Habitat segregation among the age groups of *Gasterosteus aculeatus* (Pisces: Gasterosteidae) in the middle St. Lawrence estuary, Canada

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Previous studies of migratory populations of sticklebacks (Pisces: Gasterosteidae) have been exclusively limited to their biology on the spawning grounds during the spring breeding season. In 1985 and 1986, we studied the ecology of the threespine stickleback (*Gasterosteus aculeatus*) in three subhabitats of the middle St. Lawrence estuary before, during, and after the breeding season: (*i*) the open waters of the estuary, (*ii*) a series of intertidal salt marsh pools, and (*iii*) two tidal rivers (Rivière des Vases and Rivière Trois-Pistoles). In spring, our catch data in the various subhabitats showed that adults moved from the open waters of the estuary towards the tidal rivers and tide pools. Catches of adults in all subhabitats subsequently declined, whereas the young of the year (age 0+) became increasingly abundant. In this area, *G. aculeatus* live for 2 years and are physiologically capable of breeding during their first summer as adults. However, we found age-related differences in habitat use between the two adult year classes. Age 1+ fish were never more abundant than age 2+ fish in Rivière des Vases, in the tide pools, and in the open waters of the estuary, whereas age 1+ fish were more abundant than age 2+ fish in Rivière Trois-Pistoles. Throughout the breeding season, gonadosomatic indices of female *G. aculeatus* were the same for the two age groups. Total lengths of age 0+ fish captured in the various subhabitats suggest that the major spawning period is limited to May and June. Age 0+ fish do not leave the tide pools for the open waters of the estuary before having attained a certain minimum size.

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Jusqu'à présent, les études portant sur les populations migratrices d'épinoches (Pisces: Gasterosteidae) ont été limitées à leur biologie sur les sites de frai, pendant la saison reproductrice printanière. En 1985 et 1986, nous avons étudié l'écologie de l'Épinoche à trois épines (*Gasterosteus aculeatus*) dans trois sous-habitats différents de l'estuaire moyen du Saint-Laurent, avant, pendant et après la saison reproductrice : (*i*) les régions côtières de l'estuaire moyen, (*ii*) une séric de mares intertidales et (*iii*) deux rivières tidales (la Rivière des Vases et la Rivière Trois-Pistoles). Au printemps, nos captures ont montré que les adultes quittent l'estuaire du Saint-Laurent pour coloniser les mares intertidales et les rivières tidales. Par la suite, les captures d'adultes dans l'un ou l'autre des sous-habitats diminuent au profit des jeunes de l'année. Dans cette région, *G. aculeatus* vit 2 ans et est physiologiquement prêt à se reproduire dès le premier été. Toutefois, dans les trois sous-habitats, nous avons trouvé des distributions qui différaient selon l'âge des individus. Dans la Rivière des Vases, dans les marelles et dans l'estuaire, les poissons âgés de 1 an n'étaient jamais plus abondants que les poissons de 2 ans tandis que la situation inverse prévalait dans la Rivière Trois-Pistoles. Les indices gonadosomatiques des femelles *G. aculeatus* étaient indépendants de l'âge des femelles. Les longueurs totales des jeunes de l'année capturés dans les différents sous-habitats montrent que l'effort reproducteur majeur survient au cours des mois de mai et juin. Le moment où les alevins quittent les mares intertidales pour l'estuaire du Saint-Laurent semble relié à l'obtention d'une taille minimale dans les mares.

Introduction

The threespine stickleback (*Gasterosteus aculeatus*) is one of the most intensively studied noncommercial fish species. This is probably due to its extensive geographical distribution and its great convenience for behavioural, physiological, and ecological studies (Wootton 1976, 1984). *Gasterosteus aculeatus* can either be a permanent freshwater resident or a member of an anadromous (migratory) population.

An anadromous population of *G. aculeatus* is located at Isle-Verte, Quebec, on the south shore of the St. Lawrence estuary. At the end of April or early May, the fish leave their overwintering habitats in the St. Lawrence estuary and enter intertidal salt marsh pools and tidal rivers for 2 or 3 months to breed. After this date, the young of the year (age 0+) and surviving adults presumably return to the open waters for the overwintering period, where they may serve as important prey items for a variety of predatory fish (Clemens and Wilby 1961; Blouw and Hagen 1984; Scott and Scott 1988).

