Evolutionary Ecology Research, 2004, **6**: 631–658

Role of early life-history constraints and resource polymorphism in the segregation of sympatric populations of an estuarine fish

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ABSTRACT

In marine ecosystems, evolutionary studies of reduced gene flow among fish populations in the absence of strong physical barriers have tended to focus on mechanisms to increase survival of the critical early life-history stages. In contrast, ecological resource partitioning among later life-history stages has received considerable attention in studies of freshwater ecosystems. Few studies have considered both mechanisms simultaneously and none have documented their influence on sympatric co-existence in an estuarine environment. Despite the fact that they are highly mobile and exploit a dispersive environment, the two sympatric populations of rainbow smelt (*Osmerus mordax*) found in the St. Lawrence Estuary, Canada, appear to be spatially segregated along the north (north-shore population) and south (south-shore population) shores of the estuary. The existence of population-specific spawning sites and times as well as nursery areas would indicate selective pressures acting on the early life-history stages. If resource partitioning contributes to segregation, we would also expect to identify population-specific morphological adaptations correlated with distinct feeding niches. Spawning of the two populations was temporally and spatially segregated. The north-shore population spawns approximately 2 weeks before the south-shore population directly on shallow shoals in the fluvial estuary, whereas the south-shore population spawns in small tributaries along the south shore of the middle estuary. Larval populations are also clearly segregated among discrete nursery habitats, representing the first documented case of larval segregation between sympatric populations of a fish with a pelagic larval stage. Larvae of the north-shore population exploited all channel habitats within the estuarine turbidity maximum and to a minor degree adjacent shoals and small bays. In contrast, larvae of the south-shore population were largely confined to the south shore shoals and large shallow bays at the downstream limit of the estuarine turbidity maximum. Adult smelt populations are morphologically distinct and reflect a benthic/pelagic dichotomy in morphology. However, the phenotype–habitat association is not paralleled by the expected benthivorous/planktivorous dichotomy in diet and feeding apparatus morphology. These population-specific adaptations may serve to maximize foraging efficiency within distinct environmental settings (deep channels *vs* shoals) rather than favouring

Keywords: adult morphology, benthic/pelagic ecotypes, diet overlap, early life-history constraints, ecological speciation, larval retention areas, mtDNA, *Osmerus mordax*, rainbow smelt, recruitment, St. Lawrence middle estuary.

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the exploitation of distinct prey. Selective pressures acting on the survival of the pelagic early life-history stages, as well as resource polymorphisms occurring at later stages, contribute to maintaining genetic isolation between rainbow smelt populations.

INTRODUCTION

Aquatic systems have provided many examples of reduced gene flow among populations despite their lack of strong physical barriers. Notable examples include the development of the great rift cichlids species flock (Echelle and Kornfield, 1984; Meyer, 1993), the occurrence of sympatric species pairs in northern temperate lakes (Skúlason and Smith, 1995; Smith and Skúlason, 1996; Taylor, 1999) and overlapping marine species pairs/populations (Grant *et al.*, 1988; Johns and Avise, 1998; Roques *et al.*, 1999, 2001; Ruzzante *et al.*, 1999; Stepien *et al.*, 2000; Withler *et al.*, 2001). However, evolutionary studies of such cases have tended to focus on different mechanisms acting in marine and freshwater systems (for reviews, see Palumbi, 1994; Robinson and Wilson, 1994) that are rarely studied simultaneously (but see Chouinard and Bernatchez, 1998). There are numerous examples in freshwater systems of ecological resource partitioning among adult or juvenile morphotypes. Such ecological processes are pivotal in the evolution of species by favouring divergent natural selection that ultimately leads to reproductive isolation (Schluter, 1996, 1998, 2001). Two reviews (Robinson and Wilson, 1994; Smith and Skúlason, 1996) list several examples of sympatric populations for which co-existence is correlated with the exploitation of different ecological resources often related to benthic/pelagic habitat differences. Studies on sticklebacks, salmoniforms (salmon, whitefish, trout, charr and smelts), centrarchids and cichlids have provided much of the evidence concerning resource partitioning among sympatric morphotypes (Robinson and Wilson, 1994). Although trophically dichotomous pelagic and benthic morphotypes are common in freshwater examples of sympatric species pairs studied to date, other phenotype–resource associations have been identified, namely depth distribution (Jacobson and Vetter, 1996; Turgeon *et al.*, 1999) and spatial distribution (Potvin and Bernatchez, 2001).

In marine systems, little is known about the mechanisms leading to genetic isolation of sympatric pairs. Generally speaking, studies of genetic isolation among marine populations have emphasized the impact of larval-mediated gene flow due to an extended pelagic stage (Doherty *et al.*, 1994, 1995), potential barriers to dispersion (Bowen and Grant, 1997; Grant and Bowen, 1998; Waters *et al.*, 2000), local recruitment (Jones *et al.*, 1999; Swearer *et al.*, 1999, 2002; Warner and Cowen, 2002), habitat preference and physical oceanography (Rocha-Olivares and Vetter, 1999; Muss *et al.*, 2001). Marine sympatric species pairs may also be the result of different colonization patterns following the allopatric speciation of isolates (Grant *et al.*, 1988).

Since recruitment (i.e. survival to the adult stage) is essential for population persistence, many marine fishes exploit spawning sites that favour the transport of larvae into highly productive areas to maximize early survival rates. Many of these zones are spatially well-defined and they include estuaries, gyres and upwelling zones (Cushing, 1975; Sinclair, 1988; Mann, 1993). Since the beginning of the nineteenth century (e.g. Hjort, 1914), larval survival has been considered the principal factor controlling marine-fish population dynamics, as over 99% of the young do not survive the larval stage (Dahlberg, 1979). Spawning locations, spawning times and larval nursery locations are not randomly

associated; only specific combinations may allow population persistence and these might induce selective pressures leading to population isolation. For pelagic species relying on nursery areas to sustain large population sizes (e.g. Atlantic herring), Iles and Sinclair (1982) have proposed that the number of populations (stocks) of a species is defined by the number of physical settings in which populations can complete their life cycle. Formally stated as the Member-Vagrant hypothesis (Sinclair, 1988), its proof resides in a correlation between the number of stocks and the number of nursery areas.

As both resource partitioning and early life-history constraints may promote genetic isolation among sympatric marine populations, here we investigate the two mechanisms to account for the maintenance of genetic isolation between sympatric rainbow smelt (*Osmerus mordax*) populations in the St. Lawrence middle estuary. Two major mtDNA clades (Acadian [A] and Atlantic [B]) representing two glacial races of rainbow smelt occur in northeastern North America (0.7% net sequence divergence estimate; Taylor and Dodson, 1994). The St. Lawrence middle estuary is the secondary contact zone between the two glacial races, contact occurring approximately 8000 years ago (Bernatchez, 1997). Based on the frequency of mtDNA clades found among samples of middle estuary smelt (either from spawning runs or commercial fisheries), two genetically differentiated populations have been identified (pairwise $Fst = 0.178$, $P < 0.001$; Bernatchez and Martin, 1996). Adults appear to be spatially segregated along the two shores, but samples used in the former study (Bernatchez and Martin, 1996) cannot rule out the possibility of mixing within the system. The north-shore population (NSP) is composed of 87.1% clade B, whereas the south-shore population (SSP) is composed of 80.9% clade A (Bernatchez and Martin, 1996). Based on the high-energy, macrotidal nature of the estuary, conditions should have favoured the mixing of the two founding races. Pigeon *et al.* (1998) reported that larvae of both populations were found throughout the middle estuary, but the rarity of SSP larvae cannot preclude the possibility that this population exploits an unknown nursery area. The dispersal capacity of the adult stage, in the order of 40 km per day in estuaries (Vladykov and Michaud, 1957; Magnin and Beaulieu, 1965), and their 3-month pelagic larval period (Able, 1978; Dodson *et al.*, 1989), indicate high dispersal potential. Therefore, the observation that two sympatric populations co-exist suggests the operation of one or more isolation mechanisms. Outside the middle estuary, the two races have hybridized, showing that divergence during past glaciations has not reached the level of reproductive isolation (Baby *et al.*, 1991; Taylor and Bentzen, 1993a,b; Taylor and Dodson, 1994; Bernatchez, 1997).

Estuarine ecosystems are hydrodynamically energetic and highly heterogeneous in terms of physical habitat and community structure. The existence of population-specific spawning sites and nursery areas within this kind of system would indicate the prevalence of selective pressures on early life-history stages, as documented previously for marine species. On the other hand, if resource partitioning in post-metamorphic fish is the primary cause of sympatric co-existence, we would expect to identify population-specific adaptations that correlate to distinct niches, as documented primarily in freshwater species. As the nature of estuaries differs from that of freshwater systems, any such resource polymorphism may be expressed differently. Although theoretical and field investigations have shown that both mechanisms can promote genetic isolation, no studies have documented their relative influence on sympatric populations in an estuarine setting. Estuaries may offer a different balance of ecological processes governing sympatric divergence where resource partitioning and early life-history constraints may play distinctive roles.

