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The spatial and temporal distribution of young-of-the-year *Osmerus mordax* in the Great Bay Estuary

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Synopsis

Juvenile smelt, *Osmerus mordax*, were collected from four eelgrass, *Zostera marina*, beds in the Great Bay Estuary, two within Great Bay and two located nearer the coast. Lapillar otoliths were used to estimate the ages of the smelt and to calculate daily somatic growth based on the widths of otolith increments. Smelt collected from the Bay sites were consistently younger and shorter in total length than smelt collected from the coastal sites. A repeated measures analysis of variance found significant differences among growth trajectories of smelt grouped by their dates of 'birth'.

Introduction

The determination of 'birth' rates, growth rates, and death rates of individuals within a population provides valuable information on the short- and long-term consequences of population dynamics (Caswell 1989). For fisheries biologists, estimates of these population rates are often difficult to obtain. The animals are mobile, may spend different parts of their lives in geographically separate places, and individuals of genetically separate populations may intermingle at some life intervals (Sinclair 1988). Realistically these organisms may experience different growth rates and mortality rates in each of these locations and in each phase of their life history (Iles & Sinclair 1982). It therefore becomes necessary to evaluate separate intervals of the life history in order to understand the importance of these intervals to the overall life cycle.

In order to determine a growth rate and age for an individual within a population, repeated measurements can be made at regular intervals and a growth rate computed from the change in size over time. This requires that individuals be marked and recaptured. A second approach is possible for fish because of information on the age and growth of the organism recorded in scales and otoliths (Panella 1971, Campana & Neilson 1985). Unlike traditional methods used for other organisms, fish scales and otoliths offer the investigator the advantage of containing information already recorded about the life of that individual.

For most species of fish, otoliths increment with a 24 hour periodicity. By counting the number of increments of an otolith it is possible to arrive at an estimate of the age of the fish in days. By measuring the distance between increments it is possible to arrive at an estimate of the proportion of growth occuring during that interval (Pannella 1971, Campana & Neilson 1985).

The rainbow smelt, *Osmerus mordax* (Mitchell), exhibits a spatially complex life history. Adult smelt spend the summer in coastal waters, the eggs, embyos, and larvae reside in freshwater rivers, and the larvae and juveniles spend their early life in estuaries (Bigelow & Schroeder 1953).

The Great Bay Estuary, a 45 km^2 area, is the largest estuarine region between Cape Cod, Massachusetts, and Brunswick, Maine. Great Bay itself is supplied by three main rivers and drains via Furber Strait and Little Bay to the Piscataqua River (Figure 1). Previous work in the Great Bay Estuary (Sale & Gestring unpublished data) and elsewhere (Adams 1976, Bell & Westoby 1986a, 1986b, Sogard & Able 1991, Pollard 1984) has shown eelgrass, *Zostera marina* (L.), and other seagrass beds to contain higher concentrations of juvenile fish than adjacent unvegetated habitats. Juvenile smelt constitute the most numerous species caught in the eelgrass beds of the Great Bay Estuary (Sale & Gestring unpublished data).

