

Larval transport, vertical distribution, and localized recruitment in anadromous rainbow smelt (*Osmerus mordax*)

I.R. Bradbury, K. Gardiner, P.V.R. Snelgrove, S.E. Campana, P. Bentzen, and L. Guan

Abstract: We examined larval dispersal and behaviour in rainbow smelt (*Osmerus mordax*) from the Salmonier River estuary, Newfoundland, during 2003–2005. Riverine ichthyoplankton surveys indicate that larval transport into the estuary is restricted to a two-week period in late June. A passive drifter experiment and the spatial distribution of larvae and juveniles suggest limited dispersal and low export from the estuary. The estuary exhibited low inflow and stratification in summer and high inflow with a stable freshwater layer in fall. Summer and fall winds are primarily onshore. We hypothesised that larval vertical swimming behaviour limits dispersal and export. Larval vertical position and swimming ability were examined through lab-based experiments conducted 0–10 and 90 days after hatching. Measurements of swim speed indicate an order of magnitude ($p < 0.001$) improvement in swimming capacity between larvae and juveniles. One-week after hatching, larvae displayed consistent negative geotaxis, whereas juveniles were generally deeper and displayed negative geotaxis in light and positive geotaxis in the dark. The contrasting light-mediated geotactic behavior between development stages corresponds to ontogenetic shifts in swimming abilities and seasonal changes in estuarine circulation. We suggest that the interaction between behaviour, ontogeny, and hydrography results in limited transport and a tendency for estuarine-scale recruitment, despite an extensive pelagic period.

Résumé : Nous avons étudié la dispersion et le comportement des larves de l'éperlan arc-en-ciel (*Osmerus mordax*) dans l'estuaire de la rivière Salmonier, Terre-Neuve, en 2003–2005. Des inventaires de l'ichthyoplancton de la rivière indiquent que le transport des larves vers l'estuaire se fait seulement durant une période de deux semaines à la fin de juin. Une expérience avec un dériveur passif, d'une part, et la répartition spatiale des larves et des jeunes, d'autre part, laissent croire que la dispersion est limitée et l'exportation faible dans l'estuaire. Il y a une arrivée d'eau réduite et une stratification peu marquée dans l'estuaire en été; à l'automne, l'apport d'eau est important et il s'établit une couche stable d'eau douce. Les vents d'été et d'automne soufflent principalement vers le bord. Nous émettons l'hypothèse selon laquelle le comportement de nage verticale des larves limite la dispersion et l'exportation. Nous avons examiné la position verticale et la capacité de nage des larves dans des expériences de laboratoire faites 0–10 et 90 jours après l'éclosion. Les mesures de la vitesse de nage montrent une amélioration de l'ordre de 10 fois ($p < 0,001$) de la capacité de nage entre les stades de larve et de jeune. Une semaine après l'éclosion, les larves montrent une géotaxie négative soutenue, alors que les jeunes se retrouvent généralement en eau plus profonde et montrent une géotaxie négative durant l'éclaircissement et une géotaxie positive durant l'obscurité. Le changement contrasté de comportement géotaxique d'un stade à l'autre du développement sous l'influence de la lumière correspond à des modifications ontogéniques de la capacité de nage et à des changements saisonniers de la circulation de l'estuaire. Nous croyons que l'interaction entre le comportement, l'ontogénie et l'hydrographie a pour conséquence de limiter le transport; le recrutement a ainsi tendance à se faire à l'échelle de l'estuaire, malgré la longue période pélagique.

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Introduction

Estuaries are highly productive regions that provide critical habitat for the early life stages of many marine fish and

invertebrates (Bakun 1996). Dispersal, connectivity, and population structure within estuarine species may be regulated through life cycle closure associated with limited larval dispersal (Sinclair 1988). Measures of larval transport for

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fishes and invertebrate larvae are often elusive, complicated by interactions of hydrography (e.g., DiBacco et al. 2001), behaviour (Christy and Morgan 1998; Metaxas 2001; Cowen et al. 2006), and ontogeny (e.g., Hare et al. 2005), all of which are species-dependent. Nonetheless, understanding dispersal is critical to the conservation of many coastal populations, some of which are currently exhibiting dramatic declines in abundance (Sale et al. 2005).

In many instances, populations are structured in concert with estuarine dynamics (e.g., Bernatchez and Martin 1996; McLean et al. 1999). Indeed, the scale of dispersal in many estuarine species is inconsistent with predictions based on passive transport (e.g., Thorrold et al. 2001), a paradox that is often attributed to active behavioral modifications to drift trajectories (e.g., Cowen et al. 2000). However, for most invertebrate larvae and the early stages of many fish larvae, horizontal swimming ability may contribute little to horizontal displacement (Bradbury and Snelgrove 2001).

In areas of high current shear typical of many estuaries, active manipulation of vertical position may allow selective transport of larvae in response to tides or light conditions (e.g., Dauvin and Dodson 1990; Davis 2001). Active vertical migration has been demonstrated in multiple species of planktonic fish larvae, including walleye pollock (*Theragra chalcogramma*; Davis 2001) and bay anchovy (*Anchoa mitchilli*; Schultz et al. 2000). Regular vertical movements allow larvae to choose flow speed and direction, thereby influencing retention or transport to nursery grounds and sites favourable for survival (e.g., Davis 2001; de Graaf et al. 2004; Lee et al. 2005).

Rainbow smelt (*Osmerus mordax*) are small, schooling, pelagic fish that occur along the Atlantic coast of North America from Pennsylvania to Labrador (Scott and Scott 1998). Most populations are anadromous; adults migrate to inland rivers at night during the spring to spawn and then return to sea during the day (Scott and Scott 1988). Spawning migrations are usually restricted spatially and spawning usually occurs just above the head of tide (McKenzie 1964). Eggs are negatively buoyant and adhere to bottom substrate, with egg stage durations that range from 10 to 20 days. Larvae actively synchronize hatch timing to dusk (Ouellet and Dodson 1985a; Bradbury et al. 2004) and are approximately 5–6 mm after hatching and negatively buoyant in fresh and brackish water. Yolk sac absorption usually occurs at 7 days after hatching, and flexion occurs at approximately 31 days after hatching or at a standard length of 10–15 mm (Sirois et al. 1998; Bradbury et al. 2004). Upon hatch, larvae are transported to the estuary where they develop. Several studies suggest that larval smelt may use vertical migration to enhance estuarine retention (e.g., Ouellet and Dodson 1985b; Laprise and Dodson 1989), though there has been disagreement regarding the specific environmental cues involved (Rogers 1940; McKenzie 1964; Dauvin and Dodson 1990).

Our primary goal was to describe the dispersal of larval smelt and to evaluate active contributions (i.e., behavioral modification of vertical distribution) to dispersal trajectories. We address this goal through three interlinked approaches. First, we examine the spatial extent of horizontal dispersal during the pelagic larval stage within both the river and the estuary in order to estimate export from the estuary. Second,

we examine the role that active alterations in depth play in horizontal displacement through hydrographic surveys, a passive drift experiment, and measurements of larval swim speed. Finally, we examine larval depth preference at 1–10 days and 90 days of age in response to various cues such as light and flow combinations. These experiments assume that cue responses observed in a lab setting are similar to responses in the field.

Materials and methods

Study location

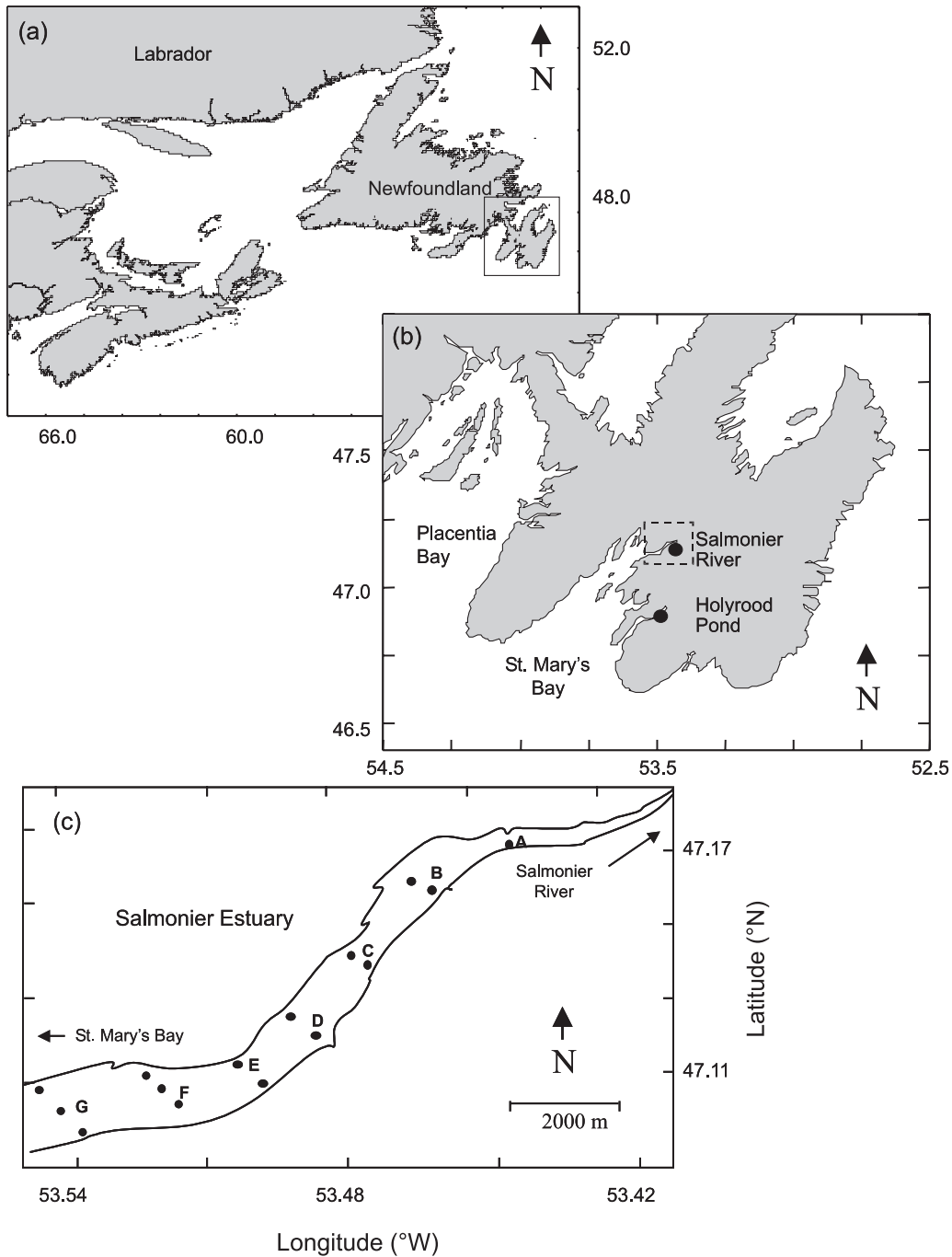
Salmonier River estuary is located at the head of St. Mary's Bay on the south coast of the Avalon Peninsula (Fig. 1). The estuary is approximately 13 km long from the tidal head to where it empties into the bay, and widths range from 1.3 km at the mouth to 0.31–0.10 km at the head. Inflow into the estuary varies seasonally from high inflow periods in fall and spring ranging from 25 to 50 m³·s⁻¹ to low inflow periods during summer characterized by flows of 1–3 m³·s⁻¹. Oceanographic current patterns within St. Mary's Bay have not been studied. Modelling studies suggest currents are dominated by an inshore branch of the Labrador Current resulting in a counterclockwise flow that exits the bay on the western side (Sheng and Thompson 1996). Oceanography in neighbouring Placentia Bay is of similar shape and orientation and has been studied more extensively. Predominant currents and transport of pelagic eggs and larvae in Placentia Bay support the prediction of a counterclockwise flow with alongshore current speeds ranging from 0 to 5 cm·s⁻¹ entering on the eastern side and exiting on along the western side with retention times of approximately 30 days (for details regarding flow and transport in Placentia Bay, see Bradbury et al. (2000, 2003)). It is likely that similar conditions exist in St. Mary's Bay, although retention times may be decreased given its smaller size in comparison with Placentia Bay.

