

The effects of bird predation on an estuarine stickleback (Pisces: Gasterosteidae) community

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Eight species of birds fed on a community of sticklebacks living in salt marsh pools along the southern shore of the St. Lawrence estuary in May and June when the fish breed. Three birds, the black-crowned night heron (*Nycticorax nycticorax*), the bronzed grackle (*Quiscalus quiscula*), and the ring-billed gull (*Larus delawarensis*) accounted for 80% of the estimated captures. Bird predation removed about 30% of the sticklebacks in the marsh. Significantly more male than female *Gasterosteus aculeatus* and *G. wheatlandi* were eaten, indicating selective predation is playing a role in structuring this fish community.

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Huit espèces d'oiseaux se sont nourris au sein d'une communauté d'épinoches vivant dans un marais salant le long de la rive sud de l'estuaire du Saint-Laurent en mai et juin, c'est à dire à l'époque où ces poissons fraient. Trois espèces d'oiseaux, le bihoreau à couronne noire (*Nycticorax nycticorax*), le goéland à bec cerclé (*Larus delawarensis*), et le mainate bronzé (*Quiscalus quiscula*) sont responsables de la capture de 80% des poissons. Environ 30% des épinoches du marais ont été victimes de la prédation par les oiseaux. Des expériences ont montré de façon significative que les mâles de *Gasterosteus aculeatus* et *G. wheatlandi* sont mangés en quantité supérieure aux femelles, ce qui indique que la prédation sélective joue un rôle dans la structuration de cette communauté de poissons.

Introduction

Predation plays a major role in structuring some communities (e.g., Paine and Vadas 1969; Connell 1975; Stroud and Clepper 1979; Batra 1982), but it remains a difficult subject to study in nature. This is especially true in fish communities, where the aquatic medium often limits opportunities to make observations, fish are highly mobile, and predators are often scarce. These difficulties have led many fish biologists to modelling approaches for studying predator-prey interactions. Modelling, by necessity, greatly simplifies or ignores many of the mechanisms of predator-prey interactions. Equations containing all the relevant variables would be mathematically intractable. Yet natural selection acts on these mechanisms, permitting animals with effective counter-predator strategies to leave more progeny and presumably resulting in the widespread distribution of the counter-predator trait within the population (Moodie 1972; Seghers 1974; Reist 1983; Giles and Huntingford 1984). Thus, field studies of the details of predator-prey interactions are important.

Three species of sticklebacks (Gasterosteidae) migrate into salt marsh tide pools along the south shore of the St. Lawrence estuary near Isle Verte, Québec, to breed in May and June. During this time eight species of piscivorous birds enter the marsh and feed on the sticklebacks. Observation of predator activity at the site is easy and the manipulation of prey within the tide pools is feasible. This situation provides an excellent opportunity to quantify predator-prey interactions in the field.

Here we report on the patterns of selective predation observed in the marsh. Specifically, we collected data to evaluate the impact of bird predation upon the structure of the stickleback community and to determine if differential predation was occurring as suggested by FitzGerald and Dutil (1981).

Materials and methods

Study site

Observations were conducted in May and June of 1982 and 1983 in

the *Spartina patens* zone of the National Wildlife Area near Isle Verte, Québec. This zone contains an extensive series of tide pools ranging in surface area from 1 to approximately 1000 m². Further details of the study site are given by Reed and Moisan (1971), Worgan and FitzGerald (1981), and Ward and FitzGerald (1983). Three sticklebacks, the threespine (*Gasterosteus aculeatus*), the blackspotted (*G. wheatlandi*), and the ninespine (*Pungitius pungitius*), spawn in these pools in May and June. While we have also captured fourspine sticklebacks (*Apeltes quadracus*) and mummichogs (*Fundulus* sp.), they are rare strays and the only other fishes found. With the exception of some *P. pungitius*, most sticklebacks have finished spawning and have either died or returned to the St. Lawrence estuary by July.

There are behavioral differences between male and female sticklebacks. Males establish territories, build nests, and defend eggs and fry. Females and nonterritorial males form loose shoals and spend much of their time foraging and resting.

