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Patterns in Seasonal Abundance, Growth and Biomass of the Atlantic Silverside, *Menidia menidia,* in a New England Estuary

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ABSTRACT: Patterns in seasonal abundance (no. per m^2 surface area), growth and biomass (g per m^2 surface area) of an annual fish, the Atlantic silverside, *Menidia menidia* (L.) were investigated in a marsh and more seaward bay region of Essex Bay, Massachusetts from August 1976 to May 1978 using a quantitative beach seining technique. Silverside abundance varied greatly by season and year class during the study period. Abundance was high in 1976 but winter mortality (99%) left an adult density of only .01 per m^2 surface area in the marsh during spring 1977. Resultant 1977 year class density in the marsh was 1.88 per m^2 by late fall 1977 but winter mortality again produced an adult density of .01 per m^2 in spring 1978. Abundance was generally higher in the marsh than in the bay region especially during spring and late fall when catches in the bay were negligible. Based on catch rate comparisons, the summer and fall juvenile abundance of the 1976 year class was much higher than the juvenile abundance of the 1977 year class. Coincidentally, mean lengths and condition of the abundant 1976 year class in the late fall were significantly lower than those of the 1977 year class, suggesting density dependent population regulation. In both years, juveniles grew rapidly and reached full adult size by November when an offshore movement to deeper waters outside Essex Bay occurred. Biomass peaked in the marsh region in late fall 1977 at 7.8 g per m^2 wet weight. Winter mortality was size selective, favoring larger individuals. The annual life history design of *M. menidia* including an offshore winter movement and high winter mortality suggests that silversides represent an important pathway of energy flow from marsh to offshore trophic systems.

Introduction

Recognition of the importance of salt marshes and estuaries as vital habitats for numerous forage species and the juvenile stages of many commercial fishes has emphasized the need to understand patterns of energy flow between marshes, estuaries and open waters. Studies have dealt with primary production and the transport of the detritus-based energy and nutrients to and from marsh surfaces (Teal 1962; Odum and de la Cruz 1967) or with metabolism and energy flow through entire marsh-embayment systems (Nixon and Oviatt 1973). Recently the role of cyprinodontid fishes in transferring energy from marsh to open water as secondary production has been discussed (Valiela et al. 1977; Kneib and Stiven 1978; Meredith and Lotrich 1979) but the population dynamics of other abundant, perhaps less easily studied, marsh species remain poorly known.

Atherinid fishes, particularly those of the genus *Menidia,* rival cyprinodontids in abundance among fishes inhabiting the shore zone of marshes and estuaries of eastern North America. The Atlantic silverside, *Menidia menidia* (L.), is an ubiquitous member of the coastal fauna throughout its range from northern Florida to Nova Scotia. Estuarine ichthyofaunal surveys often cite *M. menidia* as the most numerous species encountered; e.g. Anderson et al. (1977) in South Carolina, Richards and Castagna (1970) in Virginia, Hillman et al. (1977) and Briggs (1975) in New York, Mulkana (1966) in Rhode Island, and Chesmore et al. (1973) in Massachusetts. Atlantic silversides can

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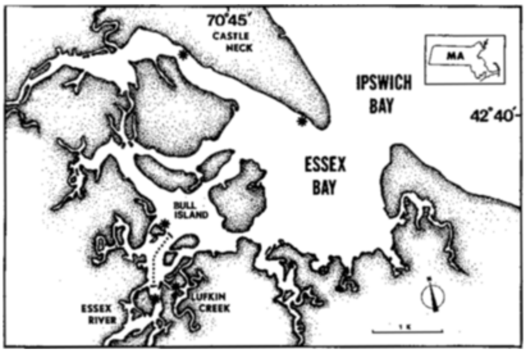

Fig. 1. The Essex Bay estuary located in Essex County, Massachusetts. Seining stations (*) and trawling location (dotted line) are indicated.

also dominate the catch of adult fishes in intertidal salt marsh creeks (Shenker and Dean 1979). The importance of silversides as forage for such gamefish as striped bass (*Morone saxatilis*), Atlantic mackerel (*Scomber scombrus*), bluefish (*Pomatomus saltatrix*) and others has been frequently noted (Merriman 1941; Bayliff 1950; Bigelow and Schroeder 1953; Schaefer 1971). Despite the obvious ecological importance of *M. menidia* only Bayliff (1950) has described its life history in detail and no studies have dealt with seasonality of growth, abundance, biomass or mortality.

Menidia menidia is one of the few annual fishes inhabiting temperate marine waters and is the most northerly distributed member of the Atherinidae in the western Atlantic. A protracted spawning season extends from May to July in the Gulf of Maine; eggs are adhesive and stick to intertidal vegetation within salt marshes (Bigelow and Schroeder 1953; Conover, unpublished data). The young-of-the-year become quite numerous in shallow inland waters and grow rapidly until winter when, in northern populations, they become rare in the shore zone (Warfel and Merriman 1944; Bayliff 1950; Hoff and Ibara 1977), are captured well offshore (Clark et al. 1969; Fahay 1975) and to depths of 49 m (Hildebrand and Schroeder 1928). Conover and Murawski (1982) have recently described the winter seaward migration and offshore distribution of Atlantic silversides over the inner continental shelf. In spring, adults returning to the shore zone are much less numerous and some apparently die during the spawning season although two-year-old individuals are occasionally found (Bayliff 1950). Such a life cycle suggests that *Menidia menidia* is potentially an important secondary producer and exporter of biomass from marsh-estuarine areas to deeper, offshore waters.

