

## On the Defence Strategy of *Physa fontinalis* (L.), a Freshwater Pulmonate Snail

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**Summary.** *Physa fontinalis* (L.) gives a characteristic, chemically mediated escape response when stimulated by the majority of British leeches and flatworms. The snail responds rapidly and consistently to contact with all the molluskivorous leeches but also to three species which may be considered harmless. However, no response was given to *Erpobdella octoculata*, the most abundant and widespread of the harmless leeches. The flatworms generally evoked less strong reactions. The adaptive significance of the pattern of responsiveness is discussed. A weaker shell-shaking response is elicited in conspecifics and it is shown that this 'antisocial' behaviour leads to a relatively spaced-out dispersion pattern. A possible adaptive advantage is the reduction of risk of detection by shell-crushing fish predators, to which the snails are otherwise extremely vulnerable.

### Introduction

In contrast to marine gastropods, freshwater snails are generally thin-shelled and lack the strong sculpturing, occluded apertures and low spires by which marine forms resist the attacks of shell breaking and shell entering predators (Vermeij and Covich, 1978; Palmer, 1979). Exceptional forms are found among the snail faunas of ancient lakes and river systems and it is thought their occurrence is associated with the evolution of specialised molluskivorous animals (Vermeij and Covich, 1978). Highly specific avoidance and escape responses elicited by predators are also common among marine molluscs (Clark, 1958; Feder and Christensen, 1966; Mackie, 1970; Phillips, 1976). Such chemically mediated behavioural responses are virtually absent in the freshwater fauna, a notable exception being the pulmonate *Physa fontinalis* (L.), together with some of its congeners. Degner (1921) described how *P. fontinalis* reacted with vigorous shell shaking and leaping movements when the molluskivorous leeches *Glossiphonia complanata* (L.) and *G. heteroclita* (L.), or their mucus, came into contact with the snail's sensitive finger-like extensions of the mantle which stretch over the outer surface of its ovoid, truncate shell. Wrede (1927) and Frieswijk (1957) made further observations and noted that leeches in other genera as well as deionized extracts of leech tissue and even strong solutions of certain salts could evoke the response.

The aim of the present work was to quantify the responses elicited in the snail by all the species of the British freshwater leech fauna (Hirudinea) (except *Haementeria costata*, recently discovered in England [Elliott et al., 1979]), and nine species of flatworms (Tricladida), in order to test the following three hypotheses; Firstly, that a taxonomic pattern might exist with species eliciting similar strengths of response when compared with confamilials but dissimilar strengths of response when compared with species of different families; Secondly, that a trophic pattern might be discernible with leech species which are natural enemies of freshwater snails eliciting strong responses and non-snail predators eliciting weak or no responses; and thirdly, that the pattern might be influenced by the relative abundance of the various predators and thus reflect the frequency of contacts between predator and prey.

We also studied the social behaviour of the snails since it had been noted that they themselves sometimes elicited weak shell-shaking responses in conspecifics. The results of this aspect of the study are discussed in terms of the role of such 'antisocial' behaviour in the determination of dispersion pattern, and the possible adaptive significance of 'spacing out' in this species.

