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Effects of vertebrate predation on freshwater gastropods: an exclosure experiment

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Abstract

A field experiment with predator exclosures was performed in a pond in Southern Sweden to evaluate the effects of vertebrate predators on the diversity, density and distribution of freshwater gastropods. Ten exclosures (1 × 1 × 1.5 m) were erected in the nearshore vegetation at a waterdepth of 0.5–0.7 m in early June 1983 so that they included different amounts and species of macrophytes. The exclosures and cageless controls were sampled for macrophytes and gastropods at the end of the summer. The density of gastropods in the controls, exposed to predators, was positively correlated to the abundance of macrophytes. No such correlation existed in the exclosures. Further, the density of gastropods was significantly higher in the exclosures than predicted by the regression between gastropods and macrophytes in the controls. There was no difference between species composition of gastropods between controls and exclosures, but the number of species and the density of gastropods were lower in the macrophyte stands dominated by *Scirpus lacustris* than in the more complex stands dominated by *Sparganium erectum*. These results indicate that vertebrate predation is a major structuring force of benthic freshwater gastropod communities.

Introduction

In recent years, the role of interspecific competition as a major structuring force in natural communities has been questioned (see e.g. Strong *et al.*, 1984). Earlier studies assumed that the community existed in a equilibrium state and that resources were limiting population density. Recent studies, however, suggest that variable or harsh conditions commonly result in non-equilibrium communities, where resources are not limiting and thus, competition is a negligible structuring force (e.g. Wiens, 1977; Wiens, 1984). According to Connell (1975), predation is the dominant force affecting community structure when disturbance is low and competition only comes into action at intermediate disturbance levels. Another hypothesis states that competition should predominate at the top carnivore and primary producer levels, whereas organisms of intermediate trophic status (i.e. herbivores) should be regulated by predators (Hairston *et al.*, 1960; see also Schoener, 1982). It has also been suggested that predation could yield results identical to those predicted by competition theory (Jeffries & Lawton, 1984; Holt, 1984). This emphasizes the importance of experimental studies on the effects of predation on community structure.

In freshwater environments size-selective predation is known to have a profound effect on the community structure of zooplankton (see review by Zaret, 1980). The role of predation in structuring benthic macroinvertebrate communities is more controversial. Thorp & Bergey (1981) found no conclusive evidence of a freshwater equivalence to the 'keystone' predators in marine intertidals (Paine, 1966). On the other hand, changes have been reported in species richness, density, size and distribution of macroinvertebrate prey in relation to predation (Henrikson & Oskarson, 1978; Covich, 1981; Crowder & Cooper, 1982; Bohanan & Johnson, 1983; Gilinsky, 1984; Morin, 1984; Thorp & Cothran, 1984). These studies have focused on the effects of predation on insects and crustaceans, whereas comparatively little has been done on the effects of predation on the structure of freshwater gastropod communities.

In small lakes and ponds in southern Sweden the number of gastropod species was correlated with area, isolation and the number of macrophyte species (Brönmark, 1985). The number of macrophyte species was hypothesized to be a measure of habitat heterogeneity. Harman (1972) showed that gastropod species diversity increased with substrate diversity and explained this change by reduced competitive exclusion due to increased availability of microhabitats. However, increased habitat heterogeneity also decrease the risk of predation due to increased number of prey refugia and reduced foraging efficiency of the predator (Kohn & Leviten, 1976; Stein & Magnuson, 1976; Savino & Stein, 1982; Anderson 1984).

In order to further elucidate the effects of predators and habitat heterogeneity on diversity, density and distribution of freshwater gastropods a field experiment with predator exclosures was performed. Exclusion of vertebrate predators was predicted to give an increase in the density of gastropods. Changes in species composition could result due to differential susceptibility to predation.

Material and methods

The field experiment was performed in a small (1 ha) eutrophic pond 40 km south of Lund, southern Sweden, inhabited by 12 gastropod species. The perimeter of the lake was lined with a belt of emergent vegetation with *Sparganium erectum*, *Scirpus lacustris* and Carex spp. as dominant species. The dominant submerged macrophyte was *Elodea canadensis*.

