The breeding-season population structure of three sympatric, territorial sticklebacks (Pisces: Gasterosteidae)

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Animals breeding only once late in life should spend most of the time during their one reproductive season attempting to reproduce. Contrary to this prediction, we found that the individuals of three species of sticklebacks (Pisces: Gasterosteidae) spent very short periods of time on their breeding ground. Tidal flooding of the site controlled patterns of fish immigration and emigration. Inundations early in the breeding season brought in new immigrants which replaced most resident fish. However, towards the end of the breeding season there was less immigration and a higher percentage of the residents remained in their pools. We expected to see movements among pools by surplus males searching for sites to establish a territory; instead, few fish moved among pools, and most of those that did were females. A high energetic cost of breeding in this unstable habitat may best explain these residency patterns.

I. INTRODUCTION

Breeding systems based on territorial behaviour are commonly encountered in nature and presumably permit animals to realize the highest reproductive success possible for a particular time and place (Huntingford, 1984; Vehrencamp & Bradbury, 1984). Within these systems individuals (usually males) or male-female pairs occupy an area and aggressively defend it from intruders. The defended space contains one or more limited resources which are necessary for successful reproduction (Brown, 1969), and competition to establish territories is often intense. Those animals which do not succeed in obtaining territories usually do not breed.

In a territorial breeding system the same animals often occupy the same place for the entire breeding season, leading to a stable population structure on the breeding grounds (Krebs, 1971; LeBoeuf, 1972; Bedard & LaPointe, 1984; Taborsky, 1984). This stability develops in part because the resident or residents may become relatively immune from attempts by conspecifics to displace them from the territory (a prior residence effect; see Wilson, 1975; Beaugrand & Zayan, 1985). Subordinate individuals may undergo physiological changes which reduce their aggressiveness and hence their tendency to challenge a territory holder (Rowell, 1974). In addition, in colonially nesting species a 'dear enemy' effect may develop, whereby the frequency and intensity of aggressive interactions between familiar neighbours are reduced (van den Assem & van der Molen, 1969; Peeke *et al.*, 1971; Thresher, 1979). At the same time, several individuals who share a common boundary may jointly attack intruders in the region where their territory boundaries abut (Dominey, 1981; Gross & MacMillan, 1981). Non-residents attempting to displace

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territorials in the colony may be subjected to concurrent attacks by several territory owners, which would make it difficult for the intruder to win space.

Many populations of sticklebacks (Gasterosteidae) undertake a spring migration to specific breeding sites where their polygamous breeding system develops. Males establish and defend territories and provide parental care to eggs and young (Wootton, 1984). Both males and females can spawn repeatedly under laboratory conditions during the reproductive season (Wootton, 1976). In many field populations individual fish make only one reproductive migration, with the members of the breeding year class dying after spawning (Craig & FitzGerald, 1982; Wootton, 1976, 1984). Current life history theory predicts that animals breeding only once late in life should invest most of their time and energy into reproduction in the one season available to them (Horn & Rubenstein, 1984). This suggests that sticklebacks should spend most of their time during the breeding season on the breeding grounds, which would lead to a stable population structure where the same individuals occupied the same sites for the reproductive period. However, no studies have succeeded in systematically following the structure of any population of these fish during their reproductive period, due to the difficulty of observing and marking the individual fish.

At Isle Verte, Quebec, three species of stickleback (the threespine, *Gasterosteus aculeatus* L., the black-spotted, *G. wheatlandi* Putnam, and the ninespine, *Pungitius pungitius* L.) migrate each spring from the St Lawrence estuary to salt marsh tide pools where they breed. Abundant food supplies are available to the fish here (Worgan & FitzGerald, 1981 *a, b*; Ward & FitzGerald, 1983 *a, b*; Walsh & FitzGerald, 1984), so breeding activity is probably not affected by a lack of this important resource. The fish can move between the St Lawrence estuary and the pools, or from pool to pool, only during the tidal flooding of the marsh which occurs about twice a month. Most of the tide pools are small (< 50 m^2 surface area) and shallow (< 0.5 m deep). These conditions permit the relatively easy capture (by seining) and subsequent marking of all fish in a pool, and allow the identification of movements of tagged fish from one pool to another. By seining and marking after each tidal cycle in selected pools it is possible to quantitatively describe stickleback population structure at this site.