The purpose of this paper is to describe some aspects of the population dynamics of the Atlantic silverside in a New England estuary including seasonal patterns in abundance, growth, biomass, relative mortality and condition. This research is part of an ongoing project concerning the population ecology of *Menidia* in the Gulf of Maine region.

Study Area

Essex Bay is a small estuary (5.8 × 4.7 km MHW) located just north of Cape Ann, Massachusetts (Fig. 1). The bay is protected from the open waters of Ipswich Bay by Castle Neck, a sand spit. A series of islands extending north to south separates the estuary into an eastern section consisting of Essex Bay proper (hereafter referred to as the "bay region") and a western section consisting of an extensive system of *Spartina* marshes (939 ha) and tidal creeks that border the only major freshwater tributary in the area, the Essex River (referred to as the "marsh region"). Historically, the river has supported spawning runs of alewives (*Alosa pseudoharengus*), rainbow smelt (*Osmerus mordax*) and Atlantic salmon (*Salmo salar*: Chesmore et al. 1973). Conditions in the marsh are estuarine with salinities ranging from 11.5 to 30.7‰ ($\bar{x}$ = 25.0, SD = 3.6, n = 25) while salinities in the bay region are higher, ranging from 23.8 to 29.0‰ ($\bar{x}$ = 27.0, SD = 1.4, n = 25; Conover 1979). Average tidal amplitude is 2.7 m (U.S. Coast and Geodetic Survey) and tidal exchange has been estimated at 75% by volume (Chesmore et al. 1973). The shallowness of the marsh-bay complex and a high tidal amplitude preclude salt wedge formation or temperature stratification.

Materials and Methods

Exploratory collections were made on an intermittent basis from August to November 1976 at various sites in Essex Bay, Massachusetts, using three types of gear: (1) a

6.4 mm mesh seine (46 × 1.8 m); (2) a 3.2 mm mesh seine (15.2 × 1.2 m); and (3) a 3.8 cm stretch mesh otter trawl (6 m head rope, 7 m foot rope, 60 mm mesh cod end liner). Data used from 1976 included *Menidia* catch rates (n = 21 seine collections; n = 8 ten min trawls) and total length, weight and condition (an index of thinness) of specimens captured. The 1976 sampling data also provided criteria for selecting permanent collecting stations and gear. During 1976–78, collections and visual observations of *M. menidia* were also conducted at Hodgkin's Cove, Cape Ann, Massachusetts, located approximately 5 km east of Essex Bay and site of the University of Massachusetts Marine Station.

In 1977 we established five sampling stations selected to represent typical habitats within the marsh and bay regions (Fig. 1). The marsh stations included (1) Lufkin Creek (LC) located in a narrow tidal creek approximately 12 m wide, (2) Essex River (ER) located in the main stem of the Essex River and (3) Bull Island (BI) located in an open tidal channel approximately 30 m wide. Both the Essex River and Bull Island stations had firm substrates of sand and mud, whereas Lufkin Creek contained very soft mud. The two bay region stations were (1) at the mouth (MO) located just inside the seaward entrance to Essex Bay and (2) Castle Neck (CN) located near the edge of the marsh region. Both bay stations had firm substrates of fine, shifting sand.

The estimation of fish population size and/or density in estuaries has long been a difficult problem. Where the system under study is small and semi-enclosed, tagging has proven useful (Nixon and Oviatt 1973; Valiela et al. 1977). Drop nets are sometimes applicable to species which dwell near the bottom in highly turbid waters where flotation devices do not affect distribution. However, these methods are not practical for small, mobile, schooling fishes such as silversides which do not easily survive handling and which inhabit the upper water column. For these reasons, *Menidia* densities in Essex Bay were estimated by an areal census. Our method involved seining with the fine mesh netting through a large area of known size and estimating the proportion of fish captured by a seine haul. We made biweekly quantitative seine hauls from 16 April to 19 November 1977 and from 6 May to 31 May 1978 at the five sampling sites. All quantitative samples were taken by following a standardized seining technique using a 1.6 mm mesh seine (46.3 × 1.8 m) equipped with a 0.8 mm mesh bag. At each end of the seine, 12.8 m of net were gathered and the remaining 20.7 m midsection was stretched parallel to shore after wading to a depth of 1 m. The net was then walked parallel to shore to the desired position, whereupon two lead weights with attached floats were dropped to mark the boundaries of the area seined. We then quickly brought the slack net-ends to shore thus enclosing a 200–400 m^2 rectangular area completed by the shoreline. The surface area seined was measured after the seine haul was completed. At each station we repeated this procedure seaward from the first set 15–30 minutes later, except at Castle Neck where only one set was made. At Lufkin Creek, the seining technique involved stretching the mid-section of the net along one bank and pulling the slack ends quickly to the opposite shore, thus enclosing a 20.7 m segment of the creek. All quantitative seining was performed within 1–2 h of low tide when much of the Essex marsh-bay complex was <1 m deep. Temperature and salinity of the nearshore water column (<1 m deep) were measured each time fish were sampled using a YSI Model 33 salinometer/temperature meter.