### Methods

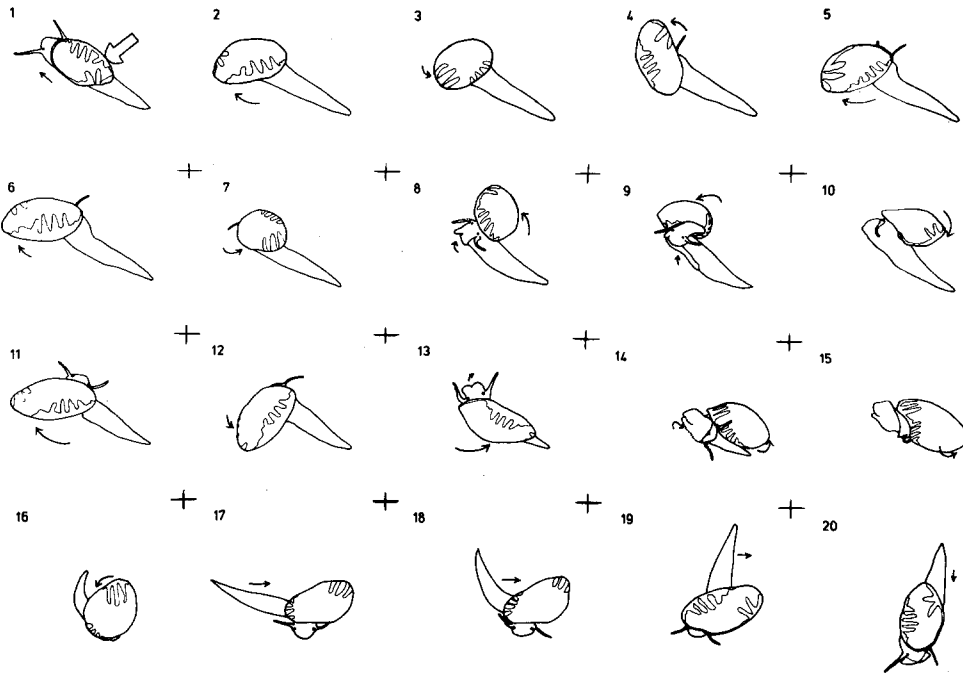
#### Escape Response

Snails with a maximum shell dimension of 7–11 mm were collected in May 1975 from a small weeded stream which enters the River Cherwell at University Parks, Oxford. Leeches and flatworms were obtained from several British and Irish locations. Snails were used within 36 h of capture having been stored overnight at room temperature in aerated aquaria. All experiments were conducted at approximately 20° C. Predator escape behaviour was studied using single snails crawling across the base of 9 cm diameter petrie dishes which contained an 0.7 cm depth of stream water. The snails were given 30 min to settle and then reactions were observed when a small portion of leech tissue, consisting of the anterior sucker and front segments, was placed in contact with the mantle digitations. Entire animals were used in the case of experiments involving flatworms.

A typical escape response was characterized by means of time-lapse cinematography filming at a rate of 4 frames per second and is illustrated in Fig. 1. Thirty replicates were performed for each leech or flatworm predator and snails were not used in more than one replicate. The response of the snail was categorized as either strong or weak. Strong reactions involved vigorous shaking

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**Fig. 1.** Time-lapse analysis of a strong escape response of *Physa fontinalis*. Note the sensitive mantle digitations over the shell. The broad arrow in frame 1 indicates where leech stimulation was applied. The position of the body and shell is shown at .25 s intervals, the 20 frames representing a 5 s record. The direction of movement of the shell is indicated by arrows. Vigorous shell shaking commenced within .25 s of stimulation. Detachment of the foot from the substrate began in frame 5 and was complete by frame 15. Frames 16–20 represent the free floating snail propelled by its own momentum over a distance of approximately 3 cm before regaining the substrate and crawling away. (The snail's shell length was 0.8 cm).

of the shell and body followed by detachment of the foot from the substratum so that the body's momentum carried it several centimetres from the stimulus source (see Fig. 1). Weak reactions involved only the shell-shaking behaviour. Tests were regarded as giving a negative result if no response was noted within 30 sec.

#### *Sociability Index and Dispersion Strategy*

During the course of investigations of the behavioural ecology of *Biomphalaria glabrata* (Say), a South American freshwater pulmonate, a model was developed which makes it possible to compare the 'sociability' of different snail species under uniform conditions (Simpson et al., 1973). The sociability index is simply defined as the average fraction of animals remaining in a group after a unit of time (one minute in the present investigation). Latency of collision,  $L$ , is the average time that animals remain in contact after encountering each other. The sociability index,  $S$ , is defined by:

$$S = e^{-(0.69315)/L}$$

For this aspect of the study, snails were placed 15 at a time in a clear perspex container,  $10 \times 10 \times 3$  cm, containing water 1 cm deep. Snails were tested one hour after capture having been allowed to become acclimatized in the experimental chamber for that period. The durations of 50 encounters were recorded with a stopwatch to obtain the average latency of collision and thus the sociability index. An encounter was taken to be any contact between snails other than just shell to shell contacts. Encounters

occurring in contact with the sides of the perspex container were ignored in this investigation. On the rare occasions when encounters led to copulation the contact was timed until sexual activity became evident with eversion of the penis.