Previous studies have examined the reproductive ecology and diet of *G. aculeatus* in this area (see FitzGerald and Wootton, 1986, and references therein), but these studies were restricted to the breeding grounds. Studies on the biology of *G. aculeatus* outside of the breeding habitat are essentially anecdotal (e.g., Brown and Cheng 1946, cited in Wootton 1984; Jones and John 1978; Parin 1968, cited in Wootton 1984), although the period of time spent in these habitats represents the major portion of its lifetime. This absence of data outside of the breeding habitat and during nonbreeding periods limits our understanding of stickleback ecology and life history. This last point has recently been emphasized by several authors (e.g., Bell 1984; Blouw and Hagen 1981; Craig and FitzGerald 1982; Whoriskey *et al.* 1986; Wootton 1984).

Craig and FitzGerald (1982) studied the life history parameters of *G. aculeatus* in Rivière des Vases, a small tidal creek in the Isle-Verte area. When examining the length–frequency histogram, they found that *G. aculeatus* were able to live for 2 years. However, the length–frequency histogram also showed that the age 1+ fish represented only about 23% of all the adult *G. aculeatus*. This surprising result was probably not a sampling error, having been previously reported in another migratory population of *G. aculeatus*, which reproduces in rock pools on the St. Lawrence estuary's north shore (Coad and Power 1973). In this population, only 1% of all the adults found on the breeding grounds were age 1+ fish. Thus, these studies suggest that during their first summer, a significant proportion of age 1+ *G. aculeatus* remains in the St. Lawrence estuary and postpones reproduction until it reaches age 2+.

The present study was undertaken to examine this spatial

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segregation among the age groups of *G. aculeatus* in three subhabitats of the St. Lawrence estuary: tide pools, tidal rivers, and the open waters of the estuary.

Our first objective concerned the temporal distribution of fish in the three subhabitats and the relative abundance of the two age groups. We postulated that before the breeding season, *G. aculeatus* are located in the estuary where age 1+ adults are more abundant than age 2+ adults. We further postulated that the majority of the age 2+ adults then leaves the open waters and enters the littoral breeding grounds to reproduce, whereas most of the age 1+ fish remain in nearshore waters. Finally, we postulated that after the breeding season, only age 1+ fish are found in the St. Lawrence estuary, since mortality is apparently complete after 2 years (Craig and FitzGerald 1982).

Our second objective concerned the reproductive state of the two age groups. Since age 1+ *G. aculeatus* apparently delay reproduction for 1 year, we postulated that the gonads of the age 1+ fish caught during the breeding season will be less developed than those of the age 2+ fish. Because information dealing with all aspects of the life cycle of anadromous age 0+ *G. aculeatus* is scarce, our last objective was to study the distribution and growth of the young of the year among the various subhabitats.

Material and methods

Study site

The study area is located between the villages of Isle-Verte and Trois-Pistoles, on the south shore of the St. Lawrence estuary (Fig. 1). In 1985 and 1986, we sampled three subhabitats in this region: (*i*) tide pools, (*ii*) tidal rivers, and (*iii*) open waters of the St. Lawrence estuary. The tide pools are located in the *Spartina patens* zone of a salt marsh, on the Isle-Verte National Wildlife Area, and are flooded every 9–15 days during spring tides. For additional information concerning the marsh, see Reed and Moisan (1971).

The tidal rivers studied, Rivière Trois-Pistoles, Rivière Verte, and Rivière des Vases, are the three largest rivers in the area of Île Verte (Fig. 1). However, since the catches in Rivière Verte represented less than 2% of the total catches in the tidal rivers, data from this river were eliminated from all subsequent analysis. Rivière des Vases flows through a salt marsh and is adjacent to a series of tide pools. Here, our sampling site was located 0.5 km from the river's mouth, where the width of the river was approximately 30 m (measured at mean water level) and the bottom was a sand–mud mixture. Rivière des Vases is further described in Lambert and FitzGerald (1979). Rivière Trois-Pistoles was the larger of the two rivers. At our sampling site, located 1.0 km from the river's mouth, the width of the river was 140 m (measured at mean water level), and the substrate was characterized by fine to coarse gravel with some large boulders. In both rivers, the choice of sampling sites was determined by ease of sampling.

In the estuary, the three stations sampled in 1985 (Fig. 1) were the south (station A) and north (station B) channels of Île Verte and Île aux Basques (station C). Because catches were low at station C in 1985, it was replaced the following year by a station located at the eastern end of Île Verte (station D). Again, because of low catches, both stations C and D were subsequently pooled with station B and considered as our "offshore" station, as opposed to "nearshore" station A.