The purpose of this study was to (1) establish pat-

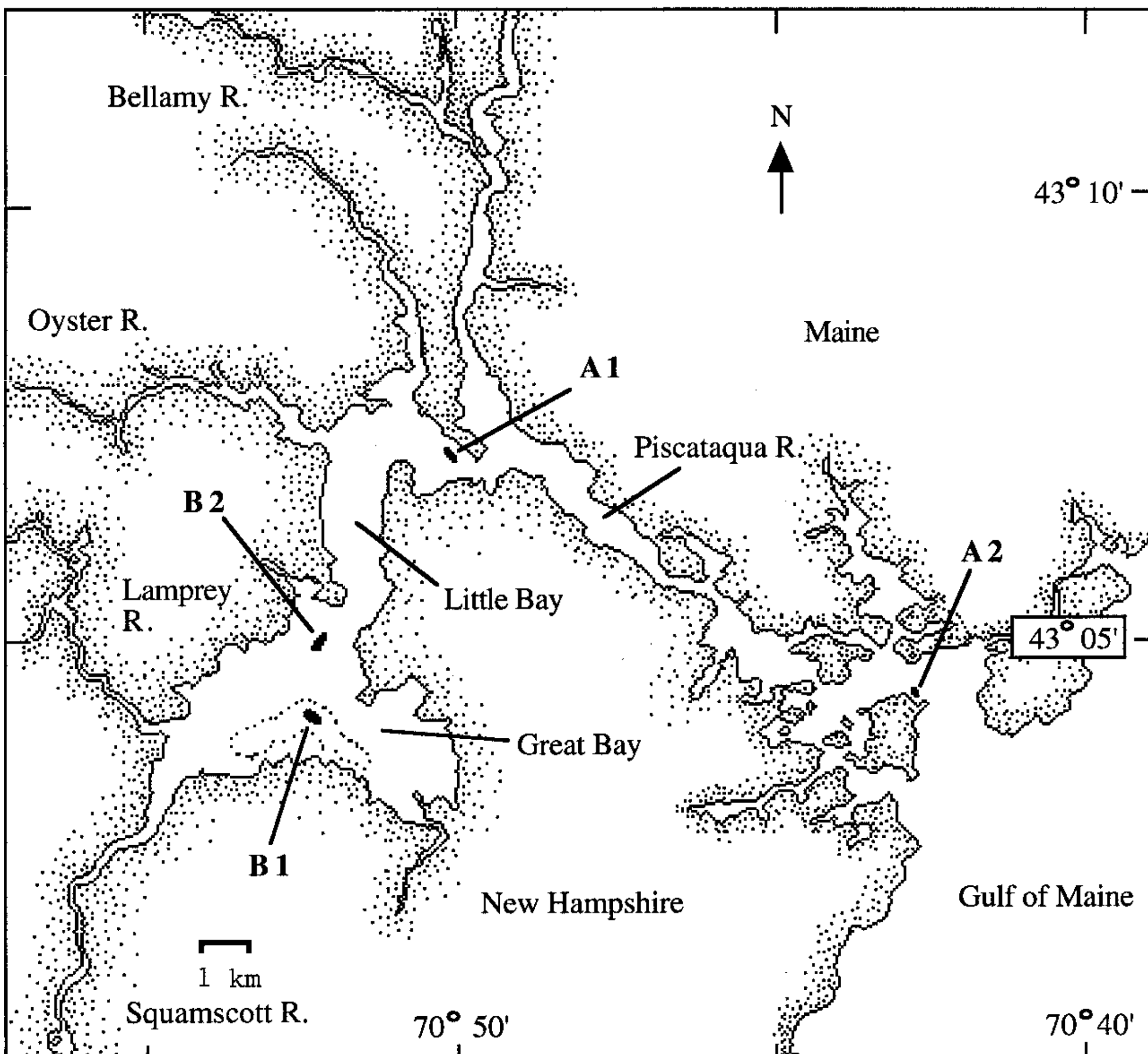

Figure 1. The Great Bay Estuary system. The four sites used in this study are shown.

terns of growth of juvenile smelt during the first growing season, (2) determine if there is a spatial component with regard to smelt age and size, and (3) compare the growth of juvenile smelt among age cohorts.

Materials and methods

Collection of fish

Four sampling sites were established within the Great Bay Estuary. The sites were chosen based on the presence of eelgrass and depth of water. Two of the chosen sites were located within Great Bay itself: B2, an isolated bed approximately 22 m^2 in area, and B1, part of a much larger contiguous bed of 2 km^2 in area (Figure 1). The remaining two sites were located along the Piscataqua River: A1, an isolated bed approximately 26 m^2, and A2, an isolated bed of 18 m^2 in area close to the mouth of the estuary.

Collections of fish began in July 1991 and continued monthly through November. Site A1 collections commenced in August and site A2 was added in September. Samples were taken using a purse seine modified from Kingsford & Choat (1985). The net is approximately 14 m × 2 m with a 1 mm mesh and is capable of sampling approximately 16 m^3 of water. Each site was sampled when water depth was 1.0–1.5 m. A sample consisted of three purses of the seine in quick succession over the vegetated region. Fish collected were identified, counted, and measured to the nearest 1 mm. A subsample of smelt were haphazardly chosen, placed into labelled plastic bags, one bag per purse, placed on ice, and taken to the laboratory.

Preparation for the analysis of otolith microstructure

The smelt were placed into 95% ethyl alcohol to preserve otolith microstructure. Three months later, the smelt were removed from the 95% ethyl alcohol and the total length was remeasured to the nearest 1 mm. One lapillar otolith from each smelt was placed into a Jensen grinding jig (Jensen 1990) and the anterior edge of the otolith was ground using 4000 grit paper until the grinding plane approached the nucleus of the otolith. The posterior edge of the otolith was then ground until the new plane of grinding approached the plane of grinding on the anterior edge of the otolith. The resulting thin section was used in all data collection relating to otolith structure.

