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FOOD RESOURCE PARTITIONING BETWEEN SYMPATRIC POPULATIONS OF BRACKISHWATER STICKLEBACKS

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SUMMARY

(1) The diets of juvenile and adult sympatric sticklebacks (*A. quadracus*, *G. aculeatus*, *G. wheatlandi* and *P. pungitius*) were compared with the abundance of potential prey in the environment.

(2) The sites exhibited differences in salinity and temperature and these were related to the observed differences in stickleback population structure.

(3) Site A had a greater abundance of potential prey than site B. Within each site, areas with abundant aquatic vegetation had higher densities of potential prey than vegetation-poor areas.

(4) Adults of all four species appeared in the breeding areas in early May and were no longer present by the end of June. Juveniles appeared in late June, except for juvenile *G. wheatlandi* which did not appear until July because of their later breeding period. Juvenile *Gasterosteus* left the breeding areas by late August, while juvenile *A. quadracus* and *P. pungitius* remained.

(5) Food niche overlap was greatest between adult *G. aculeatus* and *P. pungitius*, while adult *G. wheatlandi* overlapped least with any species. Where *A. quadracus* was found in sympatry with the other species, overlap occurred with *G. aculeatus* and *P. pungitius*. The same relationships held for juveniles.

(6) In four of the five areas, niche breadth and overlap were greater in areas of high potential-prey density and lower in areas of low potential-prey density. In the fifth area, niche overlap was high at low potential-prey densities. Because niche breadth varied between sites, no firm conclusions could be drawn about niche breadth relationships between the species.

(7) Adult and juvenile sticklebacks exhibited similar microhabitat partitioning, although it was more pronounced in juveniles. *A. quadracus* fed predominantly from the benthos, while *G. wheatlandi* fed mainly in the water column. *G. aculeatus* and *P. pungitius* fed from both the benthos and water column. *P. pungitius* usually foraged amongst algal mats.

(8) It is proposed that interspecific competition was not a factor in these environments, because of the abundance of potential prey and microhabitat segregation.

INTRODUCTION

Closely related, morphologically similar species frequently co-occur in ecological communities (Schmitt & Coyer 1982). The question that arises is, how do these species coexist if they are able to utilize the same resources? Several mechanisms have been

FIG. 1. Collection site A, Slaughter House Ponds.

proposed for the coexistence of competing species (see Pianka 1976). Resource partitioning is one such mechanism, generally occurring along the dimensions of habitat, food, or time (Schoener 1974). In fish communities, resource partitioning is usually a result of interspecific competition for those resources, either in the past or ongoing (e.g. Werner & Hall 1977).

Various combinations of four species of stickleback (Gasterosteidae) commonly occur in sympatric populations along the east coast of Canada; they are the three-spine stickleback (*Gasterosteus aculeatus* L.), the black-spotted stickleback (*Gasterosteus wheatlandi* Putnam), the nine-spine stickleback (*Pungitius pungitius* L.) and the four-spine stickleback (*Apeltes quadracus* Mitchill). The aim of this study was to examine mechanisms that might allow this coexistence. The diet and feeding behaviour of each species, together with the dietary overlap between the four species were examined. From these data, a pattern of resource usage emerged, which allowed an evaluation of the importance of resource partitioning in the structuring of sympatric populations of Gasterosteidae.

MATERIALS AND METHODS

Study area

This study was carried out during the spring, summer and autumn of 1982 near St. Andrews, New Brunswick. St. Andrews lies at the tip of a peninsula bordered by the St. Croix River and estuary on the west, and Passamaquoddy Bay on the south and east (45°5' N; 67°5' W). Collections were made at two sites: site A on the east coast of the peninsula, site B approximately 10 km north-east of St. Andrews along the eastern coast of the peninsula.

Site A consists of one large brackishwater pond plus a series of smaller ones, located in a saltmarsh. The ponds are surrounded by grasses, mainly *Spartina* sp., and are separated from Passamaquoddy Bay by a gravel sill (Fig. 1). The marsh is flooded only during spring tides higher than 8.0 m, which occur approximately once per month. At these times, the largest pond (A-3) is connected to the bay by a narrow channel (Fig. 1). Collections were made regularly from two ponds: A-1 and A-3. Pond A-3, for the purposes of this study, was further subdivided on the basis of substrate and vegetation differences into sites A-3a and A-3b (Fig. 1). Water depth and salinity at site A were variable, depending on tidal flooding, rainfall and evaporation (Table 1). Water temperature ranged from a low of 5.0 °C in late April to a high of 28 °C in July (Table 1).

Site B is a large inlet bordered by a coniferous forest and is flooded by each tide. At the mouth of the inlet there is an abandoned, breached dam which somewhat retards the flow of water. The top of the inlet is fed by a freshwater stream (Fig. 2). At low tide, four distinct ponds are visible, each interconnected, but at high tide only the uppermost pond (B-4) is distinguishable; B-4 is flooded only during spring tides (Fig. 2). The descriptions contained in Table 1 refer to conditions at low tide.

Salinity at site B is affected by both rainfall and freshwater run-off from Mitchell Brook. As a result, the salinity of surface waters was found to be much lower than underlying waters at both sites B-2 and B-3. Site B-1 exhibited more uniform conditions, due to a more vigorous mixing of water, while site B-4 contained freshwater only. Water temperatures at site B varied from a low of 5.0 °C to a high of 22.0 °C.

Sample collection

All collections were made during low tide periods between 09.00 and 14.00 hours. Fish samples and physico-chemical measurements were taken from sites A and B on seven occasions from April 1982 to September 1982.

Environmental samples were collected before the fish samples to minimize disturbance of the environment. Benthic samples were taken using a 21.0 × 15.5 cm handnet with a 50 µm mesh. An area of the bottom, approximately 525 cm², was removed to a depth of 1.0 cm and promptly placed in a plastic bag containing a 10% formalin-seawater solution as preservative. Disturbance was kept to a minimum so that fish did not have an opportunity to feed on prey exposed through sampling. Planktonic samples were collected by sweeping a 30.0 × 15.5 cm handnet (50 µm mesh) just below the surface, through a distance of 240 cm resulting in a sampled volume of approximately 110 litres. The contents of the net were rinsed into a plastic bag and preserved in the same fashion as

TABLE 1. Physical and chemical properties of study sites A and B

Site	Area (m ²)	Depth range (cm)	Salinity range (‰)	Temperature range (°C)	Substrate	Vegetation
A-1	650	20-25	15-28	5-28	Mud & silt	Filamentous green algae
A-3a	26 000	5-85	15-28	5-28	Mud & gravel	<i>Zostera</i> None
A-3b		10-100	15-28	5-28	Mud & silt	Filamentous green algae
B-1	1 800	2-30	25-30	5-20	Gravel	None
B-2	4 600	2-100	5-28	5-22	Mud & sand	None
B-3	3 600	5-120	5-24	5-22	Mud & silt	None
B-4	250	5-30	0-0.5	5-22	Mud & silt	<i>Zostera</i>

FIG. 2. Collection site B, Mitchell Brook; M.L.W. (—) mean low water line; M.H.W. (---) mean high water line.

the benthic samples. Both benthic and planktonic samples were rinsed with freshwater after 24 hours fixation time, and placed into a solution of rose bengal and 70% ethanol for staining and permanent preservation. Samples were sorted and potential food items counted using a dissecting microscope. Because of high benthic densities, samples were subsampled (Hickley 1975). The number of species was used as a description of diversity (Green 1979).