Ichthyoplankton and oceanographic data collection

Dispersal from Salmonier River

Smelt spawning locations in Salmonier River were identified through interviews with local residents and subsequent snorkelling surveys during the spring of 2002. Larvae hatched uniformly at dusk and were sampled nightly at 2200, 10 m downstream of the spawning ground, during June 2003–2005 as they drifted from river spawning beds to the downstream estuary. Sampling is described in detail by Bradbury et al. (2004), but in brief, drift samples of eggs and larvae were sampled with a 30 cm ring net of 333 µm Nitex® mesh fitted with a flowmeter (General Oceanics Inc., Miami, Florida) approximately 10 m downstream from the Salmonier River spawning site. Water depth was <1 m and single 15-min samples were taken every night (at 2200) throughout the hatch period beginning in early June and continuing until all eggs in the river had hatched (early July) in order to describe seasonality in spawning and hatch patterns. River water temperature measurements were made with an ethanol thermometer at the time of sampling, and all plankton samples were preserved in 95% ethanol and identified to species level.

Fig. 1. (a) Map showing location of St. Mary's Bay in relation to Newfoundland, Canada. (b) Map of study sites indicating location of Salmonier River and Holyrood Pond. (c) Transects and oceanographic stations in Salmonier River estuary are indicated (●).



Dispersal within the estuary

Estuarine ichthyoplankton and hydrography were sampled across seven transects distributed throughout the estuary (Fig. 1, A–G) during 3–5 July 2005. Ichthyoplankton was sampled using a 1 m ring net towed obliquely across each transect through the water column for 10 min. Volumes filtered were estimated with a flowmeter (General Oceanics Inc.), and samples were processed as described above. Fifteen hydrographic stations (Fig. 1, ●) were sampled using a CTD (conductivity–temperature–depth) profiler (SBE 25 (15–18 November 2004) or SBE 19 (3–5 July 2005); Sea-Bird Electronics, Inc., Bellevue, Washington). Data was ex-

amined graphically to determine both vertical stratification and horizontal extension of surface penetration of freshwater into the estuary. Seasonal shifts in vertical stratification allowed examination of the magnitude of inflow and its penetration into the estuary, as well as potential export. Wind data were obtained from the Canadian Atmosphere and Environmental Service for Argentia, Placentia Bay (approximately 50 km away), for July to December of 2003, 2004, and 2005. Wind data were rotated 25° to align with the long axis of the estuary. Wind direction and speed were converted to wind stress (Large and Pond 1981) and filtered using an 8th-order Butterworth lowpass filter to allow inter-

pretation of drag force per unit area transferred to water surface.

To examine predominant drift of surface water, a passive drifter release was conducted on 25 June 2005. Oranges were chosen as drifters because they are positively buoyant, visible at great distance, and biodegradable. Similar releases have been conducted and resulted in good approximations of predominant flow and transport of pelagic Atlantic cod eggs located in the upper mixed layer around coastal Newfoundland (e.g., Bradbury et al. 2000). A total of 1191 individually labelled oranges were released from the spawning location within the Salmonier River at 2200 to coincide with seasonal and daily peaks in hatch. Admittedly, given that they break the water surface, these oranges may be more responsive to wind stress and may therefore be more responsive to wind-driven flow than particles at depth. Nonetheless, the shallow depth of many parts of the river and negative geotaxis of larvae (see below) suggest that the drifter study is a reasonable approximation of passive drift. Oranges were recovered over the next 30 days based on visual surveys of beaches throughout St. Mary's Bay.

Early juvenile smelt were sampled within the Salmonier River estuary to provide the dual function of data on spatial and size-frequency distributions necessary to place the swim speed data within context of the larger population. Sampling took place during the fall (October to November) of 2003 and 2004 at each of 25 sites that spanned the estuary from river inflow to St. Mary's Bay. Sites were chosen based on distribution around the estuary, accessibility by small craft, and the presence of eelgrass (*Zostera* spp.) habitat. A 25 m demersal seine with 19 mm stretched mesh was deployed 50 m from shore. The seine samples 880 m² of habitat from the substrate to 2 m above the bottom and has a capture efficiency of 95% (Gotceitas et al. 1997).

Larval and juvenile swim speeds

Eggs were transported from the Salmonier River to the Ocean Sciences Centre of Memorial University and placed in aerated water from the river maintained at 10 °C. Eggs hatched within 15–20 days and yolk sac larvae could be maintained for approximately 10 days. Efforts to get the larvae to feed were unsuccessful, and larval data are therefore limited to individuals that were still feeding on yolk sac. On repeated trips to the Salmonier River estuary in the fall, juveniles were collected with the beach seine described above, but efforts to transport them to the lab were unsuccessful and resulted in high mortality. We therefore transported the swim tunnel (see below) to the river and conducted swim trials on freshly collected juveniles of unknown age. Nonfeeding preflexion larvae were held for a period during which no visible effects on survival were observed (<10 days). Postflexion juveniles captured in the field were acclimatized to the lab and held for a maximum of 12 h to minimize containment-associated behaviours.

To evaluate larval swimming abilities, larvae for a given developmental stage (reported as size) were selected haphazardly and carefully transferred to a small (60 mL total volume) Blazka swimming tunnel. A swimming tunnel is a tube through which flow is created via a small impeller connected to a variable-speed motor. Larval fish are placed in the tube and flow is altered via the impeller to test swim-

ming ability by determining the flow speed at which a larva can no longer maintain its position in the tube (see Beamish 1978). Larvae were allowed to acclimate to the tunnel for 10–15 min in static flow. Swimming capacity was determined using a modified critical swimming velocity (U_{crit}) test (Brett 1964), where current velocity was increased gradually from static in 1 cm·s⁻¹ increments every 2 min until the larvae could no longer maintain position for a full 2-min period. This measure of swim speed represents an upper end of swim potential, and sustained swim speeds are typically much smaller (L. Guan and P.V.R. Snelgrove, unpublished data). The equation used to calculate the U_{crit} of larvae followed Brett (1964):

$$U_{crit} = U + [(t/t_i)U_i]$$

where U represents penultimate speed, U_i represents velocity increment (1.0 cm·s⁻¹), t represents time swim in the final velocity increment, and t_i represents set time interval for each velocity increment (2 min).

The methodology for juveniles was similar to that used with larvae except that a larger swim tunnel (1.6 L volume) was required and the speed increments (U_i) for juvenile swim speed trials were 2.5 cm·s⁻¹. Ryland (1963) described the transverse velocity gradient in a tube 1.6 cm in diameter, which is similar in size to the tunnel used for the preflexion larvae examined in this study, and noted that velocity near the wall was lower than at the centre because of drag. All the reported swim speeds were for larvae near the centre of the tube to minimize the influence of the boundary layer on swim speed estimation. Nonetheless, we cannot completely rule out a minor boundary layer effect.

Vertical movement behavioural experiments

Fertilized smelt eggs were acquired from Holyrood Pond and the Salmonier River during spring spawning 2005 (Fig. 1). The Holyrood Pond population spawned first (May 2005), followed by the Salmonier River (June). To collect eggs, burlap pieces (1 m × 4 m) were placed over the substrate at locations where spawning had been observed the previous night (see Bradbury et al. (2004) for details on egg collection). Given the negative buoyancy and adhesive nature of the eggs, they quickly accumulated on the burlap, and we observed no effect of the burlap on spawning adults. Burlap pieces remained in the river until covered with fertilized eggs (typically several days), at which point the burlap was carefully transported to a nearby lab and the eggs were reared in 80 L aerated freshwater tanks maintained at 13 °C. Water quality was monitored until hatch with 50% water exchanges every second day. Because water exchanges in holding tanks were conducted on a 2-day cycle, the majority of larvae included in behavioural experiments were between 1 and 2 days old.

Initial experiments were performed on newly hatched preflexion larvae (0–10 days after hatching, noting that larvae feed primarily on yolk reserves during this period; Sirois et al. 1998) and experimental design followed Davis (2001). Larvae were added to clear plastic columns (182 cm tall, 15 cm diameter, 2 mm thick). Because larvae occur in both low salinity and brackish areas of the estuary, separate experiments were conducted with either fresh (0 psu) or brackish (15–20 psu) water obtained from the Salmonier River

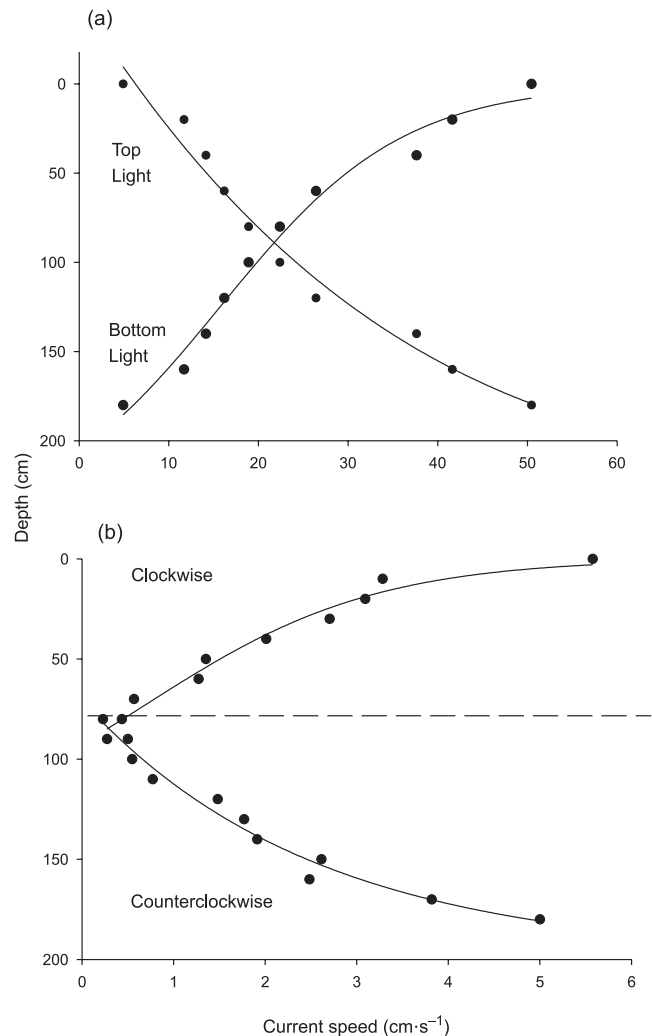
estuary. Larvae were added at a depth of 10–20 cm below the surface, taking care to minimize stress and damage. In the brackish water experiments, larvae were added well below the surface (~50–60 cm depth) to eliminate entrainment in the freshwater layer that might result from addition near the top of the column. In all treatments, larvae were negatively buoyant and, in the absence of vertical swimming, quickly descended to the bottom of columns.