Otolith data collection

All measurements of the radii and fine microstructure of the otoliths were made using the image-analysis software package OPTIMAS (BioScan[1]). The otolith was viewed under a binocular microscope using a 20× lens and the longest segment from the nucleus of the medial edge was measured (Figure 2a). The increments of the otolith were viewed under a 100× oil immersion lens (Figure 2b). The number of increments was counted from the nucleus to the medial edge in order to arrive at an estimate of the age of the smelt at the time of capture. Using the frame grabbing capabilities of OPTIMAS[1] and a 100× oil immersion lens, a line was drawn from the nucleus to the medial edge of the otolith. OPTIMAS produced a cumulative measure of the distance of each increment from the nucleus. This procedure also produced an independent estimate of the age of the smelt. The total catch of smelt by site by month is summarized in Table 1. The numbers in parenthesis indicate the number of smelt from which fine microstructure data was extracted. All statistical computations were performed using SYSTAT (Wilkinson[2]). Information concerning the analyses other than MANOVA was referenced in SYSTAT (Wilkinson[2]) and Winer et al (1991). The MANOVAs were referenced in Bray & Maxwell (1985).

In order to determine if otolith measurements could reliably be used to estimate growth, the natural log of the maximum radius from the nucleus to

1 BioScan, 1991. OPTIMAS, Incorporated of Edmunds, Washington.

2 Wilkinson, L. 1990. SYSTAT: The system for statistics. SYSTAT, Inc., Evanston. 724 pp.

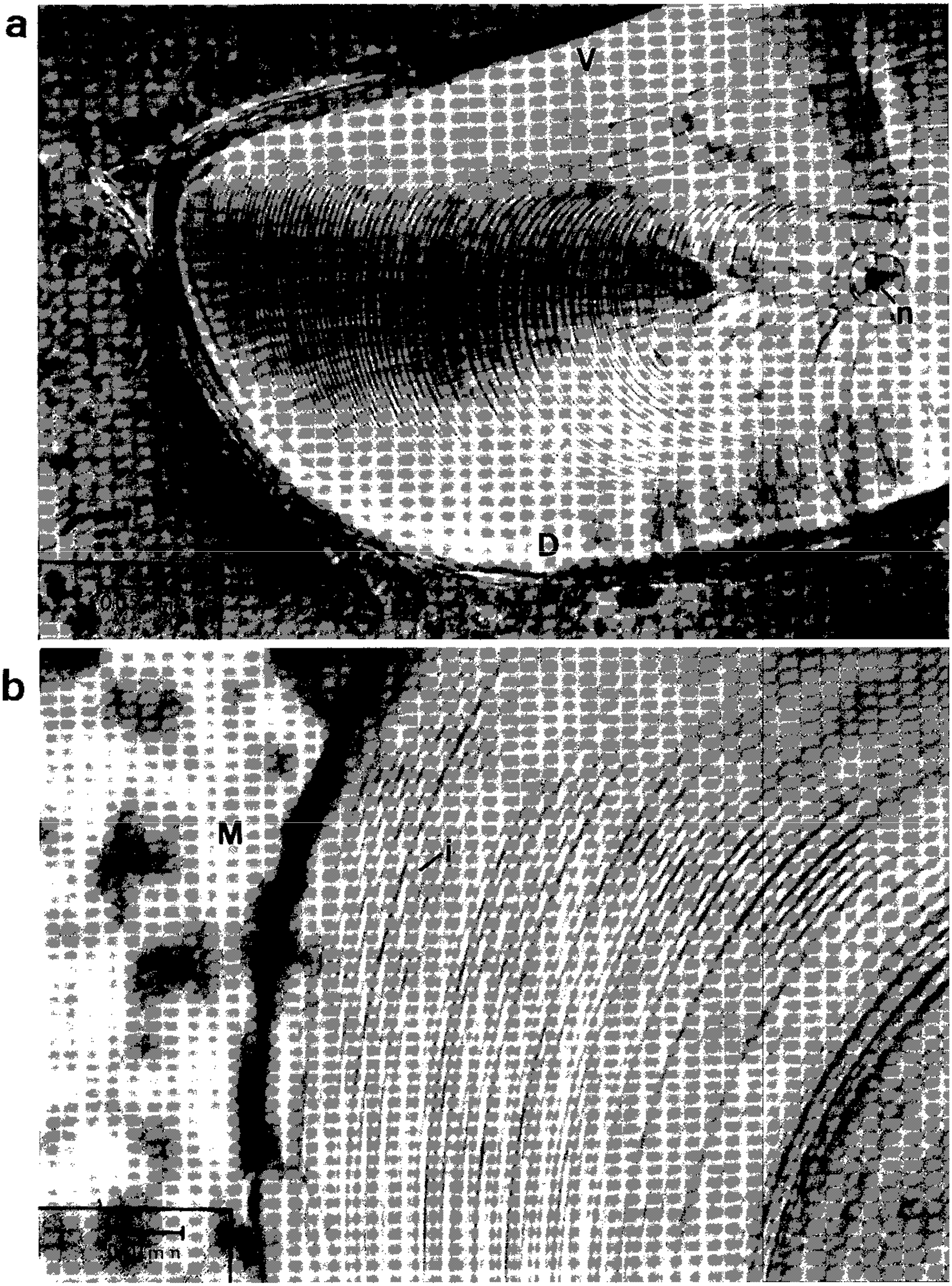

Figure 2. a – Prepared smelt otolith (n = nucleus, D = dorsal edge, V = ventral edge, M = medial edge. b – Prepared smelt otolith (M = medial edge, i = increment).

the medial edge of the otolith was regressed on the natural log of the total length of that particular smelt (alcohol length). A coefficient of determination (r^2) was produced to indicate the strength of the association between otolith growth and somatic growth.