A number of anatomical and color differences also exist between these species. Sticklebacks have dorsal and pelvic spines which may serve as effective counter-predator devices in some circumstances (e.g., Wootton 1976). *Gasterosteus aculeatus* has the longest and stoutest spines followed by *G. wheatlandi* and *P. pungitius*. *Gasterosteus aculeatus* also has lateral plates which may confer additional protection. There are important size differences among the species, but not between sexes of the same species. *Gasterosteus aculeatus* (mean standard length (SL), 63.7 mm) is the largest, followed by *P. pungitius* (43.8 mm SL) and *G. wheatlandi* (33.2 mm SL) (Craig and FitzGerald 1982). Finally, during the breeding season the three species are sexually dichromatic. Females of all species are cryptically colored and blend into the background of the pools. Male *G. aculeatus* develop bright blue eyes and red abdomens while the bodies of *G. wheatlandi* take on a general green sheen. Male *P. pungitius* are jet black with contrasting white pelvic spines. These anatomical and behavioral differences provide a potential choice of prey to avian predators.

In 1982 we identified nine possible predators of sticklebacks. They were the great blue heron (*Ardea herodias*), the black-crowned night heron (*Nycticorax nycticorax*), the herring gull (*Larus argentatus*), the ring-billed gull (*L. delawarensis*), the black-backed gull (*L. marinus*), the greater and lesser yellowlegs (*Totanus melanoleucus* and *T. flavipes*), the American crow (*Corvus branchyrhynchus*), and the bronzed grackle (*Quiscalus quiscula*). Of these species, only the

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grackle breeds in the study site, nesting within abandoned hunting blinds.

We studied bird predation upon the sticklebacks by (i) direct observations of foraging, (ii) regular censusing of all bird species in May and June, and (iii) enclosure experiments that allowed us to compare predation upon fish in unprotected pools with recoveries from protected pools.

Foraging observations

Data on bird feeding behavior were collected between 0600 and 1800 during May and June of 1982 and 1983. Observers equipped with 10 × 50 binoculars were stationed either at ground level with no cover, within hunting blinds, or in a cabin atop a 6.5 m high tower. During all of these observations we were sufficiently close to see a fish in a bird's beak. In some instances, we could also see the flight reactions of fish in a pool as the predator attacked. The duration of these observations varied from 1 to 20 min, depending on how long the birds remained in the marsh. They often left the site immediately after a capture. During the observations we noted the total number of attacks, the number of captures, and the total time that a bird spent foraging on sticklebacks. We also tried to avoid making repeated observations on the same birds, but since they were not marked we cannot rule out the possibility that some repeats occurred; however, bird populations in the area are large (Reed and Moisan 1971; Godfrey 1979; Tremblay and Ellison 1980), so we feel few if any repeated measures were made.

Censusing

Bird censusing was done from 16 May to 24 June 1983, on every Monday, Wednesday, and Friday during three time periods: 0800–1000, 1200–1400, and 1600–1800. Counts were made from the tower in a 5489 m² area which contained 3293 m² of tide pool area and was situated 200 m east of the tower's base. At the beginning of each time period we counted all birds within the site and recorded whether they were feeding. These counts were repeated at 0.5-h intervals until the observation period was finished. All five values were then averaged and the averages were used in the analyses.

To establish correlations between bird feeding activity and meteorological events, concurrently with censusing we recorded (i) wind speed and direction, (ii) air temperature, (iii) tide pool water temperature, (iv) surface area of tide pools covered with ripples, and (v) rainfall. Wind speeds were estimated from visual cues (see Villeneuve 1949). Air and water temperatures were continuously recorded with Peabody–Ryan model J thermographs. Rainfall was scored on a qualitative scale from 0 to 3 for no, light, moderate, or heavy rainfalls, respectively. Rain was a rare event occurring in only 7 of the 54 study periods. These data were obtained at 0.5-h intervals at the same time as the census data and averages were once again used for the analyses.

