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Winter mortality, growth, and behavior of young-of-the-year of four coastal fishes in New Jersey (USA) waters

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Abstract Winter mortality has been hypothesized to select for large body size in young-of-the-year (YOY) fishes, yet substantiation of winter mortality and its cause(s) are available for few estuarine or marine species. We examined seasonal length distributions of wild populations of four common marine species, black sea bass (*Centropristis striata*), tautog (*Tautoga onitis*), cunner (*Tautogolabrus adspersus*), and smallmouth flounder (*Etropus microstomus*), and mortality (i.e., frequency of death), growth, and behavior of their YOY in the laboratory at ambient winter temperatures (mean 7°C, range 2–13°C) during a 135-day period (December 1992 through mid-April 1993) to establish potential causes of their mortality in the field. Young-of-the-year black sea bass experienced 100% mortality when water temperatures decreased to 2–3°C in February, emphasizing the importance of winter emigration from estuaries in this southern species. The low mortality of two labrid species, YOY tautog (14%) and YOY cunner (3%), was consistent with their northern distribution and year-round occurrence in estuarine and nearshore coastal waters. Laboratory mortality of YOY smallmouth flounder (33%) was higher for small (<35 mm total length) fish, suggesting that this small species may experience high winter mortality in estuaries and nearshore coastal waters. Seasonal differences in fish length result potentially from several mechanisms (e.g., mortality and/or migration) that are difficult to assess, but our laboratory experiments suggest that seasonal temperature changes cause size-specific mortality of YOY smallmouth flounder and offshore migration of YOY black sea bass.

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Introduction

In their first winter of life, individuals of marine and estuarine temperate fishes may experience net energy deficits due to low temperature and food scarcity (see Sogard 1997 for review). Small individuals may also accrue an energy deficit due to their relatively high weight-specific standard metabolic rates, relatively low weight-specific energy reserves, and osmoregulatory stress (Calder 1984; Thompson et al. 1991; Johnson and Evans 1996; Hurst et al. 2000). As a result, size-dependent physiological capacities may result in low or even negative growth rates and high and size-dependent mortality rates of young-of-the-year (YOY) fishes during winter (Conover and Ross 1982; Henderson et al. 1988; Conover and Present 1990; Shuter and Post 1990; Hurst and Conover 1998; Hurst et al. 2000).

Size-dependent winter mortality may affect many life history traits such as migration, growth, and reproduction (e.g., Fox and Keast 1990, 1991; Snyder and Dingle 1990; Conover 1992; Lankford 1997) and reportedly impacts species composition, trophic structure, and other aspects of poikilotherm ecology (e.g., Persson 1986; Hall and Ehlinger 1989; Shuter and Post 1990; Atkinson 1994; Johnson and Evans 1996). Effects of mortality may be pronounced along the Atlantic coast of North America, where average winter water temperatures decline about 1°C with each degree of latitude and the annual range in sea surface temperatures exceeds 20°C (Schroeder 1966). However, most information available on winter mortality, growth, and behavior of estuarine and marine fishes is restricted to subtropical faunas and is concentrated on severe storm impacts (e.g., Gunter 1947; Hoff 1971; Gilmore et al. 1978), although an improved understanding is developing for temperate estuarine fishes (Schwartz 1964; Moss 1973; Able and Fahay 1998; Hurst and Conover 1998; Hurst et al. 2000).

Purposes of this study were (1) to compare length distributions of estuarine populations of YOY of four temperate estuarine/marine fishes between fall and spring for evidence of size-selective winter mortality, and (2) to examine mortality, growth, and behavior of YOY of those species in laboratory aquaria at ambient winter temperature. These four species, black sea bass [*Centropristis striata* (Linnaeus)], tautog [*Tautoga onitis* (Linnaeus)], cunner [*Tautogolabrus adspersus* (Walbaum)], and smallmouth flounder [*Etropus microstomus* (Gill)], are abundant and widely distributed in estuaries and nearshore waters on the continental shelf of the Mid-Atlantic Bight, but they have different geographic centers of abundance (Nichols and Breder 1927; Bigelow and Schroeder 1953; Richardson and Joseph 1973; Grosslein and Azarovitz 1982; Able and Fahay 1998). Temperature tolerances of adults and/or large juvenile black sea bass, tautog, and cunner differ from each other (e.g., Schwartz 1964; Olla et al. 1974, 1975). Winter distributions and physiological tolerances of their YOY have not been reported.

Materials and methods

Evaluation of size-selective mortality in natural populations

Size-selective winter mortality in Great Bay, New Jersey (39°30′N, 74°20′W) was determined from seasonal changes in mean length of fish (e.g., Shuter et al. 1980; Toneys and Coble 1980) caught in fall (November and December), winter (January, February, and March), and spring (April and May). In all four species, lengths of individuals captured within a season were similar. We therefore combined capture dates within a season and species for the purpose of examining seasonal growth patterns. Black sea bass, tautog, and cunner were caught with modified Gee minnow traps (length, 45 cm; diameter, 23 cm; mesh, 0.64 cm^2; Memphis Net and Twine, Memphis, Tenn.) and with rectangular "experimental" traps (33×46×91 cm, 4×45-cm "V" opening, and 6 mm^2 mesh) set in a dredged subtidal embayment at the Rutgers University Marine Field Station (RUMFS) near the confluence of Great Bay and Little Egg Harbor and in Schooner and Hatfield creeks. Minnow traps were modified by enlarging one opening from a 2-cm circle to a 2×5-cm oval to increase the size range of the catch (Able and Hales 1997). Usually, 14 traps were checked 6 days per week from fall 1992 through spring 1993, but traps were not fished in the periods of 11–15 December 1992 and 1–8 February 1993 due to severe weather. Total length of all specimens was measured and recorded.

