

Long-term dynamics and community structure of freshwater gastropods exposed to parasitism and other environmental stressors

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SUMMARY

1. Freshwater communities are subject to various abrupt environmental disturbances and increasing pollution levels in their habitat. According to the nature and the periodicity of disturbances (i.e. punctuated, recurrent or continuous), one may expect different kinds of response of the target gastropod communities.
2. The gastropod community of a French lake has been investigated for 10 years to study its responses to three main environmental disturbances: supra-seasonal droughts, recurrent proliferations of cyanobacteria and parasitism by trematodes. The relationship between this latter factor, considered as a continuous stressor, and the gastropod community was a particular focus.
3. A total of 13 280 gastropods belonging to 17 species (mostly Pulmonata with Planorbidae as the dominant family) have been sampled in the lake over the 10-year time series. Species composition of the gastropod community varied strongly during the study period as did species richness (0–14, mean of 6.5 ± 0.4 species) and abundance of gastropods (0–4456, mean of 192 ± 72 individuals). Trematode larvae belonging to 11 morphotypes of cercariae were detected in 15 of the 17 species of gastropods and had a total prevalence of 2.9%.
4. Droughts (punctuated stressor) were responsible for the disappearance of nearly all gastropod species, and thus represent a severe environmental stressor for them. Nevertheless, the extent of this stressor was limited since the gastropod community was highly resilient.
5. Recurrent proliferations of toxic cyanobacteria (recurrent stressor) coincided with the large decline of the gastropod community, corresponding to a strong decrease in abundance and species richness. Intoxication of gastropods by toxic cyanobacteria was demonstrated by the bioaccumulation of microcystins in all gastropod tissues.
6. Trematode parasitism (continuous stressor) did not affect the gastropod community despite the possibly strong impact of parasites on some host species (those with monthly prevalence as high as 100% at some times). Indeed, abundance and species richness of gastropods were scarcely influenced by trematode prevalence or species richness.

Keywords: cyanobacteria proliferations, droughts, environmental stressors, gastropod community, trematodes

Introduction

One of the biggest challenges facing ecologists is to understand how, and to what extent, environmental perturbations influence animal and plant community

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structure, species coexistence and biodiversity. Freshwater systems are habitats characterized by particularly harsh variation in environmental conditions in space and time (Humphries & Baldwin, 2003; Lytle & Poff, 2004). These naturally harsh features are accentuated by the increasing degradation of freshwater habitats due to anthropogenic pollution (Abromovitz, 1996) that greatly affects organisms that spend their entire life in freshwater systems. Among them, gastropods (Pulmonata Basommatophora and Prosobranchia) constitute a substantial part of freshwater biomass (Habdija, Lajtner & Belinic, 1995). Gastropods often play key roles in structuring aquatic communities because they are an important link between primary producers (as herbivores and detritivores associated with macrophytes and as grazers of periphyton) and higher consumers (Kerans *et al.*, 2005). Gastropods are also often adapted to fluctuations in environmental conditions in freshwater habitats [e.g. survival during hibernation and aestivation periods, general ecological tolerance] (Hubendick, 1962; Dillon, 2000). They are invariably among the first successful immigrants to newly established freshwater bodies (Boycott, 1936; Lassen, 1975; Dillon, 2000), having highly efficient passive dispersal and a capacity for self-fertilization (most pulmonates) or parthenogenesis (many prosobranchs). Despite all these characteristics, abrupt changes are often observed in natural communities of freshwater gastropods (e.g. Russel-Hunter, 1961; Hubendick, 1962; Brown, 1997) and are generally difficult to understand due to the multiplicity of abiotic and biotic factors interacting in the field. However, several studies have demonstrated the role played by some environmental factors such as predation that can control or decimate populations of freshwater gastropods in certain conditions (Lodge *et al.*, 1987; Cardona, 2006; Turner & Chislock, 2007).

In the present study, fluctuations in the composition and abundance of a gastropod community were investigated for 10 years (1994–2004) in a shallow eutrophic lake subjected to several major environmental disturbances of contrasting nature (drought, proliferation of toxic cyanobacteria, parasitism by larval trematodes) and occurrence frequency (respectively punctuated, recurrent and continuous).

Drought episodes result not only in habitat loss, but also in progressive deterioration of water quality (Magoulick & Kobza, 2003), decreased food resources

and increased predation pressure and intra- and/or interspecific resource competition (Dudgeon, 1983). Thus, when supra-seasonal droughts occur in a lake, they are expected to strongly impact freshwater gastropods despite the strategies gastropods have to survive seasonal drying events, such as aestivation and desiccation-resistant eggs (Aldridge, 1983; Schwartz & Jenkins, 2000).