Sampling date and methodology

From 21 April to 7 July 1985 we sampled monthly, during spring and neap tides, in all three subhabitats and at all stations. Since previous studies had shown that breeding activities were greatly reduced after the end of June (FitzGerald 1983; Whoriskey *et al.* 1986), we only sampled during spring tides from 7 July until 10 November. After this date, the ice cover prevented access to the tidal rivers and coastal areas. In 1986, we only sampled stations A and B from 21 April to 23 June to document the gonad condition of the females caught in the estuary and the distribution of the age groups of *G. aculeatus* in this subhabitat.

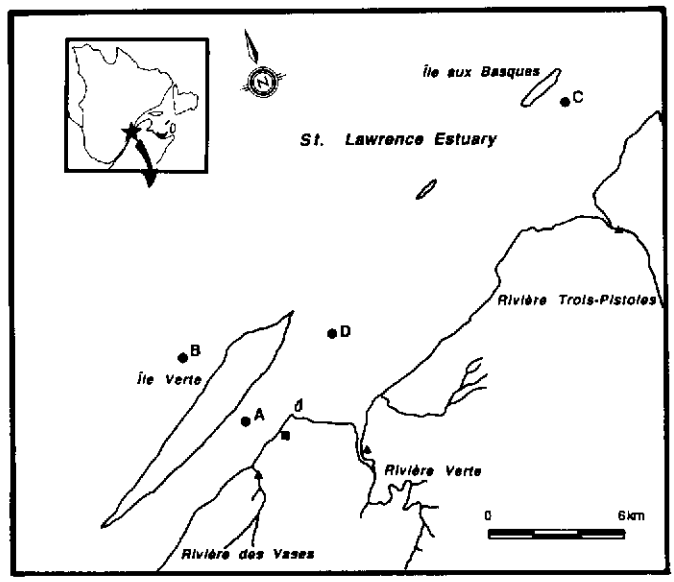

FIG. 1. Location of the various sampling sites. Circles represent estuarine stations, triangles are the different tidal rivers, and the square shows the location of the tide pools.

In the tidal marsh, we selected three tide pools with comparable perimeters of 30.2, 28.6, and 25.3 m, and each pool was seined three times. In the tidal rivers, three 1-min seine hauls were made. The seine measured 2 × 12 m (height × length). The mesh size was 6 mm, which prevented the escape of age 0+ fish that were more than approximately 3 days old (Hardy 1978).

Sampling in the St. Lawrence estuary was done from a 6.40-m Boston Whaler, using a 1.2 × 1.5 × 4.9 m (height × width × bag length) pelagic trawl equipped with a General Oceanic flowmeter. The net was hauled for 20 min against tidal currents at an average speed of 2–3 knots; between 10 and 14 hauls were made on any particular sampling date. This net was divided into three successive panels, with mesh sizes of 38.1, 25.4, and 12.7 mm at the cod end. Sampling was always performed near the surface, as preliminary trials proved this method to be the most successful. We frequently observed sticklebacks associated with patches of floating algae, as reported by previous authors (e.g., Bigelow and Schroeder 1953; Parin, 1968, in Wootton, 1984; Scott and Scott 1988).

In 1985, when age 0+ *G. aculeatus* were first observed in the tide pools, every second sample in the estuary was collected using a 0.5-m standard plankton net (0.569-mm mesh size) equipped with a General Oceanic flowmeter to sample for age 0+ fish. Since sampling ended before the first appearance of young of the year in 1986, we only used the pelagic trawl. Catches in the estuary were standardized as the number of fish/10^4 m^3, which represented our catch per unit effort (CPUE). Surface, midwater column, and bottom temperatures and salinities in the estuary were measured using a Beckman portable salinometer, in order to examine the relationships between catches and physical variables. However, we found no evidence of consistent relationships between temperature or salinity and the nearshore distribution of fish (Kendall's rank correlation test). All samples were preserved in 10% formalin.

We conducted two marking experiments in 1985 to describe possible movement patterns among the subhabitats. The fish were individually marked in the tide pools on 12–16 May and 11–15 June by clipping their first and second dorsal spines, respectively. All individuals that were recaptured in either subhabitat were counted and sexed.

Laboratory analysis

The sticklebacks collected were counted, sexed, and measured to the nearest 0.1 cm (total length). The total, somatic, and gonad weights of females were measured to the nearest 0.0001 g after carefully absorbing all excess water with blotting paper. Gonadosomatic indices

(GSIs) were calculated as (gonad weight/somatic weight) $\times 100$. To determine growth of age 0+ fish, we measured the total length of 30–200 randomly chosen fish, depending on the sample size.