Smallmouth flounder were collected with a 2-m beam trawl (6 mm^2 mesh) at three sites near Beach Haven Ridge (8–15 m) and in deeper (15–24 m) waters on the continental shelf during 1991–1992. Daily water temperatures were not recorded at Beach Haven Ridge, but comparison of water temperatures at RUMFS and surf temperatures at Atlantic City (a site for which long-term daily information is available, and which has been used as a predictor of oceanographic events at Beach Haven Ridge) indicated that winter temperatures at the ridge were within 1–2°C of those at Atlantic City (Able et al. 1992).

Young-of-the-year were distinguished from older age classes using (1) regional length frequency information (Sogard et al. 1992; Able and Hagan 1995; Able and Fahay 1998) and (2) previously published age–growth studies for black sea bass (Wenner et al. 1986), tautog (Sogard et al. 1992), cunner (Serchuk and Cole 1974; Dew 1976), and smallmouth flounder (Able and Fahay 1998). In all of the above examples there was a clear break in the length frequency between the age classes.

Laboratory experimental design

Young-of-the-year were collected from mid-November to early December 1992 with traps or beam trawls adjacent to RUMFS in Great Bay, New Jersey. Daily water temperatures and salinities during this period ranged from 0.3 to 10.7°C and 21‰ to 32‰, respectively. All fish were maintained in laboratory aquaria (40 l) at ambient conditions on a flow-through system; fish were fed daily and dead individuals were removed.

The laboratory was set up to provide an ambient-temperature treatment with natural variation (i.e., seasonal and diel changes). Water from a polyhaline creek (Schooner Creek, salinity range 26–31‰) adjacent to RUMFS was pumped continuously to an outdoor settling tank, to the laboratory where it was filtered to remove particles >5 μm, and then to 12 aquaria in two replicate water baths. The 12 aquaria in each water bath received water continuously at approximately 1 l min^{-1}; water volume was maintained by a drain in the wall of each aquarium. Temperature (using a thermometer) and salinity (using an AO Model 10419 refractometer, American Optical Corporation, Buffalo, N.Y.) were measured in both water baths each morning and afternoon. Temperature and salinity did not differ between the replicate water baths [analysis of variance (ANOVA), $P=0.95$ and 0.34, respectively]. Water temperatures in the laboratory paralleled water temperatures measured at midday at a field site adjacent to the laboratory but were slightly (1.5°C) warmer. About 4 cm of clean beach sand, artificial eelgrass mats, and several lengths of PVC pipe were placed in all aquaria, the latter two as refugia.

Healthy, actively feeding fish were measured [total length (TL) in millimeters] and sorted into three size categories (small, medium, and large), except for smallmouth flounder, which were sorted into only two size categories (small and large) due to the small size range of available specimens (Table 1). Lengths of fish included in the experiment largely overlapped length ranges of YOY in natural populations in fall (Table 1). Individuals were randomly allocated from all size groups (except for black sea bass) among six 40-l aquaria [5 fish per aquarium for black sea bass (total $n=30$), 6 fish per aquarium for tautog and cunner (total $n=36$), 8 fish per aquaria for smallmouth flounder (total $n=48$)]. This allocation resulted in two replicate water baths holding three aquaria containing all size groups of each species. All size treatments, though combined within aquaria, were considered independent because of

Table 1 Initial total length (mean ± SE, mm) of fish in each size category (small, medium, and large) for laboratory experiment and field collections in the fall for each species

Species	Laboratory				Field
	Small	Medium	Large	Overall	Overall
Black sea bass	45 ± 3.7	59 ± 0.8	72 ± 1.7	59 ± 2.4	63 ± 1.0
Tautog	45 ± 1.3	58 ± 2.0	86 ± 2.0	63 ± 3.1	58 ± 0.8
Cunner	39 ± 1.3	46 ± 1.4	55 ± 1.8	47 ± 1.4	47 ± 0.7
Smallmouth flounder	32 ± 0.6	–	40 ± 0.7	36 ± 0.7	29 ± 0.8

(1) the absence of aggression among individuals, (2) the provision of refugia for all specimens, and (3) the ad libitum feeding regimen (see below). For black sea bass (known to be cannibalistic in aquaria when fish size differed), fish of the same size group were placed in a single aquarium in each water bath. Comparison of total lengths of fish at the start of the experiment (Table 1) indicated that for each species (1) TL differed significantly among designated size groups [TL of small fish less than TL of medium fish (except for smallmouth flounder, which lacked this size category) less than TL of large fish], and (2) TL did not differ between or within replicates.

