Given the considerable overlap in diet between triclads and leeches, how can these groups co-exist? Because *D. lacteum* and *E. octoculata* feed almost exclusively on *Asellus* and chironomids respectively, with limited dietary overlap with other species, the level of interspecific competition between each of these species and the other members of the guild is likely to be relatively

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Food partitioning by lake-dwelling triclads and glossiphoniid leeches: field and laboratory experiments

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Abstract The triclads *Polycelis tenuis* and *Dugesia polychroa* and the glossiphoniid leeches *Glossiphonia complanata* and *Helobdella stagnalis* are abundant on the stony shores of productive British lakes. All species are food limited and there is considerable overlap in the diets of these triclads and leeches. This paper investigates interactions between the two groups using field and laboratory experiments to try to identify the mechanism of their co-existence. Triclad and leech numbers were manipulated inside experimental enclosures, matched by controls, erected on the stony shore of an eutrophic English lake. Increasing the numbers of *P. tenuis* and *D. polychroa* prior to the reproductive season in spring resulted in a significant decrease in the numbers and body size of *G. complanata* and *H. stagnalis* compared with control populations in the summer months, and vice versa. However, increases and decreases were temporary with a readjustment of numbers and body size to control levels in the autumn after reproduction had ceased. It is suggested that increasing the numbers of either group elevated the severity of both intra- and interspecific competition for food. The "condition" of prey may, in part, determine the strength of competition, and this was examined in laboratory experiments in which different densities and ratios of *P. tenuis* and *H. stagnalis* were offered either live of recently crushed *Asellus aquaticus*. In monospecific controls, growth rates of *P. tenuis* were greater when fed on crushed than live *Asellus*, but there was no significant difference in the growth of *H. stagnalis* fed either live or crushed prey. In mixed cultures of predators, *P. tenuis* and *H. stagnalis* were the superior competitors when fed on crushed and live *Asellus*, respectively. However, when competitive pressure was low, at low densities of predators, the presence of *H. stagnalis* in mixed cultures fed on live prey was beneficial to the growth of *P. tenuis*. These results are explained in terms of the greater ability of triclads to detect damaged prey, leaking body fluids, due to their sophisticated chemosensory system, and the ability of leeches to capture live prey due to the presence of suckers. It is concluded that co-existence of the two groups in British lakes is assisted by the partitioning of food on a live or damaged basis.

Key words Triclads · Leeches · Lakes · Food · Competition

Introduction

The most numerous invertebrate predators inhabiting the stony shores of productive British lakes comprise a guild of tricald and leech species. Commonly, the guild includes the triclads *Polycelis nigra* (Müll.), *P. tenuis* (Ijima), *Dugesia polychroa* (Schmidt) and *Dendrocoelum lacteum* (Müll.), and the leeches *Glossiphonia complanata* (Linn.), *Helobdella stagnalis* (Linn.) and *Erpobdella octoculata* (Linn.). Populations of these species are food limited (Reynoldson 1966, 1983; Martin et al. 1994a), and there is much overlap in their diets (Reynoldson and Davies 1970; Reynoldson 1975; Young 1981; Young and Spelling 1989). However, co-existence of the triclads is possible because each genus has a food refuge, that is a food type for which it is the superior predator and therefore eats more, thus reducing the severity of interspecific competition for food (Reynoldson and Davies 1970). Thus the *Polycelis* species feed extensively on oligochaetes, *D. polychroa* on snails, and *D. lacteum* on crustaceans, particularly the isopod *Asellus*. *Polycelis nigra* and *P. tenuis* can co-exist in productive lakes because of differences in their feeding behaviour (Reynoldson et al. 1981). Co-existence of the leech species is also assisted by the occurrence of food refuges with *E. octoculata* feeding heavily on chironomid larvae and *G. coplanata* on snails; though oligochaetes feature prominently in the diet of *H. stagnalis*, it is more of a generalist feeder on a wide variety of taxa (Young and Spelling 1989; Martin et al. 1994b).

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Given the considerable overlap in diet between triclads and leeches, how can these groups co-exist? Because *D. lacteum* and *E. octoculata* feed almost exclusively on *Asellus* and chironomids respectively, with limited dietary overlap with other species, the level of interspecific competition between each of these species and the other members of the guild is likely to be relatively low. Competition is likely to be more severe between the other triclad and leech species, particularly between the *Polycelis* species and *H. stagnalis*, because the diet of each is wide with great overlap, particularly oligochaetes and *Asellus*, and between *D. polychroa* and *G. complanata* because both feed heavily on snails (Young 1981).