To address these issues, we examined the spatial and temporal exploitation of distinct estuarine habitats by the two smelt populations. Segregation between the populations was assessed and quantified for the entire duration of the larval and early juvenile stages. Spawning sites, spawning periods and nursery areas for each population were identified and the extent of population mixing evaluated. Resource partitioning was assessed by comparing the morphological characteristics, spatial distribution and feeding niches of adult smelt.

METHODS

Study site

The St. Lawrence middle estuary stretches over 150 km from Orleans Island to the Saguenay Fjord but measures only 17 km wide on average (Fig. 1). The sharpest salinity gradient (0 practical salinity units [PSU] to 20 PSU) is found over 50 km in the upstream portion of the middle estuary. Estuarine two-layer circulation in this portion of the estuary contributes to the creation of the estuarine turbidity maximum, where concentrations of suspended particulate matter and plankton are maximal. River outflow (annual outflow at Québec City is 12,600 $m^3 \cdot s^{-1}$; SLC, 1996), topography and tidal amplitude (6.9 m at spring high tides; Fisheries and Oceans, 1990) result in a highly dynamic oceanographic setting with tidal current speeds of up to 3.5 $m \cdot s^{-1}$ (Frénette *et al.*, 1995). Bathymetry of the middle estuary is characterized by important shallow mud flats along the south shore (e.g. Ste-Anne Bay covers 176 km^2; D'Anglejan *et al.*, 1981) and deep channels (15–100 m deep) along a steep rocky shoreline on the north shore. Although shallower than the north shore channel, middle and south shore channels are also present. The fluvial estuary (influenced by tidal movement without saline intrusion), stretching 160 km upstream from the middle estuary, is a narrow river-like region with some important shallow shoal areas.

Location of spawning grounds

All known spawning locations in the St. Lawrence Estuary are located in south-shore tributaries and are exploited by smelt belonging to the south-shore population (Trencia, 1991; Bernatchez and Martin, 1996; Trencia and Fournier, 1999). To locate the spawning sites of the north-shore population, we focused our survey in the fluvial estuary due to historical records demonstrating high abundance of smelt in this region during the fall season. The lower section of the fluvial estuary was surveyed three times in spring 1997 to detect the presence of eggs and larvae. The first cruise, on 16 May, was conducted between the western tip of Orleans Island to 140 km upstream in the fluvial estuary, covering approximately 100 km (position +40 to +140 km on Fig. 1). Two additional cruises (19 May and 24 May) concentrated on the 60-km stretch of the fluvial estuary located immediately upstream of Orleans Island (from +40 to +100 km on Fig.1). Between five and nine sites were surveyed along the fluvial estuary depending on the date. A minimum of two samples was taken at each site in the main channel. Larvae were collected with 1-m diameter plankton nets (500 μm mesh size). The entire water column was sampled by 15-min step oblique tows and the volume of filtered water was measured by a flowmeter (General Oceanics Inc.) fixed to the net. Specimens were preserved in 95% ethanol for sorting and

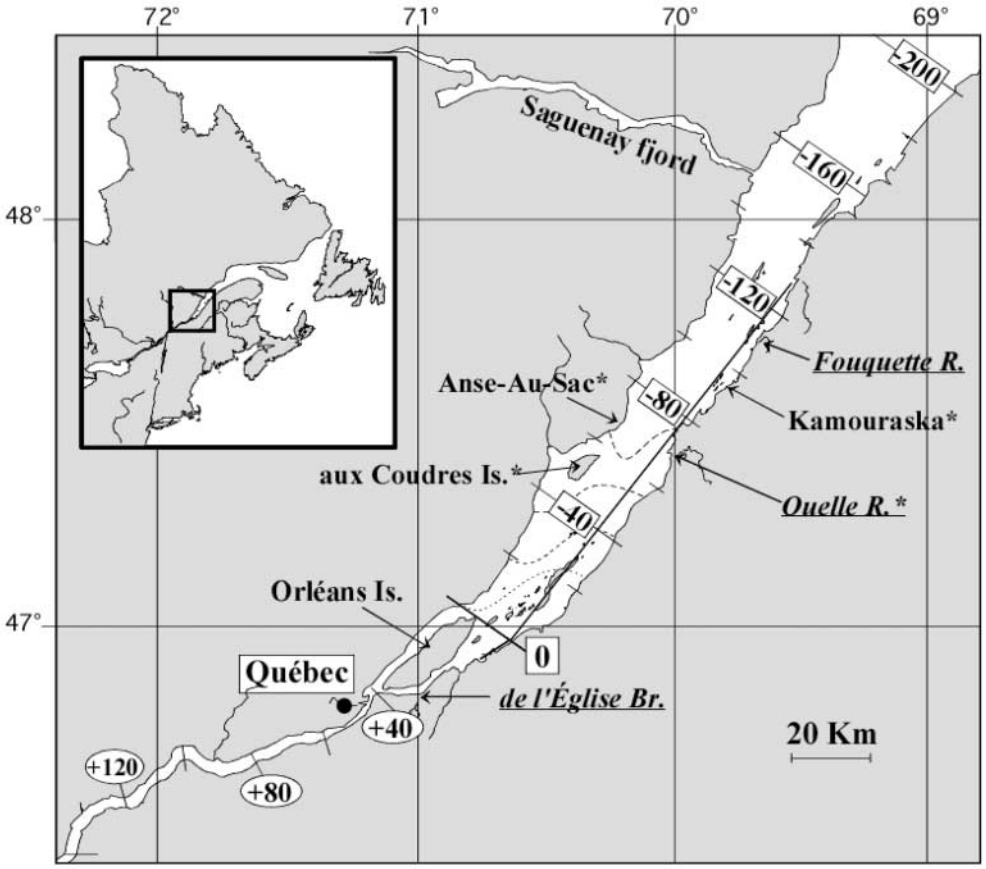

Fig. 1. Study area showing distances measured from the upstream extent of saline intrusion (positive values are located in the fluvial estuary, negative values in the middle estuary), the location of the south-shore population spawning grounds (underlined names), position of isohalines at high tide (starting with the smaller dotted lines; 0.5 PSU, 10 PSU, 20 PSU and 30 PSU) and sites where adults were collected during 1997–1998 (marked with an asterisk).

genetic identification. Population identification of drifting larvae was confirmed by the analysis of mtDNA-clade frequency.

Although spawning smelt can be easily seen and sampled in the small, shallow spawning tributaries exploited by the south-shore population, aggregations of spawning fish cannot be observed directly in the St. Lawrence River. Rather, spawning sites of the north-shore population in the fluvial estuary were inferred based on the drift pattern of yolk-sac larvae of known age. Net water movement in the fluvial estuary is approximately 25 km per day downstream (Paquet, 1993). We sampled all sites located in the fluvial estuary during the ebb tide. The most upstream sites where yolk-sac larvae were still present were considered close to spawning sites. To confirm the proximity of the spawning site to larvae sampling sites, a subsample of larvae were aged with otoliths, using the protocol of Sirois *et al.* (1998). Tributaries located in this region were surveyed to identify evidence of egg deposition.

Location of larval nurseries

Genetic analysis of larvae sampled in the channels of the middle estuary revealed that they almost all belong to the north-shore population (Pigeon *et al.*, 1998). Thus, no significant concentration of SSP larvae has yet been found, suggesting either very low abundance or the fact that they are found elsewhere. The only areas not previously sampled for larvae in the estuary were shallow habitats (i.e. <5 m in depth). Thus, in 1997, all shallow areas of the middle estuary were surveyed on three occasions, 21–23 May (11 sites), 21–23 June (28 sites) and 21–23 September (28 sites). To quantify the extent and duration of larval retention in southern shoals, we used a finer sampling grid in 1998 (35 sites) concentrating on south-shore shoals from Orleans Island to nearly 200 km downstream (Fig. 1). We sampled at four periods, 21–23 May, 18–21 June, 17–19 July and 18–21 August.

Except for the first cruise in 1997 (21 May), all samples from shoals were paired with an adjacent sample in the main channel. All the samples were taken between mid-flood tide and mid-ebb tide when tidal flats were submerged. Samples taken in the main channel used the same procedures as described for spawning site localization. For samples taken in shallow water (<3 m), we used a standard 1-m diameter plankton net (mesh size 500 μm) equipped with a flowmeter (General Oceanics Inc.). The net was mounted laterally to minimize net avoidance caused by the bow wave. Samples were conserved in 95% ethanol before sorting and genetic analysis.

Morphological analysis

The morphology of the two populations was compared using principal component analysis and a discriminant analysis. Seventy-five adults collected from each spawning tributary in 1998 were used in the analysis. Samples were obtained from all spawning sites of the south-shore population – namely, de l'Église Brook, Ouelle River and Fouquette River (Fig. 1). Adults of the north-shore population could not be caught on spawning sites, as their early spawning coincided with the spring flood. However, post-spawning NSP adults were caught at Aux Coudres Island on 16 April at a time when no other population had yet started to spawn. The genetic identity of all individuals caught in 1998 was confirmed by mtDNA analysis. Eighteen morphometric variables and two meristic counts were calculated (Fig. 2) using digitized pictures processed with an image analysis system (SigmaScan 3.0). The selection of morphological variables was based on two criteria: relevance to trophic ecology (see Gatz, 1979) and their independence of abdominal distention. This was done to avoid any bias due to sex, stages of sexual maturity or levels of gut fullness.