Fish were fed a diet of *Artemia* spp., chopped fishes, shrimps, and clams, and a prepared meal that included the above and *Spirulina* spp., chopped spinach, beef heart, vitamins C and E, and cod liver oil ad libitum twice per day. Uneaten food was removed each day. Even when their activity was reduced, all fish were provided an opportunity to feed by placement of food near each individual. The number of fish that fed during the observation period was recorded. Fishes were observed for signs of disease and parasitism during feeding and periodically at other times. The timer-controlled artificial lighting schedule was adjusted monthly so that fish experienced natural photoperiods throughout the experiment.

The experiment ran until 15 April, when the water temperature in Great Bay adjacent to the laboratory was >12°C. Long-term records indicated that water temperatures would continue to increase due to seasonal warming (Able et al. 1992). Fish in all aquaria were then counted, measured to the nearest millimeter TL, and weighed to the nearest 0.1 g (Ohaus Model C501 electronic balance, Florham Park, N.J.).

Laboratory mortality

Survival analysis was used to assess the occurrence and timing of mortality among size classes of YOY black sea bass, tautog, and smallmouth flounder. It was not possible to analyze differences in mortality among size classes of cunner with this method due to overall low mortality ($n=1$ individual) during this experiment. The observed data were fit to an accelerated failure time model based on the Weibull distribution using size class as the covariate (Chambers and Leggett 1989). The parameters of this model were estimated using maximum likelihood analysis, and the Chi-square statistic tested the null hypothesis of no effect of size class on mortality (Allison 1995).

Laboratory growth and behavior

Growth rates of fish in each aquarium were determined as the difference in mean TL at the beginning and end of the experiment divided by mean duration of survival. Behavior of fish was observed to provide insights into behaviors (Table 2) that could influence mortality (e.g., diminished feeding) or indicate imminent mortality (e.g., stress) and influence energy use (e.g., swimming, resting). Data gathered consisted of about 5 min of observation per aquarium at least once every 3 days just before, during, and after the morning feeding. Attempts were made to minimize the effects of the observer upon fish behavior (e.g., no sudden movements, etc.). It was not possible to observe and record consistently the size of fish exhibiting behaviors. The number of fish exhibiting specific behaviors (Table 2) was recorded, and the frequency of each behavior on a given day was plotted as a percentage of the number of fish that exhibited that behavior in each aquarium. These percentages were then arcsin- and rank-transformed for ANOVA (for reasons described above; Conover and Iman 1981) and analyzed with ANOVA for effects of temperature (and fish size groups for black sea bass). Results of arcsin- and rank-transformed data rarely differed from ANOVA of untransformed data, so only analyses of untransformed data are provided. When temperature affected fish behavior, temperature ranges over which each behavior occurred were determined.

Results

Seasonal length distributions

Temperatures in the field ranged from 0 to 26°C with highest temperatures during fall (mean 16°C, range 8–26°C) and lowest temperatures in winter (mean 5°C, range 1–10°C). Temperatures varied during spring (mean 10°C) ranging from 0 to 20°C.

Fish lengths from field collections differed from fall to spring for all four species (Fig. 1). Total lengths of YOY black sea bass (<110 mm TL; Fig. 1) differed between fall 1992 (mean 66 mm) and spring 1993 (mean 88 mm; $P<0.01$) with YOY individuals, <70 mm TL, making up the majority of the collection in fall (67%) but a small proportion in spring (19%). Nearly 24% of YOY collected in spring were larger than the largest YOY collected in fall. Only a single black sea bass was collected in winter.

Mean lengths of YOY tautog (<120 mm TL, Fig. 1) trapped in fall (60 mm) and winter (56 mm) were significantly smaller than the mean length of those caught in spring (67 mm, ANOVA, $P<0.05$, Student-Newman-Keuls SNK, $P<0.05$). Small tautog (TL <50 mm) made up approximately 45% of the catch in fall but only 16% in spring. Lengths of YOY cunner (<110 mm TL, Fig. 1) trapped in Great Bay were smaller in fall (49 mm) and winter (51 mm) than in spring (58 mm, ANOVA, $P<0.05$, SNK, $P<0.05$). Small fish (TL <50 mm) made up the majority of the catch in fall (60%) and winter (55%), but a much smaller percentage (15%) in spring.

Table 2 Common behavior patterns recorded in the laboratory for all species

Behavior	Description
Swimming	Active swimming at any level in aquarium
Shelter use	Use of either type of structure (PVC pipe or artificial seagrass) with fish relatively inactive (not necessarily motionless)
Resting	Motionless (or nearly so) fish, perched on pelvic fins on the substratum (except smallmouth flounder)
Burying	Complete or partial burial of fish within substratum
Stress	Any behavior indicative of stress, including gasping at the surface (aquatic surface respiration), "coughing" or exaggerated opercular movements, disoriented swimming or drifting
Aggression	Any agonistic behavior (chasing, biting, fin-nipping, etc.)
Feeding	Ingestion of food

