

INTRASPECIFIC COMPETITION IN STICKLEBACKS (GASTEROSTEIDAE: PISCES): DOES MOTHER NATURE CONCUR?

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SUMMARY

(1) Experimental manipulations of adult densities of two species of sticklebacks, *Gasterosteus aculeatus* and *G. wheatlandi* were conducted to study intraspecific competition in the field.

(2) Territory sizes were compressed at higher densities for both species.

(3) The percentage of males of both species able to build nests decreased at higher densities, but measures more closely correlated with reproductive success, i.e. the chances of getting at least one clutch of eggs and the number of eggs per male, were unrelated to density.

(4) The unpredictable effect of density upon egg production suggests that the populations of sticklebacks at the site are not being regulated by intraspecific competition.

(5) We argue that unpredictable environmental factors (temperature, dissolved oxygen cycling, water evaporation) mask any effects of intraspecific competition in the population regulation of the two species in the salt marsh.

INTRODUCTION

Intraspecific competition for resources can limit a population's size (Giller 1984) through predictable negative effects upon individual growth, survival, and especially reproduction (Christian & Davis 1964; Tanner 1966; Healey 1967; Doidge, Croxall & Baker 1984; Svane 1984; Vickery & Nudds 1984; Thresher 1985; Petranka & Sih 1986; Ross & Almeida 1986). These negative effects occur when the level of a finite, critical resource falls below the threshold needed by individuals to ensure survival and reproduction. As the population density increases, competition should decrease the profitability of the optimal resources currently used by all members of the population.

Some experimental laboratory studies (e.g. van den Assem 1967; FitzGerald & Keenleyside 1978; Stanley & Wootton 1986) have shown significant effects of intraspecific competition in fish. For example, van den Assem found density effects upon territory size and parental success (measured by the number of eggs hatched at the end of the parental cycle) in three-spine sticklebacks (*Gasterosteus aculeatus* L.). Territory sizes were smaller in high density situations, and males with smaller territories received fewer eggs than those with larger ones. Males with small territories were also more likely to have had eggs stolen by rival males. Although this important study forms the basis of a hypothesis for

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the behavioural regulation of populations in sticklebacks (Wootton 1985), there is no direct evidence of density-dependent effects upon reproductive success for free-living fish.

Sticklebacks (Gasterosteidae) are excellent subjects for studies of intraspecific competition because of their abundance and ease of manipulation (FitzGerald & Wootton 1986). Breeding sticklebacks are intensely territorial and aggressively attack both conspecifics and heterospecifics in defence of their territory (Gaudreault & FitzGerald 1985; Rowland 1983). We have been studying the ecology of sticklebacks in tide pools, where adult densities can be as high as 40 fish m^{-2} during the breeding season (Whoriskey, FitzGerald & Reeb 1986) but density varies seasonally and among pools. Due to the frequent aggressive interactions among males and the high fish densities, we considered that intraspecific competition for nest sites may be an important potential determinant of individual reproductive success. However, there are good reasons to suspect that environmental conditions may override biotic factors such as intraspecific competition in regulating population size and individual reproductive success. Tide pools are a highly variable environment within which daily temperature variations average 12 °C but can be as high as 18 °C and dissolved oxygen concentrations can cycle daily from 0.04 mg l^{-1} to 20 mg l^{-1} . These environmental changes can have severe effects on the fish by reducing the effectiveness of their anti-predator responses, or by diverting them away from reproductive or parental care activities to life-saving behaviours or by killing them (Reeb, Whoriskey & FitzGerald 1984; Whoriskey *et al.* 1985). In addition, unpredictable warm weather can dry out some pools and kill all the resident fish. In such a stochastic environment it is reasonable to ask whether such environmental vicissitudes are more important than intraspecific competition in regulating population sizes?