It can be postulated that as snails enter the breeding season, which in England usually begins in April (Duncan, 1958), their aversion to intraspecific contact will lessen. This hypothesis was tested by obtaining values for sociability index, and proportion of snails exhibiting intraspecific shell shaking, each week for the period from 8 March to 26 April 1975.

Thomas (1973) has reported that snails of the species *Biomphalaria glabrata* when placed uniformly in a homogeneous environment formed aggregates such that their dispersion pattern quickly became significantly different from random. The relationship between 'sociability' and dispersion pattern for *Physa fontinalis* was investigated by placing snails in a perspex box containing 1 cm of water and marked with a grid of 3.5 cm squares. Snails were placed initially one per square and thereafter at five minute intervals for 30 min the numbers of snails in each square were recorded. Dispersion indices ( $\chi^2$ ) were calculated from the data to determine whether the patterns were significantly different from random (i.e. clumped).

$$\chi^2 = S^2(N-1)/\bar{X}$$

where  $S^2$  = variance

$N$  = number of squares

$\bar{X}$  = mean number of snails per square

Similar experiments have been performed on two other species of snail, *Planorbis planorbis* (L.), a common British pulmonate,

and the South American *Biomphalaria glabrata*. All were similar in size. Their values for sociability and dispersion indeces can be compared with those of *Physa fontinalis*.

Note that the dispersion index,  $\chi^2$ , can only validly be used to compare dispersion patterns when mean densities and size of sampling units are not significantly different (Elliott, 1977). These conditions were met here.

## Results

### Escape Response

The results of the escape response experiments involving leeches are given in Fig. 2. There is considerable variation in the ability of the leech species to evoke a strong response such as that shown in Fig. 1. Five of the fifteen species invariably stimulated a full response, one never did and the rest were intermediate. When the results are combined for families (Table 1) it is clear that the Glossiphoniidae ranked first. The proportion of strong responses was significantly higher than for any other family ( $2 \times 2$  contingency table  $\chi^2$  tests,  $P \ll 0.001$  in each case). The Erpobdellidae ranked second, evoking significantly more responses than the Hirudidae ( $P < 0.05$ ) but not the Piscicolidae ( $P < 0.1$ ). The Piscicolidae and Hirudidae were not significantly different in their ability to evoke responses. Within the leech families there was marked variation in the results. The flatworms demonstrated less variation in their ability to evoke strong responses (Fig. 3). Species in the genera *Dugesia* and *Dendrocoelum* evoked the largest number of reactions. As a whole, flatworms evoked significantly fewer responses than glossiphoniid or erpobdellid leeches (Contingency table test,  $P < 0.001$  in both cases) but a similar number when compared with piscicolid and hirudid leeches.

### Sociability and dispersion indices

*Physa fontinalis* has a very low sociability index (varying between 0.0014 and 0.1). Individuals, when they encountered one

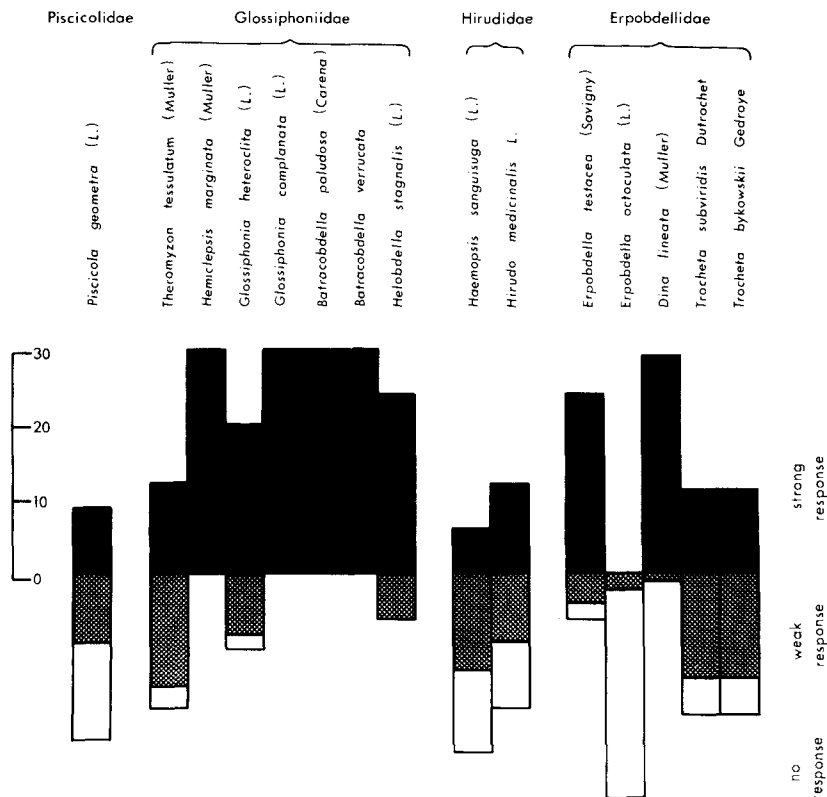
**Table 1.** Proportion of individual leech applications which evoked a strong escape response in *Physa fontinalis* when results are combined for the four leech families