Principal component analysis was used to remove the size effect on morphometric variables. Moreover, to minimize bias related to allometry (e.g. bias caused by the comparison of small versus large fishes; see Rincón, 2000), the analysis included smelt representing all adult cohorts found in the populations studied.

Morphometric variable residuals about the first principal component and meristic counts were used together in a discriminant analysis as both are independent of fish size. A stepwise discriminant analysis was carried out to delineate populations (by maximizing Euclidean distance between the north-shore and south-shore population). The discriminant function was then used to evaluate the percentage of reclassification and *a posteriori* error estimates for the discriminant analysis were used to assess the robustness of observed differences.

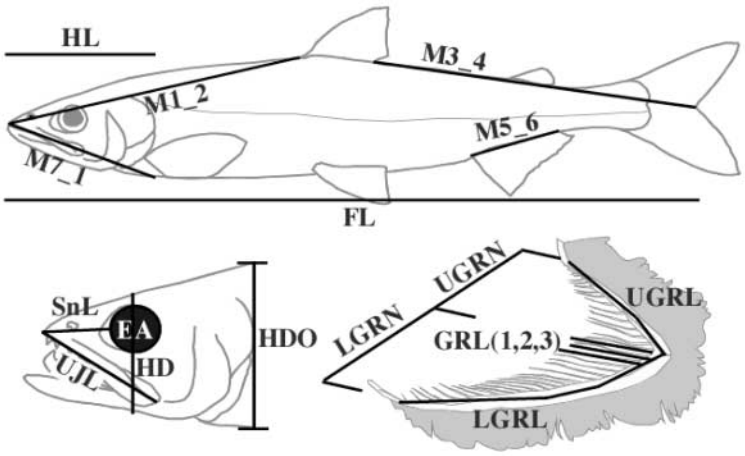

Fig. 2. Measurements taken on adult smelt. *Abbreviations*: FL = fork length; HL = head length; HDO = head depth behind the operculum; M1_2 = distance between snout and dorsal fin; M3_4 = distance between dorsal fin to the end of the caudal fin fork; M5_6 = anal fin length; M7_1 = distance from pectoral fin to snout; HD = head depth; UJL = upper jaw length; SnL = snout length; EA = eye area; UGRN = upper gill raker number; LGRN = lower gill raker number; UGAL = upper gill arch length; LGAL = lower gill arch length; GRL1 = first gill raker length; GRL2 = second gill raker length; GRL3 = third gill raker length.

Student's *t*-tests were used to compare morphometric and meristic values obtained for the two populations. Sequential Bonferroni corrections were used to correct for multiple tests. To diminish the size effect, log-transformed ratios {√(variable/length)} were used for Student's *t*-tests (Reist, 1985).

Feeding regimes of St. Lawrence middle estuary smelt

The gut contents of 180 adults were analysed. The first sample set was collected in October 1997 and included 40 adults from Aux Coudres Island and 40 adults caught along the south shore on the shoals near Ouelle River (Fig. 1). These two sites face each other and are separated by 17 km. The second sample set was collected in August 1998; 25 smelt per site were analysed and included two locations along the north shore (Aux Coudres Island and Anse-au-sac) and two from the south shore (Ouelle River and Kamouraska shoals; Fig. 1). For the 1998 samples, we identified population admixture at each of theses sites using mixed stock analysis on adults. Prey items were identified to the lowest possible taxonomic level; occurrence, dry weight and abundance were recorded. To prevent bias in the calculation of occurrence created by extreme observations (i.e. very few large prey items or many small prey items in a small minority of gut contents), we determined for each fish the proportion (for either number or weight) of each prey item and then averaged to calculate the sample estimate of prey occurrence. Schoener's (1968) niche overlap index (D) was calculated using individually adjusted proportions of prey items in the diet. Two estimates were used to compare diet: (1) numbers of each prey item and (2) weight. The Mann-Whitney U-test was used to determine whether any differences observed are related to population-specific feeding niches (as expected for ecotypes) or site-specific regimes (as expected for opportunistic feeding).

Genetic analysis

Samples of smelt larvae containing fewer than 200 individuals were entirely sorted. Samples containing more than 200 larvae were partitioned. Between 25 and 50 individuals per sample were used for genetic analysis.

Identification of mtDNA clades was accomplished with the test developed by Pigeon *et al.* (1998) adapted for the present study. A small 288-pb fragment of the ND6 subunit of NADH dehydrogenase was used for the polymerase chain reaction (PCR)/restriction fragment length polymorphisms (RFLP) analysis. A diagnostic restriction site (recognized by *Dde*I) was used to generate either the clade A (Acadian Race) or B (Atlantic Race) electrophoretic migration pattern. Briefly, entire individuals were used for larvae smaller than 15 mm, and 100 μg of tissue was used for larvae >15 mm. After two 15-min soakings in distilled water, tissue was placed in 50 μl of extraction buffer (10 nM Tris-HCl (pH 8.0), 50 mM KCl, 0.5% tween 20, proteinase K 250 $\mu g \cdot ml^{-1}$). Incubation was performed at 65°C for 4 h followed by protein denaturation (95°C for 15 min). Aliquots where centrifuged at 13,000 $rev \cdot min^{-1}$ for 15 min. The aqueous phase containing the DNA was then precipitated overnight at −20°C with 2 × volume of 95% ethanol. Tubes where centrifuged for 30 min (13,000 $rev \cdot min^{-1}$) and the precipitate was then left to dry before resuspension in TE buffer (Tris 10 mM, pH 8.0; EDTA 1 mM).

Amplification was carried out in 50 μl with 200 μM of each dNTP, 400 mM of each primer (ND56R450V and NDR56R250 from Pigeon *et al.*, 1998), 2.5 mM $MgCl_2$, 10 mM Tris-HCl (pH 8.3), 50 mM KCl and 500–1000 ng of DNA. The PCR was performed with an Ampliton II Thermocycler (Thermolyne) using the following profile: preliminary denaturation at 95°C for 2 min and then 35 cycles of amplification (denaturation at 94°C for 1 min, annealing at 45°C for 1 min and elongation at 72°C for 45 s). A final extension step was performed at 72°C for 10 min.

Restriction fragments were generated by digestion with *Dde*I. Digestion of amplified DNA (10 μl of amplified DNA) was completed overnight at 37°C in the presence of 0.5 μl *Dde*I (with 4 μl OPA 10 × buffer) in a total volume of 20 μl. The DNA fragments were electrophoretically separated on 2% agarose gels with ethidium bromide for 3 h at 80 V and banding patterns were revealed under UV.

Mixed stock analyses

The contribution of the two populations in samples was assessed using the method of Lane *et al.* (1990). This method compared the frequency of an allele in a given sample to the frequency of this allele in the reference spawning populations. The rationale is that departure from the frequency of a reference population must be caused by the presence of individuals from the other population. For a two-allele/two-population array, the contribution of population #1 in a sample is defined as:

$$X = (P_m - P_2)/(P_1 - P_2)$$

where P_m is the frequency of haplotype A in the sample and P_1 and P_2 are the frequencies of the same haplotype in reference populations #1 and #2, respectively.

As error estimates based on Taylor series expansions used by Lane *et al.* (1990) tend to minimize such estimates, we provided our own error estimates based on simulation. In total, 1000 bootstrap resamplings were obtained for various sample sizes (n = 5 to 500) obtained

from known population admixtures (100% NSP, 75% NSP, 50% NSP, 25% NSP and 100% SSP); the total number of individuals within each simulated sample was 1000. Haplotype frequencies (baseline) used to create these 'mixed' samples were set by the observed frequencies found in 'pure' samples of both populations (see below). Standard deviations were calculated for each population admixture and for sample sizes. As the mixed stock is expressed as a relative percentage of each population, the standard deviation is equivalent to an error estimate expressed as a percentage.

The compositions of both mtDNA alleles of the two populations (NSP, SSP) reported by Bernatchez (1997) and by Pigeon *et al.* (1998) were not based solely on samples of spawning adults. Thus, bias related to the mixing of individuals on feeding grounds was likely to occur. To correct this, we analysed 50 adults caught on each of the three spawning sites of the south-shore population in 1998 to generate an unbiased estimate of mtDNA clade frequencies for this population. For the north-shore population, we used 250 drifting larvae captured in 1997 in proximity to the NSP spawning site and before the SSP hatching period.