Ageing of the fish

Because of their size, the identification of age 0+ fish was unequivocal. However, in the case of age 1+ and age 2+ adults, Rao's method of moments (Rao 1948) was used to objectively assign the fish to either one of the adult year classes. This method decomposes the frequency distributions of lengths and provides the relative percentage for each of the adult year classes as well as their respective average total lengths and standard deviations. Otolith reading of 116 adults captured between 19 and 27 April 1986 confirmed the results of the length–frequency analysis and enabled us to verify that there were no fish older than 2 years old.

Statistical analysis

Differences in seasonal and monthly abundances of the two adult year classes were tested for equality with a χ^2 goodness of fit test (Sokal and Rohlf 1981). The GSIs of the two adult age groups and total lengths of age 0+ fish were compared using the Wilcoxon (two samples) or Kruskal–Wallis (more than two samples) nonparametric comparisons, since the data were not normally distributed. Significantly different samples were further compared using a modification of Dunn's nonparametric multiple comparison test for unequal sample sizes (Zar 1984). The level of significance for all tests was 0.05, and all statistics were performed on Statistical Analysis System programs (SAS Institute Inc., Cary, NC), except for the nonparametric multiple comparisons, which were done by hand.

Results

Abundance in the subhabitats

In 1985 (Fig. 2), the highest number of adults ($22.4/10^4$ m^3) at station A occurred on 28 April, and was followed by low ($4.2/10^4$ m^3) CPUE values on 28 May. High ($12.9/10^4$ m^3) CPUE values were again obtained on 27 June, but after 3 August, no adult fish were captured at this station. Age 0+ fish were first caught at station A on 3 July and their highest ($55.0/10^4$ m^3) CPUE values were recorded on 3 August.

At station B (Fig. 2), a low ($0.5/10^4$ m^3) number of adults was found on 21 April; this value subsequently increased to 10.6 and $20.6/10^4$ m^3 on 7 May and 27 May, respectively. However, on 27 May, because of logistic problems, we only made four trawl hauls at midtide. This phase of the tide cycle, characterized by the fastest tidal currents, was always the period of highest catches. Therefore, the CPUE on 27 May was probably an overestimation of the abundance of *G. aculeatus*. After 27 May, the abundance of adults remained low for the rest of the season, and none was caught after 25 July. Age 0+ fish were first captured on 2 July and their maximum CPUE values were recorded on 25 July ($22.0/10^4$ m^3).

In Rivière des Vases, Rivière Trois-Pistoles, and in the tide pools (Fig. 3), the highest numbers of adults were attained between 27 and 29 June, at the time when the lowest CPUE values for adults were recorded in the south channel of the estuary (Fig. 2). Age 0+ fish first appeared in all three subhabitats on 3 July.

In 1986, at station A (Fig. 4), catches of adult fish were highest ($172.2/10^4$ m^3) on 19 April, whereas at station B, maximum ($27.6/10^4$ m^3) abundance occurred on 16 May. After these dates, CPUE values for adults remained low for the rest of the breeding season.

Relative abundance of the age groups in the subhabitats

In 1985 we captured a total of 11 202 sticklebacks, and in all the subhabitats, except Rivière Trois-Pistoles, age 0+ fish were the most abundant age group for this species (Table 1). Seasonal

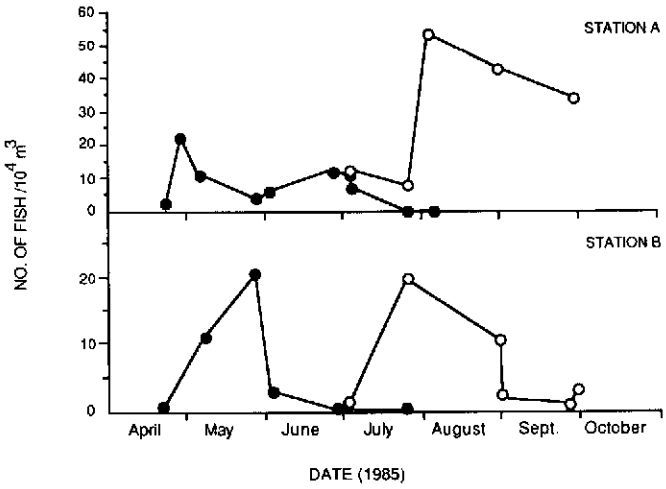

FIG. 2. Abundance of adult (●) and age 0+ (○) *G. aculeatus* at stations A and B of the middle St. Lawrence estuary in 1985.