Here we present a test of the prediction that the fish would remain in the pools for the entire breeding season. We documented immigration and emigration patterns between the tide pools and the St Lawreence estuary to identify the residence times of fish in the marsh. We also observed the movement patterns of fish between pools in the marsh. Surplus males were present at this site (FitzGerald, 1983; Whoriskey, 1984), suggesting space was a limited resource. We predicted that the fish which moved from one pool to another would be mostly surplus males, which had little chance of establishing a territory in their original pools. In contrast, territorial males and females which are successfully spawning should stay in place rather than risk movements to unknown sites where their reproductive success might decrease (Greenwood, 1980). We also observed sex ratios in these pools. In polygamous systems females are predicted to be the sex limiting mating frequency (Partridge & Hill, 1984). This occurs because the female energetic investment in gametes is much greater than the male cost of producing sperm (e.g. Wootton *et al.*, 1980, but see Nakatsuru & Kramer, 1982). Due to this energetic imbalance, males are capable of spawning more often, and with more partners, than females. This
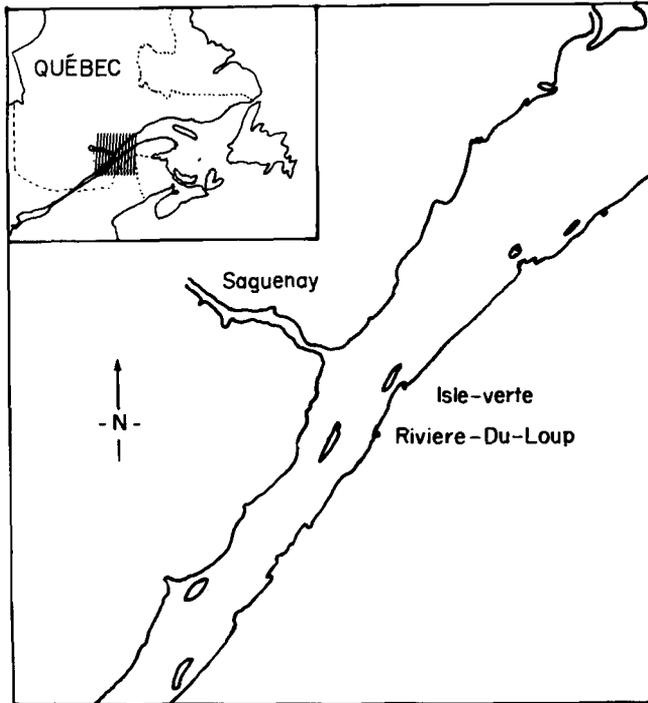
FIG. 1. The study site.

should lead to intense inter-male competition for the limited number of females present (Trivers, 1972). In contrast, most females are assumed to have free access to mates when they are ready to reproduce (Huntingford, 1984; Partridge & Hill, 1984; Warner, 1984). While these predictions should hold when the male:female ratio in a population is approximately 1:1, if the sex ratio became significantly biased towards females, males could become a limiting resource. In collecting data on the male:female ratio we hoped to identify times when male-male, or female-female competition for mates would be most intense.

II. MATERIALS AND METHODS

THE SITE

We worked in the extensive series of tide pools contained within the *Spartina patens* zone of the Isle Verte National Wildlife Area, near Rivière du Loup, Quebec (Fig. 1). Most of these pools are flooded at intervals of 9–15 days during peak high tides, and have no connection with either the estuary or the other pools except during floodings. Further descriptions of the area and its fauna can be found in Reed & Moisan (1971) and Ward & FitzGerald (1983 *a, b*); additional information on the fish resident in the St Lawrence estuary near the site is given by Dutil & Fortin (1983). The three species of sticklebacks (*G. aculeatus, G. wheatlandi* and *P. pungitius*) all breed in these tide pools. The only other fishes found in the pools are rare mummichogs, *Fundulus* sp., and fourspine sticklebacks, *Apeltes quadracus*. Only one of each of these two species was found among the 3330 fish examined in this study, so we considered them as strays and excluded them from our analysis.

Due to the limitations imposed by the time it took to mark the fish, we observed the populations in only two pools. However, we believed these pools were representative of fish population structure at the site. We verified this assumption on 10 May 1982 and 3 May 1983 (the start of the breeding season) by completely seining out and counting the fish within 11 different pools. We tested for significant differences among pools in the densities of males and females of all species, and found none. In addition, on 17 June 1979 Worgan & FitzGerald (1981*a*) also found no significant differences in the species composition or densities of fish in pools equidistant from the St Lawrence estuary. Given these similarities, we felt justified in reducing the number of pools studied to two.