The efficiency of the quantitative sampling technique in capturing *Menidia* was assessed during August 1977 by setting and anchoring a second 1.6 mm mesh seine at three sides of an approximately 300 m^2 square completed by the shoreline. The regular sampling net was led around the inside perimeter of the anchored seine such that no fish were allowed to get between the nets. The seine was retrieved repeatedly through the impounded zone by the above method until all *Menidia* were caught. The percentage of *Menidia* caught in each haul relative to the total provided an estimate of the percent loss over or under the seine as it was retrieved. It did not estimate losses that could occur under normal operation of the seine due to fish skirting the ends as the net was set. Such losses should be minimal, however, because of high turbidity in the sampling areas, the large size of the sampling area, the relative lack of disturbance during setting of the net, and the quickness with which the ends were brought to shore (usually 2–4 sec). The 1.6 mm mesh of the seine permitted capturing of *Menidia* from the post-larval (12–15 mm) to adult stages. To obtain additional adult specimens in the spring when densities were low and to provide catch rate comparisons with 1976, we also made supplemental collections with the 1.6 mm and 6.4 mm mesh seines during 1977 and 1978. Ten min trawls were also made in the Essex River during 1977.

Specimens were immediately preserved in 10% buffered formalin mixed in seawater. Specimens from 1976 were washed and placed in 40% isopropyl alcohol about one month after fixation in formalin. Weight loss due to preservation was tested; mean weight loss in 10% formalin was 3.3% (SD = 1.5) after 30 days, and with subsequent storage in 40% alcohol, the specimens lost 12.8% (SD = 2.3) of their original fresh weight. Because specimens from 1976 and 1977 were preserved differently, corrections to original fresh weight were necessary.

In the laboratory, total length, wet weight and sex were recorded from a random subsample of approximately 100 fish from the first haul at each station and date, except Castle Neck where only density in numbers was recorded. If 100 fish were not available in the first haul, additional specimens were measured from the second haul. We determined sex by dissection of all fish in the subsample that were over 30 mm total length. In late fall, year class was identified by presence or absence of an annular mark on scales from larger specimens. Growth was determined by pooling measurements for individuals from all sites captured during the same collecting period. Biomass (g per m^2) of fish collected for each site and date was computed by applying mean fish weight at each station to numbers caught (no. per m^2) since total weight of catch was not recorded in the field. Mean biomass (g per m^2) in the marsh and bay regions of Essex Bay was computed by averaging biomass estimates for stations within these two regions for each collecting period.

Condition (K), an index of relative "thinness," was calculated as:

$$K = \frac{(\text{Corrected total weight} - \text{gonad weight}) \times 100}{\text{total length (cm)}^3}$$

(Ricker 1975).

Removal of gonad weight before computing K factors allows for comparisons of somatic weight reserves between seasons without confounding weight changes due to gonad maturation.

Results

Abundance Indices

Atlantic silversides were extremely abundant in summer and fall 1976 relative to the remainder of the study period. Catch rates (no. per m seine fished) averaged 17.5 per m at Bull Island (n = 5, SE = 4.9), 19.5 per m at the mouth (n = 6, SE = 7.9), 12 per m for all 1976 seine collections (n = 21, Se = 2.9), and 74.4 per ten min. trawl in the Essex River (n = 8, SE = 43). We caught no *Menidia* with seines or trawls in Essex Bay in mid-November 1976, nor in March 1977. During April, May and June 1977, about 1% of the population returned to the shore zone as estimated from catch rates of 0.2 per m for all spring seine hauls (n = 45, SE = 0.3) and 0.0 per ten min trawl in the Essex River (n = 10, SE = 0.0). The juvenile abundance of the 1977 year class in summer and fall was much less than the juvenile abundance of the 1976 year class. Catch rates at the mouth of 2.6 per m (n = 8, SE = 0.8) and in the Essex River of 5.7 per ten min trawl (n = 14, SE = 1.8) were significantly less than in 1976 ($p < .05$, Mann-Whitney U-test). Catch rates at Bull Island of 15.4 per m (n = 12, SE = 3.8) were only slightly less than in 1976 but this was probably because *Menidia* were concentrated in the marsh region under conditions of low abundance (Table 1). Furthermore, in 1976, silverside schools were extremely evident both in Essex Bay and in exposed, open waters of Hodgkin's Cove but in 1977, *Menidia* were never sighted or captured in Hodgkin's Cove and were much less evident in shallow, inland waters even in Essex Bay. These data serve only to demonstrate that silversides were much more abundant during the exploratory phase of our study in 1976 than at any other time throughout the rest of the

TABLE 1. Mean density (nearest 0.01 no. per m^2 ± 1 SE) and biomass (nearest 0.1 g per m^2 ± 1 SE) of the 1977 year class of Atlantic silversides in the marsh (n = 3) and bay (n = 2) regions of Essex Bay, Massachusetts during the July–Nov. growing season.