Ten 1 × 1 × 1.5 m exclosures were erected in the vegetation belt 10–15 m apart at a depth of 0.5–0.7 m in such a way that they contained a varying amount of the macrophytes *S. erectum* and *S. lacustris*. The exclosures extended 0.7–1 m above the water level and were uncovered. The exclosures consisted of a wooden frame (5 × 2 cm) with screening (mesh size 1.5 mm) stapled to the sides. The experiment was initiated 8 June 1983 and terminated 7–8 September 1983. The water level in the lake decreased considerably during the summer which was extremely dry. One partially dried out exclosure was omitted from the analysis. The water depth within the remaining nine exclosures was measured as a mean of 5 readings at the termination of the experiment. In earlier cage experiments snails have readily colonized the sides of the cage, thus confounding the results (Thorp & Bergey, 1981). No snails were found on cage sides in this study, either at the termination of the experiment or at the regular inspections during the summer. As a control a 1 × 1 m square was sampled 1 m beside the exclosure before sampling of the exclosure commenced. The control was sampled in the same way as the exclosure. The sampling procedure started by cutting off and discarding the emergent parts of the macrophytes. The remaining part and the submerged macrophytes together with their fauna were removed and collected in a polythene bag. Then the upper 5 cm of the sediment were removed and sifted in a sieve (mesh size 0.5 cm) and the remainders were added to the macrophyte parts in the bag. The samples were deepfrozen at the return to the laboratory; thawed and sorted at a later date. Macrophytes were sorted to species, dried at 105 °C for 24 hours and weighed. The abundance of macrophytes was expressed as g dry weight m^{-3} because the water depth was slightly different among samples. Gastropods and leeches were determined to species and counted.

The pond was inhibited by one pair of Mute Swans (*Cygnus olor*), one pair of Rednecked Grebe (*Podiceps grisegna*) and two pairs of Coot (*Fulica atra*). The swans feed mainly on aquatic vegetation, but invertebrates, including molluscs, are occasionally found in the gut contents. The grebe feeds chiefly on invertebrates and to a certain extent on fish. Coot has been reported to be omnivorous, though plant material generally predominates. Of the animal prey recorded in the gut contents the main part consisted of molluscs and insects (data on bird food choice from Cramp & Simmons, 1977, 1980).

The fish in the pond are perch *Perca fluviatilis*, roach *Rutilus rutilus* and tench *Tinca tinca*. They are all known to feed on invertebrates, and molluscs are an important part of the diet of roach and tench (Hartley, 1942; Kempe, 1962; Kennedy and Fitzmaurice, 1970).

Results

A total of 12 gastropod species was found in the samples (Table 1). The number of species in any one sample depended on the dominant type of vegetation. Macrophyte stands dominated by *S. erectum* (samples 1–7, Table 1) had a significantly richer gastropod fauna (11.2 ± 0.8 species; x ± S.D., n = 12) than stands dominated by *S. lacustris* (7.7 ± 1.0 species, n = 6; Mann-Whitney, $p < 0.001$). Further, the dry weight of macrophytes was significantly higher in the *S. erectum* stands than in the *S. lacustris* stands (1316 ± 698 and 450 ± 172 g DW m^{-3}, respectively; Mann-Whitney, $p < 0.001$).

The density of gastropods was significantly higher in the *S. erectum* stands than in the *S. lacustris* stands (618 ± 259 and 315 ± 119 gastropods m^{-2}, respectively; Mann-Whitney, $p < 0.005$). The total density of gastropods in the controls (exposed to predators) was positively correlated to the dry weight of *S. erectum*, *E. canadensis*, the combined weight of *S. erectum* and *E. canadensis* and the total weight of macrophytes in the sample (Table 2). Snail density was, however, inversely correlated to the dry weight of *S. lacustris*. In the exclosures total density of the gastropods and dryweight of macrophytes were not correlated, except for *E. canadensis*.