This paper examines interactions between the triclads, *P. tenuis* and *D. polychroa*, and the glossiphoniid leeches, *H. stagnalis* and *G. complanata*, in field experiments involving numerical manipulations of predators in enclosures built on the stony littoral zone of an English lake. It also investigates the occurrence of competition in laboratory experiments in which different densities and ratios of *P. tenuis* and *H. stagnalis* were offered either live or recently crushed *Asellus acquaticus* (Linn.), which comprises a considerable portion of their diet. The rationale was to find out if either predator had a competitive advantage under the different conditions of this food.

Materials and methods

Field experiments

Numerical manipulations of leeches and triclads were performed inside enclosures built on the stony shore of Crose Mere, an ion-rich, eutrophic, lowland lake situated in Shropshire, England (52°50′N, 2°45′W; Nat. Grid Ref. SJ 430305). The stony littoral zone supports substantial numbers of *P. tenuis*, *D. polychroa*, *H. stagnalis*, *G. complanata* and *E. octoculata*, with only small numbers of *P. nigra* and *D. lacteum*. The first four species, those involved in the current study, breed in spring through the early autumn, with the exception of *G. complanata* which ceases to reproduce in early summer (Young and Ironmonger 1982a; Spelling and Young 1987). The triclads deposit eggs in hard-walled cocoons attached to the substratum, *G. complanata* in soft-walled cocoons also attached to the substratum, and *H. stagnalis* in soft-walled cocoons carried by the adults. The young of triclads are free-living on hatching from cocoons, whereas those of the glossiphoniids are carried initially on the underside of the parents. The leech species have a predominantly annual life cycle with adults dying soon afer breeding (Young and Ironmonger 1982a; Spelling and Young 987), whilst the triclads live for more than 1 year, though some ndividuals shrink and die in the post-reproductive period (Reynoldson 1966). The stony shore also supports large populations of prey organisms such as oligochaetes, the crustaceans *Asellus quaticus* (Linn.) and *Gammarus pulex* (Linn.), and chironomids, nd smaller populations of snails and caddisfly larvae. Reynolds 1979) provides further physical, chemical and biological informaon on the lake.

The design of the enclosures has been described fully by Marn et al. (1994a), who investigated food limitation in leech popuations in Crose Mere. Each enclosure comprised a natural bay, olated from the lake by a screen consisting of an inner, stiff, coarse-meshed, plastic frame attached to an outer fine-meshed .0×0.05 mm) monofilament polypropylene fabric, which providd a barrier to the movement of macro-invertebrates. Experimental ays were matched by control bays (no manipulations) in a ranomized block design.

The following two experiments were performed: (1) the numerical increase of *P. tenuis* and *D. polychroa*, and (2) the numerical increase of *G. complanata* and *H. stagnalis*. In each experiment, the numbers of manipulated animals were increased by about 20% at the beginning of the experiment, immediately after the first sample had been taken in the spring (see below). Based on information obtained in the spring sample, this level of manipulation would have resulted in statistically significant differences in numbers between the control and experimental sites. The triclads and leeches used in the experiments were obtained from another stony shore in Crose Mere, on the opposite side of the lake from the experimental area. The populations of the predators had a similar age and size structure to those in the experimental area.

Experimental procedure was identical to that used by Martin et al. (1994a). Briefly, each experiment was conducted in six experimental enclosures, each with an area of approximately 20 m², with six matching controls, hereafter referred to as experimental and control sites, respectively. The experiments were conducted in separate years, with each lasting about 9 months from March, prior to triclad and leech reproduction, to early November, after reproduction had ceased. Samples of invertebrates were obtained using substrate trays (36.5×21.5×5 cm) filled with the natural substratum of the lake shore, which in the experimental area has a similar substratal composition along its length and width, and buried in the lake floor for 2 months to allow for natural colonization prior to sampling. On each sampling occasion, two trays, one in shallow and one in deep water, were used in each of the six experimental and control sites. The stony shore in the experimental area of Crose Mere is narrow and, at normal water levels, has a maximum width of 6 m and a maximum depth of 1 m. In each experiment, samples were obtained on three occasions: early March, prior to manipulation and triclad and leech reproduction; in July; and in November when reproduction had ceased. Sampled trays were returned to the laboratory where triclads and leeches were removed, counted, and the body length of each triclad and the wet weight of each leech measured. Soft-bodied triclads are fragile and difficult to wet weigh, and in most previous field studies of triclads, body size has been expressed in terms of body length (Reynoldson 1966). Additionally, in the spring sample, all macroinvertebrates in the trays were removed, identified, counted, and the wet weight per tray of each taxon recorded. This was to investigate whether similar standing crops of prey organisms existed in the experimental and control sites prior to the start of the experiment.