Sticklebacks were collected using a two-man seine 4.0 m long $\times$ 1.0 m deep with a 5.0 mm mesh. Fish were killed and fixed immediately in a 10% formalin-seawater mixture and after 24 hours preserved in 70% ethanol. Regurgitation of stomach contents was not a problem. Prior to seining each site, measurements of temperature and salinity were made at both the surface and bottom of the water column using battery powered meters.

Stomach analysis

Stomach analysis was performed separately on young-of-the-year and adults for each species on each date. To increase the sample size, sample dates were later combined to form one sample of adults and one of young-of-the-year for each site. Where combined sample sizes were sufficient, adult populations were subdivided by sex to determine if there were any sexual differences in diet.

In the laboratory, standard length (S.L.) was measured to the nearest 0.1 mm for each specimen. The entire digestive tract was then removed and placed in a solution of rose bengal and 70% ethanol for 24 hours, which effectively stained the contents for later examination. The specimens were sexed by examining the gonads. Only the contents of the stomach were analysed, thus reducing errors in determining diet resulting from

differential digestion rates of prey (Berg 1979). Material in the stomach showed little sign of digestion. Prior to removal of contents, stomach fullness (empty, quarter full, half full, three-quarters full, full, distended) was estimated by eye. Prey items were then separated into taxonomic categories and counted.

Three measurements of each prey type in the stomachs were made: (i) the relative abundance of a food item in the diet of a fish species, the number of prey of a given type found in all fish examined expressed as a percentage of the total number of prey found; (ii) the percentage contribution by volume of each food category to the total stomach contents estimated by eye and; (iii) the percentage frequency of occurrence, i.e. the percentage of a population that had consumed one or more of a particular prey item (Berg 1979).

Exclusive use of any one of the above three measurements can often be misleading (Berg 1979). However, combining these measures into one index gives a more accurate representation of the diet as it balances their inherent biases (George & Hadley 1979). The index of relative importance (I.R.I.) (Pinkas, Oliphant & Iverson 1971) is one such index and was used here. I.R.I. was calculated as:

$$\text{I.R.I.} = (\%N + \%V) \times \%FO$$

where $\%N$ is the numerical percentage of a food type, $\%V$ is its volumetric percentage and $\%FO$ is its percentage frequency of occurrence. Although this index has come under some criticism (MacDonald & Green 1983), it is valuable in ranking prey items in order of dietary importance (Cailliet 1976).

Niche breadth

Niche breadth is the 'distance through' a niche along some particular line in niche space and it is used primarily as an inverse measure of ecological specialization (Colwell & Futuyma 1971). We used the Petraitis (1979) likelihood measure (W) as a measure of niche breadth. W incorporates an expression of potential prey availability and is approximately equal to the chi-square goodness-of-fit test. W ranges from a value of 0 (specialist feeder) to 1.0 (generalist feeder) and measures the likelihood that the observed proportional resource usages are the same as the proportions available (Unger & Lewis 1983).

$$W = (\lambda)^{1/N}$$

$$\ln \lambda = \sum_i n_i \ln(a_i) - \sum_i n_i \ln(P_{xi})$$

where P_{xi} = the proportion of prey item i in species x ; n_i = the amount of resource i used; a_i = the number of prey i in the environment; and N = the total number of resources used.

Niche overlap

Niche overlap is defined as the region of niche space shared by two or more contiguous niches involving one or more resource categories (Colwell & Futuyma 1971). We used the overlap indices of Schoener (1970) (C_{xy}), and Hurlbert (1978) (L). Values for C_{xy} range from 0 (no overlap) to 1 (complete overlap) with values greater than 0.6 considered to be biologically significant (Wallace 1981).

$$C_{xy} = 1 - 0.5 \left(\sum_i |P_{xi} - P_{yi}| \right)$$

where P_{xi} = the proportion of prey item i in the diet of species x and P_{yi} = the proportion of prey item i in the diet of species y .

L is a measure of dietary similarity that includes a measure of potential prey abundance. It measures the degree to which the frequency of interspecific encounters is higher or lower than it would be if each species used each resource state in proportion to its abundance (Hurlbert 1978).

$$L = (A/XY) \sum_i (X_i Y_i / a_i)$$

where A = the total number of available prey; X = the total number of prey in species X ; Y = the total number of prey in species Y ; X_i = the total number of prey i in species X ; Y_i = the total number of prey i in species Y ; and a_i = the number of prey i in the environment. For two species occupying mutually exclusive niches, L equals 0 and L equals 1.0 when both species use each potential prey category in proportion to its abundance. When $L > 1.0$ there is a convergence of diets, with both species using the same prey categories, but with some prey categories being used more intensively than others (Griffiths 1986). No levels of significance have ever been given for L .

Feeding behaviour

Qualitative and quantitative observations were made of the feeding behaviour of all four species *in situ* using mask and snorkel. *Gasterosteus aculeatus*, *G. wheatlandi* and *P. pungitius* were observed at site A-3 in June and July, while *A. quadracus* was observed at site B-4 in July. General feeding behaviour and feeding habitat were recorded for both adults and juveniles. In particular, the number of darts each stickleback made to each of three possible feeding locations (just below the surface, in the general water column, and close to the substrate) was recorded.

RESULTS

Potential prey

The most abundant organisms in the biota samples collected from site A were diatoms, nauplii, nematodes, ostracods, harpacticoid and cyclopoid copepods (Table 2). There did not appear to be any discernible pattern in either the total numbers of potential food types collected, or the number of different potential food items over the collection period. On most dates, sites A-3a and A-3b had greater numbers of prey than site A-1, even when diatoms were omitted from consideration.