The cumulative distances from the origin to each increment in turn were converted to a series of individual increment widths. The final outermost increment was discarded as it represents only a partial day of growth for the smelt. If there is a strong correlation between otolith growth and somatic growth, then each individual distance of the increment represents the growth of the smelt for that particular day in its life. Histograms of growth by day for each smelt (as determined from otolith increment data) were produced and viewed subjectively.

The total length of each smelt was plotted against the estimated age of the smelt as taken from OPTIMAS increment counts. The r^2 produced indicated the strength of the association between the total length of the smelt and its age. The purposes of such a plot were to determine the reliability of using the total length as an estimator of age and to describe the pattern of growth with age.

MANOVAs

A multiple analysis of variance (MANOVA) was used to determine if smelt caught in different sites differed in their ages and/or total lengths. Age and total length represented the dependent variables while site represented the independent variable. Separate MANOVAs were performed for each month due to missing cells.

Table 1. Total smelt catch by site and month. Numbers in parentheses denote smelt used in otolith analyses.

Month	Site B1	B2	A1	A2
Jul	59	296	*	*
Aug	481 (10)	44 (10)	172 (10)	*
Sep	14 (7)	6 (2)	87 (10)	375 (10)
Oct	46 (10)	164 (10)	29 (10)	153 (10)
Nov	5 (3)	7 (7)	0	4 (3)

* Site not sampled.

Otolith blocks and growth trajectories

A mean was computed for each block of ten increments beginning at the nucleus and proceeding toward the medial edge of the otolith (blocks i, ii, iii, ..., x, with block i innermost). Mean growth computed in this way represents the mean growth of the smelt for a ten-day interval.

The estimate of age for each smelt was used to determine its date of 'birth' (hatching date). Smelt

Table 2. The mean and SD of smelt lengths and ages for each site for each month.

Month	Site	Length (mm) mean	Length (mm) SD	Age (days) mean	Age (days) SD
Aug	B1	45.8	3.9 a	96.1	3.4 a
	B2	42.7	6.0 a	92.7	6.6 a
	A1	56.5	6.5 b	110.9	11.2 b
Sep	B1	51.3	5.5 a	117.4	4.3 a
	A1	54.6	7.2 a	113.0	6.0 a
	A2	66.8	5.3 b	129.0	6.7 b
Oct	B1	51.1	8.8 a	133.3	7.6 a
	B2	47.0	3.2 a,b	136.4	5.2 a
	A1	58.3	8.0 b	135.6	9.9 a
	A2	66.3	8.2 c	147.7	8.5 b

Lower case letters denote means which are significantly different. Comparisons are made separately for length and age and for each month.