This study had several specific objectives. The first was to determine if results of van den Assem's classic laboratory study on intraspecific competition in three-spine sticklebacks applied to a field situation. The second objective was to evaluate the effects of adult density upon two closely related sticklebacks which differ in their level of aggression (Gaudreault & FitzGerald 1985; Rowland 1983). To accomplish these goals we experimentally manipulated fish densities in tide pools. We report the effects of adult density upon male reproductive success in the three-spine stickleback *G. aculeatus* and the black-spotted stickleback *G. wheatlandi* Putnam. We also quantified the production of eggs by the two species to determine if increased competitive interactions among the males would regulate population size by decreasing the number of recruits available to the population.

MATERIAL AND METHODS

The site

We worked in the *Spartina* zone of the saltmarsh located in the Isle Verte National Wildlife area, near Riviere du Loup, Quebec. The site contains an extensive network of tide pools ranging in size from 1 to 1000 m^2 , although most pools range from 10 to 50 m^2 . Pool substrate (mud) and relief (flat) were homogeneous both within and among pools (Ward & FitzGerald 1983). These pools have no interconnections between them. Further details of the site and its fauna can be obtained from Reed & Moisan (1971) and Dutil & Fortin (1983).

The fish

There are three species of sticklebacks in the pools. In addition to the three-spine and black-spotted sticklebacks (*G. wheatlandi*) large numbers of nine-spine sticklebacks

TABLE 1. Study protocol. Pools were stocked with single species populations of either *Gasterosteus aculeatus* or *G. wheatlandi*, one density per pool. Four replicates of the density series were conducted for each species. The densities indicated for each replicate were all established concurrently. Densities of 32 fish m^{-2} were used in only two of four replicates for each species. Male:female ratios in all pools were 1:1. G.a. = *G. aculeatus*, G.w. = *G. wheatlandi*

Replicate	Date started	Date finished	Year	Densities (one each) no. fish m^{-2}	Territory size measured	
					G.a.	G.w.
1	13 May	21 May	1982	4, 8, 16	Yes	Yes
2	30 May	9 June	1982	4, 8, 16	Yes	Yes
3	18 May	24 May	1983	4, 8, 16, 32	No	Yes
4	31 May	6 June	1983	4, 8, 16, 32	Yes	No

(*Pungitius pungitius* L.) occur. We have described interspecific interactions elsewhere (FitzGerald & Whoriskey 1985; Gaudreault & FitzGerald 1985), so in this study we limited ourselves to intraspecific interactions. We attempted density manipulations with *P. pungitius* in 1982, but the fish failed to spawn. FitzGerald (unpublished data) also found that these males failed to reneest after manipulation. This species may be thermally partitioning the habitat with the other species by concentrating its reproductive activities in very cold or very hot temperatures, which were not encountered during our experiments (Lachance, FitzGerald & Magnan 1987). We excluded this species from our density manipulations and used only the two *Gasterosteus* species. These are not permanent residents of the pools, but migrate to the site from the St. Lawrence estuary to breed during May and June of each year. Surviving young and adult *Gasterosteus* return to the estuary after the breeding season, which ends by mid-July. Migrations can occur only when peak high tides flood the marsh, which usually occurs at intervals of 9–15 days. Individual fish stay in the pools, an average of 9–15 days (Whoriskey, FitzGerald & Reeb 1986). During the period between flood tides, the fish are trapped in the pools in which they have settled.

G. aculeatus is the largest fish at the site (6.37 cm average standard length (S.L.), followed by *P. pungitius* (4.38 cm S.L.) and *G. wheatlandi* (3.32 cm S.L.) (Craig & FitzGerald 1982). With the exception of rare occurrences of mummichog (*Fundulus* sp.) and four-spine sticklebacks (*Apeltes quadracus* Mitchill), these are the only fish in the pools. Males of all three species attempt to establish territories, and if successful build nests, court females and provide parental care to eggs and young (FitzGerald 1983; Wootton 1976, 1984). Females at least of *G. aculeatus*, spend much of their time resting and feeding (Whoriskey *et al.* 1985).

Field manipulations

Experiments were conducted in May and June of 1982 and 1983, in periods between successive tidal floodings of the marsh (Table 1). Previous studies at the site indicated that the duration of the experiments (about 1 week) was close to the period that a given individual spends in the marsh attempting to breed (Whoriskey, FitzGerald & Reeb 1986).