The effects of predator exclosures on gastropod density could not be analysed straight forwardly as the difference between exclosures and controls, because gastropod density was correlated with the amount of macrophytes, which varied among the samples. Therefore, the relationship between macrophytes and gastropods in the controls was used as a null-hypothesis. The regression of gastropod density with the combined dry weight of *S. erectum* and *E. canadensis* (SpElo) was used because this yielded the highest coefficient of determination ($R^2 = 0.823$). The density of gastropods in the exclosures was significantly higher than predicted by the regression from the controls (Wilcoxon signed ranks, $p < 0.05$; Fig. 1).

There was no difference in species composition between controls and exclosures but the correlation between density and macrophyte dryweight was higher for several gastropod species in the controls than in the exclosures (Table 2). In the exclosures *Lymnaea peregra* was significantly correlated to *E. canadensis* only, while in the controls this species was significantly correlated to four of the macrophyte variables. A similar pattern was shown by *Physa fontinalis*, *Anisus vortex* and *Bathyomphalus contortus*.

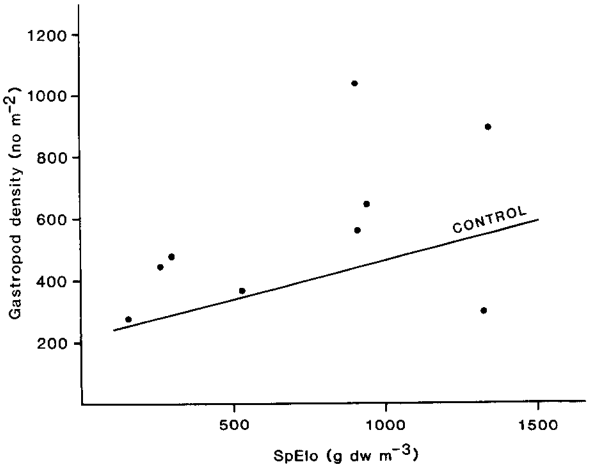

Fig. 1. The density of gastropods in relation to the abundance of *S. erectum* and *E. canadensis* (SpElo) in exclosures (points) compared with the predicted density from controls (regression line: $y = 0.246x + 214.3$, $R^2 = 0.82$, $p < 0.001$).

Table 1. The abundance of gastropods, leeches and macrophytes in controls and exclosures. The abundance of gastropods are expressed as number m^{-2}, and for macrophytes as $g\,m^{-2}$. C = Control, E = Exclosure.

CAGE	1		3		4		5		6		7		8		9		10	
TREATMENT	C	E	C	E	C	E	C	E	C	E	C	E	C	E	C	E	C	E
GASTROPODS																		
Lymnaea stagnalis	11	8	45	13	6	9	9	14	9	12	9	2	2	1	6	2	6	41
L. peregra	9	19	34	44	43	100	6	14	7	8	11	10	1	1	2	–	–	8
L. auricularia	–	–	–	25	40	23	161	30	121	66	318	33	18	2	18	36	67	28
Physa fontinalis	1	4	13	16	6	39	4	6	6	6	3	3	–	–	–	–	–	–
Planorbarius corneus	3	8	15	24	4	6	1	4	2	1	1	–	5	–	5	–	4	–
Anisus vortex	74	5	222	194	245	200	42	165	136	281	28	8	–	2	–	–	–	–
Bathyomphalus contortus	2	–	349	241	296	301	4	79	74	75	–	–	–	–	–	–	–	–
Gyraulus albus	91	52	152	213	168	234	55	203	87	67	199	63	116	120	107	233	193	278
G. crista	35	60	4	33	5	35	1	30	1	1	38	92	14	41	21	148	21	74
Hippeutis complanatus	21	14	7	31	23	33	2	14	4	–	3	4	–	2	–	–	–	3
Acroloxus lacustris	154	122	15	25	28	34	22	69	112	31	28	136	56	97	25	18	3	29
Bithynia tentaculata	1	3	50	32	12	18	5	13	3	5	18	10	–	1	6	8	7	14
Total density	402	295	906	891	876	1032	312	641	562	553	656	361	212	267	190	445	301	475
No of species	11	10	11	12	12	12	12	12	12	11	11	10		9	8	6	7	8
LEECHES																		
Glossiphonia complanata	–	2	2	8	5	5	1	9	23	1	3	–	–	–	–	–	–	–
MACROPHYTES																		
Sparganium erectum	112	88	67	53	82	20	102	46	115	64	80	73	7	25	7	14	–	–
Elodea canadensis	12	11	54	47	68	25	32	25	17	5	2	4	25	18	16	45	93	74
Scirpus lacustris	–	–	–	–	–	–	–	–	4	–	–	5	60	36	47	52	75	78