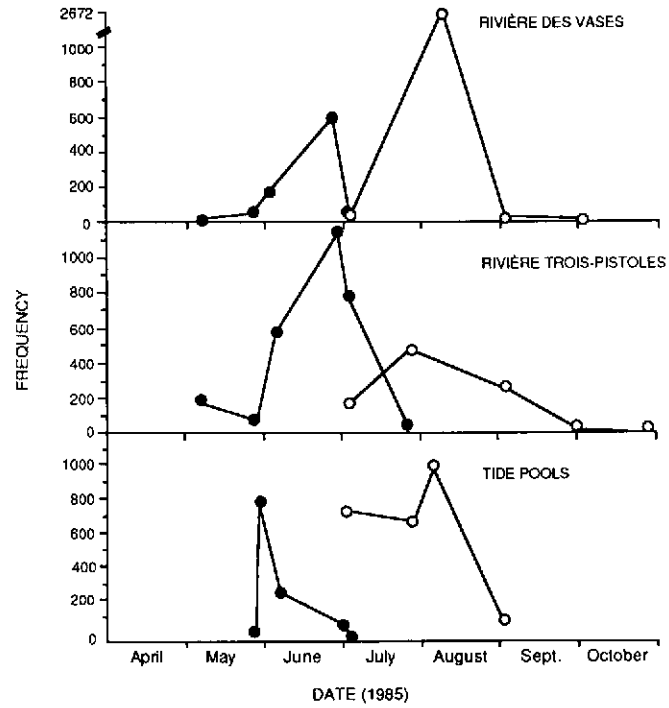

FIG. 3. Abundance of adult (●) and age 0+ (○) *G. aculeatus* in Rivière des Vases, Rivière Trois-Pistoles, and in the tide pools in 1985.

data showed that age 2+ fish were significantly more abundant than age 1+ fish in the estuary ($\chi^2 = 98.62$; df = 1; $P < 0.001$) and in Rivière des Vases ($\chi^2 = 41.48$; df = 1; $P < 0.001$) (Table 1). In the tide pools, the proportion of the two year classes was similar ($\chi^2 = 1.77$; df = 1; $P > 0.05$), whereas in Rivière Trois-Pistoles, age 1+ adults outnumbered age 2+ adults ($\chi^2 = 98.62$; df = 1; $P < 0.001$) (Table 1).

We also performed a separate analysis for each month of the breeding season when sample sizes were sufficient. In all the subhabitats, these monthly results corroborated the seasonal data concerning the relative abundance of age 1+ and age 2+ *G. aculeatus* (Fig. 5). In 1986, 1417 adult fish were captured in the St. Lawrence estuary. The combined data show that the age 2+ fish were more numerous than the age 1+ fish ($\chi^2 = 670.62$; df = 1; $P < 0.001$) in this subhabitat (Table 1). At station A, age

TABLE 1. Abundance (N) and relative percentages of the two age groups of *Gasterosteus aculeatus* caught in the tide pools, tidal rivers, and open waters of the middle St. Lawrence estuary

		Age group							
		0+		1+		2+		Total	
Habitat	Year	N	%	N	%	N	%	N	%
Estuary	1985	736	63.6	109	9.4	313	27.0	1158	100.0
	1986	—[a]	—	221	15.6	1196	84.4	1417	100.0
Tide pools	1985	1468	54.1	647	23.8	600	22.1	2715	100.0
Tidal rivers									
Riv. des Vases	1985	2691	75.9	332	9.4	520	14.7	3543	100.0
Riv. Trois-Pistoles	1985	926	24.5	2112	55.8	748	19.7	3786	100.0

[a]In 1986, only adults were sampled.

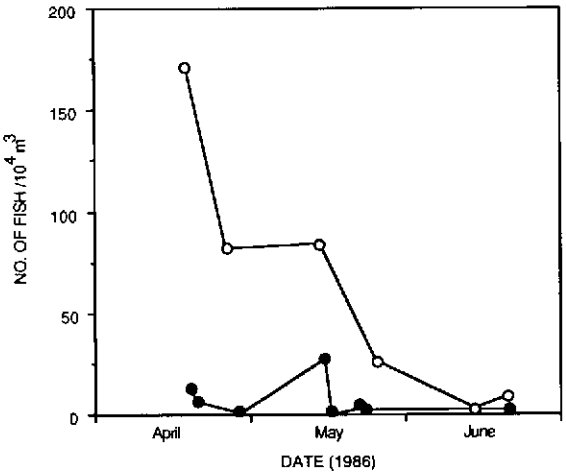

FIG. 4. Abundance of *G. aculeatus* at stations A (○) and B (●) of the middle St. Lawrence estuary in 1986.