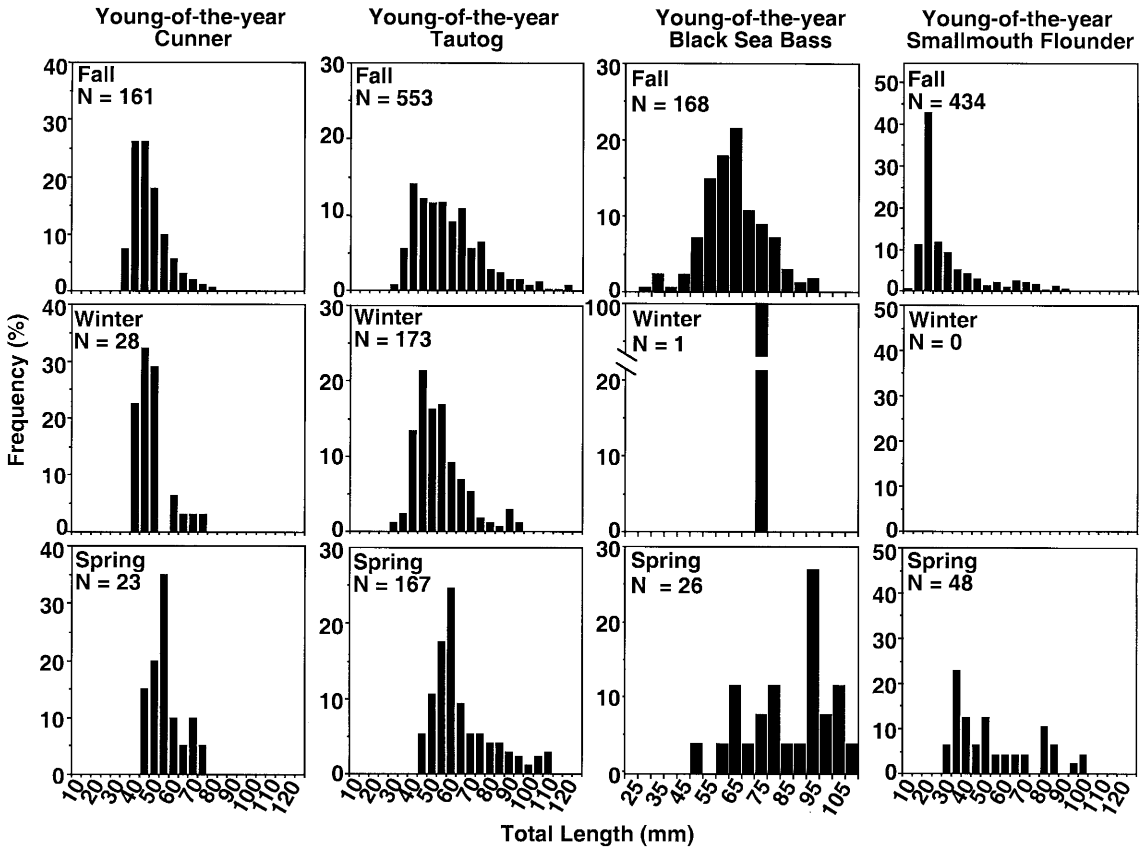

Fig. 1 Total length distributions of field collections of young-of-the-year (YOY) black sea bass, tautog, cunner, and smallmouth flounder in fall, winter, and spring. Black sea bass, tautog, and cunner were collected in Great Bay, New Jersey; smallmouth flounder were collected offshore in the vicinity of Beach Haven Ridge

Mean lengths of YOY smallmouth flounder (< 105 mm TL, Fig. 1) from beam trawl collections at Beach Haven Ridge in fall (31 mm) and spring (60 mm) were significantly different (ANOVA, $P < 0.01$). Fish < 35 mm TL, which accounted for more than 66% of all specimens collected in fall, were almost completely absent (< 5%) from collections in spring.

Mortality in laboratory experiments

Temperatures in the aquaria (mean 7°C, range 2–13°C) approximated a mild winter (Fig. 2). Water temperatures of 2°C occurred for less than 1 week, about 3 weeks shorter than the average based on temperature data from 1976–1990 for Great Bay (Able et al. 1992).

Mortality patterns in laboratory experiments differed among species (Fig. 2) and occurred without any external indicators of disease (e.g., white spots, frayed or bloody fins, visible fungus, etc.). Black sea bass did not survive winter water temperatures in Great Bay (Fig. 2). Mortality in all aquaria was low until early February, when it increased sharply when water temperatures dropped to 2–3°C. However, some individuals survived until March, when water temperatures had increased to 7–8°C. There were no significant differences in occurrence or timing of mortality among size classes ($df = 2$, $\chi^2 = 1.93$, $P = 0.382$). Tautog were fairly tolerant of winter temperatures: total mortality was only 14% (Fig. 2). Mortality of small (16%), medium (0%), and large (25%) tautog did not differ ($df = 2$, $\chi^2 = 0.13$, $P = 0.935$). Cunner were the most tolerant of winter temperatures of the four species that were examined. Mortality was 3%, with death of only one fish (Fig. 2). Analysis of mortality differences between size classes was not possible. Total mortality of smallmouth flounder was 33% (Fig. 2) and was size selective, even though the difference in mean length between large and small fish was only 8 mm. Mortality was higher for small (50%) than for large (17%) fish ($df = 1$, $\chi^2 = 4.22$, $P = 0.040$).