Family	No. of species	Proportion of strong responses
Glossiphoniidae	7	176/210; 84%
Erpobdellidae	5	75/150; 50%
Piscicolidae	1	9/ 30; 30%
Hirudidae	2	18/ 60; 30%

another, were observed to actively repulse each other usually moving apart as soon as contact was made. In approximately 25% of recorded encounters one, or both, snails exhibited a shell shaking aversion reaction which consisted of swinging the shell until the other snail was dislodged or contact was broken. The mantle fringes were the sensitive area as in the case of the predator escape response but the reaction was much weaker and detachment of the foot from the substratum never occurred.

Figure 4 shows how dispersion index changed with time for the three species of snail tested in simple laboratory arenas. There is a clear relationship between sociability index and degree of clumping. *Physa fontinalis* never attained a dispersion pattern which was significantly different from random. *Planorbis planorbis* with the higher sociability index of 0.29 attained a significantly clumped distribution within 5 min and maintained it throughout the experiment. The South American *Biomphalaria glabrata*, noted for its tendency to clump in field and laboratory (Jobin, 1970; Simpson, Thomas and Townsend, 1973), had a very high sociability index (0.60–0.75) and attained a distribution very significantly different from random in the experiment.

The sociability of *Physa fontinalis* varied seasonally as can be seen from Fig. 5, and there appears to be an inverse relationship between sociability index and the proportion of snails showing



**Fig. 2.** Proportion of stimulations which resulted in strong, weak or no escape responses for each of 15 species of leech in 4 families

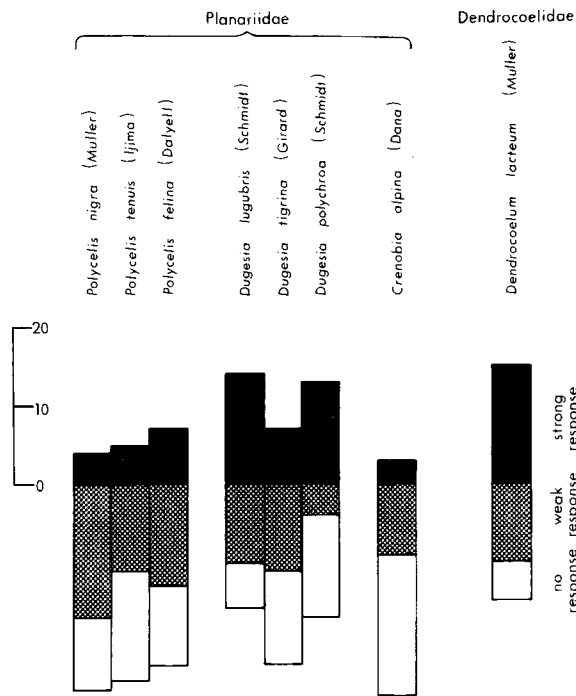


Fig. 3. Proportion of stimulations which resulted in strong, weak or no escape responses for each of 8 species of flatworm in 4 genera in 2 families