Enclosure experiments

To determine the intensity of bird predation upon fish, in 1983 six pools were selected for use in enclosure experiments. They were as close together as possible in the study site and were matched for size (28.2 and 26.0, 12.0 and 10.8, and 14.4 and 14.5 m² surface area for the three pairs), depth, shape, substrate, and percent algal cover. These pools were initially seined free of fish then restocked at the maximum recorded prevailing natural densities (2.52–2.94 *G. aculeatus*/m² tide pool area, 4.68–5.71 *G. wheatlandi*/m², and 4.40–2.91 *P. pungitius*/m², respectively). Following restocking, one of each pair of pools was closed off with 2.5-cm mesh chicken wire and the pool was left undisturbed for the experimental period, after which all fish were seined out and counted. Three replications (18–24 May, 31 May–8 June, and 16–20 June) of this procedure were made during periods when the marsh remained unflooded, giving us a total of nine protected and nine unprotected pools for statistical comparisons. Some natural mortality occurred in each pool, possibly owing to fluctuations in temperature and dissolved oxygen (see Ward and FitzGerald 1983).

Statistical analyses

Statistical procedures follow Zar (1974). Feeding observations of

ring-billed and herring gulls did not differ significantly, so we pooled data for the two species. We also had difficulty distinguishing between the greater and lesser yellowlegs, so feeding and census observations of these two species were also pooled. The relationships between the census and meteorological data were analyzed with the maximum R^2 multiple regression procedure (Helwig and Council 1979). Some of our variables were not normally distributed, but since multiple regression techniques are quite robust to departures from normality, this probably has a minimal effect on the probability of accepting or rejecting the null hypothesis (Zar 1974). Aggressive interactions or competition have been reported between some of the bird species we studied (e.g., Wiens 1965; Quinney and Smith 1980). To determine if there were any associations among the different birds using the marsh, we calculated Spearman rank correlation coefficients between abundances of pairs of the 11 most commonly occurring bird species in the marsh. This group included eight fish predators (yellowlegs observations were pooled) plus the black duck (*Anas rubripes*), the black-bellied plover (*Squatarola squatarola*), and the red-winged blackbird (*Agelaius phoeniceus*). This gave us a total of 55 coefficients and, with the significance level set at $p < 0.05$, two or three correlations are expected to be "significant" just by chance because of type I errors.

Estimates of the number of fish removed from the community by each bird species were made by multiplying the census data times the average number of captures per minute. We assumed that the birds mainly foraged between 0800 and 1800 (10 h/day), because no birds were seen in the marsh between 0500 and 0800 or 1800 and 2000 (6 days' data). The variance of our estimate of the number of fish caught by each bird species during the breeding season ($V(\bar{x}, \bar{y})$) is a function of the variance of the estimate of the number of birds foraging at the site and the variance of the number of fish caught per minute. $V(\bar{x}, \bar{y})$, which was used in the determination of the 95% confidence limits for the estimated number of fish captured, was calculated as

$$V(\bar{x}, \bar{y}) = \frac{Sx^2}{n_1} \cdot \frac{Sy^2}{n_2} + \frac{Sx^2}{n_1} \cdot \bar{y}^2 + \frac{Sy^2}{n_2} \cdot \bar{x}^2$$

where \bar{x} is the mean number of birds foraging at the site, Sx^2 is the variance of the number of birds foraging at the site, n_1 is the number of census observations, \bar{y} is the mean number of fish caught per minute, Sy^2 is the variance of the number of fish caught per minute, and n_2 is the number of observations of birds foraging.

To estimate the number of fish in the marsh at the start of the study, we determined fish densities in six census pools and multiplied them by the total tide pool area at the site. Peak high tides, which occur at intervals of 9–15 days, bring new fish into the marsh and often replace 50–100% of those already present. Two of these floodings occurred after the initial population estimate, so prior to each flooding we marked all fish in two pools to estimate the number of previous residents (i.e., fish already censused) present after the tidal cycle. These values were used to correct the counts in the six census pools for previous residents before calculation of the number of fish at the site. The initial estimate and those following the two flooding cycles were summed to give the total number of fish present at the site during the study. We were unable to compute 95% confidence limits on this total estimate because we could find no suitable technique to combine the variances of the three partial estimates. The upper and lower bounds reported are the largest 95% confidence limits found among the three partial estimates.