	Density		Biomass	
Date	Marsh	Bay	Marsh	Bay
7/5	0.23 ± .13	.01 ± .01	0.01 ± 0.01	0
7/18	1.13 ± .68	.04 ± .04	0.2 ± 0.06	0
8/1	2.57 ± .95	.11 ± .11	1.1 ± 0.3	0.2 ± .17
8/15	1.36 ± .70	.12 ± .01	1.5 ± 1.3	0.3 ± .02
8/29	1.09 ± .57	.26 ± .12	1.9 ± 1.0	0.4 ± .24
9/10	0.45 ± .09	.48 ± .26	1.0 ± 0.4	1.4 ± .8
9/24	2.10 ± .82	.54 ± .22	6.4 ± 4.6	1.6 ± .6
10/8	0.52 ± .23	.02 ± .02	1.6 ± 0.7	0
10/22	1.99 ± .83	0	7.8 ± 3.3	0
11/5	1.78 ± .55	0	7.8 ± 2.8	0
11/19	0.03 ± .02	0	0.1 ± 0.1	0

study. The remainder of this paper deals with densities as determined by quantitative seining.

The efficiency of the 1.6 mm mesh seine used in quantitative determinations was high. A single haul captured an average of 92% (n = 5, SE = 3.7) of the silversides enclosed by the seine. Corrections were made to absolute density accordingly. This high seining efficiency was probably enhanced by the behavior of *Menidia* once enclosed; individuals appeared to school in the center of the impounded water rather than attempt to escape under the lead lines. Because the mean length of *Menidia* caught in successive hauls differed little, we assumed that all individuals of a year class were equally susceptible to the seine. To determine if the number of fish caught in two replicate seine hauls at the same station and date were random, we performed a ranked sign test on these data. The second haul consistently showed smaller catches than the first during the summer and fall ($.01 < p < .05$) and for this reason, we used only numbers caught in the first haul for computing density and biomass during this period.

Density (number per m^2 surface area) of adults in the spring of 1977 was .009 ± .006 per m^2 (95% CL) based on data pooled from all marsh stations during May. *Menidia* were rare and not captured in quantitative seine hauls in the bay region at this time. Postlarval *Menidia* first appeared in low num-

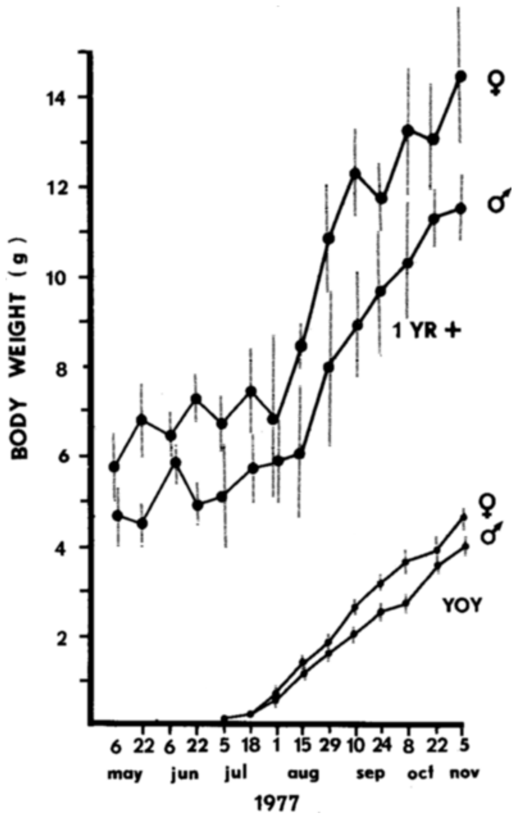

Fig. 2. Growth in wet weight of young-of-the-year (YOY) and adult (1 yr+) *Menidia* from Essex Bay. The vertical lines represent ±2 SE, which approximates a 95% CL as sample sizes approach and exceed n = 30. For the YOY curves, sample sizes range from 124 to 319 ($\bar{x}$ = 188) and for the 1 yr + curves, sample sizes range from 2 to 59 ($\bar{x}$ = 15).

bers in the upper marsh during late June and reached measurable proportions by early July (Table 1). Silversides were much more dense in the marsh region than in the bay region throughout the summer and fall of 1977 but densities were highly variable between successive dates and between stations within each region (Table 1). Recruitment of young-of-the-year to the sampling gear was complete by early August. Young-of-the-year appeared to be abundant in the marsh region from midsummer to late fall but were abundant in the bay region only in August and September. Relatively constant densities from termination of recruitment to late fall indicated high juvenile survival during the estuarine phase of life relative to

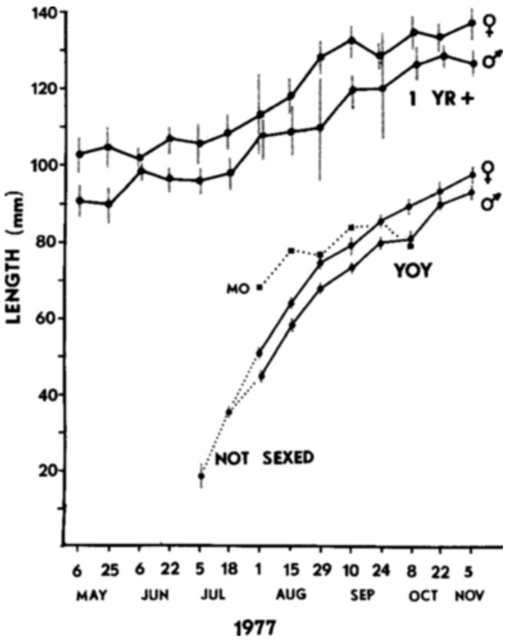

Fig. 3. Growth in length of young-of-the-year (YOY) and adult (1 yr+) *Menidia* from Essex Bay. The vertical lines represent ± 2 SE. Only mean lengths from fish collected at the mouth (MO) differed consistently from the means of all stations pooled.