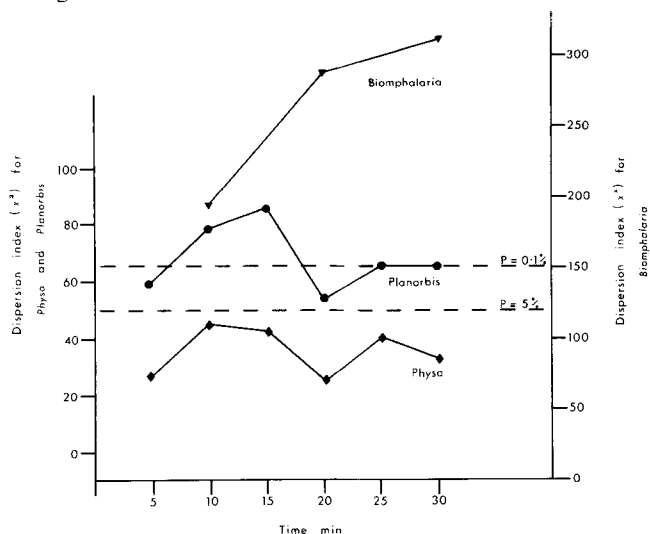


Fig. 4. Dispersion index ( $\chi^2$ ) against time in a uniform laboratory arena for 3 species of freshwater pulmonate snail. Experiments involving *Physa fontinalis* and *Planorbis planorbis* were performed with 36 snails in  $21 \times 21$  cm arenas each containing 36 grid squares. The experiment involving *Biomphalaria glabrata* was performed with 100 snails in a  $35 \times 35$  cm arena containing 100 grid squares. The  $\chi^2$  values associated with rejection of the null hypothesis of random distribution at the 5% and 0.1% level are indicated by dashed lines

intraspecific aversion behaviour. Significantly fewer encounters led to shell shaking in April than March ( $2 \times 2$  contingency table  $\chi^2$ ,  $P < 0.02$ ). One or two copulating pairs were witnessed in the field on each of 13, 21 and 26 April. Sociability increases somewhat with the onset of breeding and the aversion behaviour is clearly moderated to facilitate mating.

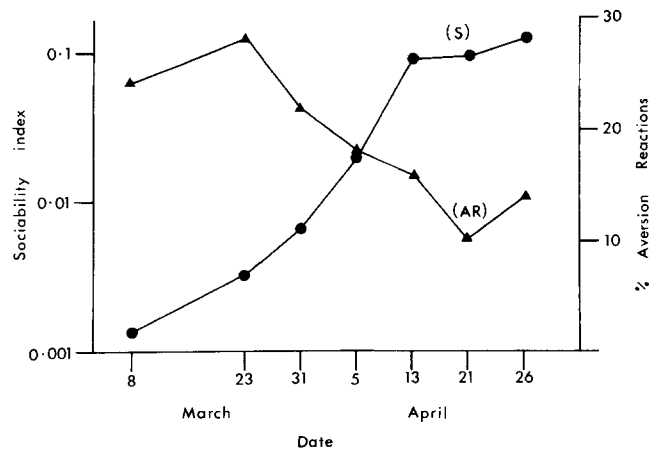


Fig. 5. Variation in sociability index (log scale) and percentage of encounters eliciting intraspecific aversion reactions in *Physa fontinalis* during March and April, 1975

### Discussion

*Physa* is known to be preyed upon by a variety of generalist predators; both invertebrates, such as flatworms, dytiscid beetles and their larvae, and vertebrates, principally fish (Boycott, 1936; Carothers and Allison, 1968; Carlander, 1969). Specialist molluski-vorous animals are rare in freshwater. In Britain, these consist of Sciomyzid (Diptera) larvae, the unusual larvae of *Hydrophilus piceus* (Coleoptera) and principally certain species of leech.

*Glossiphonia complanata* is generally regarded as a major predator of snails and, though less well studied, *Batracobdella paludosa* and *B. verrucata* are assumed to feed mainly on mollusks. *Glossiphonia heteroclita* behaves as a predator or parasite of snails and is known to overwinter in the mantle cavity (Gruffydd, 1965). Recent serological investigations (Davies et al., 1979) have shown that though the bulk of the diet of *Helobdella stagnalis* consisted of oligochaetes and chironomid larvae they also fed to a significant extent on snails. In contrast, none of the other leeches can be considered harmful to *Physa*. *Haemopsis sanguisuga* and the erpobdellids are macrophagous predators which feed on a variety of invertebrates but not normally on snails (Elliott and Mann, 1979; Klemm, 1965). *Hirudo medicinalis*, the well known medicinal leech, is a blood sucking parasite as are *Theromyzon tessulatum* on birds and *Hemiclepsis marginata* and *Piscicola geometra* on fish.

