinter growth; some have identified low or zero growth during winter for a variety of species (Able and Fahay 1998; Garvey et al. 1998; Hurst and Conover 1998), whereas others have identified significantly positive growth (Copeland and Carline 1998).

Overwinter Mortality and Size Dependence

Other studies have suggested that smaller fish experience higher overwinter mortality rates than larger fish because they have accumulated less energy reserves prior to winter and have higher metabolic rates than larger fish (see reviews by Sogard 1997; Hurst 2007). Less commonly cited reasons for size-dependent mortality are osmoregulatory failure due to cold temperatures and lethal temperatures (Johnson and Evans 1996).

In our study, the mechanisms driving overwinter mortality were not tested directly and are difficult to infer, especially for the fall cohort. Our data suggest that the relationships among fish size, temperature, and overwinter survival are complex and may differ between cohorts. The fall-spawned fish experienced

nearly all of their mortality (71%) during the period when temperature declined from 18°C to 1°C (Figure 3) in early winter, and those fall-spawned fish that died were significantly smaller than fall-spawned fish that survived the winter (Table 1; Figures 2A, 3). This suggests that transitional periods of decreasing temperature at the onset of winter are stressful for fall-spawned windowpanes, particularly the smallest individuals; however, cold temperatures throughout the remainder of the winter, including a short spell of extremely cold temperatures in February (−2°C for 2 d; Figure 3) did not result in any mortality of fall-spawned fish. Those fish that were able to survive the initial transition in temperature were able to cope with the stress of cold temperatures throughout the remainder of the winter.

In contrast, 100% of spring-spawned fish survived the period of cooling temperatures in early winter and their only mortality occurred during a short period of intense cold temperatures in February (−2°C for 2 d; Figure 3). There was no evidence of size-dependent overwinter mortality within the spring cohort (Table 1; Figure 3). The mortality pattern for spring-spawned fish suggests that low temperature was directly responsible for the deaths of some individuals. Perhaps

some spring-spawned fish, independent of their size, are vulnerable to temperatures that drop below a lethal limit during periods of extremely cold winter temperatures. A similar pattern has been observed in other species (e.g., Johnson and Evans 1996; McBride and Able 1998; Slater et al. 2007; Curran and Able 2008).

Implications for Recruitment of Age-0 Windowpanes under Natural Conditions

There are a number of bimodal spawners in the Middle Atlantic Bight, but few studies have attempted to assess the contribution of the second spawning event to the total population. For example, Atlantic menhaden *Brevoortia tyrannus*, spotted hakes *Urophycis regia*, and bluefish *Pomatomus saltatrix* exhibit bimodal patterns of occurrence in nearshore waters of the Middle Atlantic Bight. The second spawning event in these species produce age-0 fish that are small compared to the earlier spawned cohort by the time winter temperatures arrive (approximately 10–30, 10–120, and 40–140 mm TL for Atlantic menhaden, spotted hake, and bluefish, respectively; Able and Fahay 1998); however, their ability to survive or avoid winter temperatures in Middle Atlantic Bight waters remains unclear. Recent field and laboratory studies conducted with bluefish, in the South Atlantic Bight indicate that summer-spawned fish entering winter at smaller sizes compared with spring-spawned fish are capable of surviving the winter, are physiologically well-equipped to do so without seeking thermal refugia via emigration, and can contribute significantly to the adult population; however, winter severity can influence survivorship significantly (Morley et al. 2007; Slater et al. 2007).

Winter severity and thermal gradients have been shown to affect recruitment patterns in age-0 individuals belonging to a variety of other species, including the striped bass, Atlantic herring *Clupea harengus*, Atlantic croaker *Micropogonias undulatus*, black sea bass *Centropristis striata*, and bluefish (Graham et al. 1990; Hurst and Conover 1998; Hales and Able 2001; Hare and Able 2007; Morley et al. 2007). Under natural conditions, it is possible that during winters when the transition from fall to winter temperatures is more gradual or of lower magnitude, or during relatively mild winters overall, the survivorship of both cohorts could be higher than suggested by the results of this study.

Spring- and fall-spawned fish survivorship may also be altered under natural conditions if fish undergo offshore migrations into deeper ocean waters of the Middle Atlantic Bight (Morse and Able 1995). In the Great Bay–Little Egg Harbor estuarine and coastal ocean complex, bottom water temperatures from November to February of 1997–1998 and 1998–1999 were approximately 1–5°C cooler and more variable inside the estuary than in deeper, continental shelf waters (Figure 1B). Graham et al. (1990) also showed that temperatures on the inner continental shelf off the coast of Maine averaged 1–2°C degrees warmer than estuarine temperatures and remained more stable. Thus, the ability of spring- and fall-spawned windowpanes to emigrate out of shallow (8-m) estuarine habitats and into potentially warmer, deeper (>8 m) waters of the inner shelf could increase overwinter survival rates of age-0 windowpanes. Certainly, many other fishes in the temperate Middle Atlantic Bight undergo seasonal migrations either into deeper or more southerly waters to reach presumed thermal refugia (Grosslein and Azarovitz 1982; Able and Brown 2005).

Conclusions

Our results suggest that the first winter of life may be an important mortality bottleneck for both cohorts of age-0 windowpanes in the Middle Atlantic Bight but that mortality patterns are cohort specific and may be determined by different combinations of factors, as evidenced by asynchronous mortality episodes between the cohorts in our laboratory study. Further, this study provides evidence for size-selective overwinter mortality, with the smallest fall-spawned fish suffering higher mortality rates than larger fish. These results may provide insight into understanding the evolutionary significance of spring and fall spawning pulses. A potential advantage of two spawning pulses is that they provide the species flexibility to compensate for losses that may be incurred by only one of the cohorts depending on the particular suite of conditions present during a given winter. This may be particularly important for a species that inhabits a region where a wide range of environmental conditions can occur over a short period of time (Able et al. 1992). The disadvantage of two spawning pulses is that spawning comes at a tremendous energetic expense and in a given year when conditions are poor for both cohorts, the year-class may incur net overall losses. Based on abundance estimates of windowpane eggs, larvae, and juveniles, it appears that the spring cohort is numerically dominant, with densities of eggs, larvae, and juveniles in the spring being at least an order of magnitude higher than those in the fall (Berrien and Sibunka 1999; Neuman and Able 2003). This suggests that the energetic cost of fall spawning is relatively low compared with spring spawning. Thus, the advantage of producing two cohorts that together are more likely to produce higher overwinter survival rates than a single cohort may outweigh the low energetic investment made in the fall spawning event.

The first winter of life has been shown to be an important determinant of recruitment success in a number of species (see review by Sogard 1997; Lankford and Targett 2001; Hare and Able 2007; Hurst 2007), and its effect on recruitment has been shown to depend on one or a combination of the following factors: winter severity (Hurst and Conover 1998), body size (Ludsin and DeVries 1997; Garvey et al. 1998), energy reserves (Thompson et al. 1991), population density (Bernard and Fox 1997), osmoregulatory failure (Johnson and Evans 1996), and exposure to lethal temperatures (Adams et al. 1982; Graham et al. 1990). In order to make better predictions regarding the roles that fish size, temperature, and overwinter survival play in determining the population dynamics of multimodal spawners, we suggest that future studies aim to identify the causal factors responsible for producing size-selective overwinter mortality by varying prey availability and temperatures regimes (cold versus warm, constant versus variable, rapid versus slow transitions) while measuring sizes, growth rates, and energy content of individuals throughout the winter.

Acknowledgments

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