The three (numerically-dominant) potential prey types, found at both sites B-3 and B-4, were ostracods, harpacticoid copepods and nematodes (Table 3). Amphipods and dipteran larvae were found only at site B-4 while adult polychaetes were collected only from site B-3. Other than on 15 May, site B-4 had greater numbers of potential prey than did site B-3 (Table 3). Density of potential prey tended to first increase, at both sites, from early May to late July, then to decrease sharply in September. A comparison of species diversity between the two sites indicates that site B-4 had a slightly greater diversity than B-3 but neither site had a very high diversity.

Fish populations

Site A-1 contained only populations of *G. aculeatus* and *P. pungitius*, with adult *G. aculeatus* being the largest (mean S.L. = 52 mm). Young-of-the-year, of both species, were

TABLE 2. Frequency (%N) of potential food items collected from site A over the sampling period

Prey type*	29 April		13 May		28 May		13 June		27 July		30 August	
	A-1	A-3a	A-1	A-3a	A-1	A-3a	A-1	A-3a	A-1	A-3a	A-1	A-3a
Rotifera	4.1	0	5.5	0	0.9	0	0.4	0	0	0	4.1	0
Nematoda	76.1	1.8	0.9	4.2	2.8	6.1	3.1	6.9	53.8	12.3	46.0	17.8
Bivalvia	0	<0.1	0	<0.1	0	0.2	0	0.2	0	0.1	0	1.5
Polychaeta (L)	0	0	0	0.6	0	0	0	0	0	0.1	0	0
Polychaeta (A)	0	0.1	0	0.4	0	1.5	0.1	0.9	0	2.9	0	1.0
Oligochaeta	<0.1	<0.1	0.3	0.6	0	2.6	1.3	1.0	0	4.9	2.1	1.3
Acari	0.7	<0.1	0.3	0	1.4	<0.1	0	0.1	0	0.1	0	0.2
Ostracoda	1.2	0.3	0.6	4.2	2.4	1.2	2.7	0.3	8.0	4.9	15.1	5.1
Harpacticoida	1.6	0.9	3.5	2.5	8.8	4.2	0.7	2.4	16.2	9.8	17.2	7.6
Cyclopoida	0.8	1.6	<0.1	17.3	1.8	2.6	4.3	1.0	0.8	2.9	1.4	1.5
Calanoida	7.0	0.3	0.8	0.4	0.9	0.2	1.1	0.1	0	<0.1	0.7	0.2
Nauplii	8.2	0	54.7	0	76.1	0	7.8	0	11.6	0	5.1	0
Copepodites	0	0	0	0	0	0	0	0	5.8	0	4.1	0
Isopoda	0	0	0	0	0	0.2	0	0	0	0	0	0
Amphipoda	0	<0.1	0	0	0	0	0.4	0	0.7	0	0	0.2
<i>M. mucronatus</i>	0	0	0	0	0	0.3	<0.1	0.1	0	0.1	0	0
<i>Corophium</i> sp.	0	0	0	0	0	0	0.7	0	<0.1	1.6	0	0.4
Hemiptera (N)	0	0	<0.1	0	0.5	0	<0.1	0	<0.1	0	1.4	0
Diptera	0	0	0	0	0	0	0	0	0	0	<0.1	0
Chironomidae (P)	0	0	0	0	0	0	0	0	0	0	<0.1	0
<i>Chironomus</i> sp. (L)	0.2	0	<0.1	0	0.2	0	<0.1	0	1.3	0	2.8	0
<i>Cricotopus</i> sp. (L)	0	0	0	0	0	0	0	0	0	0	0	0
Tabanidae (L)	0.1	0	0	0	0	0.4	0.2	0	<0.1	0	0	0
Diatoms	0	94.8	33.2	69.9	73.5	76.8	53.9	86.8	42.2	61.4	49.9	63.4
Total no. of prey	4869	30153	13608	14316	4601	18536	12138	23720	3013	20024	2433	15776
No. of prey types	11	10545	11	12	10	13	13	11	12	9	12	11
												9

* L = larvae; P = pupae; N = nymph; A = adult.

TABLE 3. Frequency (%N) of potential food items collected from site B over the sampling period

Prey type*	Date:	15 May	27 May	15 June	30 June	26 July	3 September			
Site:	B-3	B-4	B-4	B-3	B-4	B-4	B-3	B-4	B-3	B-4
Rotifera	1.1	1.3	6.6	0	0	<0.1	0.2	0.6	2.5	1.8
Nematoda	10.1	1.7	13.1	33.0	1.9	8.7	52.0	3.3	38.1	5.0
Bivalvia	0	0	0	0	0	0	1.2	0	0	0
Polychaeta (A)	0.3	0	0	0.3	0	0	0.6	0	2.0	0
Oligochaeta	1.2	0	0.5	5.0	0.1	1.4	5.2	0	5.1	0.8
Acari	0	1.5	0	0	0	0	0	0	0	0
Ostracoda	10.9	58.1	24.1	11.2	11.7	19.0	8.6	78.8	0	60.9
Harpacticoida	73.4	22.4	43.1	50.3	84.7	69.9	32.0	16.2	43.2	28.0
Cyclopoida	1.7	0	0.5	0.1	0.8	0.2	0.2	0.3	0	0
Calanoida	0	0	0.4	0.1	0	0	0	0	0	0
Nauplii	1.2	0.2	2.8	0	0	0.2	<0.1	<0.1	0.2	<0.1
Mysidacea	0	0	0	0	0	0	<0.1	<0.1	0	0
Isopoda	<0.1	0	0	0	0	0	0	0	0	0
Amphipoda										
<i>Gammarus</i> spp.	0	0	2.6	0	0.2	0	0	<0.1	0	<0.1
Diptera										
Ceratopogonidae (L)	0	0	0	0	0	0	0	0	0	<0.1
<i>Cricotopus</i> sp. (L)	0	1.2	1.3	0	0	0.5	0	0.1	0	0
<i>Psectrocladius</i> sp. (L)	0	3.0	0	0	0	0	0	0	0	0
<i>Dicrotendipes</i> sp. (L)	0	0.9	4.5	0	<0.1	0	0	0.6	0	2.7
<i>Tanytarsini</i> sp. (L)	0	6.6	0	0	0.1	0	0	0	0	0
Tanypodinae (L)	0	0.6	0	0	0	0	0	0	0	0
Tabanidae (L)	0	0	0.5	0	0.3	0	0	0	0	0.6
Trichoptera (L)	0	0	0	0	0	0	0	0	0	<0.1
Total no. of prey	19010	2686	2941	14320	20580	13851	25997	30943	6299	8040
No. of prey types	9	11	12	7	9	8	10	10	6	10

* L = larvae; A = adult.

first collected on 13 June, *P. pungitius* being slightly larger (mean S.L. = 24 mm) than *G. aculeatus*. Neither adults of the two species, nor juvenile *G. aculeatus*, were collected in July or August. *Gasterosteus aculeatus*, *G. wheatlandi* and *P. pungitius* were collected from site A-3. As in site A-1, no adults, of any species, were collected after 13 June. *Gasterosteus aculeatus* was the largest species (mean S.L. = 52 mm), *P. pungitius* was the second largest (mean S.L. = 38 mm) but rarest, while *G. wheatlandi* was the smallest (mean S.L. = 32 mm) but most numerous species. Young-of-the-year *G. aculeatus* and *P. pungitius* were first collected on 13 June, while young-of-the-year *G. wheatlandi* were not collected until 27 July. *Pungitius pungitius* juveniles were the largest of the three species present (mean S.L. = 25 mm), *G. wheatlandi* was the smallest (mean S.L. = 18 mm).