*Physa* reacted rapidly and consistently to contact with *G. complanata*, *B. paludosa* and *B. verrucata*. Similarly, a large proportion reacted to *H. stagnalis* and *G. heteroclita*. Thus, the escape response was given to the potential leech predators, all of which are in the family Glossiphoniidae. However, comparable responses were observed in the case of the glossiphoniid *H. marginata* and the erpobdellids *E. testacea* and *D. lineata*, species which are harmless to *Physa*.

Three species of leech can be considered as widespread and abundant and therefore are likely to have been frequently encountered in evolutionary time by the widespread *Physa fontinalis* (Boycott, 1936). These are *G. complanata*, *H. stagnalis* and *E. octoculata* (Mann, 1955, 1964; McCarthy, 1975; Elliott and Mann, 1979). In view of their feeding preference it is clear that *H. complanata* must have posed the biggest threat to *Physa* and constituted a significant selection pressure. It is remarkable that *E. octoculata* should have been the only species for which no escape response was recorded. Perhaps *Physa* can specifically 'recognise' this com-

mon but harmless species thereby minimizing energy and time wastage due to unnecessary escape behaviour. Another interesting result is the fact that *G. heteroclita* evoked significantly fewer strong responses than its congener *G. complanata* ( $2 \times 2$  contingency table  $\chi^2$ ,  $P < 0.01$ ). Some degree of masking of its chemical identity would be of adaptive value to *G. heteroclita* which often adopts a parasitic mode of feeding and a tendency to spend long periods in the mantle cavities of snails.

The level of responsiveness to flatworms was in general lower than to leeches, but all species evoked some response. All the common lake dwelling triclads studied have been found to include some snails in their diet (Reynoldson and Davies, 1970; Reynoldson and Pearce, 1979a, b) so the escape reactions are probably adaptive. The species whose diet includes most snails is *Dugesia polychroa*, and from what little is known of it, the ecology of *D. lugubris* may be similar.

The escape behaviour of *Physa fontinalis* almost invariably precludes capture by leeches in the laboratory. In the case of snails moving across a substratum at depth the buoyancy provided by air in the pulmonary cavity often leads to rapid surfacing after foot detachment. For snails moving near the surface the response may be accompanied by expulsion of respiratory air and rapid sinking. Even in cases where interactions take place in 2 dimensions, escape is effected.

However, the response is clearly ineffective against another major group of predators, the shell-crushing fish. *Physa*, with its thin shell, is particularly vulnerable to fish predation and the only possibility for minimizing risk would seem to be to reduce the likelihood of being encountered. A possible adaptive advantage of the intraspecific aversion reaction and consequent spacing out of this inconspicuously marked snail is that it will reduce the likelihood of detection (Tinbergen et al., 1967; Edmunds, 1974).