In contrast to droughts, proliferations of cyanobacteria are seasonal and recurrent events, typically occurring in eutrophic waters during summer in temperate regions (Lindholm, Eriksson & Meriluoto, 1989). The high biomass of cyanobacteria during bloom episodes may alter aquatic ecosystems [e.g. disequilibria in phytoplankton supporting food webs, hypoxia, ammonia release (Chorus & Bartram, 1999)] and can result in health hazards due to the toxicity of some cyanobacterial strains (see Zurawell *et al.*, 2005 for review). Intoxication of gastropods by feeding on toxic cyanobacteria or by absorption of the toxins, as demonstrated in the laboratory, adversely affects some life history traits (survival, growth and fecundity) and results in accumulation of cyanotoxins in their tissues (Gérard, Brient & Le Rouzic, 2005; Gérard & Poullain, 2005; Lance *et al.*, 2007). Consequently, recurrent proliferations of toxic cyanobacteria are expected to cause important changes in the abundance and composition of gastropod communities.

Parasitism is as an additional stress that may regulate host populations in the field (see Esch *et al.*, 1997), especially in the case of gastropods that can be heavily infected by digenetic trematodes (Gérard, 1997, 2001a; Fredensborg, Mouritsen & Poulin, 2005). First, alterations to the physiology and metabolism of freshwater snails by larval trematodes (see Thompson, 1985; Hurd, 1990; De Kock, 1993 for reviews) can have important life-history consequences and affect survival, growth and fecundity (e.g. Gérard & Théron, 1997). Second, parasitism can modify the outcome of competition between two species ('indirect parasite-mediated competition'), by favouring or penalizing the host species or the unparasitized species (e.g. Price *et al.*, 1986; Price, Westoby & Rice, 1988; Lozano, 1991), and can also influence the choice of infected prey by predators (for reviews: Combes, 1995; Hatcher, Dick & Dunn, 2006). Third, parasite virulence may increase with host environmental stress, and fluctuations in natural gastropod populations may result from complex interactions between

parasitism and environmental conditions (Esch, Gibbons & Bourque, 1975; Morley, Irwin & Lewis, 2003; Jokela *et al.*, 2005; Morley, Lewis & Hoole, 2006).

The present study encompasses the influence on the gastropod community of the various types of environmental disturbance discussed above, but focuses in particular on the relationship between larval digenetic trematodes and community composition, something that has been poorly studied to date. Trematode parasitism was considered as a continuous stressor that was expected to significantly impact the gastropod community.

Methods

Study site, sampling and measurements

The study site is the Combours Lake, a pool (area: 10–20 ha) of hard eutrophic, shallow and stagnant water in Ille-et-Vilaine, eastern Brittany, France (48°24'N, 1°45'W). Mineral-rich and eutrophic freshwater systems support both high species richness and biomass of molluscs (Boycott, 1936; Dillon, 2000), and at the beginning of our study in 1994 the lake harboured one of the richest gastropod communities in the region, including 17 species of pulmonates (Lymnaeidae, Physidae, Planorbidae, Ancyliidae) and prosobranchs (Valvatidae) (Costil, 1993; Gérard, 1997). Gastropods were sampled in a lakeside area of 100 m length, 2.5 m width and 1.0 m maximum depth (similar sampling area in previous studies: Gérard, 1997, 2001a,b), using a pond-net (nylon mesh: 1 mm, square aperture: 0.5 × 0.5 m) to sweep the water column in the whole littoral area studied. A total of 69 samples were collected from December 1994 to October 2004, performed at the end of each month from September 1996 to September 2001, and at various intervals before and after this period (December 1994, March and July 1995, March and June 1996, June 2003, May and October 2004). Each time, water temperature and depth were measured near the shore and at 2.5 m from the shore. The pond-net contents were examined in the laboratory. Collected snails were identified according to Glöer & Meier-Brook (1994), and then dissected under a stereoscopic microscope to record parasitic infections. Larval trematodes (sporocysts or rediae and cercariae during the patent period, i.e. period of cercarial production) were observed alive and drawn with

the help of a microscope equipped with a *camera lucida*; morphotypes of cercariae were distinguished.

During the survey, severe summer droughts occurred in 1996 and 2003, resulting in the total drying out of the whole littoral area formerly inhabited by gastropods. Proliferations of cyanobacteria were observed every summer from 1997 to 2004. Against this background, with the risk of intoxication for gastropods, in May and October 2004, we assayed the tissues of all collected snails for the highly hepatotoxic microcystin-LR (MC-LR, one of the most commonly occurring microcystins produced by cyanobacteria), using High Pressure Liquid Chromatography and ELISA analytical methods described in Lance *et al.* (2006).