Results

Foraging observations

All blue herons seen in the study site were adults. They waded into the pools and pursued either individual fish or groups of sticklebacks in the "slow wade" mode (Kushlan 1976). These birds showed high capture efficiencies and high capture rates (Table 1) and swallowed fish whole.

Black-crowned night herons were "stand and wait" predators (Kushlan 1976), moving slowly up to or into a pool, freezing

TABLE 1. Observations of birds feeding on sticklebacks

	Efficiency ^a		Captures/min		N	Total observation time (min)
	Mean	SE	Mean	SE		
<i>A. herodias</i>	0.58	0.09	0.94	0.26	7	43
<i>N. nycticorax</i>	0.76	0.09	1.25	0.34	22	206
Gulls (<i>L. delawarensis</i> and <i>L. argentatus</i>)						
Wading	0.69	0.09	0.52	0.09	16	101
Diving	0.43	0.06	0.62	0.13	44	118
Swimming	0.48	0.09	0.46	0.09	14	76
<i>Totanus</i> sp.	0.16	0.09	0.38	0.15	4	31
<i>C. brachyrhynchus</i>	0.79	0.09	0.54	0.14	9	41
<i>Q. quiscula</i>	0.59	0.11	0.24	0.06	21	116

NOTE: Data was collected between 0800 and 1600.

^aEfficiency is the number of captures divided by the number of attempts made.

in place, and striking when the prey's movements brought it into range. Like the blue herons, they swallowed the prey whole and had high capture efficiencies and rates.

The ring-billed and herring gulls fished in a similar manner, using three behavioral tactics: wading, diving, and swimming. A wading gull drove sticklebacks before it until they were in striking range. The gull would then rapidly dart forward and strike with its beak. Diving was most often seen by groups of five or more gulls and occurred from a height of about 2.5 m above a pool. After one or two such attempts in a given pool the gulls moved on to another. The diving tactic appeared somewhat risky because of the shallow depths (15–30 cm) of the pools. On one occasion a gull hit its head on the bottom and for a short while was disoriented before it recovered and flew off. Gulls swam after and pecked at prey in pools where the water was too deep for wading. Of these three foraging tactics, wading resulted in the highest capture: attack ratio, but diving resulted in the most captures per minute (Table 1). The prey were consumed whole.

Black-backed gulls were rarely seen and, when they were present, only rested. Therefore, we conclude they are not important stickleback predators at Isle Verte.

The two species of yellowlegs were also waders. They usually hunted in very shallow water, darting rapidly around the pool. They did not have high capture efficiencies or rates (Table 1). Fish were again consumed whole.

Crows also waded and were quite efficient predators (Table 1), but we were unable to determine if prey were swallowed intact or torn to pieces.

Grackles are generally considered as insectivores, although some authors have reported them eating fish, including sticklebacks (Townsend 1919; Beeton and Wells 1957; Follett 1957; Weston 1963; Snelling 1968). They were predominantly waders, driving sticklebacks into shallow water before lunging and seizing the fish in their beaks. They also patrolled along the edges of pools and seized any fish that were startled out from underneath the bank. A third tactic was to seize a clump of algae (*Enteromorpha*), drag it up onto the bank, search through it, and capture any fish found.

Curiously, grackles consumed only part of their prey and this permitted us to collect a sample of abandoned captures (5 male and 11 female *G. aculeatus*, 1 male and 17 female *G. wheatlandi*, and 15 male and 13 female *P. pungitius*). Each species was caught in proportion to their abundance in the marsh, but significantly more female than male *G. wheatlandi* were taken ($\chi^2 = 14.2$, $p < 0.005$, $df = 1$, $n = 18$). The stickleback