Site B-3 contained *A. quadracus*, *G. aculeatus*, *G. wheatlandi* and *P. pungitius*. *Gasterosteus aculeatus* was the largest of the four species collected (mean S.L. = 49 mm) followed by *P. pungitius* (mean S.L. = 42 mm), *A. quadracus* (mean S.L. = 32 mm) and *G. wheatlandi* (mean S.L. = 28 mm). Juvenile *G. aculeatus* first appeared in the 15 June collection while the other three species were not present until July and September. Despite their large mean standard lengths, examinations of their gonads revealed that all fish collected in July and September were immature. *Pungitius pungitius* juveniles were the largest collected (mean S.L. = 32 mm) followed by *A. quadracus* (mean S.L. = 25 mm), *G.*

aculeatus (mean S.L. = 27 mm) and *G. wheatlandi* (mean S.L. = 17 mm). *Apeltes quadracus*, *G. aculeatus* and *P. pungitius* were collected from site B-4. Adult *G. aculeatus* were the largest specimens (mean S.L. = 52 mm) followed by *P. pungitius* (mean S.L. = 41 mm) and *A. quadracus* (mean S.L. = 30 mm). Juvenile *P. pungitius* were first collected on 15 June but were not collected again until 3 September. Juvenile *A. quadracus* were collected in July and September, while juvenile *G. aculeatus* were collected in September. No sticklebacks were collected from site B-1, and B-2 yielded only occasional specimens.

Diet

In general, a sample of ten or fifteen stomachs gave an adequate representation of the diet. This was verified by plotting the cumulative number of prey categories, found in one fish species, against a randomly pooled number of stomachs. The minimum number of stomachs necessary was estimated as the point at which the curve levelled out (Hurtubia 1973).

The diets of adults of all four stickleback species were very similar to each other in their main components. At site A, copepods, as well as hemipteran nymphs at site A-1, were the most important food items in the diet, whereas copepods and *Gammarus* were the most important at site B-3, and *Gammarus* and dipteran larvae at site B-4 (Table 4). Beyond these common prey types, differences existed in the proportion and type of lesser prey types consumed by each fish species. Adult *A. quadracus* were primarily benthic feeders, preying predominantly on chironomid larvae and *Gammarus* (Table 4). Adult *G. aculeatus*, *G. wheatlandi* and *P. pungitius* consumed a mixture of benthic and planktonic prey (harpacticoid, cyclopoid and calanoid copepods, gammarids and oligochaetes). However, plankton was more important in the diet of adult *G. wheatlandi*, while benthos was more important in the diet of adult *P. pungitius* (Table 4). Juvenile *A. quadracus* were chiefly benthic feeders, consuming mainly gammarids and dipteran larvae (Table 5). Juvenile *G. aculeatus* and *G. wheatlandi* fed mostly on plankton (copepod nauplii, calanoids and copepodites), but benthic prey (harpacticoids) was also important in the diets of juvenile *G. aculeatus* (Table 5). Juvenile *P. pungitius* consumed a greater range of benthic prey than juveniles of the other species (Table 5).

The diet of each species was found to vary in both composition and proportion, from site to site. Adult and juvenile *A. quadracus*, *G. aculeatus* and *P. pungitius* consumed greater amounts of prey in those areas which contained abundant filamentous algae (A-1, A-3b and B-4). These algal mats provided a more complex habitat and therefore supported greater numbers of potential prey (Tables 2 and 3). *Gasterosteus wheatlandi*, in contrast, consumed greater amounts of prey, in the form of nauplii and copepodites, at sites that had little vegetation (A-3a and B-3). This may be a reflection of its preference for smaller, planktonic prey and open water.

The diets of males and females, of each species, were very similar in composition, but there were differences in the importance values of the prey (Tables 6, 7). Fish eggs were more important in the diets of male *G. aculeatus*, *G. wheatlandi* and *P. pungitius* than females, but females ate greater numbers of prey. The diets of females were more diverse than those of males. Females devote much energy to egg formation, while males spend more time caring for eggs and fry, and have little time for feeding; therefore, it is not surprising that females consumed more food than males. The diets of male and female *A. quadracus* were quite similar in composition and total number, with both sexes feeding on the benthos. However, females fed on fish eggs, while males did not. In the majority of

TABLE 4. Index of relative importance (I.R.I.) data for adults from sites A and B