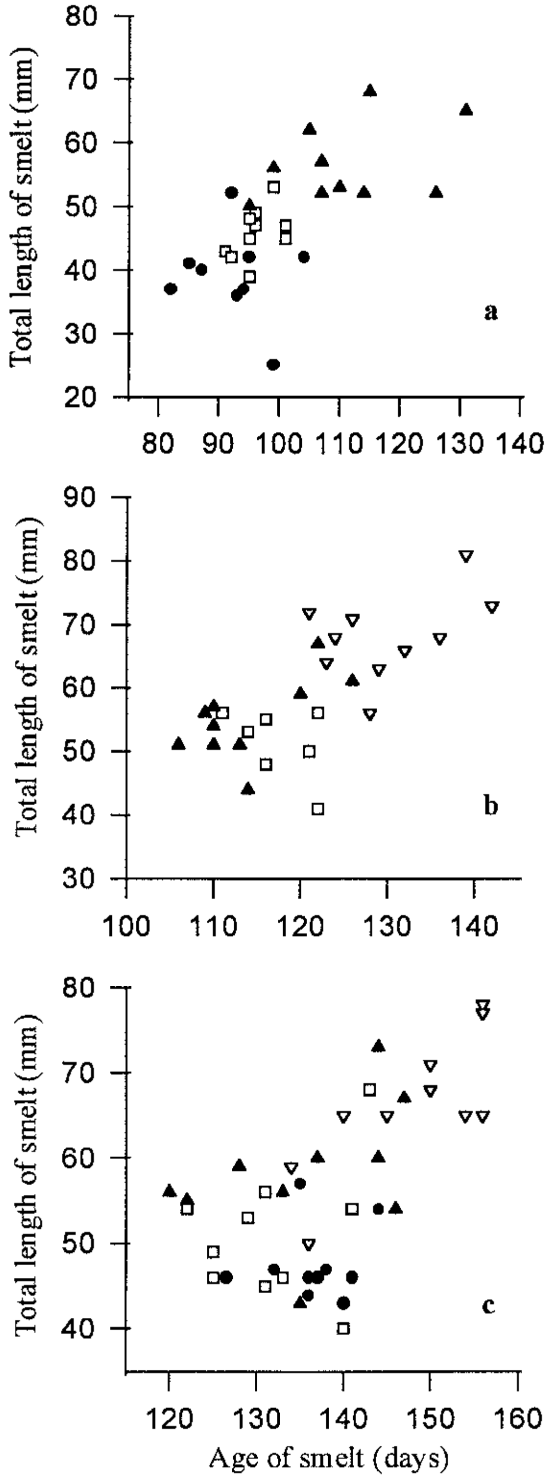

Figure 3. The relationship between the age of smelt and the total length for the months of a – August, b – September, and c – October. For each month, ● = B2, □ = B1, ▲ = A1, and ▽ = A2. Note that the axes differ in their ranges.

from different monthly collections and different sites could then be grouped by date of 'birth' according to the following schedule: born on or between (A) 20–29 April, (B) 30 April–9 May, (C) 10–19 May, (D) 20–29 May, (E) 30 May–8 June, (F) 9–18 June, and (G) 19–28 June. Data from blocks i–viii were used to derive growth trajectories for the 80 days from hatching for each group of fish. A repeated measures ANOVA with date of birth class as the grouping factor was used to determine if there were differences in the growth trajectories among smelt hatched at different times. The youngest smelt analyzed in this way was less than 90 days old. For this analysis each block represents similar periods in the ontogeny of the smelt but not necessarily the same ten calendar days.

Results and discussion

Smelt catch and correlations

The catch of smelt among sites and among months differed by up to an order of magnitude (Table 1). The largest smelt catches occurred in different months at different sites. The lack of pattern suggests that smelt are patchy in distribution at the scale of sampling (approximately 16 m^3) and therefore these data cannot be used to estimate overall abundance with any confidence.

The natural log of the total length of smelt was found to be correlated with the natural log of the maximum radius of the lapillar otolith ($p < 0.001$, $r^2 = 0.887$). Over most of the age range studied, a change in the otolith radius of 0.004 mm corresponds to a change in the total length (in alcohol) of the smelt by 1.0 mm.

The age of the smelt was correlated with total length ($p < 0.001$), but the relationship was not strong enough ($r^2 = 0.566$) to use total length as a predictor of its age. For example, a smelt of 56 mm total length ranged from 99 days old to 139 days old. Different growth rates among smelt could be due to genetic differences, or to the patchy distribution of favorable habitats with respect to food resources, optimum temperatures, or optimum salinities on a spatial scale smaller than the scale at which these fish were operating.