Laboratory experiments

Experiments on competition between *P. tenuis* and *H. stagnalis* fed on *Asellus aquaticus* combined a range of absolute and relative densities; the experimental design followed Law and Watkinson (1987) and Young et al. (1993). The experimental material was obtained from Crose Mere. Glass dishes, 18 cm in diameter and 500 ml volume, were used in the experiments; each was three-quarters filled with lake water and had a layer of gravel on the bottom to provide spatial heterogeneity, partly simulating the complex structure of a stony lake shore.

Table 1 Densities and ratios, per dish, of *Polycelis tenuis* and *Helobdella stagnalis* used in the laboratory experiments

Monospecific controls		Two-species mixtures *P. tenuis*:*H. stagnalis*
P. tenuis	*H. stagnalis*	
2	2	1:1
6	6	5:1; 1:5
10	10	5:5
16	16	15:1, 1:15
20	20	15:5, 5:15
30	30	15:15

The experiment was conducted at 14° C, which is favourable for the growth of both species (Reynoldson et al. 1965; Young and Ironmonger 1982b) and a 12 h light:12 h dark cycle. The ranges of experimental densities and ratios are shown in Table 1. Each combination of density and ratio, and control, was replicated four times.

The body length of each triclad and the wet weight of each leech was measured at the start and finish of the 3-month-long experiment. Initially, *P. tenuis* had a length range of 4–5 mm and *H. stagnalis* a weight range of 3–5 mg. To enable comparison of the two species, lengths and wet weights were converted into dry weights prior to analysis of the data; the conversion was based on regression equations obtained by dry weighing at least ten individual leeches in each milligram wet weight category and ten triclads in each millimetre length category over the spectrum of sizes used in the experiments. The leeches did not breed during the experiments but triclads produced cocoons, the numbers of which were recorded. The experiment was repeated twice using as prey, first, live, undamaged *Asellus* and, second, recently crushed *Asellus* which had been squeezed with a forceps to kill them. Eighteen *Asellus*, with a body length of about 10 mm, were added to each dish each week after the water had been changed and uneaten food removed. This number, based on pre-experimental trials, provided sufficient food for up to 13 predators to gain weight; above this particular density, competition would become increasingly severe.

Analysis of data

For each field experiment, numbers, lengths (triclads) and biomasses (leeches) were analysed using a split-plot analysis of variance (ANOVA). This provided information on variation in the data caused by experimental versus control sites, individual site differences, depths of substrate trays, and two interaction terms, between experimentals/controls and site, and between experimentals/controls and depth. For each prey taxon, numerical differences between the experimental and control sites in the spring sample, prior to any manipulations, were investigated using the Wilcoxon signed rank test (Zar 1984).

For each of the two laboratory experiments – predators fed on either live or crushed *Asellus* – four regimes were used: monospecific controls, and a series of mixed predator combinations, viz. mostly *P. tenuis*, mostly *H. stagnalis*, and equal numbers of *P. tenuis* and *H. stagnalis*. For each total density of predators, there were either three or four combinations of species, of which two were always the monospecific controls for each of the species (see Table 1). Data were analysed using regression analysis. The *t*-test was used to determine whether any differences existed between the slopes, mean weight change versus density, produced by the different predators fed on each food condition under different absolute and relative densities. Significantly different slopes would indicate differing degrees of density dependence. Comparison of weight change between control and experimental regimes was

Table 2 (a) Mean numbers (with SD) of triclads and leeches and total mean length (mm) of triclads and mean biomass (g) of leeches (with SD) per tray, and *F* values (*df*=1,5) of analysis of variance testing for differences in numbers and sizes of triclads or leeches between experimental (*E*) and control (*C*) sites in three seasonal samples in two different manipulation field experiments (*Sp* spring, *Su* summer, *Au* autumn; * $P<0.05$; ** $P<0.01$; *** $P<0.001$)