2+ fish dominated the catches for the months of April, May, and June (Fig. 5).

Recaptures of marked fish in the subhabitats

Of the 1267 adults marked in the tide pools during the first experiment (12–16 May), 71 fish were recaptured in the tide pools when we sampled for the second experiment (Table 2). In the St. Lawrence estuary, we caught three fish in 1985 and seven fish in 1986. In the tidal rivers, only six fish were recaptured, all in Rivière des Vases.

In the case of the 5986 adults marked during the second experiment (11–15 June), six adults were recaptured in the St. Lawrence estuary in 1986.

In 1986, all the recaptured fish from both marking experiments were age 2+ fish, as shown by their size distribution (males: 7.1–7.5 cm; females: 7.5–8.0 cm).

Female GSIs

We compared the GSIs of age 1+ and age 2+ females sampled in Rivière des Vases and Rivière Trois-Pistoles between 4 June and 3 July 1985 and at station A between 19 April and 27 May 1986. Out of nine samples, three showed significantly higher GSIs for age 2+ fish, and one yielded the opposite result. The remaining five samples did not show any significant differences between the two age groups. The results indicate that there were no consistent relationships between age and relative gonad size.

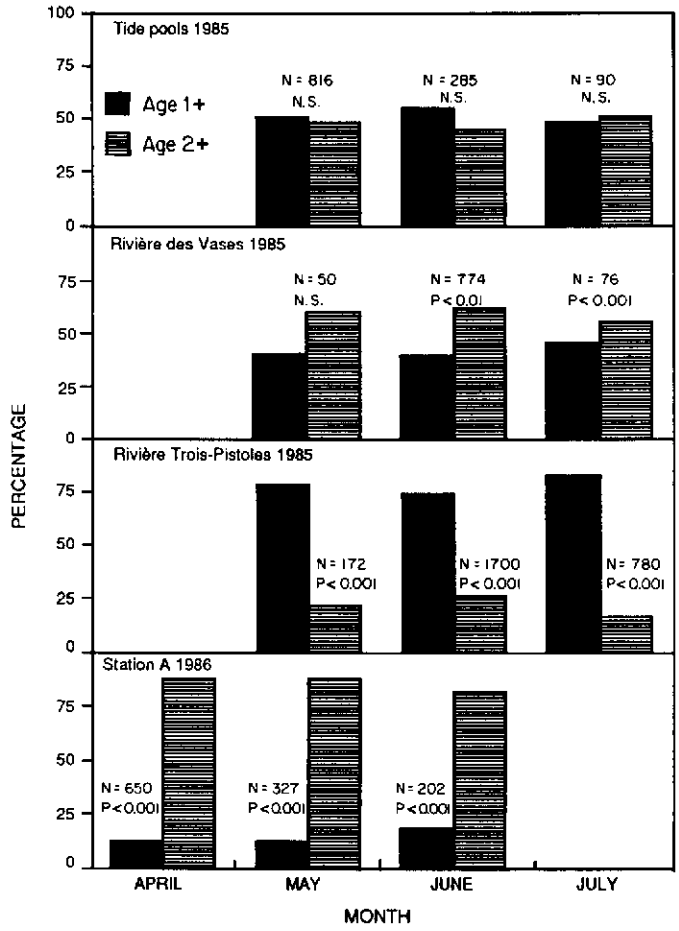

FIG. 5. Percentages of catch comprising age 1+ and age 2+ *G. aculeatus* in the tide pools, Rivière des Vases, and Rivière Trois-Pistoles in 1985 and at station A in 1986 (χ^2 goodness of fit test; starting hypothesis: age 1+ and age 2+ fish are equally abundant). N.S., not significant.