Plastic columns were covered with multiple layers of black plastic to eliminate extraneous light contamination. Plastic shades were arranged in a series of 30 cm panels that could be opened in random order to allow enumeration and avoid systematic biases. Experiments were done at varying times throughout the day and night to eliminate potential innate responses (i.e., tidal or diel) that might be unrelated to experimental stimuli.

Five different treatments were tested in fresh and brackish water: (i) top light, no flow; (ii) bottom light, no flow; (iii) no light, no flow; (iv) top light with flow; and (v) no light with flow. In all cases, preflexion larvae were exposed to a given treatment for 1 h to allow them to respond to the cues before inspection and counting. Because of their larger size and superior swimming ability, juveniles were exposed to treatments for only 15 min to allow them to respond to the cues before inspection. However, longer periods were initially tested (up to 1 h) to confirm that positions did not change substantially after 15 min. In all trials, counts were obtained at 10 cm depth increments, resulting in 18 depth interval counts per trial. Because of their small size and the potential for counting error, larvae were enumerated twice per trial and then averaged.

Fluorescent lights (13 watt) were used to simulate sunlight in all trials and were placed either above or below the tube depending on the trial (Fig. 2a). The light intensities varied from $50 \mu\text{mol photons}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ directly above or below the light source to $5.0 \mu\text{mol photons}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ at the point furthest from the source (Fig. 2a). Fluorescent lights minimized the effect of water heating on smelt behaviour. Although flow speeds in the Salmonier River estuary were not measured, flow speeds used in behavioural experiments approximated alongshore speeds common from coastal Newfoundland (Bradbury et al. (2000); see Discussion). Top and bottom flows were generated following Davis (2001). Bottom flows were created using a magnetic stirrer with a maximum flow speed of $5 \text{ cm}\cdot\text{s}^{-1}$ (Fig. 2b). Top flows were created by pumping compressed air through plastic tubing into the water to achieve flows of $5 \text{ cm}\cdot\text{s}^{-1}$ that were countercurrent to bottom flows. All flow experiments were done with simultaneous top and bottom flows to mimic actual estuarine shear conditions and create a wide range of flow and turbulence conditions within the column (Fig. 2b). Throughout all experiments, the room was kept dark and columns were maintained at $13 \text{ }^\circ\text{C}$ to match ambient water temperature of the rivers. Larvae did not show any adverse response to being held in the columns and survived and remained active for up to 10 days with no food addition (I.R. Bradbury, unpublished data). Air stones, though not present during the experiments because of the confounding effects they would have on flow, were added between trials in which limited availability necessitated reuse of larvae. The aeration ensured that

Fig. 2. Experimental treatments of (a) light and (b) flow with depth in 2 m clear plastic columns (15 cm in diameter).



oxygen gradients did not develop over time as fish selected specific depths.

Preflexion larvae (average size = 6.2 mm, $\sigma = 0.33$ mm, maximum age ~2 days old) were added to each column by taking a 1 L sample from their rearing baths, which resulted in an average concentration of 1 larva per 100 cm^3 . Concentrations varied, however, from 1 larva per 910 cm^3 to 1 larva per 16 cm^3 in some trials depending on availability. Comparisons among experiments with different concentrations of larvae indicated no concentration effect on outcomes.

Juveniles (average length = 43.9 mm, $\sigma = 9.9$ mm) were obtained in mid- to late October from the Salmonier River estuary by beach seining in eelgrass beds (Fig. 1). Because 4-month-old juveniles survived better in brackish water than freshwater, all experiments on juveniles were performed with water of salinity corresponding to the salinity where they were caught (approximately 20 psu). Juveniles were exposed to the same experimental treatments as the posthatch larvae with the exception of freshwater. Because of their larger size, juvenile numbers were maintained at lower concentrations than larvae, with an average of 1 juvenile per

467–695 cm³. Concentration had no noticeable effect on behavioural responses.

Statistical analysis

Each treatment was replicated 10 times, alternating among treatments (i.e., top light, bottom light, no light) to ensure no systematic bias. Larvae and juveniles were changed as frequently as possible, but it was sometimes necessary to reuse individuals, particularly with juveniles. In light of problems associated with centre of mass descriptions for depth distributions (Hare et al. 2005), *G* tests were used to compare observed with expected (uniform) distributions of larval or juvenile rainbow smelt. For these comparisons, the expected distribution was that either larvae or juveniles would not respond to stimuli and would be haphazardly distributed among each 10 cm depth interval. Pooled *G*-statistic (G_{pooled}) values were initially determined using the pooled number of individuals per depth range per replicate for a given treatment (Sokal and Rohlf 1995). Heterogeneity between replicates was examined using a heterogeneity *G* test (G_{het}). However, power to detect heterogeneity may be impeded significantly by low numbers in the juvenile experiments where abundances of <5 individuals per depth range and, in some trials, <1 individual were common. Additional *G* tests compared pooled results from brackish water larval and juvenile experiments to determine whether the distributions of larval and juvenile stages differed.

Results

Larval inflow

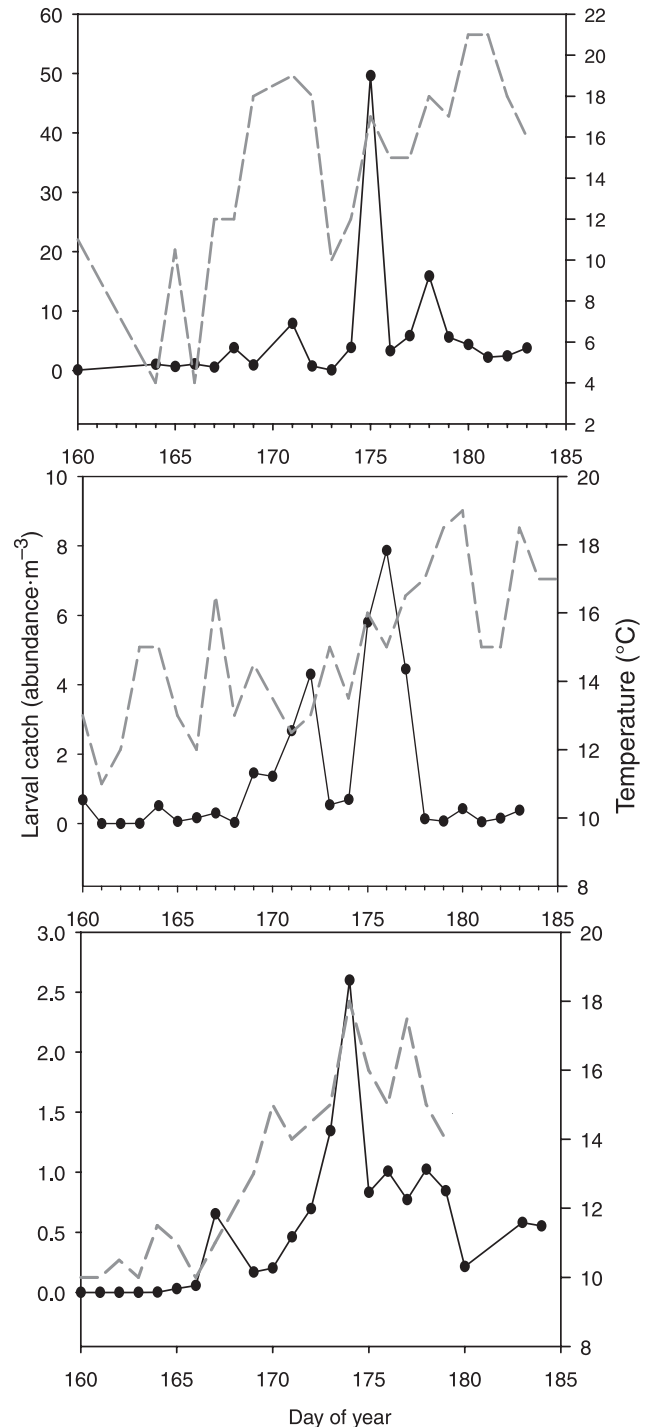
Larval flux from the Salmonier River began on approximately day 160 (9 June) each year and peaked between days 170 (19 June) and 180 (29 June) (Fig. 3). In all three years, hatch was completed by day 190. Water temperatures within the river increased from 10 to 20 °C during the hatch period (Fig. 3, broken line). In all years, the majority of larval production was restricted to a four- to five-night period (Fig. 3) with peak hatch at water temperatures of ~16 °C.

Estuarine transport, hydrography, and swimming ability

Along-estuary wind measurements throughout the summer and fall of all three years indicate that the predominant wind stress is onshore (into the estuary; Fig. 4). Intermittent offshore wind events occurred, but were rare, inconsistent, and short in duration. CTD profiles suggest strong seasonal differences in river inflow. During the summer, the freshwater layer was virtually absent and surface salinities in the upper reaches of the estuary, ranged from 25 to 20 psu, and high surface salinities (30+ psu) were observed in two-thirds of the estuary. The fall was characterized by a stable freshwater layer (Fig. 5), and a greater horizontal extension of freshwater into the estuary, as exhibited by surface salinities that rarely exceeded 15 psu, even at the transition to the bay (Fig. 6a).