Table 2. Significant coefficients between the density of gastropod species, the abundance of macrophytes (g Dw m^{-3}) and the density of *Glossiphonia complanata* in controls and exclosures.
Sparg = *Sparganium erectum*, Elodea = *Elodea canadensis*, SpElo = the combined dryweight of Sparg and Elodea, Scirp = *Scirpux lacustris*, Gloss = *Glossiphonia complanata*, *** = $p < 0.001$, ** = $p < 0.01$, * = $p < 0.05$.

CONTROLS	Sparg	Elodea	SpElo	Scirp	Total	Gloss
Lymnaea stagnalis						
L. peregra	0.835 **	0.924 ***	0.954 ***		0.960 ***	
L. auricularia						
Physa fontinalis	0.782 *	0.698 *	0.811 **		0.796 **	
Planorbarius corneus						
Anisus vortex	0.909 ***	0.866 **	0.970 ***	0.971	***	
Bathyomphalus contortus	0.744 *	0.935 ***	0.905 ***		0.927 ***	
Gyraulus albus						
G. crista						
Hippeutis complanatus	0.685 *		0.675 *		0.662 *	
Acroloxus lacustris						
Bithynia tentaculata						
Gastropods – total	0.879 **	0.774 *	0.907 ***	– 0.662 *	0.894 **	
Glossiphonia complanata						
EXCLOSURES						
Lymnaea stagnalis						
L. peregra		0.716 *				
L.auricularia						
Physa fontinalis		0.687 *				
Planorbarius corneus		0.762 *	0.746 *		0.752 *	0.663 *
Anisus vortex						
Bathyomphalus contortus		0.832 **				0.696 *
Gyraulus albus		0.692 *				
G. crista						
Hippeutis complanatus		0.869 **	0.679 *			0.746 *
Acroloxus laucustris						
Bithynia tentaculata		0.876 **				0.693 *
Gastropods – total		0.888 **				0.743 *
Glossiphonia complanata		0.778 *				

A correlation matrix between all gastropod species revealed no significant negative correlations between any species pairs in the controls, while in the exclosures the correlations between *Lymnaea peregra – Acroloxus lacustris*, *Gyraulus crista – Anisus vortex* and *Acroloxus lacustris – Gyraulus albus* were significant and negative ($r = -0.671$, $r = -0.738$ and $r = -0.698$, respectively; $p < 0.05$ in all cases).

The density of the leech *Glossiphonia complanata*, which is known to include gastropods in its diet (Wrona *et al.*, 1979), was positively correlated to the total density of gastropods, to four different gastropod species and to the macrophyte variable *E. canadensis* in the exclosures (Table 2).

Discussion

A large number of gastropod species commonly occurs in high densities in the vegetation belt of fresh waters (e.g. Soszka, 1975). When exposed to a choice between several macrophyte species in a laboratory experiment, gastropods showed a preference for specific macrophytes (Brönmark, unpubl.), and in the field macrophytes have been shown to have specific associations of gastropods (Calow, 1973; Pip & Stewart, 1976; Pip, 1978; Lodge, 1985; Pip, 1985). This habitat segregation was hypothesized to be due to interspecific competition and an increased number of macrophytes species (i.e. increased habitat heterogeneity) would thus lead to an increased number of gastropod species. Brönmark (1985) found that the number of macrophyte species was one of the variables correlated to gastropod species diversity and Harman (1972) showed that increased substrate diversity increased the diversity of gastropods. However, habitat segregation between species could also be a result of predation (Covich, 1981; Jeffries & Lawton, 1984; Holt 1984).