		<i>G. aculeatus</i>			<i>G. wheatlandi</i>		<i>P. pungitius</i>			<i>A. quadracus</i>	
Prey type*	Site = <i>N</i> =	A-1 32	A-3a 9	A-3b 28	A-3a 34	A-3b 23	A-1 30	B-3 16	B-4 53	B-3 10	B-4 46
Nematoda		14.4	4.4	21.6	92.4	35.2	49.4	0	0	0	<0.1
Bivalvia siphons		0	63.8	42.0	390.0	13.0	0	0	0	0	0
Polychaeta (L)		0	0	0	106.8	21.6	0	0	0	0	0
Polychaeta (A)		0	0	0	0.2	0.9	0	39.0	0	0	0
Oligochaeta		120.0	253.0	1245.0	2948.0	456.3	566.8	0	1.4	0	21.0
Acari		0	0	2.2	0	0	0.9	0	0	0	0
Ostracoda		40.3	9.9	102.4	9.0	31.2	6.5	3.9	230.4	0	40.8
Harpacticoida		476.0	285.6	2284.6	4470.0	8030.0	330.0	37.5	837.9	80.0	1234.8
Cyclopoida		102.5	4149.2	0.8	189.0	3.6	75.4	941.6	22.1	456.0	213.5
Calanoida		8102.8	1596.0	5090.8	4215.2	3612.7	6246.6	8610.3	504.0	908.0	352.5
Nauplii		0	0	0	129.6	1.6	17.1	0	0	0	0
Copepodites		0	0	0	12.6	0	0	0	0	113.0	76.3
Cirripedia											
<i>Balanus</i> (L)		0	0	219.6	21.0	61.6	0	0	0	0	0
Isopoda		0	0	0	27.0	0	0	0	0	672.0	0
Amphipoda											
<i>Gammarus</i> spp.		0	0	0	0	0	0	3318.9	5324.4	817.0	2448.5
<i>M. mucronatus</i>		3.5	171.6	222.5	66.0	15.6	0	0	0	0	0
<i>Corophium</i> sp.		0	247.5	11.2	3.6	13.0	0	0	0	0	0
Ephemeroptera (L)		0	0	0	0	0	0	0	1.2	0	0
Hemiptera (N)		2847.0	19.8	198.4	0.3	0	3511.2	0	2.0	0	0
Diptera											
Unidentified (P)		7.8	0	0	0	0	6.6	0	456.0	0	87.0
Ephydriidae (L)		30.6	0	1.0	5.4	0.9	51.2	0	0	0	0
Empididae (L)		0	0	0	0	0	1.2	0	0	0	0
Dolichopodidae (L)		<1.0	0	0	0	0	0	0	0	0	0
Ceratopogonidae (P)		0.9	0	0.8	0	0	3.6	0	14.4	0	2.4
Muscidae (L)		0	0	0	0	0	0.9	0	0	0	0
Chironomidae (P)		1465.2	0	187.5	0	0	633.5	0	0	0	0
<i>Chironomus</i> sp. (L)		32.3	0	0	0.3	0	176.0	0	0	0	0
<i>Corynoneura</i> sp. (L)		0	0	0	0	0	0	0	<0.1	0	2.8
<i>Cricotopus</i> sp. (L)		0	0	0	0	0	0	0	1683.0	0	1828.8
<i>Cardiocladius</i> sp. (L)		0	0	0	0	0	0	0	1.6	0	2.0
<i>Eukiefferiella</i> sp. (L)		0	0	0	0	0	0	0	17.1	0	10.8
<i>Psectrocladius</i> sp. (L)		0	0	0	0	0	0	0	1.6	0	0
<i>Heterotrissocladius</i> sp. (L)		0	0	0	0	0	0	0	19.2	0	0
<i>Orthocladius</i> sp. (L)		0	0	0	0	0	0	0	1.8	0	0
<i>Dicortendipes</i> sp. (L)		0	0	0	0	0	0	0	58.5	0	1454.4
Tanytarsini sp. (L)		0	0	0	0	0	0	0	30.0	0	5.6
Chironomini sp. (L)		0	0	0	0	0	0	0	0	0	10.4
Tanypodinae (L)		0	0	0	0	0	0	0	8.0	0	0
Trichoptera (L)		0	0	0	0	0	0	0	6.0	0	0
Hymenoptera (L)		0	0	0	0	0	0	0	0.4	0	0
Invertebrate eggs		0	0	0	0	0	0	0	0	75.0	0
Fish eggs		282.9	26.4	547.2	55.5	408.0	0.9	0	20.0	20.0	2.2
Fish fry (S.L. <1.0 cm)		6.0	0	4.5	0	3.5	195.0	0	0	0	0
Total no. of prey		3439	1292	2755	4519	2443	2067	802	1310	142	693
No. of empty stomachs		0	2	2	0	0	1	2	3	1	1

* L = larvae; N = nymph; P = pupae; A = adult.

cases, differences in total prey number between the species and between the sexes was not a result of differences in stomach fullness. Comparison of the total number of full and distended stomachs between the species at each site, indicated that there was little difference in proportion in full and distended stomachs to the total number of stomachs.

Niche breadth and niche overlap

The niche breadth values in this study varied from site to site; this resulted in differences in the ranking of each species from site to site. At sites A-1 and A-3a adult *P. pungitius* had

a greater niche breadth than adult *G. aculeatus*, while *G. aculeatus* had greater values at sites A-3b, B-3 and B-4 (Table 8). Adult *G. wheatlandi* had the largest niche breadth at sites A-3a and A-3b. The relatively large niche breadth of *G. wheatlandi* at site A-3a ($n=33$) and A-3b ($n=23$) may have been a result of the comparatively smaller sample sizes of *P. pungitius* and *G. aculeatus*. The niche breadth of juvenile *A. quadracus* and *P. pungitius* were usually wider than those of the smaller *G. aculeatus* or *G. wheatlandi* at sites A and B (Table 8). This may indicate that, as the fish grow, the range of prey available to them increases also.

Niche overlap varied from site to site with the highest values occurring at sites with filamentous benthic algae (A-1, A-3b and B-4); lower overlap values were found at the other sites (Table 8). Adult *G. wheatlandi* overlapped the other three species minimally, while adult *G. aculeatus* and *P. pungitius* overlapped greatly at site A. At site B, adult *A. quadracus* overlapped *G. aculeatus* and *P. pungitius* to a greater extent. The degree of dietary overlap agreed with the observed similarity in diet. Dietary overlap between juvenile sticklebacks was highly variable from site to site. In most cases the amount of overlap between juvenile *G. wheatlandi* and the other species was relatively low. Overlap between juvenile *P. pungitius* and *G. aculeatus* varied from significant to non-significant, depending on site. Significant overlap existed between juvenile *A. quadracus* and *P. pungitius* at site B-4 but no significant overlap was found between *A. quadracus* and the other species found at site B-3.

Feeding behaviour

Both sexes of *A. quadracus* fed exclusively on the benthos, either among benthic vegetation or from the open substrate. *Apeltes quadracus* stayed very close to the bottom, often hovering over a patch of substrate, picking at it frequently then moving on to another patch. *Apeltes quadracus* generally swam slowly but it was capable of rapid bursts when frightened. Individuals were often observed perched among strands of vegetation or among bottom debris using their pectoral fins as support.

Groups of 3 or 4 female *G. aculeatus* frequently swam together in a loose school over both algal and sediment covered areas. They often paused to feed for a few seconds (5–10) but quickly moved on when the observer approached. This behaviour made it difficult to follow an individual for any length of time, although the few individuals observed fed both in the water column and on the benthos. Nesting males made very few feeding movements over the observation periods and even these movements were difficult to distinguish from nest-tending behaviour. The few feeding movements that were made were directed towards the water column and the benthos.