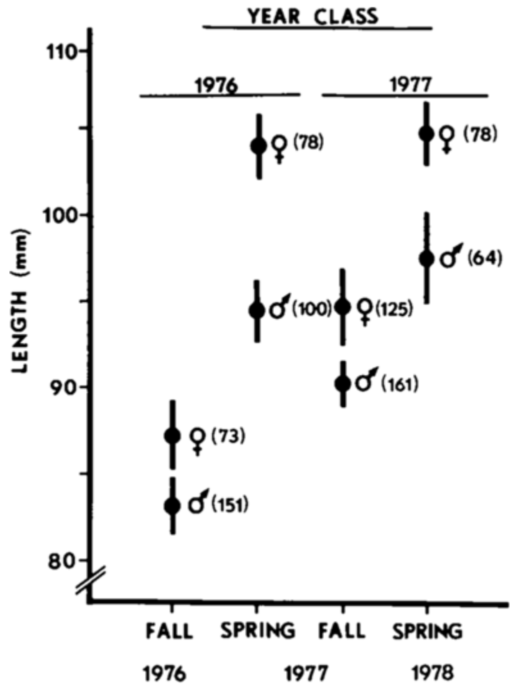

Fig. 4. Between season comparison of mean lengths by sex of Atlantic silversides from near the end of the first growing season (late October) in 1976 and 1977 as compared to mean lengths of returning fish in the spring (April and May pooled) of 1977 and 1978. The vertical lines indicate 95% CL and sample sizes are also given (n).

survival over the winter. The density of the 1977 year class averaged 1.88 ± 1.16 per m^2 (95% CL) in the marsh in late fall (22 Oct. and 5 Nov. pooled), just prior to their disappearance from the shore zone of Essex Bay as temperatures dropped to 6–8 °C in mid-November. Severe losses of 99% of the population over the winter of 1977–78 were indicated by an adult density of .009 ± .002 per m^2 (95% CL) in the marsh in May 1978.

Growth and Condition

Menidia young-of-the-year grew rapidly during 1977 reaching mean lengths and weights of 98.0 ± 2 mm and 4.8 ± 0.2 g (n = 167, 95% CL) for females and 91.5 ± 1.5 mm (n = 213, 95% CL) and 3.9 ± 0.1 g (n = 205) for males by November (Figs. 2 and 3). The growth curve from only one station, MO, deviated consistently from the growth curve for all samples pooled (Fig. 3) apparently because only larger fish dispersed to the bay region as early as August. Adults grew little in length or body weight during the May spawning season, but those that survived doubled their average weight by November.

Examination of scales over the course of the study period indicated that annular marks representing spawning checks were laid down in May and June. The spacing of scale circuli from specimens captured in early April appeared identical to that of specimens collected prior to the winter; i.e. narrowly spaced circuli or crossing over of circuli which are characteristically formed during periods of slow growth (Weatherley 1972) were not present on scales in April. The lack of winter growth rings on scales from specimens in early April probably indicates cessation of growth over the winter. This hypothesis is supported by laboratory experiments which showed that tank reared silversides ceased to feed at 6–8 °C (Conover, unpublished data) and by dramatic loss

