R.M.H. Seaby · A.J. Martin · J.O. Young

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

Received: 8 October 1995 / Accepted: 29 January 1996

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 or 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 triclad 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. complanata 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).
Given the considerable overlap in diet between triclad 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 aquatilus* (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 icon-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 hitching from cocoons, whereas those of the glossiphonids are carried initially on the underside of the parents. The leech species have a predominantly annual life cycle with adults dying soon after breeding (Young and Ironmonger 1982a; Spelling and Young 1987), whilst the triclads live for more than 1 year, though some individuals shrink and die in the post-reproductive period (Reynoldson 1966). Additionally, in the spring sample, all macro-invertebrates 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 experiments.

**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 dish was quartered 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

<table>
<thead>
<tr>
<th>Monospecific controls</th>
<th>Two-species mixtures</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>P. tenuis</strong></td>
<td><strong>H. stagnalis</strong></td>
</tr>
<tr>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>6</td>
<td>6</td>
</tr>
<tr>
<td>10</td>
<td>10</td>
</tr>
<tr>
<td>16</td>
<td>16</td>
</tr>
<tr>
<td>20</td>
<td>20</td>
</tr>
<tr>
<td>30</td>
<td>30</td>
</tr>
</tbody>
</table>

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 on the stony lake from *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 x 21.5 x 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 macro-invertebrates 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.