On the first day of an experiment, the study pools were seined free of their resident fish and restocked with allopatric populations at densities of 4–32 adult fish m^{-2} (Table 1). These pools ranged in surface area from 10 to 19 m^2 , and in depth from 15 to 20 cm.

Densities were assigned to the available pools with a random numbers table, and male:female densities were maintained at 1:1 at all densities. Care was taken to ensure that all fish were sexually mature adults. Males usually had established and started nests within 24 hours after the pools were stocked.

Cover is an important variable at the site as it can provide protection from predators to both the fish and their nests (Whoriskey & FitzGerald 1985a, b). We mapped nine pools in May 1982 and determined 10% of their surface area was covered with algae (*Fucus* sp., *Enteromorpha* sp.) or straw (*Spartina patens* Loisel) from previous years. We maintained cover in the experimental pools at 10% by determining the weight of the material covering 1 m² of pool area, then providing the appropriate weight necessary to cover 10% of each experimental pool. The material was distributed in clumps, using the same clump pattern in each of the pools.

In three of our four replicates for each species (Table 1), we determined territory size by mapping borders defended by each male against intruders. Weather conditions prevented us from doing this in the fourth replicate. Upon termination of each experiment, territorial males were collected and preserved with their nests in 5% formalin. In the laboratory the total number of eggs in each nest was counted, and the eggs present in all nests were summed to give an estimate of the production of recruits in each pool. We calculated the egg production per m² of tide pool area in order to have comparable values for pools of slightly different sizes.

Statistical analysis

The data were not normally distributed, and could not be transformed to a normal distribution, so non-parametric statistics were used. In addition, many of the variables showed significant differences among identical densities in different replicates. Therefore, we analysed our data on a pool-by-pool basis. Statistical techniques follow Zar (1974), while Kruskal-Wallis ANOVAS and Spearman correlation coefficients were calculated using Statistical Analysis Systems programs (Helwig & Council 1979).

RESULTS

Some evidence of competition among males for territories was apparent in both *G. aculeatus* and *G. wheatlandi*. As density increased, a smaller percentage of males stocked into the pools nested as did the percentage of those which obtained at least one clutch of eggs (Fig. 1; Kruskal-Wallis & Spearman tests, $P < 0.05$). In addition, mean territory size also decreased significantly ($P < 0.05$) for both species with increasing density (*G. aculeatus*, $r = -0.56$, -0.41 , and -0.72 in the three replicates where territory size was measured; *G. wheatlandi*, $r = -0.58$, -0.31 , and -0.39 in the three replicates). However, in all experiments with both species there were no significant differences among densities in the number of eggs obtained per male (all males) stocked into pools (Kruskal-Wallis ANOVA, $P > 0.20$; median scores all pools = 0; the median score was zero because of the large number of empty nests in all pools). Finally, population egg production, a measure of potential future recruits, was not predictable from an examination of the relationship between fish density and habitat area available for spawning (Fig. 2). The salt marsh tide pools are the major spawning grounds for sticklebacks in the area and 10 years of sampling sticklebacks should allow us to assume that the nine pools are representative of the salt marsh population (e.g. Worgan & FitzGerald 1981; FitzGerald 1983; Whoriskey, FitzGerald & Reeb 1986; Kedney, Boule & FitzGerald 1987).