	Polycelis tenuis			*Dugesia polychroa*			*Glossiphonia complanata*			*Helobdella stagnalis*		
	C	E	F	C	E	F	C	E	F	C	E	F
A. Increased numbers of *P. tenuis and D. polychroa*												
(a) Numbers												
Sp	46.0 (12.4)	44.9 (7.8)	0.1	1.8 (1.2)	1.7 (1.2)	0	7.3 (2.3)	7.6 (2.0)	0.1	41.9 (16.5)	41.0 (14.2)	0.9
Su	106.6 (36.9)	151.2 (49.6)	38.1**	4.2 (2.9)	8.8 (3.7)	28.9**	9.3 (1.4)	5.5 (1.5)	42.2**	161.5 (29.9)	87.9 (21.8)	29.5**
Au	112.4 (49.4)	126.5 (55.8)	0.2	6.4 (2.5)	7.5 (2.9)	4.6	11.5 (3.6)	10.5 (3.5)	1.1	35.0 (13.8)	28.3 (12.9)	0.7
(b)Size												
Sp	333.8 (83.4)	303.4 (71.0)	0.1	14.4 (9.9)	14.0 (10.1)	0.1	0.2 (0.1)	0.2 (0.1)	0.2	0.3 (0.1)	0.3 (0.1)	1.9
Su	506.5 (115.7)	657.1 (108.6)	19.2**	43.1 (13.9)	71.8 (36.3)	10.6*	0.3 (0.0)	0.1 (0.0)	62.0***	0.6 (0.2)	0.3 (0.1)	13.4*
Au	547.3 (113.2)	583.2 (119.9)	0.2	53.6 (19.1)	61.6 (21.3)	3.9	0.3 (0.1)	03 (0.1)	1.3	0.2 (0.1)	0.2 (0.1)	0.9
B. Increased numbers of *G. complanta* and *H. stagnalis*												
(a) Numbers												
Sp	42.0 (20.1)	38.5 (20.3)	0.8	3.1 (3.0)	3.3 (3.1)	0.1	20.5 (10.8)	21.7 (10.8)	0.2	42.8 (21.7)	42.5 (25.9)	0
Su	45.0 (16.8)	32.8 (15.7)	15.9*	2.2 (2.3)	1.0 (1.7)	16.0*	6.0 (3.0)	13.8 (3.4)	47.0**	55.8 (19.9)	83.1 (33.0)	17.2**
Au	76.7 (25.6)	74.0 (23.3)	0.8	4.8 (2.8)	4.8 (2.8)	0.1	14.2 (3.8)	14.0 (3.9)	0	440.3 (105.7)	426.5 (121.0)	0.7
(b) Size)												
Sp	349.4 (265.3)	270.9 (138.8)	1.9	24.8 (24.0)	26.6 (24.5)	0.1	0.3 (0.1)	0.3 (0.1)	0.1	0.2 (0.1)	0.2 (0.1)	0.1
Su	263.1 (93.7)	182.3 (89.6)	10.2*	18.6 (19.8)	8.2 (14.1)	104.7***	0.1 (0.1)	0.3 (0.1)	26.6**	0.2 (0.1)	0.3 (0.1)	13.9*
Au	415.5 (133.5)	404.4 (127.3)	0.9	30.4 (18.4)	26.8 (14.3)	0.2	0.3 (0.1)	0.3 (0.1)	0	1.7 (0.9)	1.3 (0.6)	0.6

made at each density. Variances were tested using the F_{max} test, and depending on the result, either the *t*-test or Mann-Whitney *U*-test was used to compare control and experimental data. Data for cocoon production were analysed using the *t*-test and the chi-squared test. In the chi-squared test, the expected values were the number of cocoons obtained from the control dishes.

Results

Field experiments

For each experiment, only experimental versus control data are given, because, in the ANOVA of the numerical and length/biomass data for each of the triclad/leech species, little variation occurred due to differences in site, depth, or interactions between experimentals/controls with each of site or depth. In each of the two experiments, for each of the triclad and leech species, there were no statistical differences ($P>0.05$) in the numbers and lengths (triclads) or biomasses (leeches) between the experimental and control sites in the spring sample prior to the manipulations (Table 2). The same was true for numbers and biomass for each of the main prey taxa.