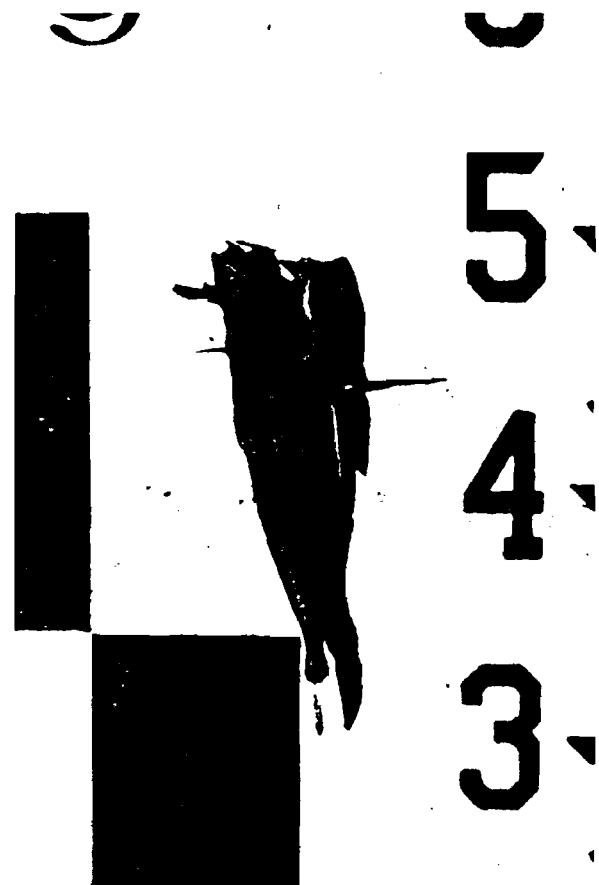


FIG. 1. Photograph of a female *G. aculeatus*, showing the characteristic grackle pattern of eating the prey's head.

cadavers most often were missing heads, though we found specimens in which the abdomen or tail sections were consumed (*G. aculeatus*, 15 fish missing only heads, 1 missing both the head and tail; *G. wheatlandi*, 16 missing only heads, 1 missing only the abdomen, 1 with both the tail and abdomen gone; *P. pungitius*, 28 missing only heads). This indicates that birds preferred eating fish heads over the other two body parts ($\chi^2 = 105$, $p < 0.005$, $df = 2$, no. of body parts consumed = 64; Fig. 1). The viscera were usually not eaten.

Censusing

Predators occurred infrequently in the marsh (Fig. 2) and spent only part of the time feeding. The most common visitors

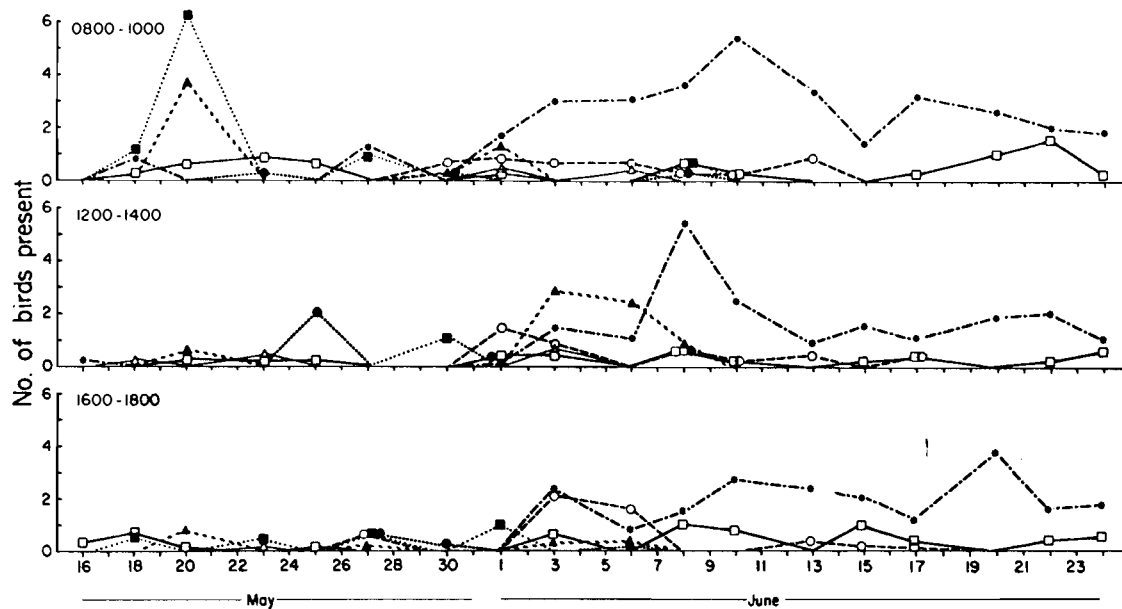


FIG. 2. Seasonal pattern of bird abundance in the 5489-m² study area during 1983. ●, *A. herodias*; ○, *N. nycticorax*; ▲, *L. delawarensis*; △, *L. argentatus*; ■, *Totanus* sp.; □, *C. brachyrhynchos*; *, *Q. quiscula*.