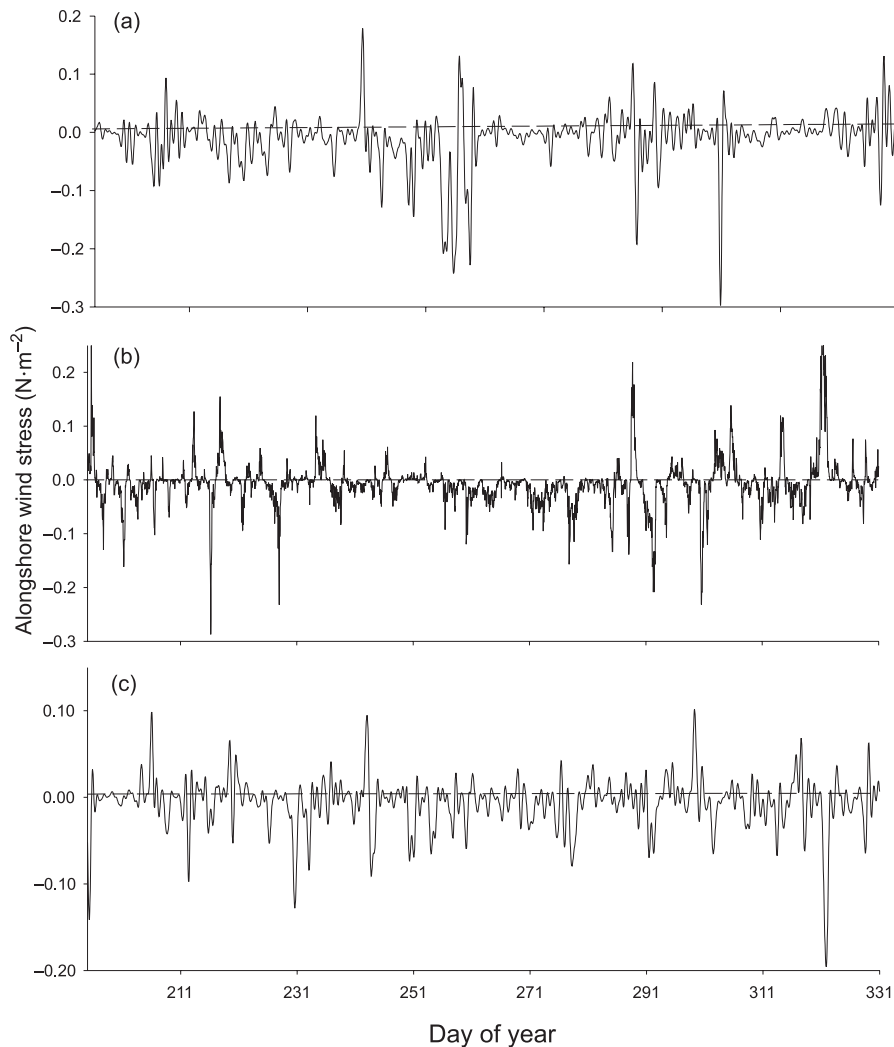
Horizontal dispersal was examined using passive drifters, as well as spatial patterns in larvae and juveniles during summer and fall, respectively. Passive drifters mirrored the extension of freshwater into the estuary in that most oranges

Fig. 3. Smelt (*Osmerus mordax*) larval abundance (● and solid lines) and water temperature (broken lines) in Salmonier River nightly at 2200 during spawning in June of (a) 2003, (b) 2004, and (c) 2005.



were recovered within the upper one-third of the estuary (Fig. 6b). Similar declines with distance were observed in smelt larval abundance in July 2005, which varied from ~600 per tow in freshwater to near zero at the exit to the bay (Fig. 6b). Similarly, juvenile catches were limited to the upper reaches of the estuary, with absence from mid- to outer

Fig. 4. Alongshore wind stress during summer and fall of (a) 2003, (b) 2004, and (c) 2005. All data were filtered with an 8th-order Butterworth filter and rotated to align with the Salmonier River estuary.



regions (Fig. 7), and significant catches (>10 individuals per tow) were limited to the same three locations in all three years (I.R. Bradbury, unpublished data).

Newly hatched preflexion larvae hatched out at sizes of 0.5 to 0.77 cm with corresponding critical swim speeds of ~ 2.7 to $3.8 \text{ cm}\cdot\text{s}^{-1}$ (Fig. 8). By contrast, swim speeds of postflexion juveniles were significantly faster ($p < 0.001$, $df = 63$); individuals ranging in size from 4.8 to 6.9 cm had corresponding swim speeds of ~ 11 to $50 \text{ cm}\cdot\text{s}^{-1}$. These two size categories corresponded to the size frequency distributions of larvae and juveniles sampled in the Salmonier River and estuary, suggesting that the swim speeds were representative of natural populations.

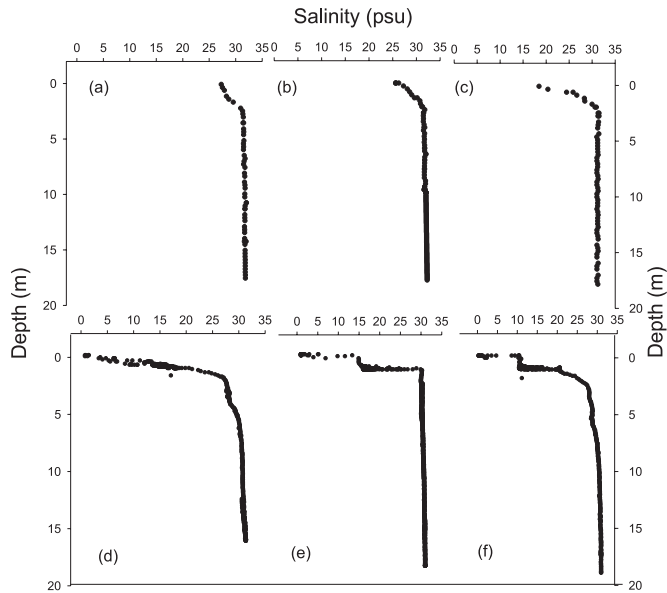
Depth-preference experiments

Experiments with larvae in freshwater indicated that the majority of individuals were found at the surface (0–20 cm), irrespective of the presence of flow or whether lighting occurred from the top or bottom of the column (Figs. 9a–9e). For top lighting, the larval vertical distribution was significantly different from a uniform distribution ($G_{\text{pooled}} = 37.64$, $p = 0.002$; Fig. 9a), although there was significant heteroge-

neity among replicates ($G_{\text{het}} = 448.26$, $p < 0.001$). In the presence of bottom light (Fig. 9b), in addition to the major peak at the surface, a substantial number ($\sim 12\%$) of individuals were also found at a depth of 170–180 cm ($G_{\text{pooled}} = 31.10$, $p = 0.02$; $G_{\text{het}} = 417.57$, $p < 0.001$; Fig. 9b). In the absence of light, larvae were again distributed primarily near the surface (0–20 cm) of the columns ($G_{\text{pooled}} = 55.27$, $p < 0.001$; $G_{\text{het}} = 436.59$, $p < 0.001$; Fig. 9c). Larvae were distributed deeper in the column (0–50 cm) in the presence of flow than in the absence of flow (0–20 cm), but individuals were nonetheless primarily near the surface in both no-light trials ($G_{\text{pooled}} = 43.88$, $p < 0.001$; $G_{\text{het}} = 173.51$, $p < 0.001$; Fig. 9d) and top-light trials ($G_{\text{pooled}} = 34.18$, $p < 0.01$; $G_{\text{het}} = 217.24$, $p < 0.001$; Fig. 9e).

Larvae in brackish water without flow were also distributed primarily near the surface (0–20 cm), irrespective of light treatment, and they were more uniform among replicates. In the presence of top or bottom light, larvae remained in the upper 20 cm of the column (top light (Fig. 10a): $G_{\text{pooled}} = 86.43$, $p < 0.001$; $G_{\text{het}} = 72.73$, $p > 0.05$; bottom light (Fig. 10b): $G_{\text{pooled}} = 119.52$, $p < 0.001$; $G_{\text{het}} = 97.29$, $p > 0.05$). With no light stimulus, larvae were again found

Fig. 5. Salinity profiles at three locations within the Salmonier River estuary during (a–c) summer (3–5 July) 2005 and (d–f) fall (15–18 November) 2004. Locations coincide with transects G, D, and A, respectively (Fig. 1).



near the surface and most individuals were within the upper 20 cm ($G_{\text{pooled}} = 112.32$, $p < 0.001$; $G_{\text{het}} = 53.4$, $p > 0.05$; Fig. 10c). In the presence of countercurrent flows, larvae were again found at the surface (0–30 cm) (Figs. 10d and 10e) and at depths of 0–80 cm in the absence of light with flow ($G_{\text{pooled}} = 124.00$, $p < 0.001$; $G_{\text{het}} = 146.57$, $p > 0.05$; Fig. 10d). With light from above, the highest numbers of larvae were within the upper 20 cm of the column ($G_{\text{pooled}} = 124.06$, $p < 0.001$; $G_{\text{het}} = 118.9$, $p > 0.05$; Fig. 10e).

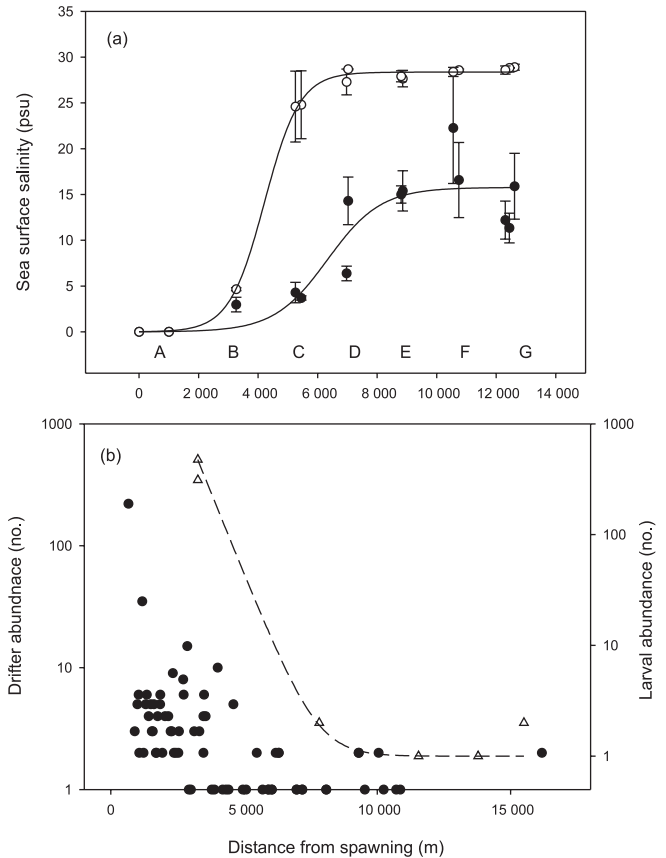
Unlike the posthatch larvae (Figs. 3–6), the juveniles showed varying responses to different treatments (Figs. 11, 12). Each of the juvenile treatments was significantly different from uniformity ($p < 0.001$). Juveniles congregated at 40–100 cm depth when light was from above ($G_{\text{pooled}} = 33.59$, $p = 0.009$; $G_{\text{het}} = 181.11$, $p > 0.05$; Fig. 11a) and in the upper half of the column (0–100 cm) with bottom light ($G_{\text{pooled}} = 11.67$, $p > 0.05$; $G_{\text{het}} = 192.1$, $p < 0.05$; Fig. 11b). When no light was present, juveniles were primarily within the bottom 10 cm of the column ($G_{\text{pooled}} = 36.82$, $p = 0.004$; $G_{\text{het}} = 200.68$, $p > 0.05$; Fig. 11c).