RESULTS

Location of spawning ground

The spawning grounds of the south-shore population are located within three tributaries of the south shore. No other sites have been reported despite important efforts to identify spawning runs within this system (Trencia, 1991; Trencia and Fournier, 1999). The spawning grounds of the north-shore population are not located in small tributaries but rather are located upstream of the middle estuary in the fluvial estuary in the vicinity of the Neuville Shoals (between +70 to +90 km; Fig. 1). High concentrations of larvae were found in this region (Table 1) at times when no larvae from the spawning sites of the south-shore population had been reported. The highest concentration (2.26 larvae per m^3) was found approximately 80 km upstream of the middle estuary. The bulk of larvae drifted downstream from 16 May (maximum 80 km upstream of the middle estuary) to 19 May (2.14 larvae per m^3, 40 km upstream of the middle estuary). The genetic analysis of 250 larvae from the survey showed that mtDNA allele B dominated samples. The haplotypic composition of this sample of larvae (88.8% B) was not different ($\chi^2 = 0.195$, $P > 0.659$) from the original haplotype frequency described for the north-shore population (87.1% B) based on adults sampled in the middle estuary by Bernatchez and Martin (1996). As no population mixing is likely to occur within our larval sample, the haplotypic composition of 11.2% A/88.8% B for the north-shore population was thus used for all further mixed stock analyses.

Based on otolith microstructure, larvae caught near Neuville on 16 May were recently hatched (average 0.5 days of age; Table 1). Since the net movement of water masses is estimated at 25 km per day in this region (Paquet, 1993), the spawning site must necessarily be within this zone. Further downstream, the mean age increased and conformed to the downstream rate of advection (Table 1).

Eggs were found only in high concentrations during the cruise of 16 May (Table 1). These demersal eggs were viable and close to hatching. Hatching of viable eggs in the water column may explain the virtual absence of eggs downstream of the Neuville shoals (i.e. downstream of +70 km; Fig. 1).

Table 1. Densities of eggs and larvae ($n \cdot m^{-3}$) sampled on three occasions in 1997, number of larvae genotyped, relative frequency of the two mtDNA clades and age of larvae

	16 May						19 May		24 May	
	Density ($n \cdot m^{-3}$)			Clade frequency			Density ($n \cdot m^{-3}$)		Density ($n \cdot m^{-3}$)	
Station[a]	Larvae	Eggs	*n*	%A	%B	Age (days)[b]	Larvae	Eggs	Larvae	Eggs
+40 North	0.41	0.00	33	6.1	93.9	2.4 (0.51)	2.14	0.00	0.72	0.4
+40 South	0.63	0.01	40	5.0	95.0		1.57	0.00	0.18	0.0
+55 North	0.94	0.00	47	8.5	91.5	1.3 (0.65)	1.12	0.00	0.10	0.0
+55 South	0.45	0.01	36	11.1	88.9		1.07	0.00	0.18	0.0
+60 North							0.07	0.00		
+60 Middle							1.03	0.00		
+60 South							<0.01	0.00		
+65 North							0.03	<0.01		
+65 Middle							0.01	0.00		
+65 South							0.00	0.00		
+70 North	0.42	0.04	45	20.0	80.0	1.3 (0.49)	0.14	0.00	0.03	0.0
+70 Middle1							0.00	0.00		
+70 Middle2							0.67	0.00		
+70 South	0.02	0.00					0.00	0.00	0.02	<0.01
+80 North	2.26	0.13	49	14.3	85.7	0.5 (0.67)	0.02	0.00	0.0	0.0
+80 South	0.02	0.01					<0.01	0.00	0.0	0.0
+90 North	<0.01	<0.01					0.01	0.00	0.0	0.0
+90 South	0.01	0.00					0.00	0.00	0.0	0.0
+105 North	<0.01	0.00								
+105 South	0.01	0.00								
+115 North	0.00	<0.01								
+115 South	0.00	<0.01								
+125 North	<0.01	0.00								
+125 South	0.01	0.00								
+140 North	0.00	0.00								
+140 South	0.00	0.00								

[a] Station codes refer to the position (north, middle, south) and distance (km) upstream from the middle estuary (see Fig. 1).
[b] Standard deviation in parentheses.

No tributaries containing eggs were found in this region. Moreover, these tributaries were also surveyed in 1998, 1999 and 2000 without detecting spawning activities or egg deposits (F. Lecomte, J.J. Dodson and S. George, unpublished data). Many of the shallow shoals of this region (roughly 35 km^2) appear to be perfectly good spawning habitat for smelt. This large potential spawning habitat may explain the high abundance of larvae found nearby.

Spawning date was back-calculated using the summation of °C*days needed for hatching (177 °C*days for average temperature below 10°C; McKenzie, 1964; Akielaszek *et al.*, 1985). Using daily water temperature measurements, summation of 177 °C*days from larvae

captured on 16 May (larvae up to 3 days old) shows that spawning had already started by the second week of April 1997, at least 2 weeks before the start of spawning of the south-shore population in south-shore tributaries.

Mixed stock analysis

Baseline haplotype composition for the south-shore population was obtained by the identification of 50 adults from each spawning run (Fouquette River, Ouelle River and de l'Église Brook; Fig. 2). The distribution of the two mitochondrial DNA clades among the three spawning runs of the south-shore population are similar ($\chi^2 = 0.038$, $P > 0.981$) to that found by Bernatchez and Martin (1996) in spawning-site samples (Table 2).

Error estimates obtained for sample sizes typical of the ones used in this study (20–30 individuals) varied from 7.5% to 16% (i.e. standard deviation of 0.075 to 0.16) depending on the population admixture (Fig. 3). Standard deviations reached the 5% level for any population admixture only with sample sizes greater than 200. The small error associated with the use of only one diagnostic restriction enzyme to identify populations thus proved that the method is sufficiently robust to assess population composition within samples of 20–30 fish.

Location of larval nurseries

Larval abundance estimates for 1997 showed high concentrations of larvae in shallow areas along the south shore (Fig. 4), maximum concentrations peaking at 2.6 individuals per m^3 in July. In 1998, the concentrations of larvae along south-shore shoals reached 66.7 individuals per m^3 in May immediately after hatching, subsequently decreasing rapidly to 2.9 individuals per m^3 in June. From June onwards, maximal concentrations appear to be relatively stable, as abundance was maintained at 1.6 individuals per m^3 in July and 1.2 individuals per m^3 in August (Fig. 5). Within shallow areas, larvae were found during the

Table 2. Origin of samples used to compare mtDNA clade distribution among sympatric populations, type of individuals analysed (larvae, post-spawners, spawners), number of observations, mtDNA clade frequencies and population-mean values used for mixed stock analyses

				Clade frequency		
Site	Type	Population	*n*	%A	%B	Reference
Neuville	Larvae	NSP	250	11.2	88.8	This study
Coudres Island	Post-spawners	NSP	50	18.0	82.0	This study
de l'Église Brook	Spawners	SSP	50	80.0	20.0	This study
de l'Église Brook	Spawners	SSP	36	75.0	25.0	Bernatchez *et al.* (1995)
Ouelle River	Spawners	SSP	50	82.0	18.0	This study
Ouelle River	Spawners	SSP	36	80.6	19.4	Bernatchez *et al.* (1995)
Fouquette River	Spawners	SSP	50	78.0	22.0	This study
Mean	Adults	SSP	222	79.3	20.7	
Mean	Larvae	NSP	250	11.2	88.8	

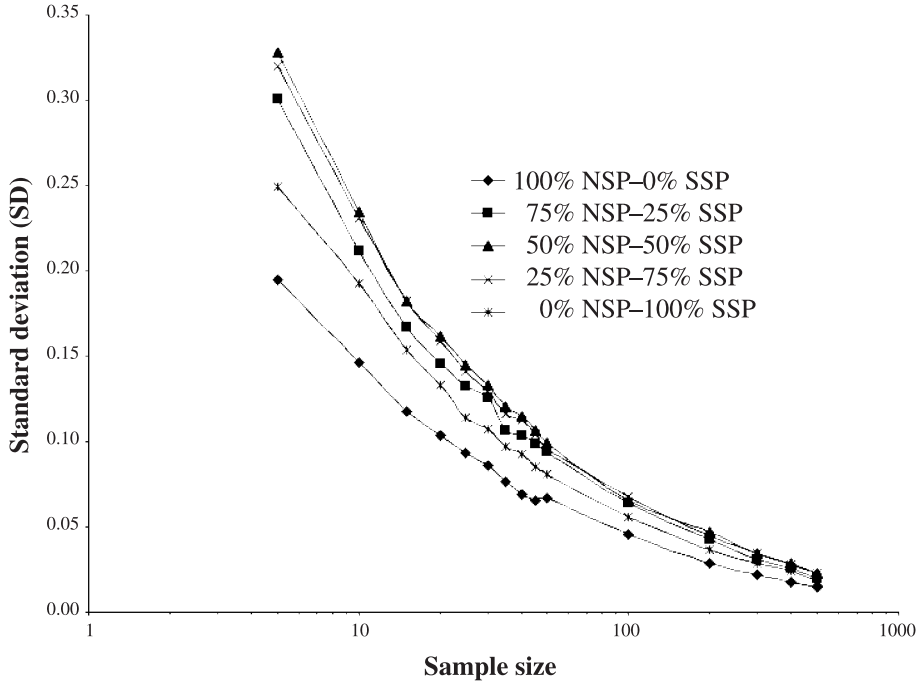

Fig. 3. Standard deviation (SD) plotted against sample size used in the calculation of the mixed stock analysis. The standard deviation for each sample size-treatment is evaluated from 1000 bootstraps taken from a known population admixture (five different compositions).