SAMPLING TECHNIQUES

The pools became accessible to migrating fish only when minimum tide heights (as reported in the tide tables) reached 3·9 m. This happened on 24–29 April, 22–28 May, 20–26 June and 19–24 July in 1982, and 27 April–1 May, 12–18 May, 25–30 May, 10–17 June, 23–28 June and 9–16 July 1983. After each flooding period we seined the pools and counted, by species and sex, the number of fish present. The sex of each individual was assessed by secondary sexual characteristics. Females of all species were cryptically coloured and often had swollen abdomens from ovarian development. Male *G. aculeatus* have bright blue eyes and a red throat and abdomen during the breeding season, while the bodies of male *G. wheatlandi* take on a green sheen. Male *P. pungitius* are jet black with contrasting white pelvic spines.

After counting, the fish were batch marked, with distinctive tags used in each pool on the different dates. Depending on our objectives, we used one of two techniques. To follow movements of fish between pools, on 10 May 1982 and 21 May 1983 we attached coloured (white in white pool, yellow in yellow pool) plastic beads, approximately 1 mm in diameter, to the upper part of the stickleback's body just behind the last dorsal fin spine. This was done with a piece of nylon thread passed through the fish's body with a surgical needle. A total of 1641 fish were tagged for the movement study in the two years. The second technique was spine clipping, which was used on 3 May and 1, 17 and 28 June 1983. Both sets of marking permitted the evaluation of immigration and emigration to and from the study pools. Before they were released back into their home pools, tagged fish were allowed to recover from the tagging procedure overnight in a holding pen placed in a tide pool. Neither the seining nor the tagging procedures had obvious effects on fish behaviour. We found no mortalities from either treatment in the holding pen, and in the following days the tagged fish were seen performing normal breeding activities.

The number of new immigrants was assessed on 28 May 1982 and all dates in 1983 by comparing the number of marked and unmarked fish in the pools. However, on 26 June and 26 July 1982 we used an alternative technique in order to assure ourselves that the tagging procedure was not adversely affecting the fish. We estimated the number of immigrants by emptying six additional pools of their fish just before the flooding cycle, and then seining them again after the cycle was finished. The six pools were similar in size to the study pools and located in the same part of the marsh as our experiment. These data provided us with an estimate of the number of immigrants per m^2 tide pool area which moved into the marsh. By multiplying the surface area of our study pools by these figures, we calculated the number of new fish moving into the community. These estimates were divided by the actual number of fish in the pools to determine the percentage of new fish present.

To check the accuracy of this estimate, in 1983 we repeated the procedure on 17 May, 1 June and 17 June and compared these results to those obtained by marking all fish. In cases where 10 or more fish moved into the pools, agreement between the two estimates was good. Values obtained by marking all fish were, on average, slightly higher (approximately 15%) than the estimates from the second technique.

To follow movements between pools, after the flooding cycles of 22–28 May 1982 and 25–30 May 1983 all pools within a 50-m radius of the study pools were minnow-trapped (1 trap per 15 m^2 for 4 h). In addition, a systematic visual survey of all tide pools within 1200 m of the originals (408 pools visited) was conducted during each year. The observer viewed each pool for 5–10 min, which was sufficient time to accurately check for tagged fish. Once spotted, marked fish were trapped with a dip-net, but where a fish could not be

dip-netted the pool was seined. Tagged fish were preserved, sexed, and the closest distance and the direction to their home pools were determined. To test the visual recapture technique, we visually surveyed nine pools as described above then seined out all their fish. We found no tagged fish among the individuals captured. Nor did we capture tagged fish from minnow traps put into eight pools which had been visually surveyed. Because of this we believe our sampling techniques were efficient.

STATISTICAL ANALYSIS

All statistical procedures follow Zar (1974). In some instances, where data from the two pools were similar, we pooled this information to clearly present general patterns. In other instances we did not pool data, in order to give some measure of the inter-pool variability at the site. Percentage data were arcsin transformed before statistical treatment. Sex ratios were evaluated on pooled data from the two pools with chi-square tests against a theoretical male:female ratio of 1:1. Inter-specific comparisons of distance moved during the flooding periods were tested with pooled data from the two pools, using the Mann-Whitney U-test or the Kruskal-Wallis ANOVA, as appropriate, because of violations of assumptions of normality and homogeneity of variance. Calculations of the mean angle of displacement were followed by evaluation of the circular standard deviation (angular dispersion). Rayleigh's test was used to determine whether there was a significant mean directionality in the pool-to-pool displacements made by each species, and a Watson-Williams statistic tested for interspecific differences in directionality.

III. RESULTS

COMMUNITY STRUCTURE

During 1982 the number of fish (composed of previous residents and new immigrants) present in the two pools on the four sampling dates was 1150 (10 May), 627 (28 May), 239 (26 June) and 29 (26 July). Two significant differences in fish density were noted between the two experimental pools in this year (Table I): both occurred on the first sampling date and they involved *G. aculeatus* and *G. wheatlandi*. These inter-pool differences were probably artifacts of the reduction of the number of study pools from the original 11 we tested to only two. We made a total of 30 comparisons of density between the two pools during the two years of this study (3 species × 10 sampling dates): with P set at 0·05 we would expect either one or two chance differences to occur, so chance differences probably account for these density deviations.

Gasterosteus wheatlandi dominated the fish community on 10 May, while *P. pungitius* was the most abundant species on 26 July when the number of fish present was small (Fig. 2, Table I). Outside of these periods the three species were approximately equally abundant. The total number of immigrants which moved into the two pools from the St Lawrence estuary during 1982 was estimated to be 409 *G. aculeatus*, 934 *G. wheatlandi*, and 601 *P. pungitius*.

In 1983 the pools were flooded more frequently than in 1982 (six times *v.* four). The number of fish present in the two pools on the respective sampling dates was 110 (8 May), 591 (21 May), 720 (1 June), 272 (17 June), 180 (28 June) and 8 (21 July). No significant differences in fish density between the two pools were noted for any of the three species on a given sampling date (Table I). *P. pungitius* dominated the fish community at the start (8 May) and end (21 July) of the breeding season (Fig. 3). On the other dates the abundances of all species were similar. A total of 292 *G. aculeatus,* 541 *G. wheatlandi* and 553 *P. pungitius* immigrated into the two pools during the 1983 breeding season.

TABLE I. Numbers of fish present, and densities (number of fish m^{-2}) of fish in the two experimental pools on each sampling date. Totals include fish which were previous residents as well as new immigrants arriving during the most recent tidal cycle. W, white pool, 43·6m²; Y, yellow pool, 19·0m² surface area

Date	Pool	Gasterosteus aculeatus				G. wheatlandi				Pungitius pungitius			
		No. Males	No. Females	No. Total*	Density	No. Males	No. Females	No. Total*	Density	No. Males	No. Females	No. Total*	Density
1982													
10 May	W	9	11	20	0·46†	67	125	193	4·42†	79	84	165	3·78
	Y	61	44	105	5·52	200	382	590	31·06	49	28	77	4·05
28 May	W	53	44	97	2·22	56	55	111	2·55	63	91	154	3·53
	Y	64	63	127	6·68	4	17	21	1·10	58	59	117	6·16
26 June	W	43	23	66	1·51	11	7	18	0·41	15	28	43	0·99
	Y	43	9	52	2·74	5	0	5	0·26	26	29	55	2·89
26 July	W	2	0	2	0·05	1	1	1	0·02	7	9	16	0·37
	Y	0	0	0	0·00	0	0	0	0·00	5	5	10	0·53
1983													
3 May	W	1	2	3	0·07	1	0	1	0·02	14	13	27	0·62
	Y	1	1	2	0·10	1	0	1	0·05	33	43	76	4·00
20 May	W	62	51	113	2·59	70	48	118	2·71	62	82	144	3·30
	Y	34	32	66	3·47	43	29	72	3·79	40	38	78	4·10
1 June	W	77	61	138	3·16	95	134	229	5·25	48	64	112	2·57
	Y	33	29	62	3·26	41	54	95	5·00	43	41	84	4·42
17 June	W	42	15	57	1·31	45	42	87	1·99	24	24	48	1·10
	Y	29	5	34	1·79	5	6	11	0·58	14	21	35	1·84
28 June	W	39	13	52	1·19	28	43	71	1·63	14	20	34	0·78
	Y	8	2	10	0·53	1	0	1	0·05	2	10	12	0·63
21 July	W	0	0	0	0·00	0	0	0	0·00	0	0	0	0·00
	Y	2	0	2	0·10	0	0	0	0·00	3	3	6	0·31

*The sex of a fish was determined from secondary sexual characteristics, but in some instances the characteristics were not sufficiently advanced for a reliable identification to be made. In these cases the unsexed fish were included in the totals column, and the totals are not equal to the sum of the male and female columns.

†Denotes a significant difference (χ^2, $P < 0.05$) in fish density between the two pools.
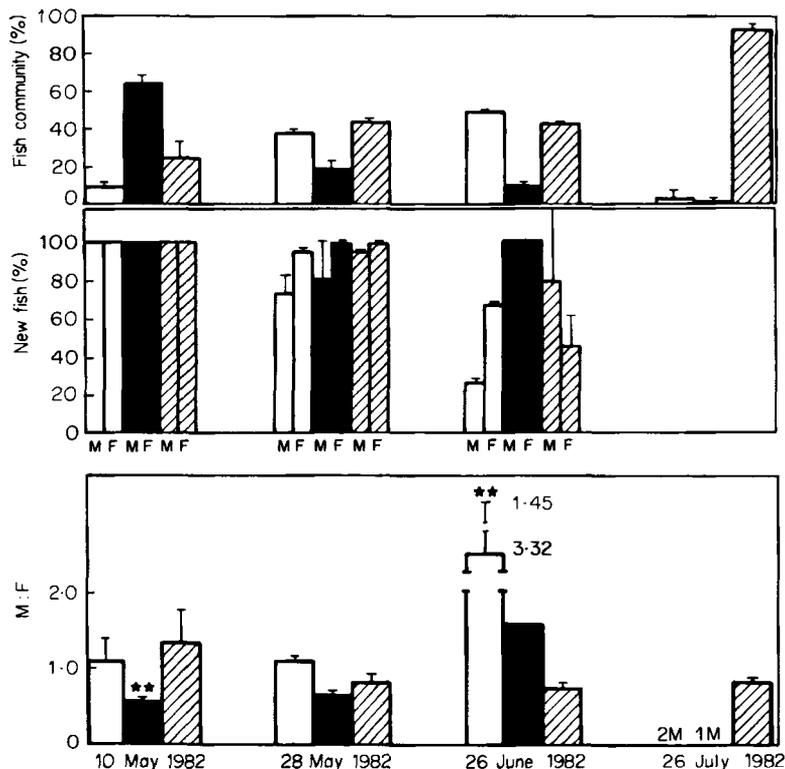
FIG. 2. Population structure, immigration patterns and sex ratios of the three species of stickleback in two St Lawrence tidal flood pools during 1982. Sampling dates are indicated above the histograms. Fish community (%) is the percentage of the total number of fish in the pool which are of the named species. Bars above the histograms are 1 S.D. New fish (%) is the percentage of the fish of a given species present on the sampling date which migrated to the marsh during the immediately preceding tidal cycle. M = male, F = female. Asterisks indicate a significant difference from a theoretical 1:1 male:female ratio (χ^2 test, $*P < 0.05$, $**P < 0.01$, $***P < 0.001$). □, *Gasterosteus aculeatus* L.; ■, *G. wheatlandi* Putnam; ▨, *Pungitius pungitius* L.

EFFECTS OF FLOODING

The effects of tidal flooding on the resident fish were similar in both years (Figs 2, 3). Nearly 100% of the fish of all species were replaced during floodings which occurred before the end of May. As immigration pressure and fish densities decreased during June, the fish, especially males, began to stay in the pools during the tidal cycle. After the tidal cycle which ended on 28 June 1983, 70–100% of the fish in the pools were previous residents (Fig. 3). The breeding season had terminated by mid-July, and most fish except a few *P. pungitius* had either returned to the St Lawrence estuary or died by this time.

Some individuals of all species moved to other pools during the inundations, but patterns of movement were different in the two years studied. These movements appeared to be affected by tidal amplitude and the prevailing winds, which established surface water currents in the marsh. In 1982 we followed the displacements after the tidal cycle of 22–28 May. At this time the maximum tide height of 4·75 m completely flooded the marsh, and the wind came constantly from the WNW at
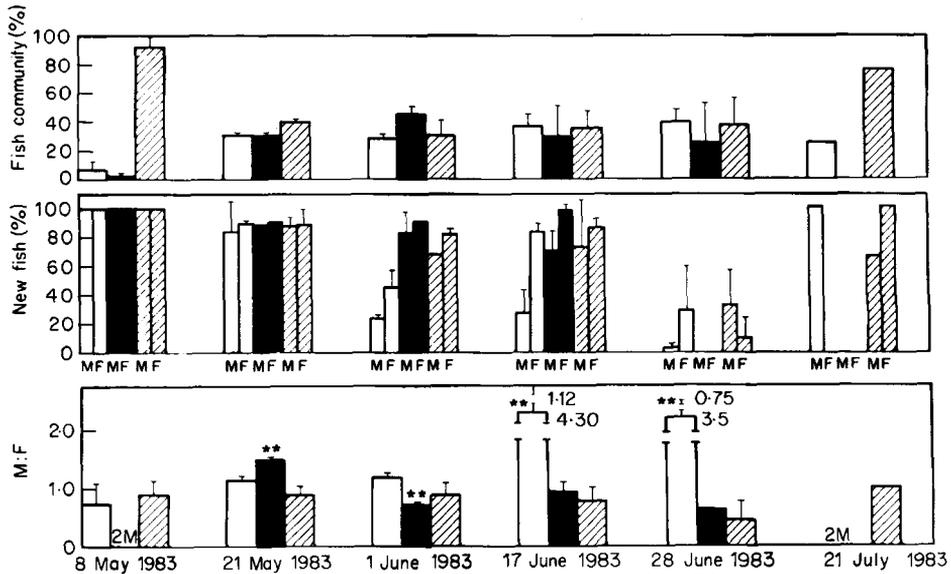
FIG. 3. Population structure, immigration patterns and sex ratios of the three species of sticklebacks in two St Lawrence tidal flood pools during 1983. Key as in Fig. 1. No fish were present in one pool on 21 July; data for this sampling are from one pool only. □, *Gasterosteus aculeatus* L.; ■, *G. wheatlandi* Putnam; ▨, *Pungitius pungitius* L.

TABLE II. Distances and directions (compass bearings) of movements of tagged sticklebacks from their home pools to other pools in the marsh. Fish were followed after the tidal cycles of 22–28 May 1982 and 25–30 May 1983. c.s.d. is circular standard deviation (Zar, 1974); M:F is the male to female ratio of fish moving to other pools in the marsh. $*P<0.05$, $**P<0.001$. Tagged fish moving (%) is the estimated percentage of the fish in the study pools which moved to other pools during the tidal cycle

Species	Distance moved (m)		Direction (°)		M:F	n	Tagged fish moving (%)
	Mean	S.E.	Mean	C.S.D.			
1982							
Gasterosteus aculeatus	121	41	120**	58	0·20*	13	10
G. wheatlandi	123	21	107**	46	0·53	24	3
Pungitius pungitius	22	15	—	—	—	2	1
1983							
G. aculeatus	5	1	353*	61	0·05**	19	11
G. wheatlandi	20	8	54*	60	1·00	16	8
P. pungitius	30	14	49*	75	0·12**	15	8

velocity 5–15 km h^{-1}, generating surface water currents in the marsh of up to 30 cm s^{-1}. The *G. aculeatus*, *G. wheatlandi* and *P. pungitius* which moved to other pools went mean distances of 121, 123 and 22 m, respectively (Table II). Only two *P. pungitius* were recaptured in other pools and since this is too few for meaningful

comparisons we excluded this species from further analyses. We found no significant difference between G. aculeatus and G. wheatlandi in the distance moved from their home pools (Mann-Whitney U-test, $P > 0.05$, $n_1 = 13$, $n_2 = 24$). The mean angles of departure of G. aculeatus and G. wheatlandi from their pools were 120° and 107° respectively, and were similar to the prevailing wind direction. In both species these directions were significantly different from a random dispersion (Rayleigh's test, G. aculeatus $z = 6.544$, $P < 0.05$; G. wheatlandi $z = 12.740$, $P < 0.001$), but between species comparisons were not significantly different (Watson-Wiliams test, $P > 0.05$). Movements in these directions took fish eastwards, parallel to the St Lawrence estuary and higher up into the marsh.

In 1983 we followed fish movements after the 25–30 May tides. Maximum tide height was 4.36 m which resulted in only partial flooding of the marsh, and there was great variability in both wind direction (30–160°) and speed (0–19.3 km h^{-1}) during the tidal cycle. Gasterosteus aculeatus, G. wheatlandi and P. pungitius moved a mean of 5, 20 and 30 m respectively (Table II), but differences among species were not significant (Kruskal-Wallis Anova, $P > 0.05$). Each species' displacements showed significant mean directionality (Rayleigh's test, G. aculeatus $z = 10.739$, $P < 0.002$; G. wheatlandi $z = 9.242$, $P < 0.005$; P. pungitius $z = 7.641$, $P < 0.05$), but there were also significant differences among the three species in the directions in which they moved (Watson-Williams test, $F = 3.27$, $P < 0.05$, Table II). Gasterosteus wheatlandi (54°) and P. pungitius (49°) moved slightly eastwards and back towards the St Lawrence estuary while G. aculeatus displacements (353°) were directly towards the estuary.

Significantly more female than male G. aculeatus (1982, $\chi^2 = 5.33$, d.f. = 1, $P < 0.05$; 1983, $\chi^2 = 15.2$, d.f. = 1, $P < 0.001$) and P. pungitius (1983, $\chi^2 = 10.89$, d.f. = 1, $P < 0.001$) displaced to other tide pools during flooding (Table II). By contrast, no significant differences were found between the numbers of male and female G. wheatlandi which moved in each of the 2 years (Table II). We also noted that only a small percentage ($< 11\%$) of tagged fish of all species were recovered after the tide cycle in other pools (Table II): presumably the rest migrated out of the marsh back to the estuary. Two of our tagged fish were recovered during incidental seining at the mouth of a tidal river emptying into the estuary near this site, supporting this suggestion.

SEX RATIOS

During 1982 there were more male than female G. aculeatus in the fish community late in the season (Fig. 2), but a significant deviation from a 1:1 male:female ratio occurred only on 26 June ($\chi^2 = 15.1$, d.f. = 1, $P < 0.001$). On 10 May the G. wheatlandi sex ratio was significantly biased towards females ($\chi^2 = 74.4$, d.f. = 1, $P < 0.001$). Pungitius pungitius sex ratios never differed significantly from 1:1 during 1982.

In 1983 a significant bias towards males was again observed for G. aculeatus late in the season (17 June, $\chi^2 = 28.6$, d.f. = 1, $P < 0.01$; 28 June $\chi^2 = 16.5$, d.f. = 1, $P < 0.01$; Fig. 3). The G. wheatlandi ratio was male-biased on 21 May ($\chi^2 = 6.82$, d.f. = 1, $P < 0.01$), female-biased during the period immediately following 1 June ($\chi^2 = 8.35$, d.f. = 1, $P < 0.01$) and not significantly different from 1:1 during the rest of the season. Pungitius pungitius sex ratios once again did not significantly differ from 1:1 during any period.

IV. DISCUSSION

Our data did not support the prediction that the population structure established at the start of the breeding season would remain stable for the entire season. Most fish which moved into the marsh stayed for only one inter-flood period, although those fish which arrived later in the season, especially males, stayed longer than those arriving earlier. Since the number of new immigrants coming from the St Lawrence into the marsh decreased as the breeding season advanced, the fish which moved out of the marsh back to the estuary did not appear to move back in again at a later date. At Isle Verte the male parental cycle lasts about 9–15 days (Reebs *et al.*, 1984), while female interspawning intervals are reported to be 19·0 and 17·5 days for *G. aculeatus* and *G. wheatlandi,* respectively (Reiffers, 1984). Thus it appears that males and females at this site spend only enough time on the breeding grounds for one spawning. This contrasts with laboratory studies which show that a male can complete up to five reproductive cycles in a breeding season and that females fed *ad libitum* are capable of producing a clutch of eggs every 3–4 days (Wootton, 1976). Kynard (1978) noted during his field work that very few male threespine sticklebacks renested after completion of a parental cycle.

Our data also do not support the prediction that the fish most likely to move from pool to pool would be surplus males searching for territories. Of the small percentage of fish in the study pools which moved to other tide pools, most were females.

We suspect that many of the fish migrating to the site may never spawn. Recent experiments have shown that some males do not establish nests, despite the presence of available space in the pools (Whoriskey & FitzGerald, 1985*a*), and that males with empty nests will often desert their territories during tidal flooding and move back to the St Lawrence estuary (FitzGerald, unpubl. data). Reiffers (1984) claims that many female ovaries may stop developing and the eggs become atretic while the females are in the marsh. Food supplies are abundant (Worgan & FitzGerald, 1981*b*; Ward & FitzGerald, 1983 *a, b*; Walsh & FitzGerald, 1984) so we do not believe a lack of potential food is affecting the fish. The stresses imposed by the harsh and unpredictable physical conditions in the tide pools may be responsible for the rapid turnover and curtailed breeding of individuals in this community. These stresses include daily water temperature fluctuations which averaged about 12° C and can. be as high as 18° C (Whoriskey, unpubl. data). Periods of extreme cold or extreme heat and very low oxygen levels also occurred during this study. On nine days in the first two weeks of May 1983 water temperature never rose above 9° C and fell as low as 2° C. *Gasterosteus aculeatus* and *G. wheatlandi* stopped most of their normal activity at these temperatures and hid under the pool banks and in clumps of algae. Some *P. pungitius* continued breeding. During June we have recorded water temperatures up to 30° C, and dissolved oxygen concentrations can fall to as low as 0·04 mg 1^{-1} (Whoriskey *et al.*, 1985). Jordan & Garside (1972) reported that the upper lethal temperature for *G. aculeatus* adapted to our salinities is about 28·5° C, and this species shows respiratory distress at oxygen levels below 2·8 mg 1^{-1} (Reebs *et al.*, 1984; Whoriskey *et al.*, 1985).