When the numbers of *P. tenuis* and *D. polychroa* were increased, numbers and total length of both species were still significantly greater in the experimental sites in the summer sample, but by the autumn no significant differences were obtained (Table 2). Conversely, within enclosures where triclad densities had been increased, numbers and biomass of both *G. complanata* and *H. stagnalis* were significantly lower in the experimental sites in the summer. However, no significant differences were found in the autumn samples.

When *G. complanata* and *H. stagnalis* numbers were elevated, statistically higher numbers and biomasses of each species were recorded in the experimental sites in the summer, but by autumn no differences were found (Table 2). In contrast, for each of the triclad species, numbers and total length were significantly lower in the experimental sites in the summer. By autumn, no significant differences were obtained.

Laboratory experiments

Regression analysis showed that for both predators, fed on either live or crushed *Asellus*, the negative relationship between growth and density, in each of the four regimes, was highly significant ($P<0.001$) (Table 3).

Table 3 Regression values and their significance levels for changes in mean dry weight for *Polycelis tenuis* and *Helobdella stagnalis*, in different experimental regimes, at a range of densities, with crushed or live *Asellus* (*Control* monospecific cultures, *Equal* equal numbers of *P. tenuis* and *H. stagnalis*, *More P.t.* more *P. tenuis* than *H. stagnalis*, *Less P.t.* less *P. tenuis* than *H. stagnalis*, *More H.s.* more *H. stagnalis* than *P. tenuis*, *Less H.s.* less *H. stagnalis* than *P. tenuis*)

Regime	Slope	*t* value	Probability level (*P*)
a. *P. tenuis* fed on crushed *Asellus*			
Control	−0.521±0.047	10.99	<0.001
Equal	−0.427±0.038	11.11	<0.001
More *P.t.*	−0.712±0.069	10.26	<0.001
Less *P.t.*	−0.736±0.042	17.62	<0.001
b. *P. tenuis* fed on live *Asellus*			
Control	−0.303±0.029	11.24	<0.001
Equal	−0.436±0.041	10.68	<0.001
More *P.t.*	−0.571±0.037	15.50	<0.001
Less *P.t.*	−0.903±0.095	9.49	<0.001
c. *H. stagnalis* fed on crushed *Asellus*			
Control	−0.060±0.003	17.73	<0.001
Equal	−0.071±0.005	12.55	<0.001
More *H.s.*	−0.080±0.005	23.74	<0.001
Less *H.s.*	−0.092±0.011	8.22	<0.001
d. *H. stagnalis* fed on live *Asellus*			
Control	−0.058±0.003	18.17	<0.001
Equal	−0.039±0.003	11.41	<0.001
More *H.s.*	−0.056±0.005	11.56	<0.001
Les *H.s.*	−0.043±0.011	4.01	<0.001

Table 4 *t*-test values and significance levels for differences between regression slopes for *Polycelis tenuis* cultures fed on crushed or live *Asellus* (*Control* monospecific cultures, *Equal* equal numbers of *Polycelis tenuis* and *Helobdella stagnalis*, *More* more *P. tenuis* than *H. stagnalis*, *Less* less *P. tenuis* than *H. stagnalis*, *C* crushed *Asellus*, *L* live *Asellus*)

	t value	Probability level (*P*)
Crushed *Asellus*		
Control C versus equal C	1.56	NS
Control C versus more C	2.40	<0.05
Control C versus less C	3.41	<0.05
Live *Asellus*		
Control L versus equal L	2.25	<0.05
Control L versus more L	5.28	<0.001
Control L versus less L	5.84	<0.001
Crushed versus live *Asellus*		
Control C versus control L	3.59	<0.001
Equal C versus equal L	0.16	NS
More C versus more L	1.80	NS
Less C versus less L	1.61	NS

Polycelis tenuis

When *P. tenuis* was fed on crushed *Asellus*, the slope of the regression line in the equal numbers of predators treatment was not significantly different from that of the monospecific control (Table 4). When in the majority or minority, slopes were significantly more negative than the control slope. Fed on live *Asellus*, the slopes of the regression lines of all the mixed species treatments were significantly more negative than the monospecific controls (Table 4). A significant difference between the slopes of the regression lines for the two monospecific controls of *P. tenuis*, fed on either crushed or live *Asellus*, was obtained, with the slope of the line relating to feeding on crushed prey being significantly more negative (Table 3). There were no other significant differ-