In flow, juveniles dispersed more evenly throughout the columns but, as with the larvae, were found closer to the surface when light was present ($G_{\text{pooled}} = 23.22$, $p = 0.14$; $G_{\text{het}} = 90.85$, $p > 0.05$; Fig. 12a) and deeper when light was removed ($G_{\text{pooled}} = 27.58$, $p = 0.8$; $G_{\text{het}} = 215$, $p < 0.05$). There was also a significant difference between the distribution of the larvae and the comparable juvenile distributions for each treatment (i.e., $p < 0.001$) with the juveniles consistently deeper than larvae.

Discussion

Estuaries have long been considered nursery grounds for a variety of marine and freshwater species (e.g., Able 2005). The role of estuaries as nursery grounds and their importance to the spatial ecology of marine organisms is directly

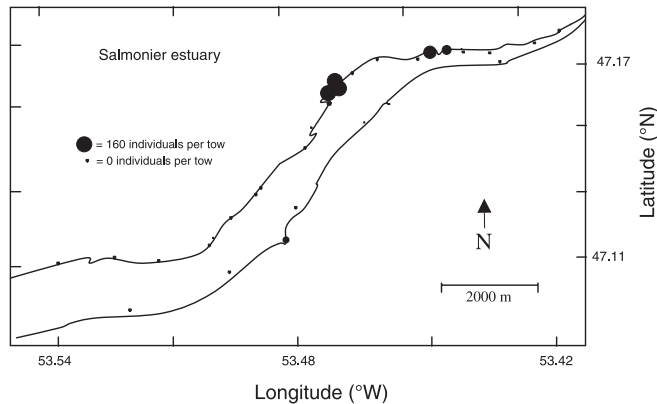
Fig. 6. (a) Changes in sea-surface salinity with distance from spawning in the Salmonier River estuary during the summer (○) and fall (●). Letters A–G refer to transects noted in Fig. 1. (b). Passive drifter (●) and smelt (*Osmerus mordax*) larval abundance (△) with distance from spawning, 3–5 July 2005. Broken line in (b) represents fit of exponential decay to larval abundance data, $f = Y_0 + 3.18 \times 10^4 e^{(0.0013X)}$, where X is distance from spawning location and f is larval abundance.



tied to the ability of pelagic larvae to maintain themselves within these areas. We demonstrate restricted larval dispersal in rainbow smelt that was limited to the upper reaches of the Salmonier River estuary. Interestingly, ontogenetic shifts in larval behavior and vertical position coincide with seasonal increases in estuarine inflow that may contribute to retention and limit larval dispersal within the estuary. Our results suggest that horizontal displacement during the larval stage within the Salmonier River estuary was on the order of 5–10 km, as shown both in larval and juvenile spatial abundance data. These data indicate clear associations with the upper reaches of the estuary and little export into the bay. Similar spatial patterns in smelt larvae have been observed in other studies (e.g., Rogers 1940; Fortier and Leggett 1982).

Bradbury et al. (2006) demonstrated significant genetic differences ($F_{ST} \sim 0.10$) between smelt populations in coastal Newfoundland, indicative of restricted connectivity between these populations. The importance of restricted dispersal to population recruitment was stressed by Sirois and Dodson (2000), who suggested that dispersal from the estuarine turbidity maximum may result in suboptimal growth and low survival. Sirois and Dodson (2000) sug-

Fig. 7. Spatial distribution of juvenile young-of-the-year smelt (*Osmerus mordax*) sampled by beach seine in Salmonier River estuary in fall 2003 and 2004.



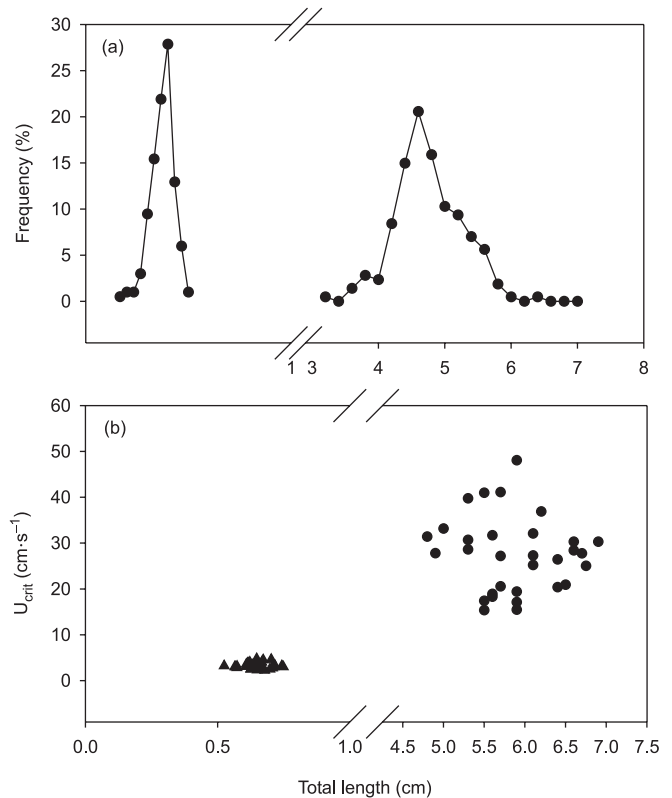
gested that retention within the productive upper reaches of the estuary was tightly linked to individual survival and was likely associated with high selection pressure. Similar linkages between survival, behaviour, and transport have been observed during late embryonic development, where hatch is synchronized to windows of low predation pressure (Bradbury et al. 2004). Nonetheless, no measures of larval survival were made here, and we can only hypothesize that limited dispersal may lead to enhanced survival as observed elsewhere.

The hypothesis of limited larval dispersal is supported by the transport of surface drifters and the intrusion of freshwater during the summer months. The reduced export of surface waters during summer is consistent with limited transport of weakly swimming larvae located in these surface waters. This retention was somewhat surprising given that export of surface water is expected to be high in moderate to high inflow estuaries (e.g., DiBacco et al. 2001). However, the seasonal variation in river inflow on the southeastern coast of Newfoundland is extremely high, varying by an order of magnitude from relatively high inflow in spring ($25\text{--}50\text{ m}^3\cdot\text{s}^{-1}$) and fall to low inflow during the summer ($1\text{--}3\text{ m}^3\cdot\text{s}^{-1}$). The timing of larval entry into the estuary coincides with low seasonal freshwater inflow evident in vertical salinity profiles that is exacerbated by consistent onshore wind.

We observed clear, nonuniform patterns in the vertical distribution of smelt larvae. Recently hatched larvae displayed consistent negative geotaxis independent of light or flow. The observation of posthatch larvae aggregating at the surface is not unusual (e.g., Dame and Allen 1996; Davis 2001; Bennett et al. 2002), and in many cases, this is associated with positive buoyancy. Smelt larvae in our trials were consistently negatively buoyant, and the cessation of swimming always led to sinking of larvae. Interestingly, preflexion larvae seemed less able to maintain themselves at the surface in freshwater than in brackish water, but they nonetheless exhibited repetitive swimming and sinking behaviours. It is likely that increased buoyancy in brackish trials played some role in the decrease in individuals at depth, though it does not explain the accumulation of larvae at the surface.

The Salmonier River estuary is an example of a coastal plain estuary, and we observed a seasonal transition from a

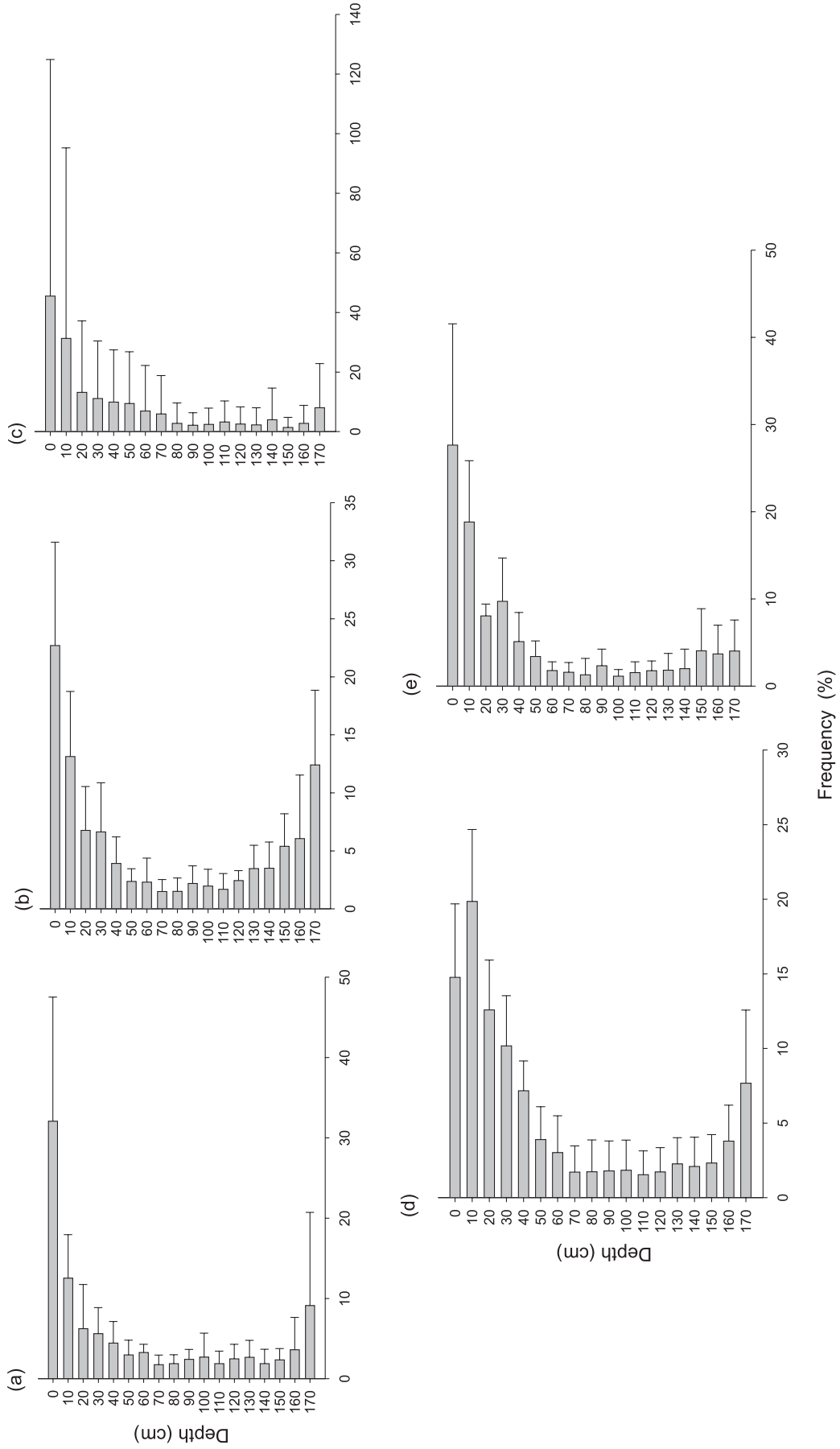
Fig. 8. (a) Larval length-frequency distributions and (b) critical larval velocity calculated for 0- to 10-day-old preflexion larvae (\blacktriangle) and 90-day-old postflexion juvenile smelt (\bullet ; *Osmerus mordax*) from the Salmonier River estuary.



highly stratified estuary in fall to a very weakly stratified estuary in summer, when circulation is expected to result from the interaction of the turbulent forces of winds, tides, and baroclinic flow. Modelling studies in stratified estuaries suggest that freshwater inflow should result in a downstream movement and potential flushing of the estuary (e.g., Hellweger et al. 2004) balanced by inflow near the bottom (e.g., Pritchard 1967). Accordingly, it has been hypothesized that estuarine larvae at the surface are advected seaward (Dodson et al. 1989; Kimmerer et al. 1998). The increased intrusion of ocean water in the Salmonier River estuary in summer is consistent with reduced river flow and onshore wind stress. Unfortunately, we lack direct measures of flow within the Salmonier River estuary, though deYoung et al. (2000) found a residency time of 5–10 days for St. John's Harbour, which has similar freshwater inflow. Their study also noted mean seaward surface currents of $\sim 4\text{ cm}\cdot\text{s}^{-1}$ and $6\text{ cm}\cdot\text{s}^{-1}$ at depth (10 m), with is consistent with the flow rates chosen for our vertical movement trials.