Male *G. wheatlandi* tending a nest site fed mainly from the benthos. Again, it was sometimes difficult to distinguish feeding movements from nesting behaviour. Female *G. wheatlandi* were primarily mid-water feeders and, on one occasion, the copepods on which they were feeding were visible in the water column. Female *G. wheatlandi* also exhibited schooling behaviour with schools of three or more individuals being common. The habit of nesting in dense growths of algae made observations of male *P. pungitius* impossible. Females were more visible and they exhibited the same schooling and general behaviour as female *Gasterosteus*. The few females observed fed from the benthos, mainly among algal mats but also from sediment-covered areas between the algal mats. Juveniles were distinguished by their small size relative to the adults. However, as they resembled each other closely, they were categorized simply as *Gasterosteus*. Juvenile *Gasterosteus* and *Pungitius* were observed always to be in large schools of ten or more individuals, while

TABLE 5. (continued)

Prey type*	<i>G. aculeatus</i>				<i>G. wheatlandi</i>			<i>P. pungitius</i>				<i>A. quadracus</i>	
	Site = N =	A-1 10	A-3a 32	A-3b 22	B-3 18	A-3a 12	B-3 31	A-1 50	A-3a 25	A-3b 35	B-3 17	B-4 15	B-4 38
Diptera													
Unidentified (P)		0	0	0	32.3	0	0	0	0	0	0	0	3.9
Tipulidae (L)		0	0	0	0	0	0	0	0	0	16.8	0	0
Ephydriidae (L)		96.0	0	3.0	0	0	0	350.3	16.0	151.8	0	0	0
Dolichopodidae (L)		0	0	0	0	0	0	0	0	1.2	0	0	0
Ceratopogonidae (L)		0	0	0	0	0	0.6	0	0	3.0	1.2	25.5	0
Empididae (L)		0	0	0	0	0	0	0.8	0	0	0	0	0
<i>Corynoneura</i> sp. (L)		0	0	0	0	0	0	0	0	0	0	0	0
<i>Cricotopus</i> sp. (L)		0	0	0	0	0	12.0	0	35.2	0	16.2	0	50.6
<i>Cardiocladius</i> sp. (L)		0	0	0	0	0	0	0	0	0	1.2	0	4535.6
<i>Eukiefferiella</i> sp. (L)		0	0	0	0	0	1.9	0	0	0	0	0	0.9
<i>Heterotrissocladius</i> sp. (L)		0	0	0	0	0	0	0	0	0	0	4.2	0
<i>Dicortendipes</i> sp. (L)		0	0	0	0	0	0	0	0	0	0	515.2	201.6
<i>Chironomus</i> sp. (L)		11.0	0	2.7	0	0	0	0	9.6	5.1	0	1.8	1.5
Invertebrate Eggs		0	0	0	812.6	0	0	0	0	0	0	0	34.0
Fish eggs		0	0	0	0	0	0	0	0	3.3	0	0	0
Fish fry (S.L. <1.0 cm)		0	9.3	4.0	0	0	0	9.6	0	4.2	0	0	3.9
Blue-green algae		0	0	56.0	0	0	0	0	0	0	0	0	0
Diatoms	4536.0	3.6	228.6	0	0	0	0	0	0	0	0	0	0
Plant seeds	0	0	0	0	0	0	0	0	0	3.0	0	0	0
Total no. of prey	1525	961	2148	2403	5833	930	2903	782	1349	1616	1021	68	489
No. of empty stomachs	0	1	0	1	1	0	3	0	2	0	0	4	2

* L = larvae; N = nymph; P = pupae; A = adult; T = cephalic tentacles.

TABLE 6. Index of relative importance values for adults, by sex, for site A

Prey type*	Site Sex N=	<i>G. aculeatus</i>				<i>G. wheatlandi</i>			
		A-1		A-3b		A-3a		A-3b	
		M	F	M	F	M	F	M	F
		10	22	13	15	8	26	11	12
Nematoda		0	25.3	19.5	46.0	5.2	151.2	12.6	66.0
Bivalvia siphons		0	0	30.0	75.0	155.0	501.4	936.0	300.0
Polychaeta (L)		0	0	0	0	252.2	84.0	0	64.0
Polychaeta (A)		0	0	0	0	0	7.2	0	2.4
Oligochaeta		0	223.1	1012.0	1922.0	95.0	4463.0	540.0	600.0
Acari		0	0	6.0	2.4	0	0	0	0
Ostracoda		4.0	69.7	18.4	322.0	53.2	3.6	108.0	8.5
Harpacticoida		240.0	576.0	2208.0	4000.0	5600.0	4190.0	7100.0	9600.0
Cyclopoida		201.0	90.0	0	2.4	540.0	114.0	25.2	0
Calanoida		6490.0	7926.1	7200.0	5336.0	2438.1	4656.0	2821.0	5060.0
Nauplii		0	0	0	0	0	195.3	14.4	0
Copepodites		0	0	0	0	0	4.0	0	0
Cirripedia									
<i>Balanus</i> (L)		0	0	368.0	217.0	0	32.3	0	252.0
Isopoda		0	0	16.0	0	10.4	64.6	0	35.7
Amphipoda									
<i>M. mucronatus</i>		0	8.0	310.0	322.0	384.3	19.0	36.0	8.8
<i>Corophium</i> sp.		0	0	18.4	16.8	107.9	12.0	25.2	8.8
Hemiptera (N)		4081.0	2730.6	60.0	486.0	0	0.4	0	0
Diptera									
Unidentified (P)		0	1.0	0	0	0	0	0	0
Ephydriidae (L)		0	67.2	0	3.2	52.0	<0.1	0	2.4
Ceratopogonidae (P)		0	1.5	0	3.2	0	0	0	0
Chironomidae (P)		1025.0	1730.1	646.0	148.0	0	0	0	0
<i>Chironomus</i> sp. (L)		22.0	39.6	0	0	0	0.4	0	0
Fish eggs		712.0	180.4	950.0	570.0	745.0	2.0	1496.0	17.6
Fish fry (S.L. < 1.0 cm)		150.0	12.6	24.8	0	0	0	19.8	0
Total no. of prey		289	3150	892	1864	592	3984	537	1907
No. of empty stomachs		0	0	1	1	0	0	0	0

* L = larvae; N = nymph; P = pupae; A = adult.

Apeltes were often solitary. Schools of juvenile *Gasterosteus* usually were found feeding either in the water column, in open areas on the bottom or among algal mats. Schools of *Gasterosteus* often swam a short distance then swam to the bottom and browsed among the debris. After a short period they would move on to a new area. Juvenile *Pungitius* fed mostly within dense mats of algae but occasionally they could be found in open areas. Juveniles were observed browsing among the algal strands in a head-down feeding posture and to periodically pick at small particles. Mixed schools of *Gasterosteus* and *Pungitius* were commonly encountered around algal mats. Juvenile *Apeltes* were found individually or in loose aggregations (as opposed to a school) of five or less. *Apeltes* fed primarily among benthic debris and vegetation, remaining close to the bottom, and were never found in the open water.