Growth in the laboratory

Growth rates at winter temperatures were sufficiently slow in all species to be difficult to perceive; that is, growth of fish was near measurement error for most species. Growth rates did not differ among small, medium, and large fish (Table 3), except for black sea bass. Growth of black sea bass (0.017 mm day$^{-1)}$ resulted from an apparent increase in TL of about 1 mm over 69 days. Growth rates of tautog (0.033 mm day^{-1}),

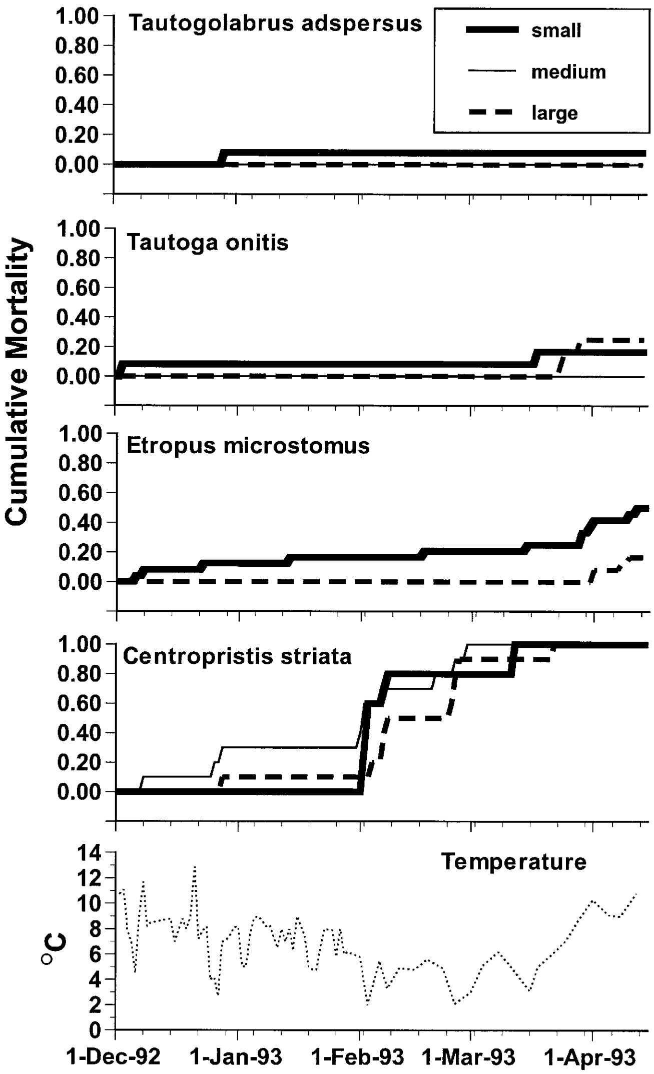

Fig. 2 Cumulative mortality (percent of average number of fish in aquarium) of small (*heavy line*), medium (*fine line*), and large fish (*dashed line*) of each replicate during the experiment (2 December–15 April) for black sea bass, tautog, cunner, and smallmouth flounder. Temperature (°C) conditions during the laboratory experiment are also shown

cunner (0.032 mm day^{-1}), and smallmouth flounder (0.029 mm day^{-1}) were based on about 4 mm of growth during the 135-day experiment.

Table 3 Absolute growth rates [(average final length –average initial length)/mean survival duration] ± 1 SE of all species and size classes

Species	Small	Medium	Large
Black sea bass	0.024 ± 0.006	0.025 ± 0.008	0.006 ± 0.003
Tautog	0.050 ± 0.006	0.015 ± 0.006	0.045 ± 0.005
Cunner	0.031 ± 0.008	0.032 ± 0.005	0.033 ± 0.005
Smallmouth flounder	0.036 ± 0.005	–	0.030 ± 0.002

Behavior

Temperature strongly affected the frequency of most behaviors of each species (Figs. 3, 4). As temperature decreased, fish fed less often, spent less time swimming, and became increasingly inactive (using shelter or burying, depending on species). Species-specific behavior rarely differed among different-sized fish. Black sea bass had low activity levels and fed erratically (Fig. 3). Frequency of feeding was generally low (37%). However, fish continued to feed until temperature decreased below 4°C in early February, and survivors resumed feeding when temperature increased above 4°C. Black sea bass shelter use increased at temperatures < 8°C. Swimming, which accounted for only 16% of observations, decreased appreciably at temperatures < 6°C but occurred at temperatures as low as 2°C. Fish buried in the sand substratum occasionally at temperatures < 6°C, apparently in response to relatively rapid decreases in temperature.

Tautog became inactive (mean swimming frequency 6%), fed erratically (mean 33%), and increasingly occupied artificial shelters (87%) as temperatures decreased (Fig. 4). Swimming frequency decreased sharply at temperatures < 8°C. Feeding was highly variable from 5 to 12°C and decreased sharply at temperatures < 4°C. Burying was observed at low temperatures (2–7°C), apparently a short-term response to sudden temperature decreases. Stress behaviors (at 2–8°C) preceded death. Like tautog, cunner became less active and fed more erratically as temperatures decreased (Fig. 4). Cunner were observed most often using shelter (94% of all observations). Swimming was observed across all temperatures (2–25°C), but its frequency decreased as shelter use increased at temperatures < 10°C. Feeding frequency (mean 41%) declined with temperature to just below 2°C, when feeding ceased. Smallmouth flounder were usually buried in the sand (approximately 95% of all observations) and were seldom observed feeding (6%), resting on the substratum (4%), or swimming (1%, Fig. 4).