TABLE 2. Multiple regression analyses (maximum R^2 improvement technique; Helwig and Council 1979) for number of feeding *L. argentatus* and *Q. quiscula* versus environmental variables. Partial correlation coefficients are given, as well as the type II sum of squares (SS), which is the SS that would be added to the error term if the variable is not included in the model

	<i>L. argentatus</i> ($R^2 = 0.46$)				<i>Q. quiscula</i> ($R^2 = 0.49$)			
	DF	SS	F	p	DF	SS	F	p
Regression	9	0.0898	4.24	<0.0005	9	26.9297	4.63	<0.0002
Error	44	0.1035			44	28.4223		
Total	53	0.1933			53	55.3520		

Environmental variable	<i>L. argentatus</i>			<i>Q. quiscula</i>		
	Partial correlation coefficient	Type II SS	p	Partial correlation coefficient	Type II SS	p
Julian day	0.0010	0.0014	<0.45	-0.0100	0.1419	<0.64
Hour of day	0.0077	0.0009	<0.55	-0.0737	0.0779	<0.73
% cloud cover	0.0004	0.0036	<0.22	-0.0093	2.3953	<0.06
Wind direction	0.0002	0.0095	<0.05	-0.0012	0.3944	<0.44
Wind speed	0.0068	0.0059	<0.12	0.0433	0.2396	<0.55
Air temperature	0.0000	0.0000	<1.00	-0.0563	1.2126	<0.18
% pool surface covered in ripples	-0.0024	0.0344	<0.0004	-0.0208	2.6645	<0.05
Water temperature	-0.0066	0.0074	<0.08	0.0673	0.7586	<0.28
Time since flooding	-0.0019	0.0022	<0.34	0.1330	10.8400	<0.002
Tide stage	0.0000	0.0000	<1.0	0.0000	0.0000	<1.00

were grackles, black-crowned night herons, and crows. Although we ran separate regression analyses (number of birds feeding regressed on selected abiotic variables) for each bird species, significant R^2 values were found only for grackles ($R^2 = 0.49$) and herring gulls ($R^2 = 0.46$) (Table 2). An analysis of the partial correlation coefficients for these data sets indicates that ripples on pool surfaces and cloud cover negatively affected grackle foraging, perhaps by reducing prey visibility. There was also a significant positive correlation between the number of grackles foraging and the time since the

marsh was last flooded. Flooding occurred about once every 7 days. After a flooding cycle is finished, pools start losing water through seepage and evaporation (see Ward and FitzGerald 1983). This loss lowers water depths and decreases pool surface area, concentrating fish in small areas. Fishing grackles may be aided by this concentration effect. There were significant negative correlations between the number of herring gulls foraging and (i) the percent of pool surface covered with ripples (ii) water temperature, and (iii) wind direction. We are unsure of the reasons why water temperature and wind direction affect

TABLE 3. Enclosure experiment results. Data are pooled samples from nine tide pools protected from bird predators and nine others concurrently subjected to natural predation

Species	Sex	Protected pools			Unprotected pools		
		No. of fish stocked	No. of fish recaptured	% recaptured	No. of fish stocked	No. of fish recaptured	% recaptured
<i>G. aculeatus</i>	♂	174	174	100*	167	137	82*
	♀	274	248	90	269	223	83
<i>G. wheatlandi</i>	♂	368	354	96*	364	261	72*
	♀	490	469	96	447	444	99
<i>P. pungitius</i>	♂	248	207	83	242	212	88
	♀	298	249	83	313	251	80

NOTE: *, statistically significant difference in the percent of fish recovered after the experimental period occurred between protected and unprotected pools (Mann-Whitney *U*-test, $p < 0.01$, $n_1 = n_2 = 9$). No other comparisons were significant at a minimum level of $p < 0.05$.

foraging behavior and it is possible they are spurious correlations as a result of type I errors.