DISCUSSION

The diet of adult and juvenile *G. aculeatus* is in general agreement with that in the literature. The importance of copepods in the diet of *G. aculeatus* collected from site A, was similar to that found for specimens collected by Worgan & FitzGerald (1981b), while

larger crustaceans and dipteran larvae were more important in the diets of *G. aculeatus* collected from site B, as was found by Walsh & FitzGerald (1984) and Zander, Moller-Buchner & Totzke (1984). Worgan & FitzGerald (1981b) questioned the importance of copepods in the diet of sticklebacks because of the transitory nature of the copepods, however, they were clearly a major component in the diets of adult and juvenile fish in our study. The diets of adult and juvenile *A. quadracus*, *G. wheatlandi* and *P. pungitius* were in general agreement with the few published studies (e.g. Cameron, Kostoris & Penhale 1973; Blouw & Hagen 1981; Imrie & Daborn 1981; Walsh & FitzGerald 1984).

The observed sexual differences in the diets of adult *G. aculeatus*, *G. wheatlandi* and *P. pungitius* agree with those in the literature (Walsh & FitzGerald 1984); no data exist for *A. quadracus*. A possible explanation for the increased number of prey in the stomachs of female sticklebacks may be that the large size of the eggs eaten by the males (1.0–1.5 mm), leaves very little room in the stomach for other food items and results in a distended stomach with low prey diversity.

Studies of dietary diversity in adult sticklebacks have shown that the largest species have the greatest niche breadth (Thorman 1983). However, Worgan & FitzGerald

TABLE 7. Index of relative importance values for adults, by sex, for site B

Prey type*	Site Sex N=	<i>P. pungitius</i>				<i>A. quadracus</i>	
		B-3		B-4		B-4	
		M	F	M	F	M	F
Polychaeta (A)		182.0	0	0	0	0	0
Oligochaeta		0	0	0	3.0	9.5	25.9
Ostracoda		6.5	3.9	270.6	214.6	24.2	57.2
Harpacticoida		45.0	27.5	1993.6	530.1	1631.7	9828.0
Cyclopoida		1018.4	930.0	19.2	25.5	281.6	166.5
Calanoida		7506.4	9037.5	195.8	671.3	189.5	465.5
Copepodites		0	0	0	0	257.4	16.0
Amphipoda							
<i>Gammarus</i> spp.		4920.0	2110.5	1570.8	7376.0	1415.1	3168.9
Ephemeroptera (L)		0	0	0	2.4	0	0
Hemiptera (N)		0	0	0	4.2	0	0
Diptera							
Unidentified (P)		0	0	1966.8	89.7	96.0	85.5
Ceratopogonidae (L)		0	0	16.8	9.9	0	8.4
<i>Corynoneura</i> sp. (L)		0	0	0	0.3	3.5	3.2
<i>Cricotopus</i> sp. (L)		0	0	745.8	2178.0	1987.5	1663.2
<i>Cardiocladius</i> sp. (L)		0	0	0	2.7	3.5	1.6
<i>Eukiefferiella</i> sp. (L)		0	0	18.7	16.2	11.0	11.2
<i>Psectrocladius</i> sp. (L)		0	0	0	3.0	0	0
<i>Heterotrissocladius</i> sp. (L)		0	0	0	34.1	0	0
<i>Orthocladius</i> sp. (L)		0	0	0	3.0	0	0
<i>Dicrotendipes</i> sp. (L)		0	0	137.7	35.2	1546.3	1377.6
Tanytarsini sp. (L)		0	0	38.5	17.1	6.5	5.2
Chironomini sp. (L)		0	0	0	0	4.5	15.2
Tanypodinae (L)		0	0	7.2	7.2	0	0
Trichoptera (L)		0	0	42.9	1.5	0	0
Hymenoptera (A)		0	0	0	0.6	0	0
Fish eggs		0	0	141.1	1.5	0	6.8
Total no. of prey		263	539	181	1129	238	455
No. of empty stomachs		0	2	1	2	0	1

* L = larvae; N = nymph; P = pupae; A = adult.

TABLE 8. Niche overlap and breadth values of adult and juvenile Gasterosteidae collected from sites A and B; N = total number; L = niche overlap (Hurlbert 1978); C_{xy} = niche overlap (Schoener 1970); W = niche breadth (Petraitis, 1979); $A.q = A. quadracus$; $G.a = G. aculeatus$; $G.w = G. wheatlandi$; $P.p = P. pungitius$

	SITE															
	A-1			A-3a			A-3b			B-3			B-4			
	N	L	C _{xy}	N	L	C _{xy}	W	N	L	C _{xy}	W	N	L	C _{xy}	W	
Adults																
P.p vs.	30	11.4	0.83	3	15.1	0.33	0.07	6	16.6	0.72	0.11	16	468.0	0.55	0.01	0.56
G.a	32	—	0.14	9	—	0.06	0.06	28	0.32	0.32	0.15	2	—	0.15	6	0.11
P.p vs.	—	—	—	3	22.1	0.57	0.07	6	9.45	0.52	0.11	16	22.9	0.06	0.01	—
G.w	—	—	—	33	—	0.18	0.18	23	0.54	0.54	0.52	4	—	0.52	—	—
P.p vs.	—	—	—	—	—	—	—	—	—	—	—	16	292.4	0.42	0.01	0.61
A.q	—	—	—	—	—	—	—	—	—	—	—	10	—	0.31	46	0.11
G.a vs.	—	—	—	9	7.3	0.29	0.06	28	6.63	0.59	0.32	2	11.1	0.06	0.15	—
G.w	—	—	—	33	—	0.18	0.18	23	0.54	0.54	0.52	4	—	0.52	—	—
G.a vs.	—	—	—	—	—	—	—	—	—	—	—	2	139.9	0.69	0.15	0.45
Aq	—	—	—	—	—	—	—	—	—	—	—	10	—	0.31	46	0.28
G.w vs.	—	—	—	—	—	—	—	—	—	—	—	4	7.0	0.13	0.52	0.42
A.q	—	—	—	—	—	—	—	—	—	—	—	10	—	0.31	—	—
Juveniles																
P.p vs.	50	2.20	0.27	25	53.1	0.60	0.15	35	0.90	0.37	0.64	17	605.9	0.27	0.01	0.60
G.a	10	—	0.24	32	—	0.13	0.13	22	0.95	0.95	0.38	18	—	0.38	2	0.80
P.p vs.	—	—	—	25	25.9	0.41	0.15	35	0.30	0.12	0.64	17	975.9	0.42	0.01	0.61
G.w	—	—	—	12	—	0.23	0.23	8	0.45	0.45	0.10	31	—	0.10	—	—
P.p vs.	—	—	—	—	—	—	—	—	—	—	—	17	235.9	0.49	0.01	0.58
A.q	—	—	—	—	—	—	—	—	—	—	—	15	—	1.47	38	0.14
G.a vs.	—	—	—	32	31.9	0.54	0.13	22	4.90	0.43	0.95	18	256.5	0.49	0.38	—
G.w	—	—	—	12	—	0.23	0.23	8	0.45	0.45	0.10	31	—	0.10	—	—
G.a vs.	—	—	—	—	—	—	—	—	—	—	—	18	62.0	0.12	0.38	0.37
A.q	—	—	—	—	—	—	—	—	—	—	—	15	—	1.47	38	0.61
G.w vs.	—	—	—	—	—	—	—	—	—	—	—	31	99.9	0.11	0.10	0.14
A.q	—	—	—	—	—	—	—	—	—	—	—	15	—	1.47	—	—