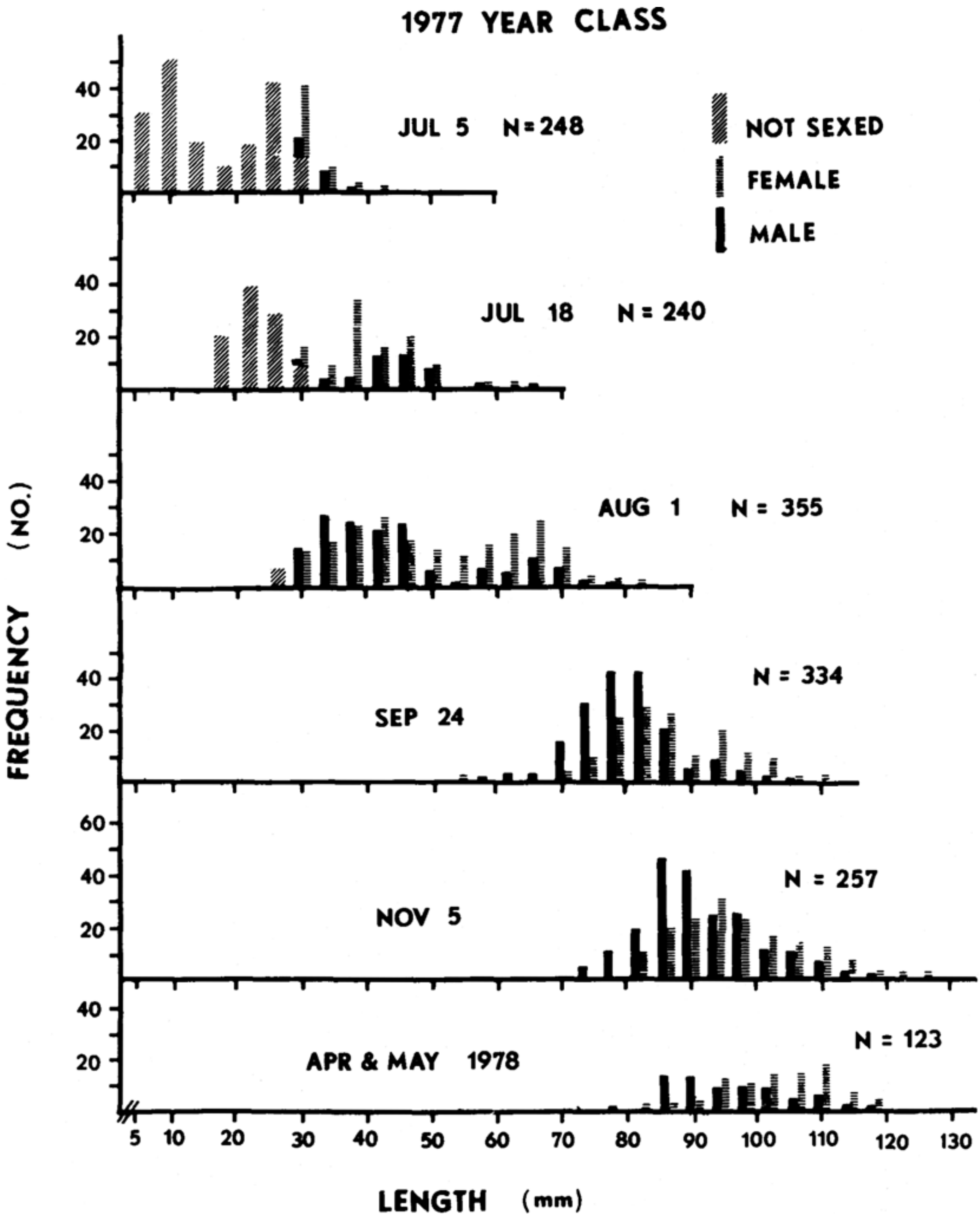

Fig. 5. Length-frequency histograms for the 1977 year class of Atlantic silversides from Essex Bay, Massachusetts.

in condition in field populations over the winter (see Fig. 6 below).

Between season comparisons of mean lengths revealed that fish of the less abundant 1977 year class attained significantly greater size by late October than did the 1976 year class the previous fall (Fig. 4). Females attained significantly greater mean

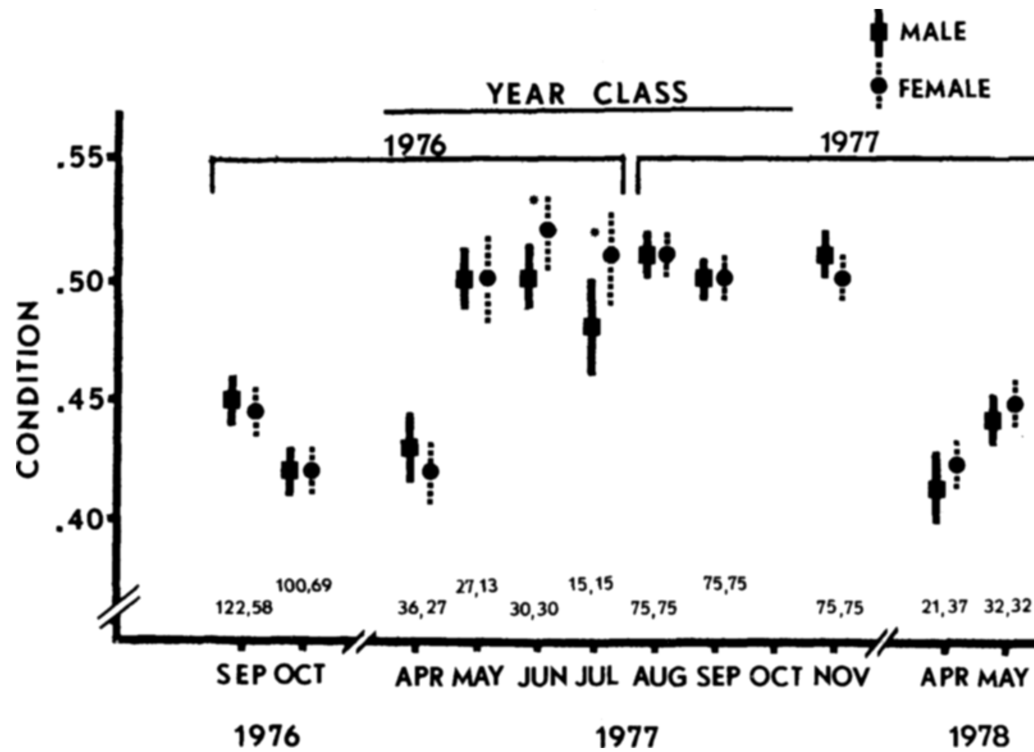

Fig. 6. Condition factors (with gonad removed) for *Menidia* pooled by month and sex. The vertical lines indicate 95% CL and sample sizes are given below each data point. An * indicates male and female conditions are significantly different ($p < .05$, Student t-test).

lengths than males in both years. Mean lengths of *Menidia* returning in the spring were significantly greater than in fall, suggesting size-selective winter mortality favoring larger individuals since winter growth is improbable. Of 407 adults examined during April–May 1977, only one was two years of age (1♀: 0.2%), while of 312 adults examined in April–July 1978, three were two years of age (1♀, 2♂: 1.0%).