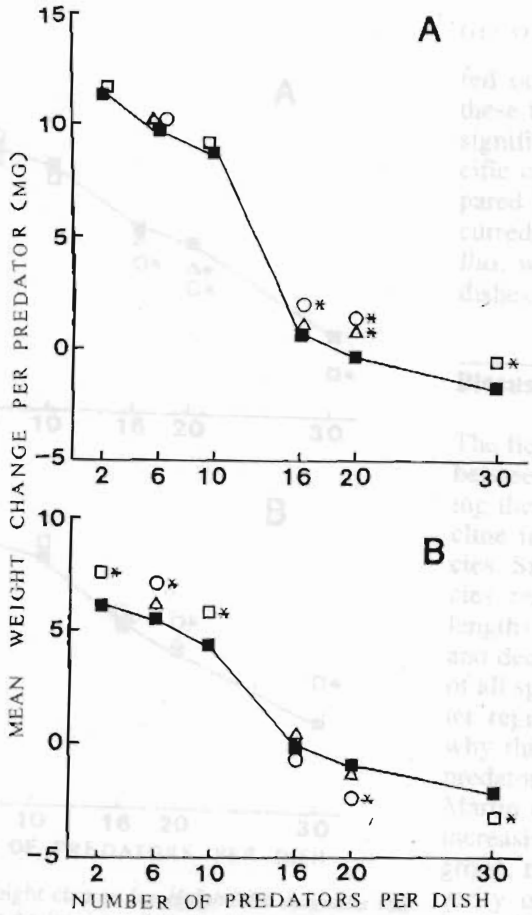

Fig. 1A,B Mean dry weight change for *Polycelis tenuis* fed on A crushed and B live *Asellus aquaticus* at a range of densities of both monospecific controls and two species combinations (■ monospecific control, □ equal numbers of *Polycelis tenuis* and *Helobdella stagnalis*, △ more *P. tenuis* than *H. stagnalis*, ○ less *P. tenuis* than *H. stagnalis*; * statistically significant difference from control)

ences between slopes for regimes of the same relative density for the two food conditions (Table 4).

At densities of 20 and 30 predators when fed on crushed *Asellus*, *P. tenuis* showed significantly higher growth in mixed species cultures than in the monospecific controls (Fig. 1A). At a density of 16 predators, growth was also significantly higher when *P. tenuis* was in the minority to *H. stagnalis*. Growth of *P. tenuis* was not affected by the presence of *H. stagnalis* when at equal densities or in the majority at densities of 16 and fewer, or when in the minority at 10 or fewer predators.

When fed on live *Asellus* (Fig. 1B), and when present in equal numbers with *H. stagnalis*, *P. tenuis* showed significantly higher growth than in the monospecific controls at densities of 2 and 10 predators. A significantly higher growth rate was also found when *P. tenuis* was in the minority at a density of 6. In contrast, with equal numbers of predators at a density of 30 and in the minority at a density of 20, *P. tenuis* showed significantly lower growth than in monospecific controls. The growth of *P. tenuis* at all densities when in the majority and at a density of 16 when in the minority was not significantly different from monospecific controls.

Table 5 *t*-test values and significance levels for differences between regression slopes for *Helobdella stagnalis* cultures fed on crushed or live *Asellus* (*Control* monospecific cultures, *Equal* equal numbers of *Polycelis tenuis* and *Helobdella stagnalis*, *More* more *P. tenuis* than *H. stagnalis*, *Less* less *P. tenuis* than *H. stagnalis*, *C* crushed *Asellus*, *L* live *Asellus*)

	t values	Probability level (*P*)
Crushed *Asellus*		
Control C versus equal C	1.64	NS
Control C versus more C	2.36	<0.05
Control C versus less C	2.81	<0.001
Live *Asellus*		
Control L versus equal L	4.48	<0.001
Control L versus more L	0.34	NS
Control L versus less L	1.32	NS
Crushed versus live *Asellus*		
Control C versus control L	0.47	NS
Equal C versus equal L	4.77	<0.001
More C versus more L	2.40	<0.05
Less C versus less L	3.15	<0.001

H. stagnalis

When *H. stagnalis* was fed on crushed *Asellus*, there was no significant difference in the slopes of the regression lines for the equal number of predators treatment and the monospecific control (Table 5). The slopes of the treatments with more and less *H. stagnalis* than *P. tenuis* were both significantly more negative than the control. When *H. stagnalis* was fed on live *Asellus*, the slope of the regression line for the equal numbers of predators treatment was significantly less negative than that for the monospecific control. The slopes of the regression lines for the treatments with more or less leeches than triclads were not significantly different to the control slope (Table 5). The slopes of the controls fed on crushed or live *Asellus* did not differ significantly. Significant differences between the slopes for each of the regimes of the same relative density, for the two food conditions, were obtained. The slope for predators fed on crushed prey was always more negative than for those fed on live prey.