MANOVA results

For the month of August, the MANOVA revealed that there was a significant difference in the composition of smelt at the three sites (Pillai trace = 0.634, $F_{4,54,0.05} = 6.270$, $p << 0.001$). A post-hoc comparison revealed that the smelt at A1 were significantly different from the smelt at B2 and B1 ($p << 0.001$). The new variate (a combination of both total length and age) explained 63.2% of the variation among sites. Smelt were longer at A1 than smelt at either B2 (univariate $F_{1,27,0.05} = 30.526$, $p << 0.001$) or B1 (univariate $F_{1,27,0.05} = 18.352$, $p << 0.001$). Smelt were also older at A1 than smelt at either B2 (univariate $F_{1,27,0.05} = 27.708$, $p << 0.001$) or B1 (univariate $F_{1,27,0.05} = 18.322$, $p << 0.001$) (Figure 3a).

For the month of September the MANOVA revealed that there was a significant difference in the composition of smelt at the three sites (Pillai trace = 0.826, $F_{4,48,0.05} = 8.450$, $p << 0.001$). A post-hoc comparison revealed that the smelt at A2 were significantly different from the smelt at A1 and B1. The new variate explained 67.4% of the variation among sites. Smelt were longer at A2 than at either A1 (univariate $F_{1,24,0.05} = 21.498$, $p << 0.001$) or B1 (univariate $F_{1,24,0.05} = 29.514$, $p << 0.001$). Smelt were also older at A2 than at A1 (univariate $F_{1,24,0.05} = 32.483$, $p << 0.001$) and B1 (univariate $F_{1,24,0.05} = 16.515$, $p << 0.001$) (Figure 3b).

For the month of October, the MANOVA revealed that there was a significant difference in the composition of smelt at the four sites (Pillai trace = 0.767, $F_{6,72,0.05} = 7.468$, $p << 0.001$). A post-hoc comparison revealed that the smelt at A2 were significantly different from the smelt at A1, B1, and B2; the smelt at A1 were significantly different from the smelt at B2. The new variate explained 54.8% of the variation among sites. The smelt at A1 were longer (univariate $F_{1,33,0.05} = 12.663$, $p << 0.001$) but not older (univaritate $F_{1,36,0.05} = 0.051$, $p = 0.822$) than smelt at B2. The smelt at A2 were longer than smelt at B2 (univariate $F_{1,36,0.05} = 36.939$, $p << 0.001$), B1 (univariate $F_{1,36,0.05} = 22.912$, $p << 0.001$), and A1 (univariate $F_{1,36,0.05} = 6.347$, $p < 0.05$). The smelt at A2 were older than smelt at B2 (univariate $F_{1,36,0.05} = 10.238$, $p < 0.01$), B1 (univariate $F_{1,36,0.05} = 19.764$, $p << 0.001$), and A1 (univariate $F_{1,36,0.05} = 11.739$, $p < 0.01$) (Figure 3c).

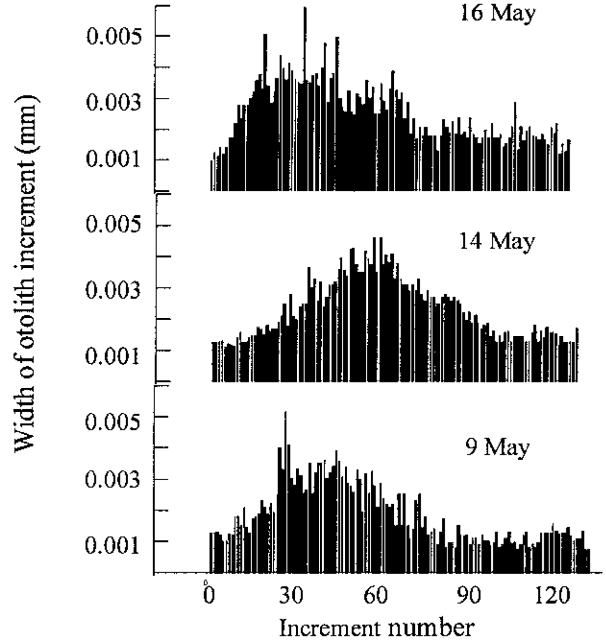

Figure 4. Histograms of the width of each otolith increment. Since otolith increment widths correlate with somatic growth, these histograms represent daily growth. Dates associated with each histogram are the estimated birth dates of the smelt.