Length-frequency histograms for the 1977 year class displayed two modes during July and August possibly indicating a bimodal spawning or larval emergence pattern (Fig. 5). These modes became less distinct by September and were indistinguishable thereafter. A comparison of the length frequencies for 5 November 1977 and April–May 1978 further supports the hypothesis that size-selective winter mortality, rather than growth, is responsible for the greater mean lengths of fish in the spring; very few *Menidia* <85 mm in length were able to survive the winter but the maximum range in size did not increase.

Condition (K) of Atlantic silversides showed strong trends by season and by year class. Since regression analysis showed that condition was not significantly related to length of fish ($p > .50$) within a year class, K factors were pooled by sex, year class and month of capture in order to make seasonal and year class comparisons. Conditions of male and female *Menidia* of the abundant 1976 year class were relatively low in September 1976 (.44♂; .43♀) and declined further by October 1976 (Fig. 6). In April 1977, members of the 1976 year class that had survived the winter still exhibited poor condition (.43♂; .43♀), but by May their condition had increased significantly. The less abundant 1977 year class maintained much higher K factors throughout the August to November growing season (.50♂; .50♀) than did the 1976 year class during the same period in the previous year. The

1977 year class lost condition over the winter but was regaining it in May 1978. Male and female conditions were significantly different ($p < .05$, t-test) only during the late spawning season in June and July. The trends in condition factors between seasons, year classes and sexes described above cannot be accounted for by changes in weight due to gonad maturation since testicular and ovarian weights were removed before the analysis was conducted.

Biomass

Mean biomass (g per m^2) in the marsh and bay regions varied greatly through the summer and fall of 1977 (Table 1). Most of this biomass was concentrated in the marsh region of Essex Bay during 1977 where it reached a mean peak of 7.8 ± 5.0 g per m^2 (95% CL) in late fall (22 Oct. and 5 Nov. pooled). Silverside biomass reached significant levels in the bay region only during August and September in 1977. These biomass estimates may be valid only for the shore zone and not open water areas; hence we did not attempt to compute a total biomass estimate for the entire Essex Bay region.

Discussion

The catch rate and density data clearly indicate that *Menidia* population size fluctuated dramatically by season. Since silversides tended to concentrate in the marsh region during late fall and spring, comparisons of abundance in the marsh between these two periods should provide a rough indication of winter mortality rates. The 99% difference between the abundance of juveniles in fall and adults in spring indicates winter mortality is severe. To determine if the magnitude of winter mortality in silverside populations from Essex Bay is characteristic of the Massachusetts coastal region as a whole, we compared spring and fall catches of Atlantic silversides in 17 independent marine resource surveys conducted in all the major bays and estuaries of Massachusetts (Mass. Div. Mar. Fish. Monogr. Ser. Nos. 1–17). These surveys usually consisted of monthly seine hauls at several sites within each bay or estuary over a one-year period. Collecting techniques were generally standardized in each individual study but varied between studies. Thus, only abundances between seasons within a study were comparable. These data indicate that spring abundances of Atlantic silversides are approximately 3% of total spring and fall numbers captured in waters north of Cape Cod but average 12% for sites south or west of Cape Cod (Table 2). This is not surprising since Cape Cod is a well-known faunal barrier (Bigelow and Schroeder 1953) and colder winters in the Gulf of Maine may result in higher winter mortality rates. The actual cause of high mortality rates during winter is unknown but could include predation and physiological stress imposed by migrating offshore and prolonged exposure to cold temperatures. High winter mortality in *Menidia* populations has also been noted by Bayliff (1950) in Chesapeake Bay, Warfel and Merriman (1944) in Connecticut and Austin et al. (1973) in New York.

This study also demonstrates that the summer–fall year class strength of juveniles can fluctuate dramatically from year to year as Bayliff (1950) and Derickson and Price (1973) have previously noted. Yet despite the great differences in juvenile abundance observed in this study, the number of adults which returned each spring was similar. Since winter mortality was size selective favoring larger fish and since year class abundance was negatively related to mean size and condition prior to winter, this suggests that a density compensatory mechanism could influence the number of fish that survive to breed each spring. Hence, fish from less abundant year classes may exhibit lower winter mortality rates than fish from abundant year classes.

The significant differences in size and condition of *Menidia* in 1976 and 1977 also suggest that silversides can reach and/or exceed the carrying capacity of the Essex Bay marsh in years of great abundance. Their abundance in Ipswich Bay along the rocky coast of Cape Ann (Hodgkin's Cove) during 1976 and their absence from this area in 1977 indicate a tendency to disperse widely in response to high density as Warfel and Merriman (1944) have previously proposed. The preferred summer–fall habitat of *Menidia* is apparently in the marsh since they were most abundant there in a low density year. The

TABLE 2. Number of Atlantic silversides captured in spring expressed as a percentage of total numbers captured in spring (March, April, May, June) and fall (August, September, October, November) in marine resource inventories of 17 Massachusetts bays or estuaries[a] arranged in order from south to north.