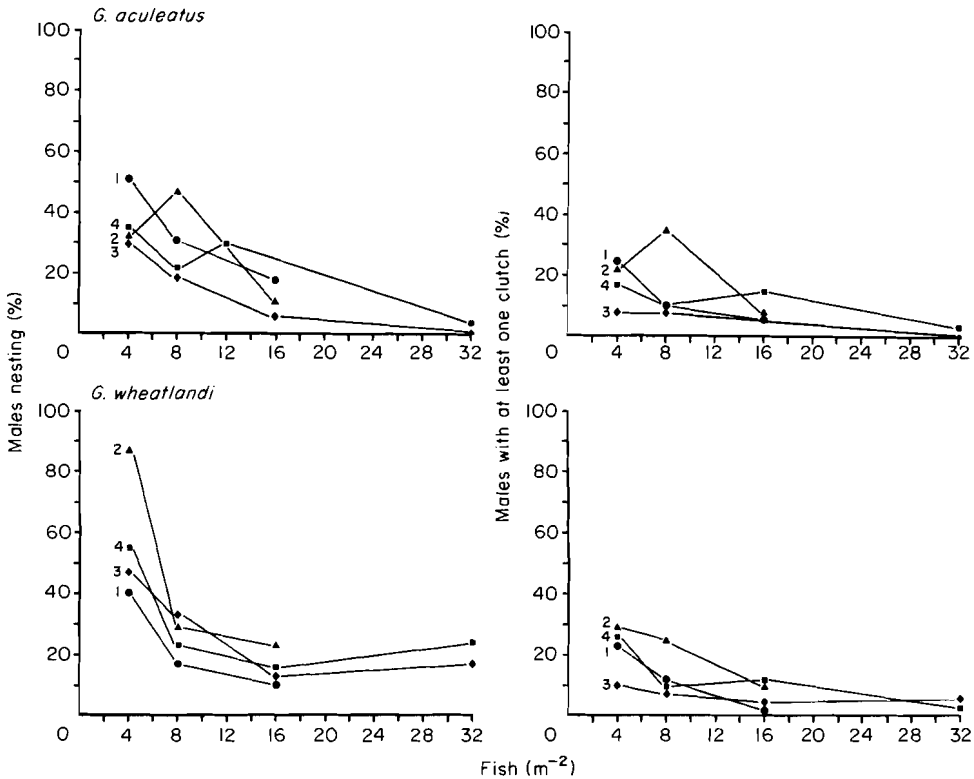


FIG. 1. Relationships between adult density and (a) the percentage of male *Gasterosteus aculeatus* and *G. wheatlandi* stocked into allopatric pools that nested and (b) the percentage of males stocked that spawned at least once. Densities are the number of fish per m² of tide pool area. Male:female densities were 1:1. 1-4 are replicates one to four, respectively.

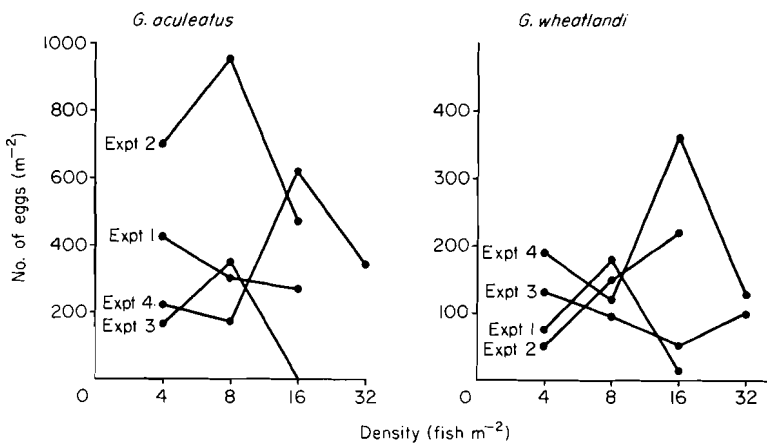


FIG. 2. Relationship between adult density and egg production in the experimental populations. Fish density is the number of fish per m² of tide pool area. Male: females ratios were 1:1. Eggs m⁻² is the number of eggs produced per m² of tide pool area. This standardized our measure to account for the slight variations in size among the different experimental pools.