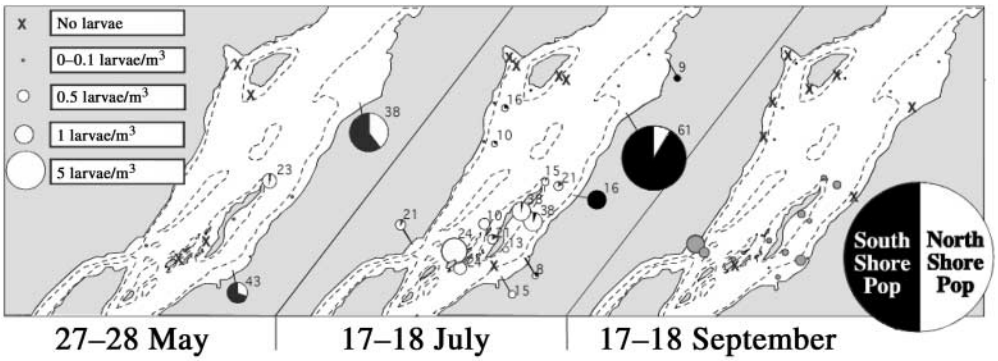

Fig. 4. Distribution of samples, larval abundance (number of larvae per m^3 and population admixture estimated by mixed stock analysis from mtDNA) for 1997 sampling cruises. The small number of larvae collected in September precludes the use of mixed stock analysis, hence pies are represented in grey (populations not identified). Dotted line represents the 2-m isobath measured at low tide. Numbers beside pies represent the number of larvae used for the mixed stock analysis.

entire growing season; by August–September, all individuals of both populations had reached the juvenile stage (with distinctive adult morphology).

Larval populations are clearly segregated among discrete nursery habitats in the St. Lawrence middle estuary (Fig. 6). The north-shore population exploited all channel

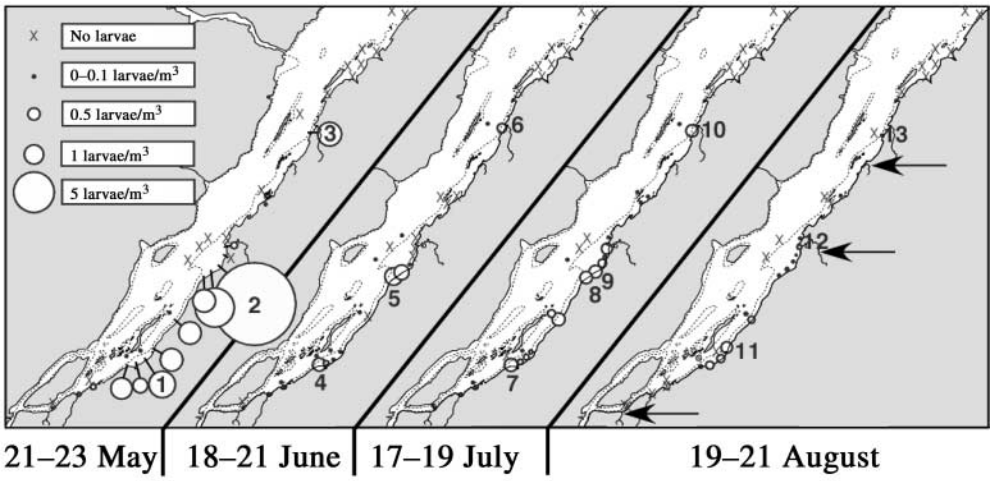

Fig. 5. Distribution of samples and larval abundance (as number of larvae per m^3) for the four sampling cruises of 1998. Dotted line represents the 2-m isobath measured at low tide. Numbers beside pies are codes referring to sites used in mixed stock analysis presented in Table 3. Arrows indicate SSP spawning sites.

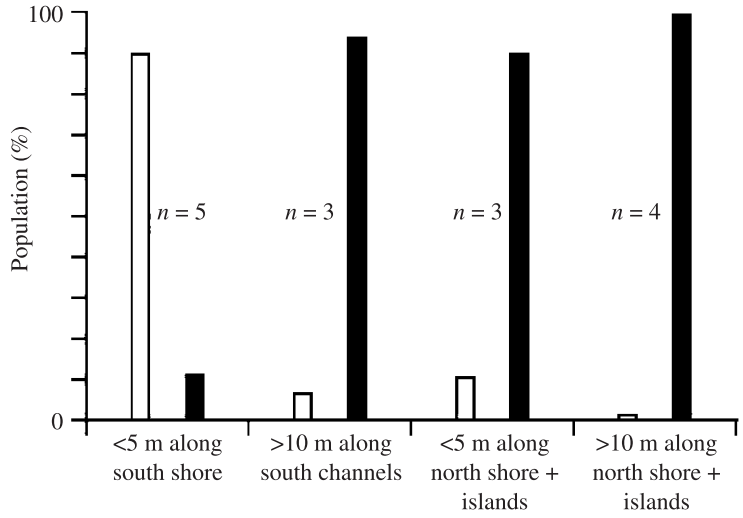

Fig. 6. Proportion of the two smelt populations collected during the July 1997 sampling survey (mixed stock analysis based on mtDNA). Samples were pooled in four different categories according to the nature of sampling sites (depth + shore). Proportions are calculated for pooled samples corrected for larval abundance within each site. n = number of sites used within each category. □, south-shore population; ■, north-shore population.

habitats of the middle estuary and adjacent shoals and small bays that are emerged during low tide (Figs. 4, 5). These observations of the distribution of NSP larvae are consistent with previous observations showing that they are concentrated in the three channels of the middle estuary with maximal abundance recorded at the head of the estuarine turbidity

maximum (Ouellet and Dodson, 1985; Dodson, *et al.*, 1989; Laprise and Dodson, 1989a,b, 1993; Pigeon *et al.*, 1998; Sirois and Dodson, 2000). In contrast, the only location where SSP larvae were present in high proportions was along the south shore shoals. Mixed stock analyses of 1997 larval samples revealed high concentrations of SSP larvae on the south shore shoals (up to 2.4 individuals per m^3; Fig. 3). In contrast, the concentration of SSP larvae outside bays never reached more than ≈0.01 individuals per m^3 (Fig. 4), comparable to the results of Pigeon *et al.* (1998). By June, larvae had aggregated in Ste. Anne Bay (the largest bay located between −50 to −75 km; Fig. 1). In 1997, the frequency of SSP larvae relative to NSP larvae in Ste-Anne Bay increased from 61% in May to 91% in June (Fig. 4). Very few individuals were caught in September 1997, thus precluding mixed stock analysis for that period. A similar result was seen in 1998 (Fig. 5, Table 3); SSP larvae were lost from the upstream sites (i.e. Montmagny Bay, −5 to −20 km; Fig. 1) but accumulated in and dominated the other two major retention areas (Ste-Anne Bay, −50 to −75 km; Rivière-du-Loup Shoals, −115 to −130 km; Fig. 1). In one sample (coded 8 on Fig. 5), NSP larvae dominated shallow areas at the edge of the Ste-Anne Bay located only 3 km away from sites dominated by SSP larvae (i.e. site coded 9; Fig. 5 and Table 3). It would appear that important concentrations of SSP larvae are not restricted to the estuarine turbidity maximum as are NSP larvae, but rather are associated with large shallow bays. Ste-Anne Bay is on the margin of the transition zone between the estuarine turbidity maximum and the more saline region of the middle estuary, while Rivière-du-Loup shoals are 75 km

Table 3. Density of larvae along the south shore of the St. Lawrence middle estuary, mtDNA clade frequencies and relative contribution of the two populations in samples analysed from four sampling periods, 1998

Date	Location	Position (km)	Density ($n \cdot m^{-3}$)	n	Clade frequency		Relative contribution	
					%A	%B	SSP	NSP
21–23 May	Montmagny Bay[1]	−13	6.83	24	71	29	0.88	0.12
	Ste-Anne Bay[2]	−62	66.75	25	64	36	0.78	0.22
	Rivière-du-Loup Bay[3]	−125	5.55	25	76	24	0.95	0.05
18–21 June	Montmagny Bay[4]	−6	1.65	25	28	72	0.25	0.75
	Ste-Anne Bay[5]	−56	2.90	25	80	20	1.01	−0.01
	Rivière-du-Loup Bay[6]	−126	0.78	15	80	20	1.01	−0.01
17–19 July	Montmagny Bay[7]	−13	0.33	25	24	76	0.19	0.81
	Ste-Anne Bay[8]	−56	1.57	24	13	88	0.02	0.98
	Ste-Anne Bay[9]	−59	1.21	25	88	12	1.13	−0.13
	Rivière-du-Loup Bay[10]	−126	1.53	24	88	13	1.12	−0.12
19–21 August	Montmagny Bay[11]	−14	1.21	25	8	92	−0.05	1.05
	Ste-Anne Bay[12]	−68	0.13	25	72	28	0.89	0.11
	Rivière-du-Loup Bay[13]	−125	0.03	15	73	27	0.91	0.09

Note: Superscript number after location name refers to stations marked on Fig. 5. Standard deviation (SD) of the estimates: for $n = 25$, SD = 0.13; for $n = 15$, SD = 0.17.

downstream of the estuarine turbidity maximum (Fig. 1). By comparing larval distribution to the location of spawning tributaries of the south-shore population (Fig. 5), this population exhibits a pattern of initial dispersal and subsequent retention that is clearly distinctive relative to that of the north-shore population.