Discussion

Available information on growth, behavior, and fish movements from field collections, our laboratory experiment approximating a mild winter, and other sources suggests that size-selective winter mortality is the most plausible cause of seasonal differences in lengths of tautog and cunner, and one of several potential causes of seasonal differences in lengths of black sea bass and smallmouth flounder. Seasonal changes in length distributions of YOY in natural (wild) populations consistent with size-selective winter mortality occurred in all species but may have resulted from several causes. Seasonal comparison of fish length to identify size-specific mortality patterns assumes that (1) samples are

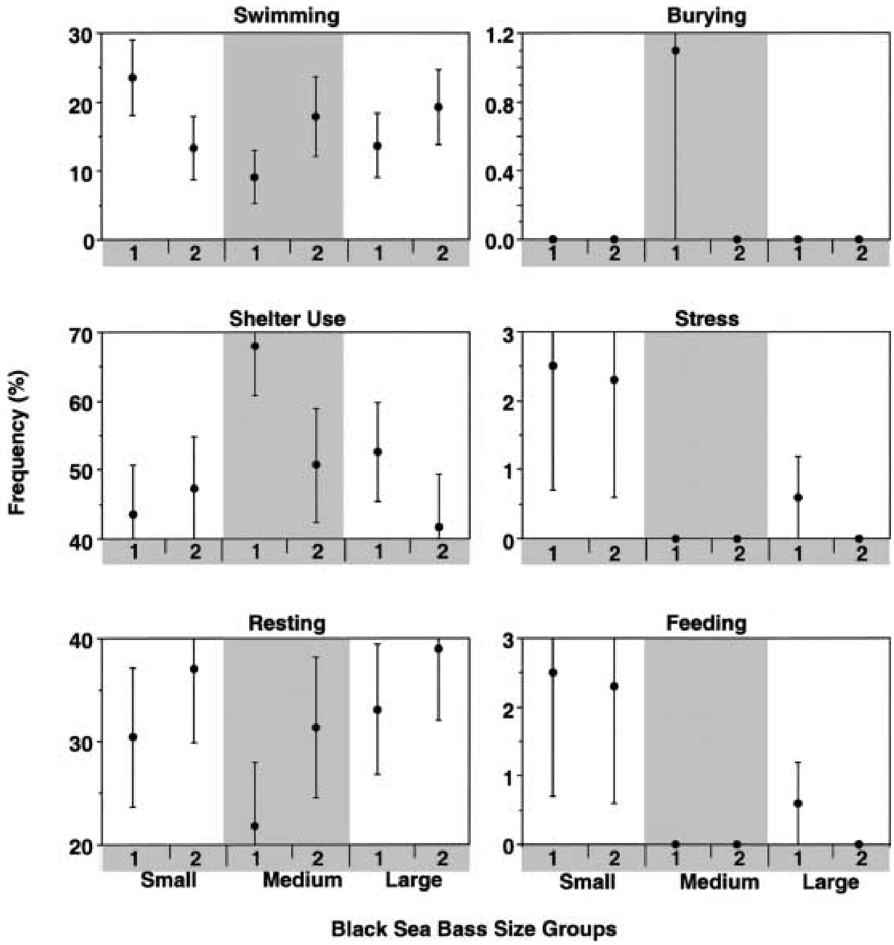

Fig. 3 Behaviors of YOY black sea bass for all size groups (small, medium, and large) of each replicate. Values given are mean frequency ± 1 SE from all observation periods every 3 days throughout the experiment. See Table 2 for description of behaviors

representative of the population and thus are not biased by gears and/or location, (2) the same population is being sampled in different seasons (i.e., the population is resident and not migratory), and (3) no growth occurs.

Seasonal length distributions

The distinction between YOY and older individuals of all species was easily made based on monthly difference in length for the same and adjacent estuarine systems (Able and Fahay 1998). There was no evidence that gear bias was a significant contributor to seasonal patterns in fish length. Length distributions of black sea bass, tautog, and cunner that were captured in traps included both recently settled YOY and larger individuals from older age classes that use estuaries, and they were similar to length distributions from 1-m and 2-m beam trawl collections in months in which both gears were used (Able and Fahay 1998). Length distributions of smallmouth flounder from beam trawl collections also included both recently settled YOY and larger individuals from older age classes.

Comparisons of seasonal length distributions of these species from other years produced similar results (see below), suggesting that mechanisms causing seasonal length differences may occur regularly. Based on samples of 461 black sea bass, 343 tautog, and 104 cunner collected with similar gears but different sampling designs during three previous winters (1990–1992), seasonal increases (>10 mm) in mean total lengths of YOY, indicative of size-selective mortality, occurred in black sea bass (one of three winters), tautog (two of three winters), and cunner (all winters). Although size-selective winter mortality presumably varies directly with environmental severity (i.e., harsher winters may cause larger size differences between seasons as a result of higher mortality of smaller fish), other patterns may be possible (e.g., mortality during harsh winters may not be size selective due to death of all fish).