(1981b) found that adult *P. pungitius* had the largest niche breadth, followed by *G. aculeatus* (which was the largest species) and then *G. wheatlandi*. They used Levins' (1968) measure of niche breadth, which should have given values ranging from 1.0 (the lowest possible value) to n (the total number of resource states) (Petraitis 1979). However, their values were consistently below 1.0, which is not possible given the nature of the index, therefore their values may not be valid. Werner & Hall (1977) proposed that species that were more efficient feeders on small prey should, in general, exhibit more generalized diets. This appears to be the case for adult *G. wheatlandi*, which display larger niche breadths than the other species.

Studies of dietary similarity between *G. aculeatus*, *G. wheatlandi* and *P. pungitius* have produced conflicting results. Some studies indicated that the diets were quite similar (*G. aculeatus* and *P. pungitius*: Hynes 1950; Thorman 1983; *G. aculeatus*, *P. pungitius* and *G. wheatlandi*: Worgan & FitzGerald 1981b), while others found little similarity (Coad & Power 1973; Walsh & FitzGerald 1984). Of these studies, only Thorman (1983) and Walsh & FitzGerald (1984) made any quantitative measurements of overlap. Our study is the first to measure the dietary overlap of adult and juvenile *A. quadracus* with the other stickleback species. Dietary overlap was found to be greatest in areas of abundant aquatic vegetation that supported greater numbers of potential prey, although at site B-3, the overlap measure L reached its highest values. Studies of other closely-related fish species, have also shown that dietary overlap increased with increasing potential food abundance (Keast 1977). As pointed out by Abrams (1980), L is greatly affected by the inclusion of resource states that are not used by the species in the community. Therefore, the unusually high values of L at site B-3 may be due to the abundance of nematodes in the benthic samples and the relative scarcity of nematodes in the diets of collected fish. On the other hand, C_{xy} has no such problems and offers a better view of overlap (Abrams 1980). The affect of rare resources on L also limits its usefulness in the comparison of overlap values from different sites, but C_{xy} is not so constrained (Abrams 1980).

Microhabitat segregation has been observed in sympatric populations of *Gasterosteus* and *Pungitius*, in relation to feeding behaviour (Worgan & FitzGerald 1981b; Walsh & FitzGerald 1984), and in other morphologically similar fish species (Schmitt & Coyer 1982). Microhabitat segregation was found in our study too, with dietary differences being related to microhabitat differences. Field observations of adult and juvenile *A. quadracus* showed them to be benthic in their feeding (chronomids and gammarids), while adult *G. wheatlandi* fed mainly from the water column (copepods, copepod nauplii and copepodites). Although adult *G. aculeatus* and *P. pungitius* fed from both the water column and benthos, *P. pungitius* fed more from the benthos (copepods, chironomid larvae and amphipods). Microhabitat segregation in juveniles was even more pronounced than in the adults. Juvenile *Pungitius* were usually associated with algal mats and were rarely observed over open areas of substrate. As a result, their diets closely reflected the potential prey associated with vegetation (i.e. dipteran larvae). Zander (1979) obtained similar results for juvenile *Pungitius* collected off the coast of Denmark. Juvenile *Gasterosteus* were usually found in small schools in open water, although they were sometimes observed feeding close to algal mats too. This habitat preference was also reflected by their diets, which were predominantly planktonic (i.e. copepods).

The appearance of adults (April–May) and juveniles (June–July) of all four species in the study areas coincides with dates found in the literature (Blouw & Hagen 1981; Craig & FitzGerald 1982). Juvenile *G. wheatlandi* appeared later than the other species, as has been observed elsewhere, indicating that this species breeds at a later date than the others

(McInerney 1969; Worgan & FitzGerald 1981a). As in other studies, no adults were found after June, indicating that they had either returned to the sea or had died. We found no dead sticklebacks although Mullem & Vlugt (1964) reported finding dead adult *G. aculeatus* in July. Juvenile *G. aculeatus* migrated to the sea from June till August, whereas juvenile *G. wheatlandi* did not move out of the breeding areas until July–September; Worgan & FitzGerald (1981a) and Craig & FitzGerald (1982) obtained similar results. Both Blouw & Hagen (1981) and Worgan & FitzGerald (1981a) found that juvenile *A. quadracus* and *P. pungitius* remained in their breeding areas until the autumn, as in our study. Snorkel observations at site A confirmed the abundance of juvenile *P. pungitius* and scarcity of juvenile *Gasterosteus*.

Although the diets of the four species were quite similar, differences in composition and abundance were evident. The measurement of niche breadth and overlap indicated, generally, that values were greatest in areas of abundant potential prey and lower in areas of low potential-prey density. Optimal foraging theory, however, predicts a specialization in diet as the absolute abundance of preferred prey types increases (Pyke, Clemens & Charnov 1977). Perhaps the reason for this discrepancy lies in the euryphagic feeding behaviour of sticklebacks. Sticklebacks, in our study and others, fed on a wide range of prey and their diet was, in part, a reflection of prey availability. It is possible, therefore, that they may not have a 'preferred' prey type. Thus, the increased diet breadth and subsequent increased dietary overlap in areas of high potential food abundance may merely have been a consequence of that increased abundance. It is unlikely, therefore, that interspecific competition for food was a factor in our stickleback communities. The abundance of potential prey in the environment may have permitted high degrees of overlap without any noticeable detrimental effects (see also Hynes 1950; Worgan & FitzGerald 1981b). The probability of interspecific competition was further reduced by microhabitat segregation. Although this segregation was not absolute, it has been observed to be of importance in structuring other stickleback communities (Worgan & FitzGerald 1981a; Walsh & FitzGerald 1984). It seems clear, therefore, that adults and juveniles of the four species of stickleback in this part of maritime Canada coexist in marginal habitats through the partial segregation of prey types and microhabitats.

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