Growth and median lengths of age 0+ fish

During the breeding season, the only significant increase in length over time occurred at station A, where age 0+ fish grew 0.187 mm/day ($R = 0.96$; df = 4; $P < 0.01$). For any given date during the breeding season, the largest young of the year were found in the estuary (station A or B), and the smallest fish were captured either in the tide pools or in tidal rivers (Kruskal–Wallis nonparametric comparisons) (Fig. 6). In the tide pools, age 0+ fish never exceeded 2.8 cm (31 August), whereas at

TABLE 2. Recaptures of adult *Gasterosteus aculeatus* in three subhabitats of the Isle-Verte area in the middle St. Lawrence estuary in 1985

Date of tagging experiment (1985)	No. of fish marked	No. of recaptures			
		1985			1986
		Estuary	Riv. des Vases	Tide pools	Estuary
May 12–16	1267	3	6	71[a]	7
June 11–15	5986	0	0	0	6

[a]All the fish were recaptured during the second tagging experiment.

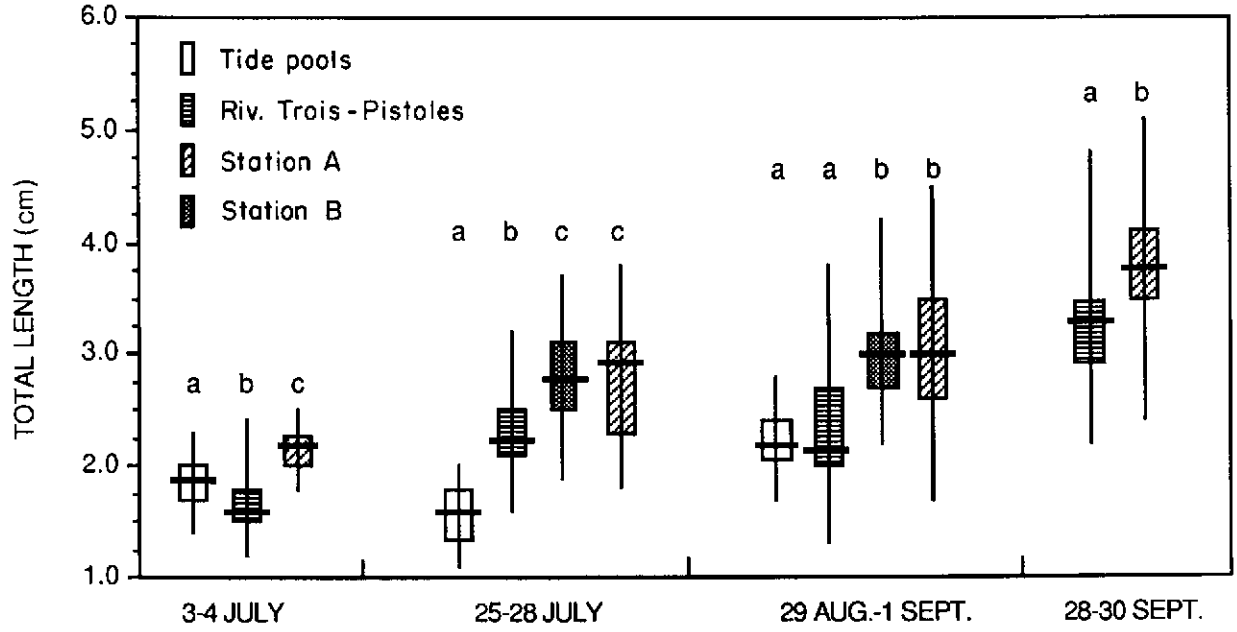

FIG. 6. Comparisons of the total length of age 0+ sticklebacks captured in the tide pools, Rivière Trois-Pistoles, station A, and station B of the estuary. Medians are represented by the horizontal lines, the lower and upper limits of the box are the 1st and 3rd quartiles, respectively, and the vertical lines indicate the range of values. Medians with the same letters are not significantly different.

station A, young of the year as long as 4.5 cm were captured during the same period of time (29 August).

Discussion

The sticklebacks that are found in the different subhabitats of the Isle-Verte area are probably members of a single population. This conclusion is based on several lines of evidence. The first is the geographical proximity of the subhabitats. In the middle St. Lawrence estuary, the displacement of surface waters by tidal currents varies from 9 to 26 km (Laprise and Dodson 1989). Thus, knowing the swimming ability of sticklebacks (Taylor and McPhail 1986; Whoriskey and Wootton 1987), fish located in the estuary could readily traverse the stretch of coastline from the Isle-Verte salt marsh to Rivière Trois-Pistoles. Secondly, our catch curves (Figs. 2 and 3) showed that decreases in the abundance of adults in the estuary early during the breeding season coincided with increases of their numbers in the tide pools and tidal rivers. Thirdly, the recaptures from our marking experiment, although not numerous, indicated that fish marked in the tide pools could be recaptured in either one of the subhabitats.