Because of inherent difficulties, seasonal comparison of fish length may detect only severe cases of size-selective mortality (Ricker 1969; Post and Evans 1989; Hurst and Conover 1998). Because we were able to detect differences in most species in most years, use of more sensitive methods to compare length distributions (e.g., quantile–quantile plots, Chambers et al. 1983; Post and Evans 1989) seemed unnecessary although it may have revealed additional differences in length comparisons from 1990–1992.

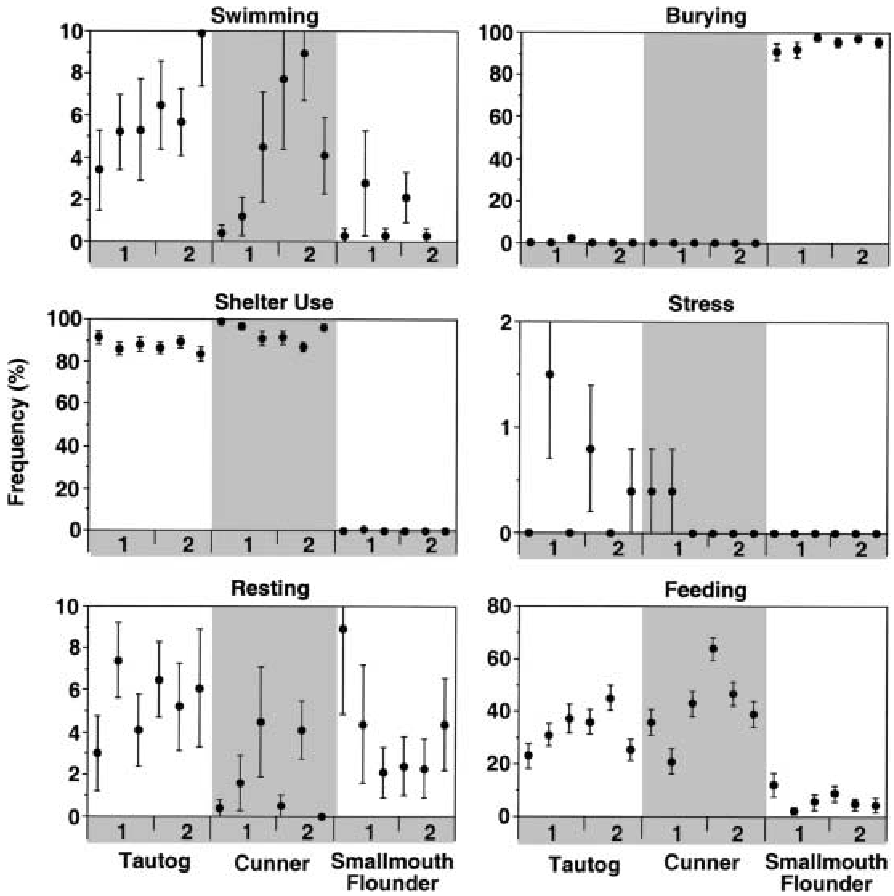

Fig. 4 Behaviors of YOY tautog, cunner, and smallmouth flounder in each aquarium of each replicate. Values given are the means of all aquaria per replicate ± 1 SE. See Table 2 for description of behaviors

Seasonal movement

Information available from other concurrent studies in the Great Bay estuary indicates that YOY tautog and cunner are locally resident throughout the year, suggesting that size-selective mortality is a plausible explanation for the seasonal difference in fish length. Individually tagged tautog and cunner were recaptured in Great Bay, New Jersey throughout the winter in the same habitats that they occupied in warmer months (Able and Fahay 1998).

Young-of-the-year black sea bass and smallmouth flounder apparently emigrate from estuaries in late fall and immigrate back into estuaries in spring. Individual YOY black sea bass captured, tagged, and released in Great Bay in summer and fall were not recaptured in winter (with one exception in early February) or the following spring (Able and Hales 1997). Black sea bass are seldom collected in winter in Great Bay or other New Jersey estuaries where they occur in warmer months (Allen et al. 1978; Able et. al. 1995; Able and Fahay 1998), but they have been collected in shallow nearshore waters on the continental shelf throughout the year (Able and Hagan 1995). Older juvenile and adult black sea bass are seasonal migrants in northern portions of their range (e.g., Murawski 1993; Able et al. 1995; Able and Fahay 1998) and appear to occupy temperature refugia on the mid-shelf of the Mid-Atlantic Bight in winter (Edwards and Livingston 1962; Able et al. 1995). Thus, emigration from estuaries appears critical for black sea bass, which experienced total mortality (100%) at low winter temperatures in the laboratory, although we cannot rule out the possibility that mortality could occur on the continental shelf as well. Our limited studies of fish movements have provided no evidence that black sea bass return to their natal nursery, suggesting that size-selective emigration in the fall or size-selective immigration in the spring are likely explanations for the seasonal differences in fish lengths. Seasonal movements of smallmouth flounder are unknown, but their absence from estuarine trawl samples during winter months in several New Jersey estuaries (Able and Fahay 1998) are consistent with emigration from estuaries in late fall.