Morphological differentiation between sympatric populations

The St. Lawrence middle estuary smelt populations are morphologically distinct but do not conform to typical benthic/pelagic morphotypes. Differentiation between the two populations is highly significant ($P < 0.001$, proportional chance criterion; Huberty, 1994) and showed a very high success of reclassification between populations (97.2%) and a corresponding small *a posteriori* error estimate (3.7%). Even considering the sampling sites as the grouping variable for the discriminant analysis (i.e. reclassifying smelt to their sampling sites), the first canonical axis separated the two populations (the first axis explaining 89.6% of the variance) while the three spawning tributaries of the south-shore population were not clearly separated (Fig. 7). Superficially, the north-shore population looks like a pelagic morphotype, as individuals have longer heads relative to body length with relatively large eyes, while the south-shore population exhibit the opposite features, similar to a benthic morphotype (Fig. 7, Table 4).

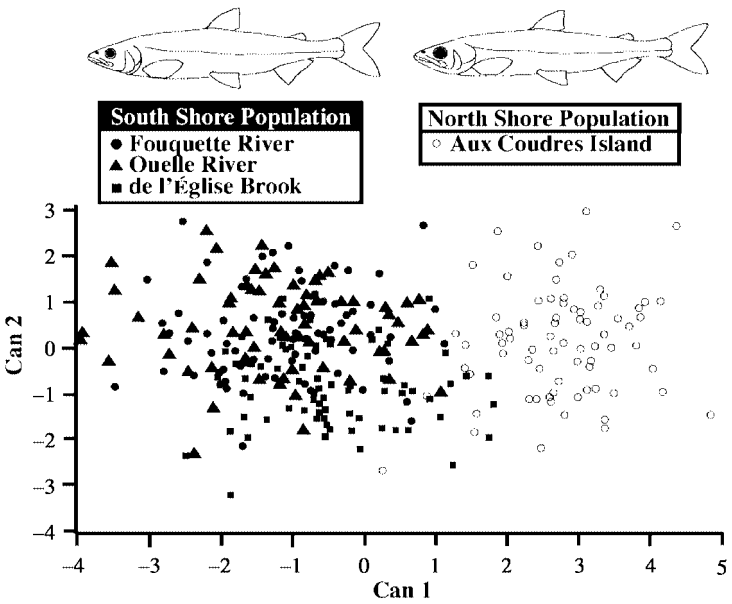

Fig. 7. Distribution of adult smelt sampled in 1998 as a function of the two principal canonical axes. Discriminant analysis was performed using 16 morphometric measurements (corrected for size effect through a principal component analysis) and two meristic counts. The grouping variable used for discriminant analysis was the sampling site. Open circles represent fish from Aux Coudres Island (NSP); filled circles, Fouquette River (SSP); filled triangles, Ouelle River (SSP); filled squares, de l'Église Brook (SSP).

Table 4. Morphological variables used in the principal component/discriminant analysis, and mean values (with standard deviation in parentheses) expressed in mm or mm^2 adjusted for a 150-mm fish for the different sites

	NSP	SSP			
Variable	Coudres Island ($n = 75$)	De l'Église Brook ($n = 75$)	Ouelle River ($n = 75$)	Fouquette River ($n = 75$)	NSP *vs* SSP *P*-value
Fork length	153.6 (14.9)	154.7 (20.9)	153.9 (18.9)	159.2 (23.5)	0.3696
Head length	32.9 (1.3)	30.1 (1.3)	29.0 (1.2)	29.2 (1.5)	<0.0001*
Head depth after opercula	21.0 (1.1)	20.7 (1.2)	21.0 (1.0)	21.6 (1.4)	0.4046
Measure 1_2[a]	69.6 (1.3)	69.3 (1.3)	69.6 (1.4)	69.7 (1.4)	0.6834
Measure 3_4[b]	67.1 (1.5)	67.2 (1.5)	66.7 (1.4)	66.6 (1.8)	0.0991
Measure 5_6[c]	20.9 (1.4)	20.6 (1.4)	21.1 (1.5)	20.8 (1.5)	0.6968
Measure 7_1[d]	34.2 (1.5)	32.2 (1.4)	32.2 (1.1)	32.4 (1.4)	<0.0001*
Head depth	14.7 (0.5)	13.6 (0.5)	13.6 (0.5)	13.5 (0.6)	<0.0001*
Upper jaw length	17.2 (0.6)	14.9 (0.7)	14.6 (0.7)	14.8 (0.9)	<0.0001*
Snout length	8.5 (0.6)	7.7 (0.7)	7.5 (0.5)	7.6 (0.7)	<0.0001*
Eye area	39.7 (3.5)	31.3 (3.1)	29.4 (2.9)	31.8 (4.1)	<0.0001*
Upper gill raker number	11.1 (0.6)	11.3 (0.6)	11.3 (0.6)	11.4 (0.5)	0.0231
Lower gill raker number	19.6 (0.9)	19.7 (0.9)	20.1 (0.7)	19.8 (0.7)	0.0055
Upper gill arch length	7.8 (0.4)	7.1 (0.3)	7.0 (0.3)	7.1 (0.3)	<0.0001*
Lower gill arch length	15.9 (0.7)	14.3 (0.6)	14.2 (0.6)	14.1 (0.6)	<0.0001*
First gill raker length	3.9 (0.3)	3.7 (0.3)	3.5 (0.4)	3.6 (0.4)	<0.0001*
Second gill raker length	3.9 (0.3)	3.6 (0.3)	3.4 (0.4)	3.5 (0.4)	<0.0001*
Third gill raker length	3.8 (0.3)	3.5 (0.3)	3.3 (0.4)	3.3 (0.3)	<0.0001*

Note: The *t*-tests comparing mean SSP and NSP values were based on log-adjusted values {log(measure/fork length)} except fork length, for which we used raw data.
* Significant once corrected for multiple tests (sequential Bonferroni correction)
[a] Measure 1_2 = snout to beginning of dorsal fin. [b] Measure 3_4 = end of dorsal fin to the caudal fin fork. [c] Measure 5_6 = length of anal fin. [d] Measure 7_1 = pectoral fin to snout.

Morphological differentiation of the feeding apparatus cannot be attributed consistently to a planktivorous (pelagic) or to a benthivorous (benthic) lifestyle. The superficially pelagic north-shore population is also characterized by the largest mouth (associated with a benthic lifestyle; Taylor and Bentzen, 1993a,b), the longest gill rakers (pelagic), the lowest density of gill rakers (benthic) and the lowest gill raker counts (benthic). Thus, St. Lawrence smelt exhibit a clear morphological differentiation (e.g. very high reclassification percentages; Fig. 7), but the two morphotypes do not correspond to the typical benthic/pelagic trophic dichotomy that evolves to exploit large benthic (benthivorous) versus small planktonic (planktivorous) prey items.

Adult feeding regimes and distribution

Comparisons of feeding regimes between populations showed that all middle estuary smelt fed upon the same prey, including *Crangon septemspinosa, Gammarus* spp., *Nereis* spp., *Mysis stenolepis, Neomysis americana*, fish (*Osmerus mordax, Microgadus tomcod,*

Gasterosteus spp.), euphausiacea and *Eurytemora affinis* (see Table 5). All prey identified, except *Osmerus mordax* and euphausiacea, are usually considered as benthic or suprabenthic organisms. Because of strong vertical mixing, suprabenthic animals are found in large concentrations throughout the water column in the middle estuary (Laprise and Dodson, 1993, 1994). Only the endobenthic *Nereis* spp. and snails are truly limited to benthic habitat.

Eighty-two per cent of the 180 fishes examined contained gut contents. No planktivorous/benthivorous pattern could be detected between the two populations, either when considering the origin of the prey (from plankton or benthos) or prey size. Schoener's Index (Schoener, 1968) revealed important overlap within and among populations using both dry weight and prey items as variables for the index (Table 6). Mean values for the comparison between the south-shore and north-shore populations are 0.599 for diet estimated by dry weight and 0.598 for diet estimated by prey items. Moreover, once we compared niche overlap among sites within the same shore to niche overlap estimated by comparing pairs of samples caught on different shores, Mann-Whitney *U*-tests showed no significant differences in diet based on both dry weight ($P = 0.906$) and number of prey items ($P = 0.556$). As such, differentiation between north- and south-shore samples are in the same range as within north- or south-shore samples. The homogeneity of feeding regimes observed between shores could not be related to population mixing as little population mixing occurred in 1998 between shores (average of $8 \pm 14\%$; Table 5).