DISCUSSION

The primary objectives of this study were (i) to determine if intraspecific competition was occurring in sticklebacks and (ii) to describe its mechanism of action. Because food is not limiting for fish at our site (Worgan & FitzGerald 1981; Walsh & FitzGerald 1984) and the fish do not injure themselves in territorial disputes, we expected to see effects on reproduction rather than growth or survival. The effects of competition may be determined by measuring either individual reproductive success or from a population viewpoint, the total production of new recruits on the spawning grounds. The usual measure of reproductive success is the number of an individual's progeny surviving to reproduce in future generations (Trivers 1972) although it is rarely possible to directly measure it in field studies. We used three measures as estimates of reproductive success. Our measures, the number of males nesting, the number of males receiving at least one clutch of eggs in their nests and the number of eggs per male should be correlated with true reproductive success. Of the three measures, the numbers of eggs obtained per male, should be the best estimate of true reproductive success and the number of males nesting the least accurate estimate. This latter measure can be considered as a measure of individual reproductive success as it represents the probability of a given male obtaining a nest. It is also a population level measure of reproductive output to the next year-class. In this study, apparently clear effects of density were documented, as evidenced by the decrease in the percentage of males nesting in a given pool. However, density effects were less evident when measured as the male's chances of receiving at least one clutch of eggs in his nest and non-existent when we take the number of eggs per male as our index of reproductive success.

With these results, it is difficult to conclude that competition affects individual reproductive success. Although a compression of territory size occurred as density increased, it is problematic whether this can be considered as evidence for competition. In his laboratory study, van den Assem (1967) found that males with large territories had more eggs in their nests than males with smaller territories. Hence, a decrease in territory size could result in a decrease in reproductive success. By contrast, in wading pools, Sargent (1982) and Sargent & Gebler (1980) found that the territory size of *G. aculeatus* did not differ significantly between males guarding large versus small numbers of eggs. In the field, FitzGerald (1983) found fewer eggs in nests located farther apart, than in nests closer together in this same species breeding in tide pools. Thus, the relationship between territory size and reproductive success is not yet well understood, but decreased territory size does not necessarily mean lower reproductive success.

Another study, conducted at Isle Verte examined competition for territories by conducting removal experiments of male three-spine sticklebacks (Whoriskey & FitzGerald 1985b). Males having nests with eggs in them were removed from their territories, and the rates of recolonization of the vacant, presumably high quality, territories by the surplus males present in the pools monitored. Only three of fifty-eight territories were recolonized in this study, suggesting again that competition is not as pervasive as we originally predicted.

The unpredictable effect of density upon the production of eggs (eggs m^{-2} of spawning habitat) is also difficult to reconcile with an hypothesis of stickleback population density being regulated by intraspecific competition. In fish of low fecundity ($< 10^4$ eggs per female per breeding season), the number of individuals in the next generation is generally

a function of the year-class immediately preceding it (Cushing 1971). Most *G. aculeatus* and all *G. wheatlandi* breed at age 1+ in the marsh (Craig & FitzGerald 1982). In fish with higher fecundities, recruitment is predicted to be independent of stock size (Williams 1975; Cushing 1971). Isle Verte sticklebacks are low fecundity fish (500 eggs or less; Craig & FitzGerald 1982) yet our results indicate that recruitment potential fluctuates independently of density. These results are interesting because Wootton (1985) recently concluded that adult fish density (and food supply) could account for changes in abundance in a Welsh population of *G. aculeatus*.

After studying sticklebacks in the field for over 10 years, the relevance of laboratory studies of competition in sticklebacks is uncertain to us. We feel, at least at our site, that environmental fluctuations can mask any competitive effects that may be occurring. We propose that environmental stresses play the principal role in determining egg production patterns. This is not to say that intraspecific competitive interactions are unimportant. While effects are not simple, competitive interactions during periods of environmental stress could have proportionally greater negative impact on male reproductive success than at times when conditions are more benign. We believe that environmental fluctuations are more than simple background 'noise' that obscure competitive patterns in field studies. However, our results do not appear to fit a recently proposed theory of competitive interactions in fluctuating environments. Strong (1986) holds that many species are characterized by density-vague population dynamics, in which intraspecific effects are negligible at intermediate population densities (8–16 fish m⁻² at Isle Verte), but pronounced at low and especially high densities. None of our measures indicated that this was occurring.

In conclusion, our results serve as a caution about the interpretation of field experiments. The measures of competition that we found easiest to use were also the least closely associated with reproductive success. It would have been very easy to make false conclusions or oversimplify the results of these experiments if only some (e.g. territory size or percentage of males nesting) of the variables were measured. While the final results are difficult to interpret, they do serve to underscore the complicated inter-relations involved in population regulation and community dynamics.

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