Daily growth and age comparisons

The daily otolith growth of three individuals collected from A2 in September and born within one week of each other are presented (Figure 4). Each of these histograms can be subjectively divided into four periods: (1) a period of approximately ten days in which growth is uniform with increment widths around 0.001 mm, (2) a period of increasing growth, (3) a period of decreasing growth, and (4) a period of uniform growth with increment widths around 0.001 mm. Since the widths of the otolith increments correspond directly to the growth in length of the smelt, each bar represents the growth for that particular day. Depending on the period in question, there was a great deal of day-to-day variation in

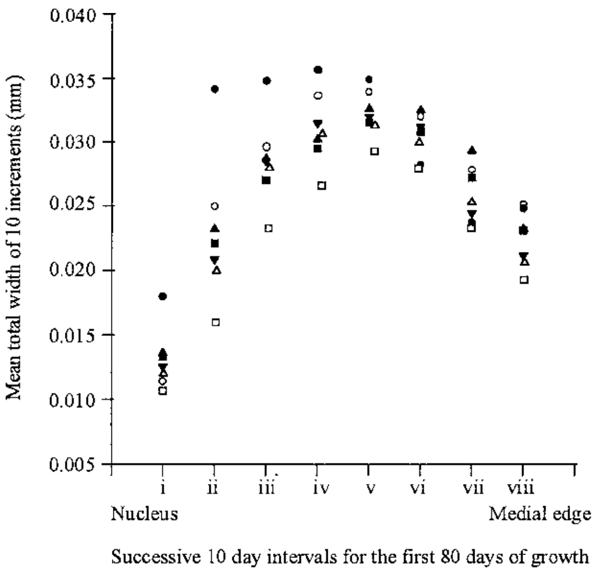

Figure 5. The mean total width of ten increments (ten days) plotted against successive ten increment blocks for smelt from four sites in Oct. The mean total width of ten increments (ten days) plotted against successive ten-increment blocks for smelt from different birth date classes (● = 20–29 April, ■ = 30 April–9 May, ▲ = 10 May–19 May, ▼ = 20–29 May, □ = 30 May–8 June, △ = 9 June–18 June, ○ = 19 June–28 June).

growth. These three histograms illustrate the flexibility in the smelts' growth profiles, which vary in the length of time spent in each of the four periods, the maximum increment width, the rate of increasing growth in period two, the rate of decreasing growth in period three, and the variation within growth periods.

The mean total width of ten increments for each birth class is plotted against each ten-increment otolith block (Figure 5). The growth trajectories of smelt were significantly different according to their date of birth ($F_{6,101,0.05} = 146.000$, $p < 0.001$). Both the block ($F_{7,707,0.05} = 1.826$, $p < 0.001$) and the block*birth class interaction ($F_{42,707,0.05} = 1.826$, $p < 0.005$) were significant. Blocks i, ii, iii, iv, vii, and viii were found to be significantly different using Tukey's post-hoc multiple comparisons test. The differences in the blocks were more pronounced during the early or late intervals of the growth trajectory. Changes during these intervals may result in greater overall variances in growth by reducing or protracting the length of the maximum growth intervals (periods two and three). The differences in the growth trajectories among birth classes may also have been the result of small temporal-scale differences in some favorable condition or resource for the smelt. The difference among growth trajectories of different birth classes could also be explained by changes in the composition of the birth class cohort over time. The two groups exhibiting the greatest growth are those smelt born between 20 April–1 May and those born betweeen 9–18 June (Figure 5). The relatively high growth rates for the 20 April–1 May class may be due to the loss over time of those smelt that did not exhibit high growth rates. However, if this were true, then we would expect to see differences in the groups according to their birth dates: 20 April–1 May would have the highest mean growth rate and each subsequent group would exhibit slightly lower mean growth rates. This type of pattern was not evident in the data.

Conclusions

For the purpose of the age and growth study of smelt in the Great Bay Estuary, the described method of otolith preparation was developed. This method produced a thin section that could be used confidently to estimate the age and growth of juvenile smelt.

Smelt born on or near the same day (similar cohorts) showed a great deal of day-to-day variability in growth. However, when these growth trajectories were viewed at a coarser temporal scale, in ten day intervals, similar cohorts follow similar growth trajectories. This suggests that there may have been differences in what the smelt were experiencing on the temporal scale of weeks and that no predictable trend in growth from cohort to cohort existed through time.

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