When fed on crushed *Asellus*, *H. stagnalis* showed significantly lower growth than the monospecific controls at the highest densities of 20 and 30 for all three regimes where *P. tenuis* was present (Fig. 2A). Also, significantly lower growth was recorded at a density of 16 predators when *H. stagnalis* was in the minority. At all other densities, the presence of *P. tenuis* did not significantly affect the growth of *H. stagnalis* compared to the monospecific controls.

When fed on live *Asellus* (Fig. 2B), growth was significantly higher than the monospecific controls only at a density of 30 when the predators were in equal numbers

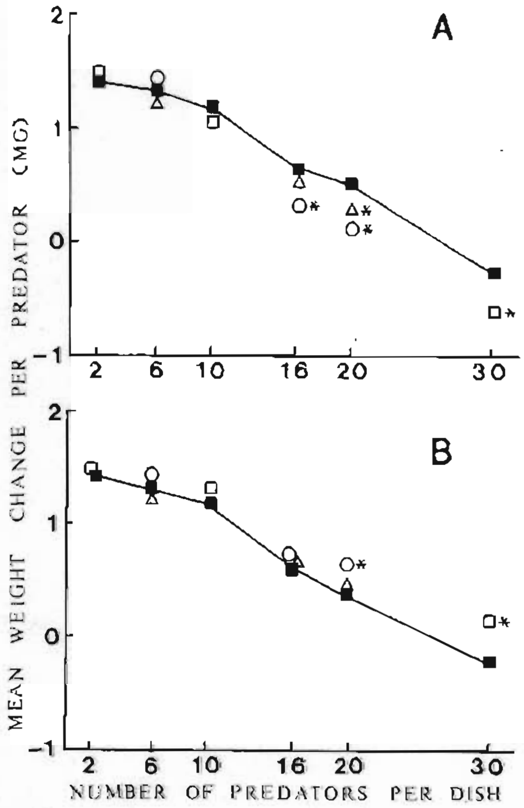

Fig. 2A,B Mean dry weight change for *Helobdella stagnalis* fed on **A** crushed and **B** live *Asellus aquaticus* at a range of densities of both monospecific controls and two species combinations (■ monospecific control, □ equal numbers of *Helobdella stagnalis* and *Polycelis tenuis*, △ more *H. stagnalis* than *P. tenuis*, ○ less *H. stagnalis* than *P. tenuis*; * statistically significant difference from control)

and at a density of 20 when *H. stagnalis* was in the minority. The presence of *P. tenuis* did not significantly affect the growth of *H. stagnalis* compared to the monospecific controls at the other densities.

Mortality

Few deaths of predators were recorded during the experiments, and these occurred only at the highest density of 30. In monospecific controls, more *P. tenuis* died when fed on live than crushed prey, 17.5% compared to 8.3%, whereas similar proportions of *H. stagnalis* died, 9.2% and 8.3% on crushed and live *Asellus* respectively. In the mixed populations, 12.5% of *P. tenuis* died when fed on live prey but none on crushed prey, and 13.3% of *H. stagnalis* died when fed on crushed prey but none on live prey.

Cocoon production by *P. tenuis*

Cocoon production was lowest at the two highest densities of 20 and 30 predators. In all situations, the triclads fed on crushed prey had a higher cocoon output than these fed on live prey. However, the difference was only significant at total densities of 6 and 16 in the monospecific controls ($P<0.05$). When the treatments were compared to the controls, the only significant difference occurred at the highest density when fed on crushed *Asellus*, when more cocoons were laid in the mixed species dishes ($P<0.001$).