There was little evidence of interspecific interference among the birds as they used the marsh. We observed no agonistic interactions between these species and only 7 of 55 Spearman correlation coefficients calculated on abundance data of pairs of species were significant ($p < 0.05$; blue heron \times black-crowned night heron, $r_s = 0.3270$; black-crowned night heron \times ring-billed gull, $r_s = 0.3647$; black-crowned night heron \times grackle, $r_s = 0.3555$; black-crowned night heron \times black-bellied plover, $r_s = 0.3695$; black-crowned night heron \times red-winged blackbird, $r_s = -0.3926$; blue heron \times red winged blackbird, $r_s = -0.3071$; yellowlegs (*Totanus* sp.) \times grackles, $r_s = -0.2801$). At best, these associations may indicate habitat preferences (e.g., Burger *et al.* 1982) rather than competition or mutualism (but see Wiens 1965; Hunt and Hunt 1973; Quinney and Smith 1980; Lenington and Scola 1982). However, with such a large number of pairwise comparisons we also expect to find two or three chance correlations owing to type I errors. Thus, these results must be treated with caution.

By combining the census and foraging data we were able to estimate the impact of bird predation upon the fish population over the study period. Assuming the birds use the marsh 10 h/day for foraging, by multiplying the number of birds feeding (census data) by the foraging data (Table 1) we calculated that the numbers of sticklebacks consumed ($\pm 95\%$ confidence limits) in the 5498-m² study area were as follows: blue heron, 1184 \pm 364; black-crowned night heron, 4725 \pm 598; ring-billed gull, 3160 \pm 429; herring gull, 144 \pm 48; the two species of yellowlegs 861 \pm 151; crows 408 \pm 74; grackles, 3750 \pm 484. The fish community was estimated to contain 49 226 fish (upper and lower bounds 67800 and 35257, respectively) (F. G. Whoriskey, unpublished data), so approximately 30% of the fish at the site were removed by predation.

Enclosure experiments

We tested for selective bird predation by comparing recoveries of fish from nine protected pools to recaptures from nine pools subjected to natural predation. Significantly higher percentages of male *G. aculeatus* and *G. wheatlandi* were recovered from protected pools than unprotected pools (Mann-Whitney *U*-test, $p < 0.01$, $n_1 = n_2 = 9$, Table 3). No other statistically significant differences were found. There were black-crowned night heron tracks on the bottom of the unprotected pools, as well as headless fish from grackle predation along the unprotected pools' banks.

Discussion

Eight of the nine potential predators were seen feeding on sticklebacks. The exception was the black-backed gull, which did not appear to affect the fish community. An examination of the foraging data (Table 1) showed that the black-crowned night heron and the great blue heron, followed by the ring-billed and herring gulls, were the most efficient predators, but grackles, night herons, and ring-billed gulls hunted more frequently in the marsh. These three species accounted for 80% of the estimated fish captures. Our data suggests that 30% of all fish entering the spawning grounds were eaten by birds; this would be a significant factor in the population dynamics of the sticklebacks in this area. But confidence limits on our estimates are large and the data must be interpreted with caution.

The birds considered in this study, with the possible exception of grackles and crows, are well-known piscivores (Harris 1965; Hunt and Hunt 1973; Kushlan 1976; Godfrey 1979). The grackle was one of the most important predators. Their behavior of removing clumps of algae to capture hidden fish is a clever way of circumventing counter-predator tactics such as protean display (Keenleyside 1979) and (or) refuging in the algae. Their habit of eating just the heads of their prey is perplexing. The spines or body armor of the two *Gasterosteus* species is formidable and may prevent further consumption, but grackles ate only the heads of *P. pungitius* which has very small spines and no armor. These anatomical defenses were inefficient against the observed bird predation, but they may have evolved in response to predation by fish (Hoogland *et al.* 1957; Giles and Huntingford 1984). We noted also that both grackles and crows preferred to chase live fish rather than scavenging the occasionally abundant dead fish which resulted from pools drying out completely.