Growth

Considerable evidence suggests that growth of fish in the estuary did not cause the observed seasonal differences in fish length. First, growth rates in the laboratory, if actually positive even in a mild winter with ad libitum feeding, were insufficient to produce observed length increases in any species. Such slow growth rates were consistent with previous studies reporting little if any growth at temperatures < 10°C in temperate marine fishes (e.g., Peters and Angelovic 1973; Malloy and Targett 1991; Sogard et al. 1992; Szedlmayer et al. 1992; Keefe and Able 1993; Able and Fahay 1998; Hurst and Conover 1998). The slow growth in the laboratory experiment did not result from dietary deficiencies or laboratory confinement because fish held at 18°C under otherwise identical conditions grew rapidly during the same time period (unpublished data). Slow growth in the laboratory was also supported by field data for three species. Individually tagged tautog and cunner that were recaptured in Great Bay did not grow from December through early June (unpublished data), and individually tagged black sea bass recaptured at the same sites did not grow in late fall (mid-November through December) or in spring (April through early June; Able and Hales 1997).

Behavior

Young-of-the-year exhibited behavioral adaptations for overwintering that are similar to those of juvenile and adult fish in both freshwater and marine environments (e.g., Cunjak 1988; Lagardere and Sureau 1989). As temperatures decreased, activity levels of all species decreased and fish increasingly used shelter or "rested" on the substratum. For black sea bass, tautog, and cunner, the reduction in swimming occurred over approximately 6–10°C, although cunner continued swimming to the lowest temperatures observed. This reduction in swimming implies that migration out of the estuary in anticipation of cold winter temperatures should occur at or before these temperatures in order not to be trapped. These temperatures generally occur during November–December in Great Bay estuary (Able et al. 1992) and generally correspond to the period of seasonal decline in the catch of YOY of these species (Able and Fahay 1998). Burial was observed in all species except cunner in response to short-term temperature decreases. The increased incidence of burial at low temperatures is important because if fish died while buried the chances of ever detecting this mortality in the field would be very low or impossible. All species fed throughout the winter, but feeding in the laboratory may have been positively influenced by food availability. Tautog and cunner have been reported not to feed in winter (Green and Farwell 1971; Olla et al. 1974; Dew 1976), but in the laboratory they fed until temperatures declined below 2–3°C. In the laboratory black sea bass fed up until their death at 2–3°C, similar to observations of larger fish (Schwartz 1964).

Mortality

Combined with knowledge of species migration patterns, mortality in the laboratory experiment suggested that size-specific mortality was plausible for some but not all species. Total mortality (100%) of black sea bass by mid-February at the relatively mild winter temperatures during the study period suggested that this species is incapable of overwintering in New Jersey estuaries. Mortality of smallmouth flounder was generally consistent with theoretical predictions; larger fish survived longer than smaller individuals. Mortality of small fish occurred late in the experiment (from mid-March to early April) after temperatures had increased from minimum values (2–3°C) in February. Such delayed mortality may indicate depletion of energy reserves (see Hurst and Conover 1998; Hurst et al. 2000) rather than a minimum temperature threshold. Low mortality of cunner in the laboratory experiment (only one fish died) precluded any possibility of a size-specific pattern, not surprising given New Jersey's location near the southern limit of their range (Hildebrand and Schroeder 1928) and the mild winter temperatures. Warmer temperatures in our laboratory experiment (field temperatures were generally 1–2°C colder) may have contributed to the difference between laboratory patterns in mortality and field observations in size distribution.

Mortality in the laboratory was consistent with available information of temperature tolerance of older, larger fish. Nearly all YOY black sea bass in our study died when water temperatures decreased to 2°C, identical to the lower tolerance reported by Schwartz (1964) for older fish (221–241 mm TL). Most, though not all, YOY tautog were tolerant of the lowest temperature in the experiment (2°C) for 1–2 days, similar to the temperature tolerance of adult tautog (2°C; Olla et al. 1974, 1975). Young-of-the-year cunner tolerated lower temperatures than the other species that were tested, a finding that is consistent with the low temperature limit reported for larger juvenile and adult cunner (–2°C, Green and Farwell 1971; Green 1974). Large smallmouth flounder in our experiment (37–52 mm TL) were tolerant of 2–3°C for 6 days, similar to the low-temperature tolerance reported for YOY summer flounder, *Paralichthys dentatus*, which has an overlapping distribution in Middle Atlantic Bight estuaries (Malloy and Targett 1991; Szedlmayer et al. 1992).

In summary, our results suggest that the first winter is an important period in the life of these temperate estuarine and nearshore marine species by causing size-selective mortality or migration (possibly size selective), depending upon species-specific physiological tolerances. Migration appears most plausible for those differences in YOY black sea bass. Either size-specific migration and/or size-specific mortality could have caused the observed seasonal length pattern in smallmouth flounder. Additional knowledge of movement patterns of these and other estuarine and marine species is clearly needed to determine mortality patterns and other aspects of their ecology. Our results support previous suggestions (Conover 1992; Sogard 1997; Hurst and Conover 1998) that size-selective winter mortality is an important influence on the ecology of estuarine and marine fishes.

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