Along-estuary wind stress may play a significant role in dictating flow regimes (deYoung et al. 2000; Brown et al. 2004). Down-estuary wind stress may favour vertical stratification, whereas up-estuary wind stress may tend to break it down (i.e., wind straining, Scully et al. 2005). Moreover, modelling studies suggest that in the presence of onshore winds, surface propagules may be transported or retained near the shore in coastal estuaries, whereas they tend to be quickly dispersed in offshore winds (Blanton et al. 1999).

Fig. 9. Average abundance (\pm standard deviation) of smelt (*Osmerus mordax*) larvae (0–7 days) with depth under various experimental treatments based on 10 replicates of each: (a) top light, no flow; (b) bottom light, no flow; (c) no light, no flow; (d) no light with flow; and (e) top light with flow. All treatments in fresh (salinity 0 psu) water collected from spawning site.



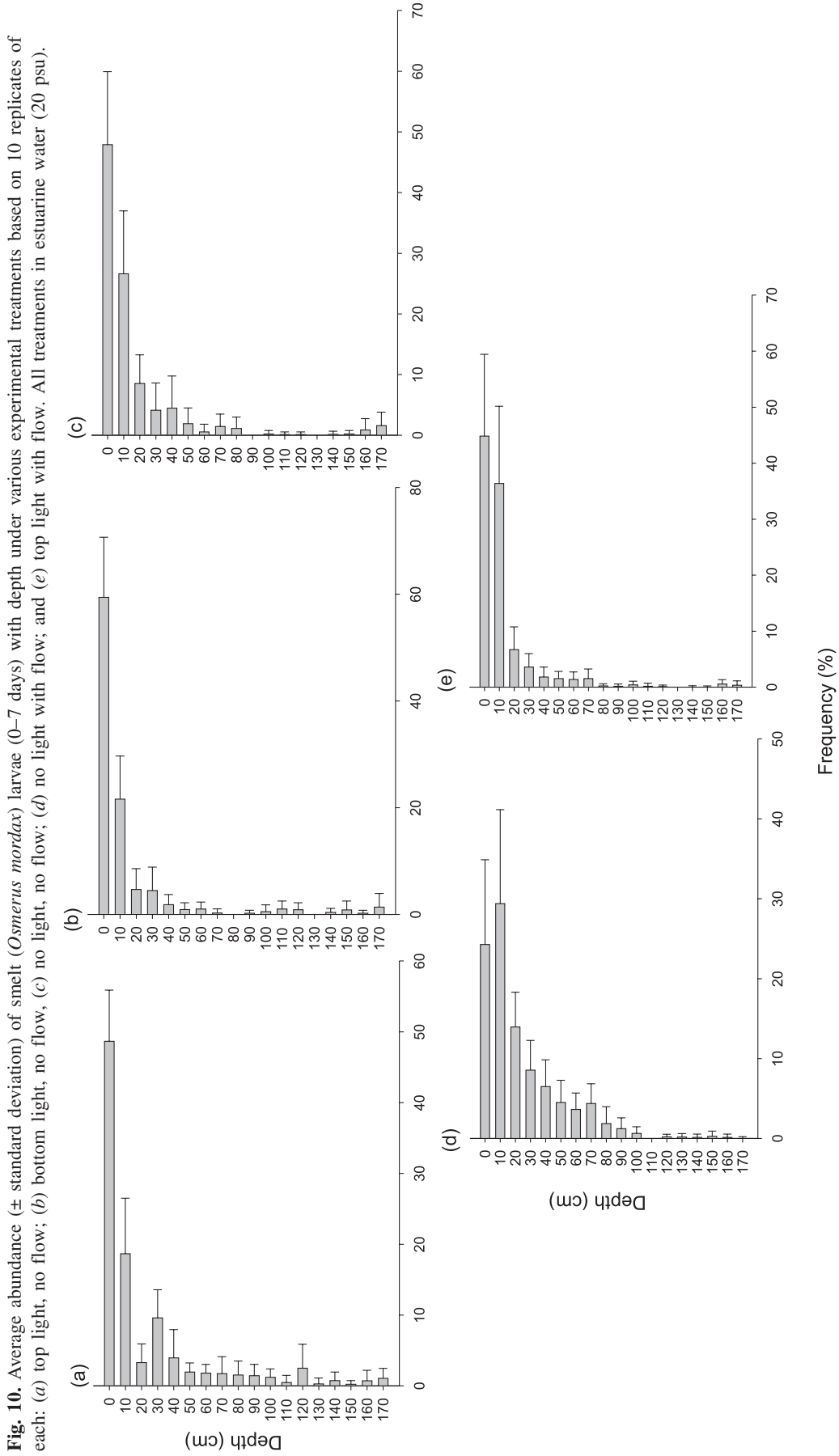
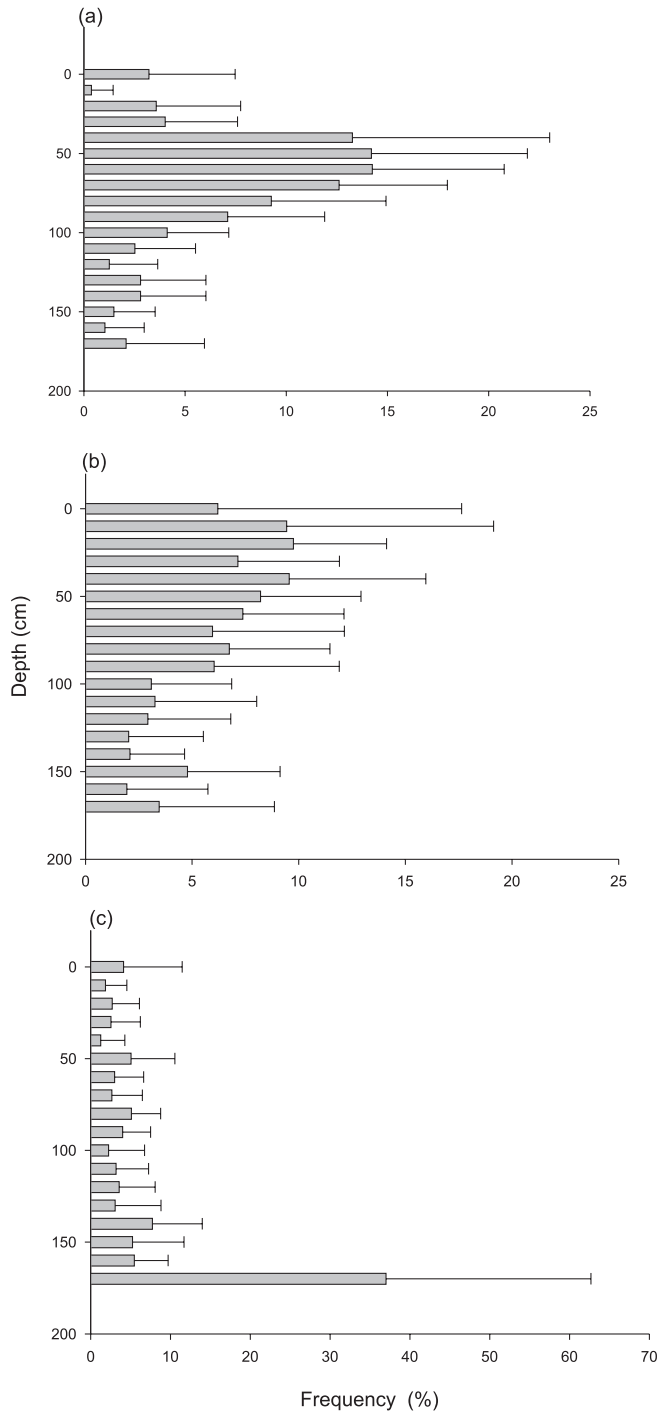


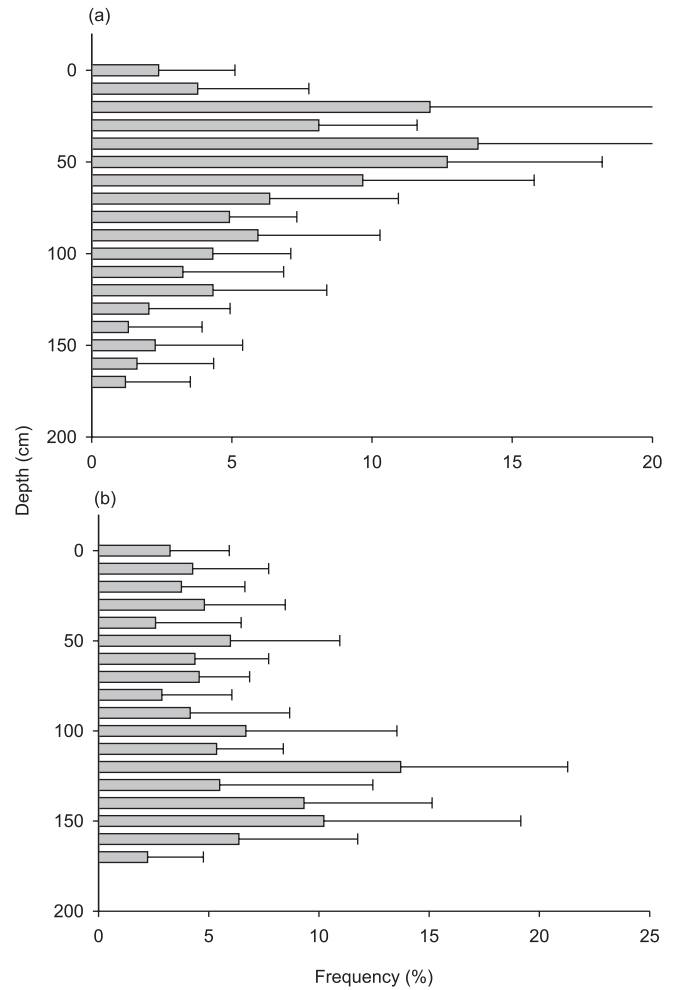
Fig. 11. Average abundance (\pm standard deviation) of smelt (*Osmerus mordax*) larvae (~90 days) with depth under various experimental treatments based on 10 replicates of each: (a) top light; (b) bottom light; and (c) no light. All treatments in estuarine water (20 psu).