Except for the herring gull and the grackle, multiple regression models of the number of birds feeding versus selected environmental variables had no significant predictive power. This may indicate that the birds were resourceful predators and the fish were fairly vulnerable to predation, so that weather plays a minor role in determining foraging patterns. Weather conditions have important effects on the feeding of terns (Dunn 1973) and plovers (Pienkowski 1983).

Abundant, alternative foods may also be affecting the number and species of birds eating sticklebacks. Two other fishes, herring and tomcod, are seasonally abundant near the site (Lambert and FitzGerald 1979; Côté *et al.* 1980) and are fed on by several of the stickleback predators (Godfrey 1979; Tremblay and Ellison 1980). A local dump and recently plowed

fields may also provide occasionally abundant food, especially for gulls (e.g., Mudge and Ferns 1982).

The enclosure experiments demonstrated that selective predation occurred on male *G. aculeatus* and *G. wheatlandi* (Table 3) and we suspect black-crowned night herons and ring-billed gulls caught these males. Though Tremblay and Ellison (1980) reported that *G. aculeatus* was the only stickleback captured by the black-crowned night heron, we cannot exclude the possibility that they also fed on *G. wheatlandi*. The ring-billed gulls made large numbers of captures and are thus also suspect, but we have no direct evidence to support this supposition.

Male sticklebacks may be easy to capture because they are attached to a fixed site, their nest, during the reproductive period. A "stand and wait" predator such as the black-crowned night heron (Kushlan 1976) could take up a position near a nest and rest silently until the resident returned. Since both *G. aculeatus* and *G. wheatlandi* males were taken in similar proportions, fish size, color, body armour, and spines seem unimportant in explaining the observed predation patterns.

Grackles were also selective predators, taking more female than male *G. wheatlandi* ($\chi^2 = 14.2$, $p < 0.001$, $df = 1$). However, they took the other sticklebacks in proportion to their abundance in the marsh. Since there were no significant differences in recoveries of female *G. wheatlandi* from protected and unprotected pools, it appears that grackles did not capture enough females from any given pool to cause significant local imbalances in sex ratios. It is possible that females hid more often than males in the algae, thus becoming more susceptible to grackle foraging tactics, but we have no data to support this suggestion.

During the course of the study we made qualitative observations of differences in the antipredator behavior of the three stickleback species. *Pungitius pungitius* is extremely skittish and hides in the algae if any movement occurs above the pools. After a disturbance it takes them longer than the other species to resume normal activities. This behavior seems to be characteristic of *P. pungitius* throughout its range (Wootton 1976). *Gasterosteus aculeatus* and *G. wheatlandi* both form shoals when threatened, which is a well-known antipredator behavior (Keenleyside 1979), but *G. aculeatus* shoals tend to occupy deeper water than those of *G. wheatlandi*. Both species will also hide in the algae at times. Large shoals of *G. wheatlandi* moving rapidly in shallow water cause extensive surface rippling which may confuse predators. Deep water may provide protection for *G. aculeatus*. However, unlike *P. pungitius*, both of these species recover from a fright relatively rapidly. Our data indicate that *P. pungitius* has the most effective behavior for avoiding bird predation at this site.

FitzGerald and Dutil (1981) hypothesized that selective predation by black-crowned night herons was an important factor in structuring the Isle Verte fish community. *Gasterosteus aculeatus* is the most aggressive (FitzGerald 1983) and most fecund species (Craig and FitzGerald 1982) at the site, yet it is not the most abundant species in the marsh. Selective predation on male *G. aculeatus* could reduce their numbers to a level which permits the coexistence of the other, similar species. Our data show selective predation on both *G. aculeatus* and *G. wheatlandi* males, so at best we provide only partial support for this hypothesis. Other sources of stress and mortality, such as interspecific interactions, intra- and interspecific egg predation, or mortality during the overwintering period in the St. Lawrence estuary may also play key roles in

reducing *G. aculeatus* numbers relative to those of the other sticklebacks.

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