By sampling in three different subhabitats, we were able to establish the chronology of appearance of *G. aculeatus* in these subhabitats. Our catch data during the spring show the departure of adult *G. aculeatus* from the estuary towards the breeding grounds, whereas at the end of the season, it can be seen that age 0+ fish leave the rivers and tide pools to overwinter in the St. Lawrence estuary. In the estuary, the turbid waters combined with high tidal amplitudes (reaching 4.6 m during spring tides) and cold surface temperatures (May and June average at station A: 9.1°C) almost certainly prevent reproduction in the estuary, in the vicinity of the study area. Although we cannot be certain about the winter distribution and life history events during the 5- to 7-month period of ice cover during which we were unable to sample, the most likely scenario is that this period is either spent in offshore areas near Isle-Verte or in the tidal rivers, as suggested by catches of *G. aculeatus* as late as 26 October 1985 in Rivière Trois-Pistoles (Fig. 3).

We found age-related differences in habitat use between age 1+ and age 2+ fish, but these differences were not as we expected. At station A, during both years, age 2+ fish were more abundant than age 1+ fish (Table 1). This result was surprising because we expected a typical age structure, where the relative proportion of fish belonging to a specific age group decreases with age (Elseth and Baumgardner 1981). Thus, following the overwintering period, a high proportion of the age

1+ fish born on the Isle-Verte breeding grounds do not gather at station A during the spring. Rather, these fish are presumably located either in neighbouring river systems or in unsampled offshore areas of the St. Lawrence estuary. Because of the high numbers of age 1+ *G. aculeatus* in Rivière Trois-Pistoles (Table 1), the former hypothesis appears the most likely.

In the tide pools and in Rivière des Vases, the relative proportion of age 1+ to age 2+ fish was higher than at station A, but the age 1+ fish were still not as abundant as expected from demographic theory (Elseth and Baumgardner 1981). Similar findings have been previously reported for another anadromous population of *G. aculeatus* (Münzing, 1959, in Wootton, 1984). In this study, age 1+ fish spent their first summer in the sea away from the breeding grounds, but this was probably because sexual maturity was reached at 2 years of age. This is apparently not the case at Isle-Verte where adults are capable of reproducing during their first summer (Picard 1988) and may return the following year to reproduce, as suggested by recaptures at station A in 1986 of fish that were marked in 1985 (Table 2). Furthermore, we found that both age 1+ and age 2+ females allocate similar proportions of their total energy into gonads. This was contrary to our second hypothesis, but supported Boulé (1988) who also failed to detect any difference in the GSIs of age 1+ and age 2+ females kept in the laboratory.

Perhaps any benefits that age 1+ fish would gain by reproducing on the breeding grounds at Isle-Verte are outweighed by the costs of competition with the larger age 2+ fish. At Isle-Verte, fish densities may be relatively high (Ward and FitzGerald 1983) and can cause a decrease in the number of males that become territorial (Whoriskey and FitzGerald 1987). Hence, if nest sites are limited, large males may be more successful in obtaining territories (Rowland 1989*a*; J. C. Belles-Isles unpublished results). In the case of females, large individuals may also be advantaged, since they appear to be courted more often than smaller ones (Rowland 1989*b*). Thus, because of their size, age 1+ fish may prefer to stay in other subhabitats, such as Rivière Trois-Pistoles, where the fish densities are probably lower than at Isle-Verte. This hypothesis is supported by large numbers of age 1+ adults in Rivière Trois-Pistoles found in 1985 (Fig. 5). Clearly, the question regarding the relative breeding success of age 1+ and age 2+ *G. aculeatus* at Isle-Verte deserves further attention.

Finally, our data on age 0+ *G. aculeatus* suggest that the fish leave the tide pools for the estuary once they have reached a length of approximately 2.2 cm (median length), which agrees with the results of Poulin and FitzGerald (1989). The ability of age 0+ fish smaller than 2.2 cm to remain in the tide pools despite tidal flooding is supported by observations of young fry accompanied by their fathers in the tide pools during periods of tidal flooding (FitzGerald *et al.* 1986). In the estuary, the gradual increase in length of age 0+ *G. aculeatus* indicates that there were no small age 0+ fish arriving from the breeding grounds after the end of June. This suggests that most of the breeding activity had taken place prior to this date, corroborating previous observations made at Isle-Verte (FitzGerald 1983; Whoriskey *et al.* 1986) and in New Brunswick (Delbeek and Williams 1987).

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