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## References

- Boycott, A.E.: The habitats of freshwater Mollusca in Britain. *J. Anim. Ecol.* **5**, 116–186 (1936)
- Carlander, K.D.: Handbook of freshwater fishery biology. Vol. I. Ames: Iowa State University Press (1969)
- Carothers, J.L., Allison, R.: Control of snails by the redear (shell cracker) sunfish. Proc. World Symp. Warmwater Pond Fish Cult. Rome. FAO Fish Report **44**, 396–406 (1968)
- Clark, W.C.: Escape responses of herbivorous gastropods when stimulated by carnivorous gastropods. *Nature* **181**, 137–138 (1958)
- Davies, R.W., Wrona, F.J., Linton, L.: A serological study of prey selection by *Helobdella stagnalis* (Hirudinoidea). *J. Anim. Ecol.* **48**, 181–194 (1979)
- Degner, E.: Ueber einen Abwehrreflex bei *Physa fontinalis* L. *Bacteria* **21**, 38–44 (1921)
- Duncan, C.J.: The life-cycle and ecology of the freshwater snail *Physa fontinalis* (L.). *J. Anim. Ecol.* **28**, 97–118 (1958)
- Edmunds, M.: Defence in animals. Harlow: Longman (1974)
- Elliott, J.M.: Some methods for the statistical analysis of samples of benthic invertebrates. Freshwater Biological Association Scientific Publication No. 25 (1977)
- Elliott, J.M., Mann, K.H.: A key to the British freshwater leeches with notes on their life-cycles and ecology. *Scient. Publ. Freshwat. biol. Ass. No.* **40**, 1–72 (1979)
- Elliott, J.M., Mugridge, R.E.R., Stallybrass, H.G.: *Haementeria costata* (Fr. Muller) (Hirudinea: Glossiphoniidae), a leech new to Britain. *Freshwat. Biol.* **9**, 461–465 (1979)
- Feder, H.M., Christensen, A.M.: Aspects of asteroid biology. In: *Physiology of echinodermata* (R.A. Booloottian, ed.), pp. 87–127. New York: Wiley 1966
- Frieswijk, J.J.: A leech avoidance reaction of *Physa fontinalis* (L.) and *Physa acuta* Drap. *Bacteria* **21**, 38–45 (1957)
- Gruffydd, W.D.: Notes on a population of the leech *Glossiphonia heteroclita*, infesting *Lymnaea pereger*. *Ann. blag. nat. Hist.* **8**, 151–154 (1965)
- Jobin, W.R.: Population dynamics of aquatic snails in three farm ponds of Puerto Rico. *Am. J. trop. Med. Hyg.*, **19**, 1038–1047 (1970)
- Klemm, D.J.: Studies on the feeding relations of leeches (Annelida, Hirudinea) as natural associates of Mollusks. *Sterkiana* **58**, 1–50 (1975)
- Mackie, A.M.: Avoidance reactions of marine invertebrates to either steroid glycosides of starfish or synthetic surface-active agents. *J. exp. mar. Biol. Ecol.* **5**, 63–69 (1970)
- Mann, K.H.: The ecology of British leeches. *J. Anim. Ecol.* **24**, 98–119 (1955)
- Mann, K.H.: A key to the British freshwater leeches with notes on their ecology (2nd edition). *Scient. Publ. Freshwat. biol. Ass. No.* **14**, 1–50 (1964)
- McCarthy, T.K.: Observations on the distribution of the freshwater leeches of Ireland. *Proc. R. Ir. Acad.* **75B**, 401–451 (1975)
- Palmer, A.R.: Fish predation and the evolution of gastropod shell structure: experimental and geographic evidence. *Evolution* **33**, 697–713 (1979)
- Phillips, D.W.: The effect of a species-specific avoidance response to predatory starfish on the intertidal distribution of two gastropods. *Oecologia (Berl.)* **23**, 83–94 (1976)
- Reynoldson, T.B., Davies, R.W.: Food niche and coexistence in lake-dwelling triclads. *J. Anim. Ecol.* **39**, 599–617 (1970)
- Reynoldson, T.B., Pearce, B.: Predation on snails by three species of triclad and its bearing on the distribution of *Planaria torva* in Britain. *J. Zool.* **189**, 459–484 (1979a)
- Reynoldson, T.B., Pearce, B.: Feeding on gastropods by lake-dwelling *Polycelis* in the absence and presence of *Dugesia polychroa* (Turbellaria, Tricladida). *Freshw. Biol.* **9**, 357–367 (1979b)
- Simpson, A.W., Thomas, J.D., Townsend, C.R.: Social behaviour in the freshwater pulmonate snail *Biomphalaria glabrata* (Say). *Behav. Biol.* **9**, 731–740 (1973)
- Thomas, J.D.: Schistosomiasis and the control of molluscan hosts of human schistosomes with particular reference to self-regulating mechanisms. In: *Advances in Parasitology* (B. Dawes, ed.) **11**, 307–394, London and New York: Academic Press 1973
- Tinbergen, N., Impekoven, M., Franck, D.: An experiment on spacing out as a defence against predation. *Behaviour* **28**, 307–321 (1967)
- Vermeij, G.J., Covich, A.P.: Coevolution of freshwater gastropods and their predators. *Amer. Natur.* **112**, 833–843 (1978)
- Wrede, W.L.: Über die Abwehrreaktion von *Physa*. *Zool. Jahrs (Zool)* **44**, 315–322 (1929)

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