Discussion

The field experiments demonstrated negative interactions between the triclads and glossiphoniid leeches. Increasing the numbers of both triclad species resulted in a decline in the numbers and biomasses of both leech species. Similarly, elevating the numbers of both leech species resulted in a decrease in the numbers and total lengths of both triclad species. However, the increases and decreases were of a temporary nature, with numbers of all species returning to control levels in the autumn after reproduction had ceased. The question arises as to why this should happen. Bearing in mind that the four predatory species are food limited (Reynoldson 1966; Martin et al. 1994a), it seem reasonable to assume that increasing the size of the established populations of one group, triclads or leeches, would result in raising the severity of both intra- and interspecific competition for food, the relative strengths of which are never easy to assess. Readjustment of numbers could have been achieved through changes in fecundity and/or mortality of adults and/or juveniles. There is evidence that triclad populations respond to alterations in food level through changes in fecundity (Reynoldson 1966, 1983), whereas leeches, at least in productive lakes, respond through changes in juvenile mortality (Spelling and Young 1987; Martin et al. 1994a).

The severity of any competition will depend on the availability of different prey types and the quantity of each prey type. At the start of the experiments, these factors were similar in experimental and control sites. Additionally, however, the "condition" of the prey organisms may be important. Triclads, with the exception of the Dendrocoelidae, which have a pseudo-sucker, are inept (Reynoldson and Young 1963) and glossiphoniid leeches, which have well-developed suckers, are efficient (Martin et al. 1994c) at capturing live, intact prey. Both groups feed on damaged, incapacitated prey which are leaching body fluids, but triclads are more successful due to their superior ability at detecting such food using their more sophisticated chemosensory system (Seaby et al. 1995; Young et al. 1995). Thus, it is conceivable that co-existence of these triclad and glossiphoniid leech species may be assisted by the partitioning of the food resource on a damaged or live basis, and the present laboratory experiments investigated this possibility.

Polycelis tenuis in the monospecific controls gained significantly more weight when fed on crushed than live *Asellus*, reflecting the predator's inability to catch and feed on live prey. In contrast, there was no significant difference in the growth of *H. stagnalis* in monospecific controls fed on either crushed or live *Asellus*, indicating that the ability of the predator to utilize the prey is unaffected by its condition. Therefore, any effects found in the mixed species cultures would be due to the presence of *P. tenuis*. In the three mixed-species regimes (equal numbers, majority, minority) fed on crushed *Asellus*, significantly increased and decreased growth of *P. tenuis* and *H. stagnalis*, respectively, in comparison to monospecific controls, occurred at high densities, indicating that *P. tenuis* was the superior competitor. When fed on live *Asellus*, the growth of *P. tenuis* was significantly higher compared to monospecific controls at low densities and significantly lower at high densities, when *H. stagnalis* was in the majority or in equal numbers. This may have been the result of *H. stagnalis* capturing and damaging *Asellus*, thus allowing prey to be utilized by the triclad when the intensity of competition is low. When fed on live *Asellus*, the presence of *P. tenuis* at high densities resulted in greater growth of *H. stagnalis*, than when it was on its own; this would reflect reduced interspecific competition, at a particular density, when *P. tenuis* was present.

Mortality of predators was recorded only at the highest density of 30 predators. For *P. tenuis* in monospecific controls, it was lowest when fed on crushed *Asellus* and highest on live *Asellus*; an intermediate value was obtained in the mixed species cultures of equal numbers, indicating the benefit to the triclad of the presence of the leech in capturing live *Asellus*. Mortality of *H. stagnalis* was similar in controls fed either crushed of live *Asellus*, and was highest in the cultures where equal numbers of the leech and triclad were present, reflecting the superior ability of the latter to exploit damaged prey. There was a trend for *P. tenuis* to produce more cocoons when fed on crushed than live *Asellus*. When in competition with *H. stagnalis* at higher densities and fed on crushed prey, the triclad produced more cocoons than it did on its own at comparable densities, indicating a superior ability to utilize damaged prey.

Thus, the laboratory experiments support the hypothesis that co-existence is achieved through the partitioning of food on a damaged or live basis. The ratio of damaged to live prey on the stony shore of a lake will be influenced both by abiotic and biotic factors. The ratio will vary from time to time, but over a long period of time, given no exceptional circumstances, it will be fairly stable. The sizes of the triclad and leech populations will depend on the absolute and relative abundance of the live and damaged food resources.

Interestingly, there was some evidence from the laboratory experiments that *P. tenuis* benefitted from the presence of *H. stagnalis* which captured live prey subsequently accessible to and utilized by the triclad. However, this occurred at low densities only; presumably as density of the predators increases, intra- and interspecific competition for food will become more severe. In British lakes, competition for food, at least during the reproductive phase, is intense, and so the presence of *H. stagnalis* would have little beneficial effect on the *P. tenuis* population.

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