Studies on the effects of predation on the structure of benthic, freshwater invertebrate communities have given contradicting results on the response of gastropods to predation. In a predator exclosure experiment Thorp & Bergey (1981) found a decrease of gastropod abundance within the exclosures but assigned this to ineffective sampling. In contrast, Macan (1977) found an increase in the abundance of *L. peregra* when trout (*Salmo trutta*) was introduced to a pond.

In this study the density of gastropods in the controls, exposed to predators, was correlated to the abundance of macrophytes (Fig. 1). There are two possible explanations for such a relationship. The main food resource of freshwater gastropods are epiphytic algae and detritus (e.g. Calow and Calow, 1975; Reavell, 1980). If food were limiting i.e. competition the main structuring force, density of gastropods would be expected to increase with increasing abundance of macrophytes, mainly due to increasing resource levels. However, it has also been shown that increased habitat heterogeneity in benthic communities reduces the effects of predation (Stein & Magnuson, 1976; Crowder & Cooper, 1982; Gilinsky, 1984) by increasing the availability of refugia and reducing predator efficiency. If food availability is the major factor affecting gastropod community structure, then a lowered predation pressure, as in the exclosures, would not affect the relationship between gastropod density and macrophytes. But if predation is the most important structuring force the outcome of excluding predators may be more complex. Since the effect of predation is most severe at the lower macrophyte densities the increase in gastropod densities would be expected to be highest in low macrophyte density patches when predators are excluded. This would yield a decreasing slope of the gastropod – macrophyte relationship and eventually the correlation between the two may disappear completely. At a later stage, when densities of gastropods have increased food may become limiting and again a positive relationship with macrophyte abundance will be found, but this time due to competition.

Several findings from the exclosure experiment indicate that predation is the most important structuring force influencing the gastropod community in this pond. First, the correlation between gastropod density and macrophyte abundance disappeared within the controls. Second, the total density of gastropods was higher in the exclosures than predicted from the correlation of gastropod density and macrophyte abundance in the exclosures. Third, in the exclosures there were negative correlations between three species pairs, but no such correlations were found in the controls. This may be due to interspecific competition coming into action when predation pressure is lowered and density of gastropods subsequently increase. However, it is hard to draw any conclusions on the existence of competition on mere correlations between species. Fourth, the negative correlation of gastropod density with the abundance of *S. lacustris* and the lower number of gastropod species in samples dominated by this species further indicates the modifying effect of macrophytes on predator-prey relationships. The complexity of the stands dominated by the non-branching *S. lacustris* is lower, as indicated by the low dryweight · m^{-3}, and this allows the predators to forage more efficiently.

The evolution of shell thickness and sculpture in gastropods has been seen as a response to predation by shell crushing predators (e.g. Vermeij & Covich, 1976; Palmer, 1980). Resistance to shell crushing varies among freshwater gastropods (Stein *et al.*, 1984; Brönmark, unpubl.). A thick shell increases the handling time, and the profitability to the predator decreases (Stein *et al.*, 1984). When exposed to a range of prey species with differing shell thickness the optimal forager should choose prey so that net energy gain is maximised. A release of predation by vertebrate predators foraging in an optimal way thus should be expected to have a more pronounced effect on thinshelled species. For several of the species the correlation between density and macrophyte abundance disappeared within the exclosures. This was especially pronounced for the thinshelled species *L. peregra*, *A. vortex*, and *P. fontinalis*.

Several studies have shown that when vertebrate predators are excluded the invertebrate predators increase in importance (Crower & Cooper, 1982; Gilinsky, 1984; Morin, 1984). Generally, leeches and flatworms are the most important invertebrate gastropod predators. In this pond only the leech *Glossiphonia complanata* was present and the abundance of this species was positively correlated to the abundance of the gastropods in the exclosures but not in the controls. This may suggest an increased importance of leeches as predators in the absence of vertebrate predators.

In conclusion, the exclosure experiment indicate that predation, rather than competition, is the major structuring force of benthic gastropod communities. Long-term exclosure experiments or studies of gastropod communities in habitats with and without vertebrate predators should be performed to further evaluate the relative importance of interspecific competition and predation in freshwater gastropod communities.

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