The descriptors used to characterize the gastropod community were: species richness (S), abundance, frequency (relative abundance of a species in the community), occurrence frequency (percentage of months a species was collected in the 69 months sampled), Shannon's diversity index ($H = -\sum p_i \ln p_i$ where p_i is the proportion of species i relative to the total number of species), Shannon's equitability ($E_H = H/\ln S$), and prevalence [relative abundance of snails harbouring trematodes (Bush *et al.*, 1997)]. Shannon's diversity and equitability were not calculated when species richness was <3 .

Cumulative frequency abundance curves of gastropods were built over the 10-year period to describe patterns of fluctuation in abundance of each gastropod species. When the maximum cumulative frequency (1.00) was attained, all individuals of a given gastropod species had been collected. Thus, the more rapidly the maximum cumulative frequency value was reached for a given species, the more quickly that species disappeared over the 10-year study. For species that were temporarily absent, cumulative frequency curves exhibited a threshold lasting several consecutive sampling dates. To facilitate inter-species comparisons, gastropod species were classified in two groups according to their occurrence frequency ($<50\%$ or $\geq 50\%$); species with low occurrence frequency ($<5\%$) were not included.

To describe the trematode community and its link to the gastropod community, several descriptors were used: trematode richness, number of trematode infrapopulations [all trematodes of a given species within an individual host (Bush *et al.*, 1997)] across all gastropod species (NTI), frequency of trematode infrapopulations (FTI), frequency of trematode occur-

rence (FTO), number of gastropod species as first intermediate host (NGH), frequency of trematode morphotypes in each component community [all trematode infrapopulations in one host species (Bush *et al.*, 1997)].

Data are reported as mean \pm standard error (SE).

Data analysis

The trend in the gastropod community and its relationship to environmental factors were explored using time series analysis. As observations in the time series must be equally spaced, analyses were performed on data corresponding to the June 1997–June 2001 period. Indeed, during this period, both a constant and short sampling interval occurred (see Fig. 1). Observed data series can be decomposed into various components: a deterministic change (trend), systematic variability (periodicity) and random fluctuations (noise). As a first step, changes in the gastropod community (abundance and species richness) over months (trends) were analysed to assess whether the gastropod community was responding or not to the recurrent environmental stressor (cyanobacteria proliferations) throughout the study. Abundances of gastropods were $\ln(x + 1)$ transformed because of the nonlinearity of data, and trends in the data series were analysed by linear regression. At a second step, we investigated periodic variability in the gastropod community over months. The approach was to quantify the relationships between successive terms of the data series. This latter investigation requires that the series be stationary, i.e. constant mean and variance over the series (Legendre & Legendre, 1998). It became so when the trend was extracted from the data series by detrending (use of deviations around the regression of gastropod data versus time). Periodicity was explored by an autocorrelation function. At a third step, we extracted the periodic component to focus the analysis on the link between variations in residuals (random fluctuations) of the gastropod community and the descriptors of parasitism (prevalence and species richness of trematodes) over months. Random fluctuations were derived from a differencing process applied to the systematic component. Differencing involves creating a new series resulting from the differences between successive periods, i.e. $X'_t = X_t - X_{t-1}$, where X'_t is an observation in the new series with $n-1$ values. A

cross-correlation function was then computed between random fluctuations of the gastropod community and each parasitism descriptor (after detrending and differencing) during the selected sampling period. Analyses were performed using STATISTICA (version 7.1, Statsoft, Maisons-Alfort, France).

Results

Species composition of the gastropod community

A total of 13280 gastropods belonging to 17 species have been sampled in the Combourg Lake over the 10-year time series (Table 1). *Gyraulus albus* (Müller) was the most abundant species (28.3%), followed by *Planorbis planorbis* (Linné) (16.0%), *Radix peregra* (Müller) (13.2%) and *Valvata cristata* Müller (10.5%). The Planorbidae family was the best represented (50.4% of the total abundance of gastropods, seven species), followed by Lymnaeidae (24.5% represented by five species), Valvatidae (the only Prosobranchia: 15.4% with three short-lived species, i.e. survival less than 2 years compared to most prosobranchs), Physidae (8.9%, one species) and Acroloxidae (0.8%, one species).

Large fluctuations occurred in species richness (0–14; Fig. 1a) and abundance of gastropods (0–4456; Fig. 1b), with a mean of 6.5 ± 0.4 species and of 192 ± 72 individuals. