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THE EFFECTS OF INTERSPECIFIC INTERACTIONS UPON  
MALE REPRODUCTIVE SUCCESS IN TWO SYMPATRIC  
STICKLEBACKS, *GASTEROSTEUS ACULEATUS*  
AND *G. WHEATLANDI*

by

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(With 2 Figures)  
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**Introduction**

Interspecific competition is said to occur when two or more species are using the same resources that are in short supply, or when one species prevents or reduces access to resources by another species (BIRCH, 1957). In spite of many field studies showing evidence for competition (see SCHOENER, 1983), one cannot necessarily assume that competition occurs between any two species sharing a trophic level or even between two very ecologically and phylogenetically similar species. EMLEN (1984) reviews cases where competition "ought" to occur between similar species but does not.

For the past seven years we have been investigating the factors structuring a community of three stickleback species, living in tide pools along the southern shore of the St. Lawrence Estuary near Isle Verte, Québec. These pools are characterized by high productivity and by rapid diel changes in temperature and dissolved oxygen (WARD & FITZGERALD, 1983a; REEBS *et al.*, 1984). Ecologists generally consider that the populations of variable habitats should remain below the limits set by resources and hence interspecific competition should play at best a minor role in their population dynamics.

Our previous studies (WORGAN & FITZGERALD, 1981a; WARD &

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FITZGERALD, 1983b; WALSH & FITZGERALD, 1984a, b) indicate that food competition is unimportant in this system despite average fish densities of 20/m<sup>2</sup> and extreme densities of 60/m<sup>2</sup> (WARD & FITZGERALD, 1983b). However male sticklebacks are highly territorial toward both conspecifics and heterospecifics (WOOTTON, 1976; FITZGERALD, 1983) during the breeding season, and on average only about 30 per cent of male *Gasterosteus aculeatus* and *G. wheatlandi* in the pools are able to obtain territories and build nests. In a previous study, WHORISKEY (1984) found there was no consistent relationship between fish density and egg production (number of eggs produced per m<sup>2</sup> of pool substrate) for either species in allopatric pools, leading him to conclude that intraspecific competition was relatively unimportant. However the role of interspecific competition among sticklebacks at Isle Verte was not investigated.

The primary objective of the present study was to determine if interspecific competition for nest sites between *G. aculeatus* and *G. wheatlandi* occurred in the pools and to what extent such competition affected the reproductive success of each species. This objective was accomplished by effecting a series of *in situ* manipulations to examine the effects upon reproductive success of behavioural interactions between the two species in pools differing in both adult density and relative species abundance ratios. Fish reproductive success in sympatric pools (this study) was also compared to that in allopatric pools (WHORISKEY, 1984) of comparable density and species abundance ratios.

## Methods

### *The fish.*

Except for occasional stray mummichogs (*Fundulus* sp.) and fourspine sticklebacks (*Apeltes quadracus*), only the threespine stickleback, *Gasterosteus aculeatus*, the blackspotted stickleback *G. wheatlandi*, and the ninespine stickleback, *Pungitius pungitius* occur in the pools. The fish migrate from the St. Lawrence estuary to the pools in late April or early May and return to the estuary at the end of June. *G. aculeatus* and *G. wheatlandi* were chosen for study as these species were considered to be the most likely candidates for competition for nest sites to occur. Both species nest in open areas of the pools, often within 10-15 cm of each other, and interspecific aggression occurs between them (FITZGERALD, 1983; ROWLAND, 1983). *P. pungitius* was not considered to be a serious competitor of the two *Gasterosteus* species because it is almost always found in dense vegetation and it is less likely to interact aggressively with the other sticklebacks. Moreover, *P. pungitius* is not easily manipulated in the field as it often fails to build nests after removal and restocking. Female *G. aculeatus* range in size from about 5.0 to 7.0 cm standard length and weigh on average 3-4 gms. Female *G. wheatlandi* range in size from about 2.7 to 4.1 cm standard length and range in weight from 0.3 to 1.1 gms (CRAIG & FITZGERALD, 1982). Male *G. aculeatus* are slightly smaller than females, but the *G. wheatlandi* males and females are similar sized.

TABLE 1. Experimental protocol

Pool no.	Pool surface area (cm <sup>2</sup> )	Adult fish/m <sup>2</sup> <sup>1)</sup> (GW:GA)	Number of fish stocked		
			G.A.	G.W.	Total
Experiment 1 (Density manipulations):					
1-1	13.5	4 (2:1)	18	36	54
1-2	20.6	8 (2:1)	56	110	166
1-3	17.0	4 (2:1)	22	46	68
1-4	18.0	16 (2:1)	96	192	288
1-5	14.0	8 (2:1)	37	74	111
1-6	11.3	16 (2:1)	60	120	180
1-7	13.0	32 (2:1)	138	276	414
1-8	15.0	32 (2:1)	160	320	480
Experiment 2 (Species abundance manipulations):					
2-1	25.0	16 (2:1)	128	256	384
2-2	27.0	16 (4:1)	86	346	432
2-3	18.0	16 (1:1)	144	144	288
2-4	15.0	16 (2:1)	80	160	240
2-5	11.3	14 (4:1)	36	144	180
2-6	21.8	16 (4:1)	70	278	348
2-7	7.0	8 (4:1)	12	44	56
2-8	7.0	8 (4:1)	12	44	56
2-9	20.6	8 (1:1)	82	82	164
2-10	17.0	8 (1:1)	68	68	136
2-11	17.0	8 (1:1)	68	68	136

<sup>1)</sup> Male: Female sex ratios were 1:1 in all experimental pools.

#### Study site.

Experiments on interspecific competition were conducted in May and June, 1984 in a tidal salt marsh approximately 20 km east of Rivière du Loup, Québec. We worked in ~~Further details of stickleback parental and aggressive behaviour are given in Wootton (Reed & Moisan, 1971; Ward & Fitzgerald, 1983a).~~

#### Field protocol.

To examine the hypothesis that individual male reproductive success (number of eggs per nest and per cent of males nesting) of *G. aculeatus* and *G. wheatlandi* was different between allopatric and sympatric species pools, we completely seined and restocked pools with fish at densities ranging from 4 to 32 fish/m<sup>2</sup>. Sex ratios were 1:1 for each species and each pool contained 2 *G. wheatlandi* for each *G. aculeatus*. Two replicate pools were obtained for each density condition. Experiments lasted 7 days because of tidal flooding. The results of this experiment, hereafter referred to as experiment 1, were compared to those of Whoriskey (1984) for allopatric pools.

To test the hypothesis that there is a specific species abundance ratio below which *G. wheatlandi* cannot coexist with *G. aculeatus*, we manipulated the species abundance in eleven tide pools (experiment 2). This hypothesis was formulated because *G. aculeatus* is more aggressive than *G. wheatlandi* and may destroy their nests (Rowland, 1983; Gaudreault & Fitzgerald, 1985) while the reverse has never been observed. The densities and relative abundance of fish used in the two experiments are given in Table 1.

*Behaviour.*

Behavioural observations were made on males fanning well-constructed nests. When a male was sighted fanning its nest, and when it appeared to be undisturbed by the observer, behavioural data were collected for 10 minutes using a Datamyte behavioural event recorder (Electrogeneral Corporation, Minnetonka, Mn). Observations were usually made between 8:00 and 18:00, weather permitting. Each male was observed only once. Time budgets were obtained by quantifying: 1) time at nest: *i.e.* male within 20 cm of his nest; 2) time away from nest: male was greater than 20 cm from his nest; 3) fanning: this involves direct aeration of eggs by pushing water into the nest with the pectoral fins; 4) aggression: chases, bites, round-about-fighting and head down threats were scored as aggression. We recorded separately aggression directed at conspecifics or heterospecifics of each sex; 5) hidden: males briefly concealed themselves in dense vegetation.

Further details of stickleback parental and aggressive behaviour are given in WOOTTON (1976). Although frequency and duration data were quantified, only % of time data are presented here.

*Nest site characteristics.*

The first males usually began defending territories and building nests within a few hours of placement in the pools, while most of the rest of the nests were finished within 2 to 3 days. A record of nest building and destruction was kept on a day to day basis. Before collecting nests the resident male was trapped by allowing it to swim into a long-handled dip net placed over its nest. After capture specimens were preserved in 10% formaldehyde.

The following information was taken for each nest before preserving it in 10% formaldehyde for subsequent counting of eggs: 1) distance from the nest to the pool bank, 2) depth of water over the nest, 3) distance to the nearest conspecific and heterospecific nest and 4) amount of cover (submerged algae) around the nest. Cover was classified as a) 0%: open, nest visible to intruder on all sides, b) 25%: nest visible on 3 sides, c) 50% nest visible on 2 sides, d) 75% nest visible on 1 side and, e) 100% nest in dense algae or concealed under a bank, but visible to an overhead observer. Finally, after nests and territorial males were collected, non-territorial males and females were removed by seining and similarly preserved.

*Laboratory protocol.*

To determine if the manipulations affected fish body and gonad size, specimens from 3 pools in experiment 1 (one replicate pool of 4, 8, 16 fish/m<sup>2</sup>) were examined. The standard length, body and gonad weights of non-territorial and territorial males and females were measured. Gonadal-somatic indices (gonad wt/body wt × 100) were also calculated.

*Statistical analysis.*

We used non-parametric procedures where data were non-normal, heteroscedastic and not transformable to a normal distribution. Our authorities for the statistical tests were SOKAL & ROHLF (1981) and SIEGEL (1956). Sample sizes and tests varied depending upon the parameter being analyzed, and are given where appropriate throughout the text.

**Results****Reproductive success.**

In some pools, up to 60% of the male *G. aculeatus* were able to nest (Figs 1 & 2), but many of these nests were empty (Table 2). In most pools only 20-30% of the males nested, but the per cent of males nesting was

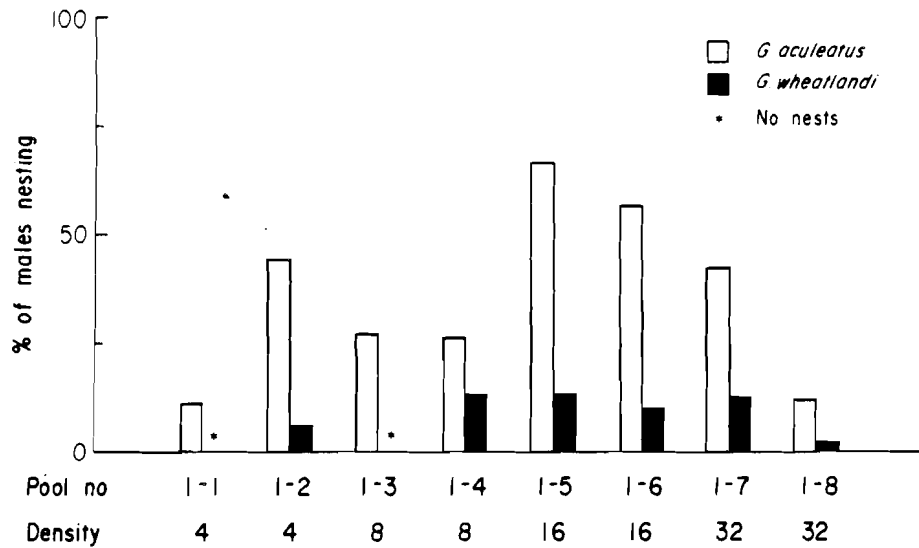


Fig. 1. Data are per cent of males nesting in pools of different adult fish densities (experiment 1).

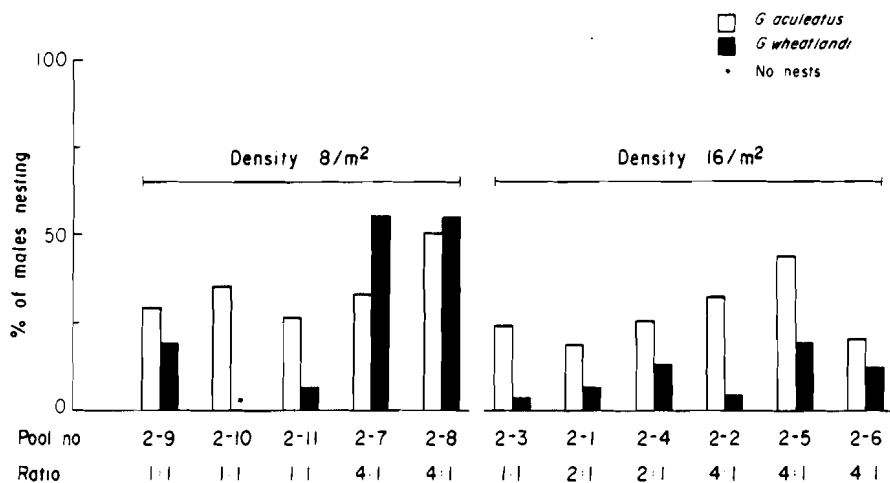


Fig. 2. Data are per cent of males nesting in pools of different adult densities and species abundances (experiment 2).

unrelated to density or to species abundance ratios. There was no evident relationship between fish density or species abundance ratios and the number of eggs per nest (Table 2, Spearman correlation and Kruskal-Wallis ANOVA tests  $p > .05$ ).

TABLE 2. Basic reproductive data for *G. aculeatus* and *G. wheatlandi* breeding in sympatry in 19 pools of different density and species abundance ratios (see Table 1)

	Pool	$\bar{X} \pm 1$ S.D. eggs/nest	
		<i>G. aculeatus</i>	<i>G. wheatlandi</i>
Experiment 1	1-1	43 $\pm$ 0 (1)	0 (0)
	1-2	384 $\pm$ 384 (2)	47 $\pm$ 0 (1)
	1-3	0 (1)	0 $\pm$ 0 (0)
	1-4	351 $\pm$ 0 (1)	0 $\pm$ 0 (2)
	1-5	93 $\pm$ 12 (1)	0 $\pm$ 0 (5)
	1-6	230 $\pm$ 115 (3)	141 $\pm$ 111 (3)
	1-7	149 $\pm$ 175 (6)	130 $\pm$ 62 (5)
	1-8	243 $\pm$ 136 (5)	278 $\pm$ 244 (4)
Experiment 2	2-1	690 $\pm$ 577 (8)	256 $\pm$ 170 (5)
	2-2	304 $\pm$ 190 (5)	51 $\pm$ 0 (1)
	2-3	212 $\pm$ 179 (9)	0 (0)
	2-4	262 $\pm$ 60 (3)	401 $\pm$ 0 (1)
	2-5	763 $\pm$ 345 (2)	157 $\pm$ 59 (6)
	2-6	361 $\pm$ 16 (2)	0 (0)
	2-7	293 $\pm$ 0 (1)	160 $\pm$ 126 (8)
	2-8	361 $\pm$ 96 (2)	215 $\pm$ 142 (8)
	2-9	735 $\pm$ 445 (10)	0 (0)
	2-10	464 $\pm$ 277 (7)	0 (0)
	2-11	649 $\pm$ 0 (1)	0 (0)

Number in brackets = number of nests examined.

TABLE 3. Reproductive success of *G. aculeatus* and *G. wheatlandi* in allopatric and sympatric pools

Variable	Species			
	<i>G. aculeatus</i> sympatric	<i>G. aculeatus</i> allopatric	<i>G. wheatlandi</i> sympatric	<i>G. wheatlandi</i> allopatric
% males <sup>1)</sup>	29.6%	14.9%	8.7%	22.6%
building nests	(200/676)	(201/1348)	(123/1404)	(282/1246)
$\bar{X}$ no. of eggs/nests	407 $\pm$ 368 (66 nests) N.S.	331 $\pm$ 466 (201 nests) N.S.	193 $\pm$ 139 (40 nests) N.S.	102 $\pm$ 177 (282 nests) N.S.

<sup>1)</sup> Data from allopatric pools from WHORISKEY (1984). Number of nesting males : number of males stocked. Significantly different between allopatric and sympatric pool situations ( $\chi^2$  tests,  $p < .01$ ) for both species.

<sup>2)</sup> N.S. = not statistically different between allopatry and sympatry.

Less than 15 per cent of the *G. wheatlandi* nested in any of the 19 pools and no males nested in 3 pools (Figs 1 & 2). The maximum number of nesting *G. wheatlandi* (18) occurred in pool 2-7 where the species abundance ratio of Gw:Ga was 4:1. There was no evident relationship between fish density and the number of eggs/nest (Table 2, Spearman correlation  $p > .05$ ).

In all pools many nests (about 70%) of both species were empty upon collection. To test the possibility that many males were not physiologically ready to spawn, we compared the gonad sizes of non-territorial and territorial males of both species, but the differences were not statistically significant (ANOVA  $p > .05$ ).

#### Allopatric and sympatric comparison.

A significantly smaller per cent of *G. aculeatus* built nests in the allopatric pools than in the sympatric pools while the opposite was true for *G. wheatlandi* ( $\chi^2$  tests  $p < .01$ , Table 3). However the average number of eggs per nest did not differ between allopatry and sympatry for either species (Wilcoxon signed rank test  $p > .05$ ).

#### Nest-site characteristics.

For *G. aculeatus* and *G. wheatlandi* there were no significant differences among pools in the nest site characteristics (Table 4). For this reason samples from all pools in Experiment 1 were pooled to test for correlations (Spearman rank order correlation test) between these variables and the number of eggs per nest. There were significant correlations between % cover ( $r_s = .368$ ,  $p < .001$ ,  $N = 185$ ), nest depth ( $r_s = .170$ ,  $p < .01$ ,  $N = 184$ ), distance to the bank, ( $r_s = .293$ ,  $p < .001$ ,  $N = 187$ ) and the number of *G. aculeatus* eggs per nest. These were the only significant correlations found.

Pooled samples from all densities were also used to test for correlations between the number of *G. wheatlandi* eggs per nest and nest site variables. There were significant correlations between % cover ( $r_s = .279$ ,  $p < .01$ ,  $N = 105$ ) and distance to the nearest heterospecific nest ( $r_s = .417$ ,  $p < .001$ ,  $N = 105$ ).

#### Male behaviour.

Males of both species showed no significant differences among pools in either frequency or duration of the measured behavioural parameters in the two experiments (Kruskal-Wallis ANOVA  $p > .05$ ). There were no

TABLE 4. Nest site variables for *G. aculeatus* and *G. wheatlandi* breeding at different densities in sympatric pools (Experiment 1)

Pool no.	<i>G. aculeatus</i>			
	M.D.	M.D.B.	M.D.C.	M.D.H.
1-1	10 ± 0 (1)	80 ± 0	—	—
1-2	12 ± 2 (12)	48 ± 31	120 ± 50	260 ± 0
1-3	12 ± 2 (3)	61 ± 43	118 ± 45	—
1-4	11 ± 4 (11)	38 ± 28	68 ± 36	155 ± 107
1-5	8 ± 2 (12)	24 ± 28	61 ± 19	71 ± 52
1-6	7 ± 3 (17)	51 ± 43	70 ± 17	107 ± 54
1-7	11 ± 3 (27)	49 ± 37	57 ± 18	50 ± 30
1-8	7 ± 2 (10)	14 ± 12	80 ± 45	183 ± 133

Pool no.	<i>G. wheatlandi</i>			
	M.D.	M.D.B.	M.D.C.	M.D.H.
1-1	*	*	*	*
1-2	7 ± 0 (1)	18 ± 0	—	78 ± 0
1-3	*	*	*	*
1-4	6 ± 1 (2)	20 ± 3	300 ± 0	23 ± 2
1-5	6 ± 3 (5)	35 ± 36	50 ± 30	53 ± 35
1-6	3 ± 1 (6)	22 ± 7	114 ± 92	77 ± 55
1-7	9 ± 3 (18)	42 ± 26	55 ± 37	28 ± 20
1-8	2 ± 6 (4)	30 ± 14	101 ± 16	45 ± 14

M.D. = Mean depth, M.D.B. = Mean distance to bank, M.D.C. = Mean distance to nearest conspecific nest, M.D.H. = Nearest heterospecific nest. — No data, \* No fish nested. Sample sizes are given in brackets in 1st column. All measurements are to nearest cm.

significant differences in behaviour between males with eggs and those with empty nests for either species (Wilcoxon signed rank tests  $p > .05$ ) so these data were pooled (Table 5).

A comparison of the % of time (time budget) spent in each activity by both species showed that *G. aculeatus* spent significantly more time hidden than *G. wheatlandi* and that *G. aculeatus* were significantly more aggressive toward conspecific and heterospecific females than *G. wheatlandi* (Table 5).

Time at nest and time fanning occupied over 65% of the time budget of both species. A Spearman correlation analysis was run between the behaviour data and the number of eggs per nest for each species. This data set was obtained by pooling data from all pools in experiment 1, as preliminary analysis showed no differences among pools. There were significant correlations between the number of eggs per *G. aculeatus* nest and aggression toward conspecific males ( $r_s = -.94$ ,  $p < .001$ ,  $N = 14$ ), ag-

TABLE 5. Time budgets of territorial male *G. aculeatus* and *G. wheatlandi* breeding in sympatry

Behaviour	$\bar{X}$ % of the time		
	<i>G. aculeatus</i>	<i>G. wheatlandi</i>	
Time at nest	44.5	52.5	N.S.
Time fanning	23.6	27.9	N.S.
Time hidden	2.7	.6	**
Aggression			
toward conspecific males	2.5	3.4	N.S.
toward heterospecific males	.6	.7	N.S.
toward conspecific females	3.5	1.6	**
toward heterospecific females	1.9	.2	**

Data were collected on males fanning well-constructed nests, empty nests included. Friedman Rank-order anova \*\*  $p < .01$ . N.S. = between species comparisons, not statistically significant.

Data were collected on 50 *G. aculeatus* and 50 *G. wheatlandi* for 10 minutes.

gression toward conspecific females ( $r_s = -.56$ ,  $p < .01$ ,  $N = 21$ ) and time spent hidden ( $r_s = -.76$ ,  $p < .001$ ,  $N = 14$ ).

By contrast those *G. wheatlandi* males whose nests contained the most eggs were more aggressive toward both heterospecific males and females, than males whose nests contained fewer or no eggs ( $r_s$  (male) = 0.43,  $r_s$  (female) = 0.43,  $p < .01$ ,  $N = 21$ ). There were no other significant correlations between any behavioural measure and reproductive success.

No statistical comparisons of behaviour were made with data collected on males breeding in allopatry as the behavioural interactions possible among fish were different.

Gonadal-somatic indices (G.S.I.).

Female gonads may compose up to 30% of the wet weight of sticklebacks, depending upon the time elapsed since the fish has spawned, while male gonad weight is about 2% of the total weight (WOOTTON, 1976). An examination of the G.S.I. values of 302 female and 130 male *G. wheatlandi* and of 131 and 118 female and male *G. aculeatus* from experiment-1 pools revealed no consistent differences between pool density and gonadal-somatic indices. However, some significant inter-pool variation occurred (one-way ANOVA,  $p < 0.05$ ).

### Discussion

In undisturbed pools at Isle Verte, *G. aculeatus* and *G. wheatlandi* live in sympatry at varying densities and relative species abundances. The first

objective of the study was to determine if reproductive success of these species was related to these two biotic variables. The second objective was to determine if interspecific interactions between the species affected their reproductive success. The following discussion considers the relationship between density and reproductive success and examines whether nest site and behavioural variables are related to changes in reproductive success. The results of this study are then compared to a previous study where allopatric populations of these species were studied in a similar manner. In addition, because *G. aculeatus* is behaviourally dominant (ROWLAND, 1983) over *G. wheatlandi* we predicted that by increasing the number of *G. wheatlandi* relative to *G. aculeatus*, the reproductive success of the former would increase.

#### Reproductive success.

There was no evident relationship between reproductive success (per cent of males spawning; proportion of males nesting) and density for either *G. aculeatus* or *G. wheatlandi*. However, in all pools of experiment 1, *G. aculeatus* built their nests several days before *G. wheatlandi* and significantly more male *G. aculeatus* than *G. wheatlandi* spawned ( $\chi^2$  tests). It is interesting to note that a significantly higher per cent of *G. aculeatus* nested in sympatry than in allopatry (Table 3), while the converse was true for *G. wheatlandi*. These results support ROWLAND's (1983) laboratory findings that male *G. aculeatus* displaces *G. wheatlandi* from their nests and that *G. aculeatus* may prevent some *G. wheatlandi* from obtaining territories and building nests. This conclusion is reinforced by the results of the species abundances manipulations (experiment 2). Only in those pools where the ratio of *G. wheatlandi* to *G. aculeatus* was at least 4:1 did an increase, albeit non significant, in the per cent of *G. wheatlandi* nesting occur. However this increase in the number of *G. wheatlandi* nesting did not result in more eggs/nest for this species.

Individual reproductive success of *G. aculeatus* and *G. wheatlandi* is highly variable among and within pools. Many males have no nests and many with nests do not obtain clutches. Some males only obtain a single clutch, while others procure several clutches. The factors that determined which males obtain territories, and of these which obtain eggs remains unknown, although nest cover, and aggression levels are often correlated with reproductive success at the site (FITZGERALD, 1983; WHORISKEY, 1984; this study). Females may preferentially prefer to mate with aggressive males having nests in cover. In studies of unmanipulated populations of *G. aculeatus* and *G. wheatlandi* we have found the sex ratios

are sometimes significantly biased towards males (WHORISKEY *et al.* MS submitted). This might increase competition for mates.

#### Nest site variables.

In all pools of the two experiments both species nested in similar areas, usually within 1 meter of the pool banks at depths of water from 1-15 cm. Both species often nested within 15 cm of each other, but despite this close proximity, there was a tendency for the average distance to the nearest conspecific to be less than to the nearest heterospecific (Table 4). ~~Because most *G. wheatlandi* nested after *G. aculeatus*, this may mean that *G. wheatlandi* is inhibited from nesting too close to *G. aculeatus*, again supporting ROWLAND's (1983) work.~~

The patterns of nest site location of both species in sympatry were similar to those observed in the allopatric pools (WHORISKEY, 1984), indicating that there is little if any interspecific effect upon nest site location. Large parts of all pools were empty of nests and males usually avoided nesting in the center of pools. Perhaps by nesting close to the banks, egg predation is decreased as one side of the nest is protected.

#### Male behaviour.

The behaviour of territorial males appeared to be unaffected by the experimental manipulations despite either the eight fold increase in density or the 4:1 ratio of *G. wheatlandi* to *G. aculeatus* in some pools. Studies where the relationship between fish density and reproductive success have been examined are often contradictory. For example, DE BOER (1981) found that damselfish (*Chromis cyanea*) nesting at high density were more aggressive and maintained their nests less than those fish nesting at low density. In contrast KODRIC-BROWN (1983) reported that the different levels of aggression accounted for little of the variance in male reproductive success in pupfish (*Cyprinodon pecosensis*). FITZGERALD & KEENLEYSIDE (1978) showed increased aggression by parental cichlids (*Cichlasoma nigrofasciatum*) and reduced reproductive success at high densities. WHORISKEY (1984) found no significant behavioural changes by male *Gasterosteus aculeatus* and *G. wheatlandi* in allopatric pools at densities from 4-32 fish/m<sup>2</sup>.

In the present study the time budgets of these two species were similar although *G. aculeatus* was significantly more aggressive than *G. wheatlandi* toward conspecific females (Wilcoxon signed rank test  $p < .05$ ). Overall, male *G. aculeatus* are more aggressive than male *G. wheatlandi*. Nesting *G.*

*aculeatus* males also spent significantly more time hidden than *G. wheatlandi* males, perhaps because of differences in susceptibility to bird predation (WHORISKEY & FITZGERALD, 1985).

#### Limiting resources.

Food supply and space to build nests are the two most obvious resources that might limit the reproductive success of *G. aculeatus* and *G. wheatlandi* in the tide pools. We discount food as a limiting resource at the site because of the abundance of food types available in the pools (WALSH & FITZGERALD, 1984b; WARD & FITZGERALD, 1983a, b; WHORISKEY, 1984). It is more difficult to determine if nesting space is in short supply. There are usually large areas of apparently suitable pool substrate available and not used. This occurs despite the surfeit of males of both species. Furthermore, in pools where male *G. aculeatus* were removed from their nests, their sites were generally left unoccupied (WHORISKEY, unpublished data). It seems that space *per se* is not limiting in the pools, although the quality of space may be, especially for *G. aculeatus*. In an experiment where 20 male and 20 female *G. aculeatus* were placed in one pool, 10 of the 20 males nested in the algae, 1 nested in the open and other males did not build nests (FITZGERALD, 1983). Comparative data are not yet available for *G. wheatlandi*. The importance of nest site location has been directly related to reproductive success in sticklebacks by KYNARD (1978) and SARGENT & GEBLER (1980) (see also WOOTTON, 1976). Both species may avoid the open pool areas to minimize nest raids (WHORISKEY, 1984) and to avoid bird predation (WHORISKEY & FITZGERALD, 1985).

#### Concluding remarks.

Most conventional mathematical models of competition (see any recent ecology text) assumes that competition is increased as a direct function of population density. This does not occur at Isle Verte. Yet we conclude that interspecific competition occurs at the site.

The lack of a relationship between adult density and reproductive success in both the allopatric (WHORISKEY, 1984) and sympatric pools (this study) suggests that density *per se* is not an important factor in stickleback population dynamics at the site. However the fact that the per cent of *G. wheatlandi* spawning is higher in allopatry than in sympatry suggests that strong interspecific effects are occurring. The lower per cent of *G. wheatlandi* males nesting in sympatry occurs probably because the larger more aggressive *G. aculeatus* can and do interfere with the reproductive

behaviour of the former (ROWLAND, 1983; GAUDREULT & FITZGERALD, 1985).

Many workers are sceptical of the traditional importance attributed to biotic processes in community structure (see STRONG *et al.*, 1984). The stickleback community along the southern shore of the St. Lawrence estuary (community is defined as a group of species living close enough together for the potential of interaction) has been remarkably constant over the years 1978-1984 (see WORGAN & FITZGERALD, 1981a, b; FITZGERALD, 1983; DUTIL & FORTIN, 1983; WHORISKEY, 1984). Usually *G. wheatlandi* and *P. pungitius* are 2-3 times more abundant than *G. aculeatus*. Yet more *G. aculeatus* obtain territories, build nests and produce eggs than do *G. wheatlandi*. This suggests that the explanation for the greater abundance of *G. wheatlandi* lies elsewhere than in competition. Studies are needed upon the early life history of the fishes in the marsh as differences in survival at the egg and fry stages between the two species may explain their differential reproductive success.

#### Summary

1. Two closely related sticklebacks nest together in tide pools along the southern shore of the St. Lawrence estuary.
2. We tested the hypothesis that interspecific interactions limit male reproductive success by manipulating both fish density and species abundance ratios. The index of male reproductive success used was the number of eggs per nest and the per cent of males building nests.
3. There was no significant relationship between reproductive success and density or abundance ratios.
4. The data of the present study (sympatric populations) were compared to a previous study (allopatric populations). A higher per cent of *G. aculeatus* bred in the sympatric than in the allopatric pools while the opposite was true for *G. wheatlandi*. There were no differences in the number of eggs per nest for either species between the allopatric and sympatric situations.
5. We conclude that interspecific interactions between *G. aculeatus* and *G. wheatlandi* may lower the reproductive success of *G. wheatlandi* when both species breed in sympatry.

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**Sommaire**

1. Deux espèces d'épinoches, étroitement apparentées, nichent ensemble dans les bassins intertidaux le long de la rive sud du fleuve St. Laurent.

2. Nous avons testé l'hypothèse que les interactions interspécifiques limitent le succès reproducteur des mâles en manipulant la densité des poissons et leur abondance relative. L'indice du succès reproducteur mâle employé était le nombre d'oeufs par nid et le pourcentage des mâles qui construisent des nids.

3. Il n'y avait pas de relation entre le succès reproducteur et la densité ou l'abondance relative des espèces.

4. Les données de notre étude (populations sympatriques) ont été comparées à une étude précédente (populations allopatriques). Un plus grand pourcentage de *G. aculeatus* a frayé en sympatrie qu'en allopatrie alors que le contraire s'est produit pour *G. wheatlandi*. Il n'y avait pas de différences dans le nombre d'oeufs par nid pour chaque espèce dans les bassins allopatriques et sympatriques.

5. Nous concluons que les interactions interspécifiques entre *G. aculeatus* et *G. wheatlandi* peuvent baisser le succès reproducteur de *G. wheatlandi* quand les deux espèces fraient en sympatrie.

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