This scenario is consistent with our drifter recoveries and our hypothesis that the dominant onshore wind stress in summer months may contribute to retention of preflexion larvae.

In addition to onshore wind stress and reduced inflow, the convergent and restrictive nature of estuarine frontal forma-

Fig. 12. Average abundance (\pm standard deviation) of smelt (*Osmerus mordax*) larvae (~90 days) with depth in response to light while exposed to countergradient current flow based on 10 replicates of each treatment: (a) top light and (b) no light. All treatments in estuarine water (20 psu).



tion may also influence larval transport (e.g., Largier 1993; Sarabun 1993). Surface flotsam and foam indicative of front formation are common in the upper reaches of the Salmonier River estuary in summer months and, in conjunction with spatial data on sea surface salinity, support the hypothesis of frontal formation well within the geographic boundaries of the estuary. Convergent flow at estuarine surface fronts has been noted to reach to tens of centimetres per second (Sarabun 1993) and can be intensified by onshore winds forcing denser water toward the front (Largier 1993). Moreover, given the role of topography in front formation, fronts may regularly recur at specific locations (O'Donnell 1993). Interestingly, the extension of freshwater beyond geographic boundaries in fall suggests that if a frontal plume exists, it may extend into St. Mary's Bay, likely reducing its close association with the upper reaches of the Salmonier River estuary.

There are several possible explanations for surface aggregation of posthatch larvae. Negative geotaxis may be linked to predator avoidance within natal rivers where high predation of smelt eggs and larvae by young salmonids has been

noted (Bradbury et al. 2004). Within estuaries, however, larval predation is thought to be lower than in rivers (Sirois and Dodson 2000). Alternatively, aggregation at the surface of posthatch larvae may be a passive process resulting from positive buoyancy and limited swimming ability. Fortier and Leggett (1982) observed no vertical migration in larvae under 10 mm, suggesting that larvae smaller than this size may be unable to cross the pycnocline and maintain themselves either in surface (capelin) or bottom (herring) waters. Beyond this critical size, the amplitude of vertical migration increased with size in these species (Fortier and Leggett 1982), suggesting a size constraint on vertical migration behavior. Similarly, larvae of the congeneric *O. eperlanus* lack functional swim bladders and, along with their poorly developed fins, possess limited control over their location within the water column until they are between 12 and 15 mm in length (Urho 2002). For the larval stages examined here, which were all well below this size threshold, our observation of near-surface aggregation but weak critical swimming speed and little other obvious strong behavioural responses is generally consistent with these other studies.

In contrast to preflexion larvae, juveniles displayed consistent changes in vertical position, which appeared to represent positive and negative geotaxis cued by light. Juveniles also had substantially stronger swim capabilities than their larval counterparts, which would be expected to have a greater impact on their dispersal and active self-recruitment potential. Although flow had no large effect on vertical position, the response was blurred by flow and distributions were more diffuse, suggesting that juveniles may use active swim behaviour to avoid areas of high flow and to choose preferred weaker flow conditions. An ontogenetic increase in the potential for active behaviour to modify vertical position in larval fish is consistent with Bradbury et al. (2003), who predicted that the critical developmental stage for active behavioural influence on spatial pattern is approximately 10 mm.

Diel vertical migration (DVM) is a common behavior in estuarine fish and invertebrate larvae (e.g., Criales et al. 2005), where larvae surface at night and migrate to deeper water during daylight hours (Poulin et al. 2002). In contrast, we observed light-mediated vertical distribution responses that are consistent with a reverse diel vertical migration (RDVM; Ohman et al. 1983). Poulin et al. (2002) observed RDVM in gastropod larvae located in an advective, upwelling zone that enhanced coastal retention. Interestingly both behaviors (DVM and RDVM) have been reported for rainbow smelt depending on locality (Rogers 1940; Nellbring 1988; Laprise and Dodson 1989). The mechanisms responsible for contrasting behaviours are unknown but may be linked to local estuarine conditions or evolutionary divergence associated with glacial refugia (e.g., Bernatchez 1997). Interestingly, RDVM should increase risk of predation by visual predators (Pearre 2003). However the association of smelt larvae with areas of high turbidity (estuarine turbidity maximum, ETM) characteristic of many estuaries (e.g., Sirois and Dodson 2000; Lecomte and Dodson 2005) may reduce this risk. Moreover, in estuaries where larval predators undergo regular DVM, RDVM may act to counter predator behaviour (Ohman et al. 1983). Admittedly, our experiments were conducted over time periods with less than a

24-h cycle, and despite clear patterns associated with light and dark treatments, we can only hypothesize that observed patterns would hold over 24-h changes in light exposure.

The larval vertical movement documented here appears to be primarily geotactic and not phototactic, given that the majority of larvae remained at the surface even with bottom lighting. Similar behaviour has been noted for walleye pollock, which congregated on the surface irrespective of top or bottom lighting (Davis 2001). Contrary to Davis (2001), we did not observe any shifts from geotaxis to phototaxis in flow trials. There was an indication of positive phototaxis in freshwater larval trials, where secondary peaks of abundance were observed at the bottom in the presence of bottom light; however, the absence of this pattern in the brackish trials makes interpretation difficult.

Several field studies have documented vertical migration in smelt. McKenzie (1964) observed that smelt larvae usually occurred near the bottom, although low concentrations were observed at the surface at night. In the St. Lawrence River, Laprise and Dodson (1989) suggested that active retention in the maximum turbidity zone was achieved through tidally cued vertical migration; their reanalysis of data from Rogers (1940) suggested that such cues could explain the observed distributions. This finding is in stark contrast with our observations that suggest that flow plays only a secondary role in determining vertical position. Of course, movement related to foraging behaviour was not examined here and may be important in field situations, but Dauvin and Dodson (1990) suggested that vertical migration in smelt was not related to feeding. Admittedly, the developmental stages examined here do not directly overlap many previous studies in the St. Lawrence, which examined larvae 8–30 mm in size (e.g., Fortier and Leggett 1982). Nonetheless, our examination of pre- and post-flexion larvae highlights significant behavioural processes associated with each developmental stage.

The potential consequences for limited larval dispersal to the spatial ecology of coastal smelt populations are extensive. We suggest that restricted dispersal results in the formation of isolated demes associated with estuarine retention areas as predicted by the “member vagrant hypothesis” (Sinclair 1988). Similar observations based on genetic (Bernatchez and Martin 1996) and morphological (Frechet et al. 1983) data for the St. Lawrence River estuary suggest discrete populations associated with local retention areas. A similar comparison of genetic diversity and morphology for populations of smelt along Canada’s eastern coast (Newfoundland, Nova Scotia, New Brunswick, Prince Edward Island) suggests that Newfoundland populations (based on 10 estuaries along the southeastern coast of Newfoundland) are subject to limited gene flow, resulting in isolated demes that respond independently to selection for morphology (Bradbury et al. 2006). Interestingly, populations in mainland Canada (i.e., Nova Scotia, Prince Edward Island, and New Brunswick) are not subject to consistent onshore winds and are characterized by significantly lower genetic structure and higher gene flow. One hypothesis for regional differences in gene flow between Newfoundland and mainland populations is that onshore winds and topography effectively retain weakly swimming, younger larvae until active behaviour can contribute significantly.

In conclusion, we observed short-distance larval dispersal in coastal smelt despite an extensive planktonic larval period. Retention appears to be the result of an ontogenetic shift in vertical behavior that coincides with seasonal changes in river inflow and predominant onshore winds. Such retention effectively restricts dispersal between estuaries, resulting in significant population structure. We suggest that larval dispersal in smelt is a complex interaction of seasonal changes in estuarine inflow and outflow, wind forcing, and ontogenetic shifts in swimming ability and behavior.