Breeding imposes an important metabolic cost on fishes. Recent studies have shown that, even when fed excess rations in relatively benign laboratory conditions, fish cannot simultaneously become reproductive and maintain their growth rate or

physical condition (Wootton & Evans, 1976; Stanley, 1983; Taborsky, 1984). The metabolic costs associated with the tolerance or adaptation to environmental fluctuations (Precht et al., 1973; Hochachka & Somero, 1984) may impose further demands on individual energy budgets. In addition to these direct costs, environmental fluctuations may impair an animal's feeding or processing of food. For example, at low temperatures our fishes' digestion rates may be slowed or stopped, and at extreme temperatures and dissolved oxygen levels the fish may divert all their time away from foraging activity to survival activities (Reebs et al., 1984; Whoriskey et al., 1985). Thus, despite the presence of a plentiful food supply, the fish may not be receiving sufficient energy to cover metabolic costs. This could drive them out of the marsh after only one inter-flood interval, but the hypothesis remains to be tested.

Another example of environmental influences upon this fish community comes from the movement data. Movements by the three species from their home pools to other sites within the marsh covered similar distances and were usually in the same direction. Since the magnitude and direction of these displacements correlated with the height of the tide and prevailing wind direction, passive transport is suggested. The fish may still partially control their displacements by choosing the moment that they move up into the water column. Movement into the current during a rising tide would presumably carry the fish up into the marsh, while movement into the current during the ebbing tide would carry them back toward the St Lawrence estuary. This type of movement, termed 'selective tidal stream transport', has already been reported in other species (Greer Walker et al., 1978; McCleave & Kleckner, 1982).

Predictable, male-biased sex ratios occurred for G. aculeatus late in the breeding season of both years. In this species, since males should be able to mate more frequently than females, shortages of reproductively active females should limit male mating frequencies throughout the breeding season. Competition between males for mates should be heightened during the times of imbalance in the sex ratio compared to periods where the ratio did not differ significantly from 1:1. In contrast, G. wheatlandi sex ratios became significantly female-biased once during the first half of the breeding season of both years, and in 1983 it also shifted from male-biased to female-biased on one occasion. This suggests that female G. wheatlandi could be limited in their mating frequency by a shortage of males during certain periods of the breeding season, and female-female competition for mates may occur at these times. During the rest of the breeding season, if competition for mates occurs it should be between males for females. For these predictions to be true, the sex ratio of the population must reflect the sex ratio of the animals which are actually capable of breeding. Unfortunately, our batch marking techniques precluded the identification of individual fish so we had no way to separate reproductively active fish from those which could not breed. Future studies looking at reproductive activity of individual fish at this site, and at the factors affecting competition for mates (including the role of mate choice, see Hay & McPhail, 1975; McPhail & Hay, 1983) would be valuable.

Despite the harsh, unstable nature of the breeding habitat, we found community structure and fish abundance patterns to be relatively stable during the two years we observed them. Ratios of G. aculeatus:G. wheatlandi:P. pungitius were 0·68:1·55:1·00 in 1982, and 0·52:0·98:1·00 in 1983. With the exception of what may

have been a strong year class of *G. wheatlandi* in 1982, the number of fish of each species and the total number of fish which moved into the pools in the 2 years were also similar. These abundance patterns must be determined by a combination of factors acting on the fish while they are breeding in the marsh and during their overwintering period in the St Lawrence estuary. While competition (Whoriskey, 1984; FitzGerald & Whoriskey, 1985), predation (Whoriskey & FitzGerald, 1985*b*), and the harsh conditions (Reebs *et al.*, 1984; Whoriskey *et al.*, 1985) all affect the fish of this community during the breeding season, the fish spend only a small part of their lives in the marsh. Factors which act on the fish during their early life history and stay in the St Lawrence estuary need to be elucidated if we are to understand exactly how this community is structured.

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