The two adult populations are clearly segregated along the two shores of the estuary (Table 5). Considering both the proximity of the shores (less than 20 km) and the swimming capacity of adult smelt (recorded movements of up to 40 km per day; Vladykov and Michaud, 1957), adult habitat selection may explain the observed distribution. The morphology of adult smelt appears to coincide with habitat type. The more pelagic-like morphology (NSP) was associated with the north shore characterized by deep channels, whereas the more benthic-like (SSP) morphology was associated with the south shore typified by important shoals and shallow bays. As such, the morphological differentiation of the two populations is related to the distinct environmental settings exploited by the populations rather than to the differential exploitation of prey types.

DISCUSSION

Population-specific spawning areas and times

Spawning times and the nature of spawning sites of the two populations are likely to favour temporal and spatial segregation during reproduction, thus reducing the probability of gene flow. Adults of the south-shore population normally start spawning during the first week of May (Ouellet and Dodson, 1985; Pettigrew and Verreault, 1999), almost simultaneously in the three south-shore spawning tributaries (Fig. 1). In contrast, the north-shore population spawn directly in the St. Lawrence fluvial estuary in the vicinity of the Neuville shoals located 70–90 km upstream of the estuarine turbidity maximum (Table 1). Back-calculation of spawning date from NSP larvae caught in 1997 revealed that spawning had started by the second week of April. An important commercial fishery for smelt that existed in the region of Neuville prior to the 1960s (Magnin and Beaulieu, 1965) probably targeted a pre-spawning migration and aggregation of the north-shore population near the spawning

Table 5. Number of gut contents examined, prey items (size ranges of prey are indicated), and diet expressed as three variables: raw number (in **bold**), mean percent dry weight (underlined in parentheses) and percent occurrence (in *italics*), for the six sites sampled to compare the diet of SSP and NSP smelt found along the north and south shores

	NSP samples			SSP samples		
Prey item (size range)	Coudres Island, October 1997 ($n = 40$)	Coudres Island, August 1998 ($n = 25$)	Anse-Au-Sac, August 1998 ($n = 25$)	Ouelle River, October 1997 ($n = 40$)	Ouelle River, August 1998 ($n = 25$)	Kamouraska, August 1998 ($n = 25$)
Crangon sp. (≈20–50 mm)	**14** (21.8) *27.5*	**10** (12.4) *28.0*	**1** (8.9) *4.0*	**15** (13.1) *17.5*	**3** (11.0) *12.0*	**20** (61.7) *56.0*
Gammarus sp. (≈5–30 mm)	**99** (33.9) *80.0*	**135** (31.1) *80.0*	**10** (29.8) *16.0*	**413** (42.3) *65.0*	**39** (52.5) *52.0*	**2** (5.7) *8.0*
Nereis sp. (≈50–150 mm)	**2** (2.6) *2.5*	**9** (4.9) *24.0*	**2** (0.5) *8.0*	**5** (1.5) *7.5*	**1** (5.3) *4.0*	**9** (25.2) *32.0*
Mysis stenolepis (≈20–24 mm)	**127** (27.8) *40.0*	**523** (51.5) *84.0*	**5** (17.7) *8.0*	**31** (25.7) *42.5*	**2** (3.3) *8.0*	**3** (3.0) *4.0*
Neomysis americana (≈3–12 mm)	**170** (10.7) *37.5*	—	—	**173** (8.6) *45.0*	**6** (3.8) *4.0*	—
Fish (≈50–100 mm)	**7** (1.6) *10.0*	—	—	**2** (8.4) *5.0*	**4** (19.6) *16.0*	**1** (4.3) *4.0*

Euphausiacea (≈15–30 mm)	—	**2** (0.1) *4.0*	**5** (24.7) *12.0*	**1** (0.2) *2.5*	—	—
Snails (<5 mm)	**9** (1.7) *10.0*	—	—	**3** (0.2) *7.5*	—	**1** (0.3) *4.0*
Eurytemora affinis (≈1.0–1.2 mm)	—	—	**70** (18.4) *12.0*	—	—	—
Others	—	**1** (0.6) *4.0*	—	—	**1** (4.6) *4.0*	—
Ratio of fish with prey	38/40	25/25	11/25	35/40	19/25	20/25
Mean no. of prey per fish with gut content	10.9	26.8	8.4	17.9	2.8	0.8
Mean weight of prey per fish with gut content (mg)	25.7	117.8	34.7	51.4	134.3	77.9
Mixed stock analysis[a]	NA	92% NSP	92% NSP	NA	101% SSP	113% SSP
No. individuals clade A/B		4A/20B	4A/20B		20A/5B	22A/3B

Note: Number of fish with prey, number of prey per gut and mean dry weight of prey also presented. The results of the mixed stock analysis of the 1998 samples are shown at the bottom of the table.

[a] Standard deviation (SD) estimated through bootstrapping: for $n = 25$, SD = 0.13.

Table 6. Schoener's Index (*D*) of trophic niche overlap between smelt populations

	NSP population			SSP population		
Site/date	Coudres Island, October 1997	Coudres Island, August 1998	Anse-Au-Sac, August 1998	Ouelle River, October 1997	Ouelle River, August 1998	Kamouraska, August 1998
Coudres Island, Oct. 1997	—	0.736	0.475	0.846	0.561	0.349
Coudres Island, Aug. 1998	0.582	—	0.456	0.705	0.506	0.256
Anse-Au-Sac, Aug. 1998	0.486	0.500	—	0.462	0.314	0.072
Ouelle River, Oct. 1997	0.828	0.517	0.549	—	0.703	0.277
Ouelle River, Aug. 1998	0.547	0.421	0.441	0.696	—	0.292
Kamouraska, Aug. 1998	0.226	0.134	0.179	0.247	0.239	—

Note: Diet was estimated by dry weight (above the diagonal) or number of prey items (below the diagonal). Both diet estimators are corrected for individual contributions to the group. The comparison of pooled samples of NSP versus SSP gives values of 0.599 for mean weight and 0.598 for number of prey items.

grounds during the fall prior to spawning. Genetic segregation between populations is thus favoured by the exploitation of distant and ecologically distinct spawning sites at different times of the year.

Population-specific nursery areas

Sympatric smelt populations of the St. Lawrence middle estuary are spatially segregated during their larval stage (Figs. 4–6). This represents the first documented case of larval segregation among sympatric populations of a fish with a pelagic larval stage. The scale of the spatial segregation is as little as 2 km between shallow areas exploited by SSP larvae and channel habitat used by NSP larvae (Figs. 4 and 5, Table 3). A small minority of NSP larvae overflows from channel habitats into neighbouring bays, but still no important population mixing occurs by the end of the growing season (Fig. 5, Table 3). The area where larval populations are in contact occurs over an approximately 20-km section of the south shore (encompassing salinities ranging from 5 to 20 PSU; Fig. 1). Within this area, no extensive mixing occurs; rather, the area appears to be exploited alternatively by the two larval populations in relation to tidal movement.

The positioning of spawning sites largely accounts for the location of larvae in population-specific nursery areas. Because three main channels are present in the middle estuary, a point source located upstream is best suited to disperse larvae into all of them. Moreover, locating spawning sites directly on the bottom of the St. Lawrence contributes to preventing stranding of shore shoals at low tide and maximizes advection towards the nursery area. The NSP nursery area and spawning site are separated by 100 km of

low-productivity fluvial habitat (Runge and Simard, 1990). Water residence time between the Neuville spawning area and the middle estuary is estimated to be 2–4 days (Paquet, 1993). Considering that smelt larvae yolk-sac reserves are exhausted within 7–8 days at ambient temperatures occurring in the St. Lawrence, it is possible for NSP larvae to reach their nursery area on yolk-sac reserves.

For the south-shore population, spawning sites are located in shallow tributaries that provide larvae direct access to their shallow nursery areas. Soon after hatching, yolk-sac larvae of the south-shore population are found throughout the south shore shoals (Figs. 4 and 5). Important cross-estuarine currents exist in the middle estuary (Ouellet and Trump, 1979; D'Anglejan *et al.*, 1981) and these were thought to account for the distribution of larvae originating from south-shore tributaries in the middle estuary channels (Ouellet and Dodson, 1985). However, considering the present data on the distribution of larval haplotypes, it is evident that cross-channel water movement does not have a strong influence on the SSP larvae, as they are retained throughout the growing season along the south shore (Figs. 4 and 5, Table 3) with little dispersion into channels (Fig. 4 and Pigeon *et al.*, 1998).

Population-specific retention mechanisms

Distinct retention mechanisms likely account for larval retention in population-specific nursery areas. Since the majority of both populations exploit physically and ecologically distinct nursery areas throughout most of their larval/juvenile stage, different combinations of water movement and behaviour are expected for these populations. Several mechanisms accounting for the maintenance of estuarine organisms are known, including passive accumulation in the estuarine turbidity maximum (Frénette *et al.*, 1995), fast growth rate (mostly for zooplankton and phytoplankton; Gupta *et al.*, 1994) and various types of behaviour patterns (Boehlert and Mundy, 1988). The NSP larvae are retained by vertical migrations that exploit tidal circulation. During flooding tide, larvae migrate to the upper water column to maximize landward movement while moving close to the bottom at ebbing tide to minimize seaward transport. As larvae develop into juveniles, greater amplitude vertical migrations result in a concentration of juvenile smelt at the head of the estuarine turbidity maximum (Laprise and Dodson, 1989b).