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References

- Able, K.W. 2005. A reexamination of fish estuarine dependence: a reexamination of connectivity between estuarine and open habitats. *Estuar. Coast. Shelf Sci.* **64**: 5–17.
- Bakun, A. 1996. Patterns in the ocean. Ocean processes and marine population dynamics. California Sea Grant College System, University of California, La Jolla.
- Beamish, F.W.H. 1978. Swimming capability. *In* Fish physiology. Academic Press, New York. pp. 101–187.
- Bennett, W.A., Kimmerer, W.J., and Burau, J.R. 2002. Plasticity in vertical migration by native and exotic estuarine fish in a fluctuating low salinity zone. *Limnol. Oceanogr.* **47**: 1496–1507.
- Bernatchez, L. 1997. Mitochondrial DNA analysis confirms the existence of two glacial races of rainbow smelt *Osmerus mordax* and their reproductive isolation in the St. Lawrence River estuary (Quebec, Canada). *Mol. Ecol.* **6**: 73–83.
- Bernatchez, L., and Martin, S. 1996. Mitochondrial DNA diversity in anadromous rainbow smelt, *Osmerus mordax* Mitchell: a genetic assessment of the member–vagrant hypothesis. *Can. J. Fish. Aquat. Sci.* **53**: 424–433.
- Blanton, J.O., Werner, F.E., Kapolnai, A., Blanton, B.O., Knott, D., and Wenner, E.L. 1999. Wind-generated transport of fictitious passive larvae into shallow tidal estuaries. *Fish. Oceanogr.* **8**(2): 210–223.
- Bradbury, I.R., and Snelgrove, P.V.R. 2001. Contrasting larval transport in demersal fish and benthic invertebrates: the roles of behavior and advective processes in determining spatial pattern. *Can. J. Fish. Aquat. Sci.* **58**: 811–823.
- Bradbury, I.R., Snelgrove, P.V.R., and Fraser, S. 2000. Transport and development of eggs and larvae of Atlantic cod, *Gadus morhua*, in relation to spawning time and location in coastal Newfoundland. *Can. J. Fish. Aquat. Sci.* **57**(9): 1761–1772.
- Bradbury, I.R., Snelgrove, P.V.R., and Pepin, P. 2003. Passive and active behavioral contributions to patchiness and spatial pattern during the early life history of marine fishes. *Mar. Ecol. Prog. Ser.* **257**: 243–245.
- Bradbury, I.R., Campana, S.E., Bentzen, P., and Snelgrove, P.V.R. 2004. Synchronized hatch and its ecological significance in rainbow smelt *Osmerus mordax* in St. Mary's Bay, Newfoundland. *Limnol. Oceanogr.* **49**: 2310–2315.
- Bradbury, I.R., Coulson, M., Campana, S.E., and Bentzen, P. 2006. Morphological and genetic differentiation in anadromous rainbow smelt: disentangling the effects of geography and morphology on gene flow. *J. Fish Biol.* **69**(Suppl. C): 95–114.
- Brett, J.R. 1964. The respiratory metabolism and swimming performance of young sockeye salmon. *J. Fish. Res. Board Can.* **21**: 1183–1226.
- Brown, C.A., Holt, S.A., Jackson, G.A., Brooks, D.A., and Holt, G.J. 2004. Simulating larval supply to estuarine nursery areas: how important are physical processes to the supply of larvae to the Aransas Pass inlet. *Fish. Oceanogr.* **13**(3): 181–196.
- Christy, J.H., and Morgan, S.G. 1998. Estuarine immigration by crab postlarvae: mechanisms, reliability and adaptive significance. *Mar. Ecol. Prog. Ser.* **174**: 51–65.
- Cowen, R.K., Lwiza, K.M.M., Sponaugle, S., Paris, C.B., and Olson, D.B. 2000. Connectivity of marine populations: open or closed? *Science (Washington, D.C.)*, **287**: 857–859.
- Cowen, R.K., Paris, C.B., and Srinivasan, A. 2006. Scaling of connectivity in marine populations. *Science (Washington, D.C.)*, **311**: 522–527.
- Criales, M.M., Wang, J., Browder, J.A., and Robblee, M.B. 2005. Tidal and seasonal effects on transport of pink shrimp post-larvae. *Mar. Ecol. Prog. Ser.* **286**: 231–238.
- Dame, R.F., and Allen, D.M. 1996. Between estuaries and the sea. *J. Exp. Mar. Biol. Ecol.* **200**: 169–185.
- Dauvin, J.C., and Dodson, J.J. 1990. Relationship between feeding incidence and vertical and longitudinal distribution of rainbow smelt larvae (*Osmerus mordax*) in a turbid well-mixed estuary. *Mar. Ecol. Prog. Ser.* **60**: 1–12.
- Davis, M.W. 2001. Behavioral responses of walleye pollock, *Theragra chalcogramma*, larvae to experimental gradients of sea water flow: implications for vertical distribution. *Environ. Biol. Fishes.* **61**: 253–260.
- de Graaf, M., Jager, Z., Vreugdenhil, C.B., and Elorche, M. 2004. Numerical simulations of tidally cued vertical migrations of flat-fish larvae in the North Sea. *Estuar. Coast. Shelf Sci.* **59**: 295–305.
- deYoung, B., Schillinger, D., Zedel, L., and Foley, J. 2000. Circulation through the narrows of St. John's Harbour: summer and fall 1999. Physics and Physical Oceanography Technical Report 2000-1. Memorial University, St. John's, Newfoundland.
- DiBacco, C., Sutton, D., and McConnico, L. 2001. Vertical migration behavior and horizontal distribution of brachyuran larvae in a low-inflow estuary: implications for bay–ocean exchange. *Mar. Ecol. Prog. Ser.* **217**: 191–206.
- Dodson, J.J., Dauvin, J.C., Ingram, R.G., and d'Anglejan, B. 1989. Abundance of larval rainbow smelt (*Osmerus mordax*) in relation to the maximum turbidity zone and associated macroplanktonic fauna of the middle St. Lawrence Estuary. *Estuaries*, **12**: 66–81.
- Fortier, L., and Leggett, W.C. 1982. Fickian transport and dispersal of fish larvae in estuaries. *Can. J. Fish. Aquat. Sci.* **39**: 1150–1163.
- Frechet, A., Dodson, J.J., and Powles, H. 1983. Use of variation in biological characters for the classification of anadromous rainbow smelt (*Osmerus mordax*) groups. *Can. J. Fish. Aquat. Sci.* **40**: 718–727.
- Gotceitas, V., Fraser, S., and Brown, J.A. 1997. The use of eelgrass beds (*Zostera marina*) by juvenile Atlantic cod (*Gadus morhua*). *Can. J. Fish. Aquat. Sci.* **54**: 1306–1319.

- Hare, J.A., Thorrold, S.R., Walsh, H., Reiss, C., Valle-Levinson, A., and Jones, C.M. 2005. Biophysical mechanisms of larval ingress into Chesapeake Bay. *Mar. Ecol. Prog. Ser.* **302**: 295–310.
- Hellweger, F.L., Blumberg, A.F., Schlosser, P., Ho, D.T., Caplow, T., Lall, U., and Honghai, L. 2004. Transport in the Hudson estuary: a modeling study of estuarine circulation and tidal trapping. *Estuaries*, **27**(3): 527–538.
- Kimmerer, W.J., Burau, J.R., and Bennett, W.A. 1998. Tidally oriented vertical migration and position maintenance of zooplankton in a temperate estuary. *Limnol. Oceanogr.* **43**: 1697–1709.
- Laprise, R., and Dodson, J.J. 1989. Ontogeny and importance of tidal vertical migrations in the retention of larval smelt *Osmerus mordax* in a well-mixed estuary. *Mar. Ecol. Prog. Ser.* **55**: 101–111.
- Large, W.G., and Pond, S. 1981. Open ocean momentum flux measurements in moderate to strong winds. *J. Phys. Oceanogr.* **11**: 324–336.
- Largier, J.L. 1993. Estuarine front: how important are they? *Estuaries*, **16**(1): 1–11.
- Lecomte, F., and Dodson, J.J. 2005. Distinguishing trophic and habitat partitioning among sympatric populations of the estuarine fish *Osmerus mordax* Mitchell. *J. Fish Biol.* **66**: 1601–1623.
- Lee, J.T., Coleman, R.A., and Jones, M.B. 2005. Vertical migration during tidal transport of megalopae of *Necora puber* in coastal shallow waters during daytime. *Estuar. Coast. Shelf Sci.* **65**: 396–404.
- Metaxas, A. 2001. Behavior in flow: perspectives on the distribution and dispersion of meroplanktonic larvae in the water column. *Can. J. Fish. Aquat. Sci.* **58**: 86–98.
- McKenzie, R.A. 1964. Smelt life history and fishery in the Miramichi, New Brunswick. *Bull. Fish. Res. Board Can.* No. 144.
- McLean, J.E., Hay, D.E., and Taylor, E.B. 1999. Marine population structure in an anadromous fish: life history influences patterns of mitochondrial DNA variation in the eulachon, *Thaleichthys pacificus*. *Mol. Ecol.* **8**: S143–S158.
- Nellbring, S. 1988. The ecology of smelts (genus *Osmerus*): a literature review. *Nord. J. Freshw. Res.* **65**: 116–145.
- O'Donnell, J.O. 1993. Surface fronts in estuaries: a review. *Estuaries*, **16**(1): 12–39.
- Ohman, M.D., Frost, B.W., and Cohen, E.B. 1983. Reverse diel vertical migration: an escape from invertebrate predators. *Science (Washington, D.C.)*, **220**: 1404–1406.
- Ouellet, P., and Dodson, J.J. 1985a. Tidal exchange of anadromous rainbow smelt (*Osmerus mordax*) larvae between a shallow spawning tributary and the St. Lawrence Estuary. *Can. J. Fish. Aquat. Sci.* **42**: 1352–1358.
- Ouellet, P., and Dodson, J.J. 1985b. Dispersion and retention of anadromous rainbow smelt (*Osmerus mordax*) larvae in the middle estuary of the St. Lawrence River. *Can. J. Fish. Aquat. Sci.* **42**: 332–341.
- Pearre, S. 2003. The hunger/satiation hypothesis in vertical migration: history, evidence and consequences. *Biol. Rev. Camb. Philos. Soc.* **78**: 1–79.
- Poulin, E., Palma, A.T., Leiva, G., Navarez, D., Pacheco, R., Navarrete, S.A., and Castilla, J.C. 2002. Avoiding offshore transport of competent larvae during upwelling events: the case of the gastropod *Concholepas concholepas* in Central Chile. *Limnol. Oceanogr.* **47**: 1248–1255.
- Pritchard, D.W. 1967. What is an estuary: physical viewpoint. *In Estuaries. Edited by G.H. Lauf.* AAAS Press, Washington, D.C. pp. 3–5.
- Rogers, H.M. 1940. Occurrence and retention of plankton with the estuary. *J. Fish. Res. Board Can.* **5**: 164–171.
- Ryland, J.S. 1963. The swimming speeds of plaice larvae. *J. Exp. Biol.* **40**: 285–299.
- Sale, P.F., Cowen, R.K., Danilowicz, B.S., Jones, G.P., Kritzer, J.P., Lindeman, K.C., Planes, S., Polunin, N.V., Russ, G.R., and Sadovy, Y.J. 2005. Critical science gaps impede use of no-take fishery reserves. *Trends Ecol. Evol.* **20**: 74–80.
- Sarabun, C.C. 1993. Observations of a Chesapeake Bay tidal front. *Estuaries*, **16**: 68–73.
- Schultz, E.T., Cowen, R.K., Lwiza, K.M.M., and Gospodarek, A.M. 2000. Explaining advection: do larval bay anchovy (*Anchoa mitchilli*) show selective tidal stream transport? *ICES J. Mar. Sci.* **57**: 360–371.
- Scott, W.B., and Scott, M.G. 1988. Fishes of Atlantic Canada. *Can. Bull. Fish. Aquat. Sci.* No. 219.
- Scully, M., Friedrichs, C., and Brubaker, J. 2005. Control of estuarine stratification and mixing by wind-induced straining of the estuarine density field. *Estuaries*, **28**(3): 321–326.
- Sheng, J., and Thompson, K.R. 1996. Summer surface circulation on the Newfoundland and Grand Banks: the role of local density gradients and remote forcing. *Atmosphere-Ocean*, **34**: 257–284.
- Sinclair, M. 1988. Marine populations. An essay on population regulation and speciation. *Books in Recruitment Fishery Oceanography*, University of Washington Press, Seattle, Wash.
- Sirois, P., and Dodson, J.J. 2000. Critical periods and growth-dependent survival of larvae of an estuarine fish, the rainbow smelt *Osmerus mordax*. *Mar. Ecol. Prog. Ser.* **203**: 233–245.
- Sirois, P., Lecomte, F., and Dodson, J.J. 1998. An otolith-based back-calculation method to account for time-varying growth rate in rainbow smelt, *Osmerus mordax*, larvae. *Can. J. Fish. Aquat. Sci.* **55**: 2662–2671.
- Sokal, R.R., and Rohlf, F.J. 1995. *Biometry*. W.H. Freeman & Co., San Francisco, Calif.
- Thorrold, S.R., Latkoczy, C., Swart, P.K., and Jones, C.M. 2001. Natal homing in a marine fish metapopulation. *Science (Washington, D.C.)*, **291**: 297–299.
- Urho, L. 2002. Characters of larvae — what are they? *Folia. Zool.* **51**: 161–186.