Study Site	Year Conducted	% Captured in Spring	Total Number Captured
	South Side or West of Cape Cod		
Mount Hope Bay-Taunton River	1969–1970	7.1	8,234
Westport River	1964	0.4	10,941
Waquoit Bay	1967–1968	31.3	3,263
Bass River	1970–1971	17.3	12,280
Pleasant Bay	1965	3.0	2,768
		$\bar{x}$ = 11.8	
	North of Cape Cod		
Wellfleet Harbor	1968–1969	10.0	8,733+
Kingston-Duxbury-Plymouth Bay	1971	1.7	13,619
North River	1965	0.0	1,000+
Hingham Bay	1970	7.7	6,636
Quincy Bay	1964	3.7	492
Dorchester Bay	1967–1968	0.1	3,294
Lynn-Saugus Harbor	1968–1969	10.0	750
Beverly-Salem Harbor	1965	3.5	1,271
Annisquam-Gloucester Harbor	1966–1967	1.2	5,648
Essex Bay	1969	0.2	1,257
Parker River-Plum Island Sound	1965	0.3	1,537
Merrimack River	1964	0.4	238
		$\bar{x}$ = 3.2	

[a] A Study of the Marine Resources of Massachusetts. Mass. Div. Mar. Fish. Monogr. Ser., Nos. 1–17.

relatively low condition of Atlantic silversides in April probably reflects a reliance on fat and other nutritive reserves during the winter which are quickly replenished in May as water temperatures warm and feeding resumes in the marsh.

The summer–fall growth rate of *M. menidia* in Essex Bay of about 20 mm per month is faster than that of populations farther south. Austin et al. (1973) reported summer growth of 10–15 mm per month in Long Island Sound, while Mulkana (1966) noted summer growth of 7–14 mm per month in a Rhode Island estuary. The summer–fall growth rate of *Menidia* in Essex Bay may be higher due to a shorter growing season in the north or because the low density 1977 year class was favored by reduced intraspecific competition for food. The winter cessation of growth noted in this study has also been reported for *M. menidia* populations farther south (Bayliff 1950; Bigelow and Schroeder 1953).

The absence of Atlantic silversides from the shore zone during winter has been noted in several previous studies (Bayliff 1950; Austin et al. 1973; Warfel and Merriman 1944; Hoff and Ibara 1977) all of which were conducted in areas from Chesapeake Bay northward. Richards and Castagna (1970) reported that silversides inhabited deep channels during winter along Virginia's eastern shore but ichthyofaunal surveys in South Carolina indicate that *M. menidia* remains abundant in intertidal marsh creeks throughout the winter (Cain and Dean 1976; Shenker and Dean 1979). Hence, southern populations may not undergo an offshore migration in winter as do northern populations. Although this study does not directly deal with the offshore distribution of Atlantic silversides in winter, this subject has been recently addressed elsewhere. Conover and Murawski (1982) examined records of the National Marine Fisheries Service bottom trawl survey program and reported that *Menidia* were captured up to 170 km offshore and to depths of 126 m but most catches occurred over the inner continental shelf within 40 km of shore and in depths less than 50 m. They also noted that silverside catches in offshore waters were most frequent in winter and negligible in summer and fall. Other authors have also reported catches of silversides offshore (Clark et al. 1969; Fahay 1975).

Menidia menidia is one of the few annual fish found in temperate marine waters of North America. This unusual life history may be an adaptation to high levels of winter mortality. Because the chances of surviving the winter are so low, it may be more advantageous for a yearling adult to expend all of its energy and effort in breeding rather than sacrificing reproductive effort to survive and breed a second year. However, in Essex Bay, silversides that survive the breeding season double their average weight in their second year and hence do not reach their full growth potential in one year; two-year-olds occasionally reach a second spawning season. This further suggests that the annual life history pattern of this species is maintained by high levels of winter mortality rather than senility at age one.

This study demonstrates that even in a low density year, silversides are important secondary producers and reach biomass levels comparable to total fish biomass in other marine ecosystems (summary in Nixon and Oviatt 1973). Based on a dry weight/wet weight conversion factor of 0.25 for *Menidia* (Conover, unpublished data), biomass values reported herein for 1977 are less than for *Fundulus heteroclitus* in a Massachusetts marsh (Valiela et al. 1977), a Rhode Island marsh (Nixon and Oviatt 1973) and a Delaware marsh (Meredith and Lotrich 1979). However, in high density years such as 1976, *Menidia* biomass could be much greater than we measured in fall 1977. Since very few adults return to "recolonize" the marsh in late spring, the winter movement and mortality patterns of *M. menidia* in northern populations could represent a one-way export of biomass from shallow marsh areas to deeper waters with nearly complete annual turnover. This life history pattern contrasts sharply with that of *Fundulus heteroclitus* which lives to 3–4 years of age (Kneib and Stiven 1978) and overwinters in marsh creeks (Fritz et al. 1975 and personal observations). Nixon and Oviatt (1973), in a classic study of energy flow through a Rhode Island salt marsh embayment, did not observe a clear pulse of net fish biomass export and suggested that marsh fish did not supply a large forage base for larger fish in open waters. However, Atlantic silversides were not an important part of the fish fauna encountered in their study, perhaps because the only open water access to their study site was through a culvert which may have affected the movement of surface dwelling fishes such as *M. menidia*. In contrast to their results, our study suggests that Atlantic silversides play a role in transporting energy from marshes to deeper, offshore waters.

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