In contrast, this mechanism may not be well suited to exploit tidal flats. Zones exploited at high tide by SSP larvae are emerged at low tide. Migrating near the bottom on ebbing tide increases the risks of stranding at low tide. Therefore, persistence at mid-depth over the entire tidal cycle may suffice for retention in large coastal bays that are often characterized by the formation of eddies contributing to the passive retention of plankton (Geyer and Signell, 1992; Archambault *et al.*, 1998). If retention of the south-shore population in shallow bays is largely passive, it may explain why few SSP larvae are retained in the deep channel nursery habitat by the end of the growing season (Pigeon *et al.*, 1998). Considering the weak larval swimming capacity relative to the tidal energy of the middle estuary, population-specific behaviour in relation to vertical migration is likely to be the primary mechanism to explain the maintenance of spatial segregation at the larval stage.

Adult morphotypes and resource polymorphism

Smelt populations of the middle estuary are morphologically distinct and reflect a benthic/pelagic dichotomy in morphology, each morphotype exploiting an ecologically different

habitat. However, the phenotype–habitat association is not paralleled by the expected benthivorous/planktivorous dichotomy in diet and feeding apparatus morphology (Taylor and Bentzen, 1993a,b; Robinson and Wilson, 1994; Smith and Skúlason, 1996). The morphological differentiation of the sympatric smelt populations shows significant differences in several variables studied; for example, eye area is 29% greater for NSP adults (Table 4). However, considering solely the feeding apparatus, variables discriminating the two populations appear to be inconsistent with either planktivorous (p) or benthivorous (b) features. The NSP 'pelagic' morphotype possesses a longer jaw (b), longer gill rakers (p), fewer gill rakers (b) and larger gill arches (p), which translate into a lower density of gill rakers/length of gill arches (b). Thus, it is difficult to identify any ecological advantage to be gained by such an inconsistent array of features for prey capture (i.e. reduced density of longer gill rakers). Analysis of the diet revealed that, without reference to their population origin, smelt consume almost any large prey. Heterogeneity in the middle estuary accounts for diet variation observed among and between sampling areas rather than population-specific feeding regimes. Although both populations are physically capable of feeding upon small planktonic prey, *Eurytemora affinis* and *Neomysis americana* are rarely found in gut contents even if they represent two of the most abundant prey in the middle estuary (concentration up to 10,000 individuals per m^3 and 100 individuals per m^3, respectively; Laprise and Dodson, 1993, 1994). If food availability was limiting, hence promoting resource polymorphism for alternate diets, one would expect to find these kind of prey in the gut contents. Moreover, the presence of *Nereis* spp. in the stomach of both populations shows that they are both capable of feeding benthically.

The two populations are spatially segregated along the two shores of the middle estuary, resulting in the differential exploitation of estuarine habitats. The deep channels typical of the north shore are exploited by the north-shore population, while the south-shore population was found along south shore shoals and in bays. Both regions are ecologically distinct environments. Channels are energetic environments as much of the water flow occurs there, creating high-speed currents (up to 3.5 $m \cdot s^{-1}$). In contrast, shoal dynamics are strongly impacted by tidal amplitude that may reach 5.8 m in this region. Analyses of smelt fishery statistics during the twentieth century along the north and south shore of the estuary revealed that both freshwater input and temperature, chosen to reflect variations in hydrology and climate, were generally positively related to north shore landings and negatively related to south shore landings (Mingelbier *et al.*, 2001). The contrasting role of hydroclimatic variables in driving abundance cycles of the two populations reflects the fundamental ecological differences that exist between shoal and channel habitats.

The absence of population-specific diets and the inconsistency in key morphological features such as gill rakers and mouth size suggest that exploitation of distinct prey types is not the primary cause of the segregation between populations. Rather, the spatial segregation of morphotypes may be correlated with the specific habitat they exploit and hence may reflect the efficiency with which they forage upon similar prey in ecologically distinct environments. In contrast, resource polymorphism within freshwater fish populations generally involves exploitation of distinct prey types. Schluter (1995) showed for sticklebacks that benthic morphs were more efficient (as assessed by growth rate) to exploit the benthic environment, while the limnetic morph performed better in open water. Such results support the idea that divergent selection acting on foraging efficiency (or energy conversion) within distinct environments could reduce the survival of morphologically intermediate hybrids. Thus, even in the absence of complete premating isolation mech-

anisms, the two morphotypes could be maintained. For lacustrine smelt populations, Taylor and Bentzen (1993a,b) demonstrated that dwarf and normal morphotypes have evolved from both glacial races. Dwarf smelt exhibit features typical of pelagic plankton feeders (small mouth, high number of gill rakers, larger eyes) and normal smelt exhibit features typical of benthic feeders, regardless of their glacial race of origin. Compared with freshwater systems, estuaries are extremely productive environments where food is not limiting but where the physical environment is highly heterogeneous. In such a situation, population-specific adaptations may be seen as a way of maximizing efficiency to capture any large prey within distinct environmental settings rather than favouring the exploitation of distinct prey within specific environments as observed in freshwater systems (Skúlason and Smith, 1995; Smith and Skúlason, 1996; Taylor, 1999).

Genetic isolation, secondary contact and ecological speciation

We have demonstrated that both early life-history constraints and adult morphological polymorphisms related to foraging habitat are potentially involved in the maintenance of the genetic isolation of the two estuarine populations. The characteristics of both populations are well correlated to the exploitation of distinct environmental settings by all early developmental stages. The ecological speciation hypothesis (Schluter, 1996, 1998, 2001) appears to be the most likely mechanism responsible for the actual ecological segregation that is reflected by marked genetic differentiation (see Bernatchez and Martin, 1996).

It is possible that part of the morphological, ecological and behavioural differences observed in this study evolved before secondary contact among the glacial ancestors of the contemporary populations. However, some mixing of the two races occurred at secondary contact, as the north- and south-shore populations retain a minority of haplotypes associated with the alternate glacial race. This indicates that isolation mechanisms have acted since secondary contact to prevent complete hybridization of the two races. The recolonization of the middle estuary by the two races did not occur at the same time, the Atlantic race (mtDNA clade B) possibly colonizing the area before the Acadian race (mtDNA clade A; Bernatchez, 1997). The secondary contact probably occurred only 7500–8000 years ago in the middle estuary when oceanographic conditions were similar to present-day conditions (de Vernal *et al.*, 1993). In the period before secondary contact, the Atlantic race conceivably adapted to the local estuarine conditions through the exploitation of the productive nursery area that is the estuarine turbidity maximum. It thus seems likely that the ecological and morphological distinctiveness of both populations is at least partially a consequence of secondary contact between the invading Acadian race and the resident Atlantic race and evolved to reduce population interactions through the exploitation of distinct niches at all life-history stages.

CONCLUSION

In fishes, the distribution of habitat structure favouring the survival of early life-history stages can lead to micro-allopatric patterns in the distribution of local populations (or demes) if the spatial distribution of appropriate habitat is well structured. The dispersal ability of the population and the ecological distinctiveness of the nursery habitat will determine to what extent population isolation is favoured. In many marine fishes, local

populations or demes are connected by high levels of gene flow to form metapopulations (McQuinn, 1997). The selective pressures associated with site-specific retention mechanisms minimizing loss of larvae due to dispersion and/or advection may favour the evolution of philopatry and the genetic isolation of sympatric populations. In the present case, the segregation of the two smelt populations has proceeded beyond the 'local-population' stage to a stage that includes an evolutionary component related to the ecological constraints influencing the survival of larvae and juveniles and possibly the foraging success of adults exploiting different hydrodynamic features of the estuarine landscape. In the highly dispersive estuarine environment, it appears that selective pressures acting on the survival of the pelagic early life-history stages as well as resource polymorphisms occurring at later stages contribute to maintaining the genetic isolation of the two rainbow smelt populations.

ACKNOWLEDGEMENTS

This manuscript is part of the senior author's PhD thesis. F. Lecomte was supported by scholarships from the Natural Sciences and Engineering Research Council of Canada (NSERC) and Fonds pour la Formation des Chercheurs et l'Aide à la Recherche (FCAR, Québec). We are greatly indebted to all those who participated in the field and lab work; from U. Laval (F. Colombani, M. Lafrance, O. Pelain, J.-Y. Anctil, P. Sirois, J.-F. Bourque, M. Lagacé, R. Pilote), Ministère de l'Environnement et de la Faune du Québec (R.O. Picard, F. Caron, S. Tremblay, G. Verrault, G. Trencia, S. George, A. Valière, J.-G. Frénette) and others (M. Dubé, G. Leclerc, P. Lecomte, H. Allard). Funding was provided by grants from NSERC (Canada) and Ministère de l'Environnement et de la Faune du Québec to J.J. Dodson. Earlier versions of the manuscript were greatly improved by constructive comments from B.W. Bowen, J. Turgeon and L. Bernatchez. This manuscript is a contribution to the program of Québec-Océan (Groupe inter-institutionnel de recherches océanographiques du Québec).

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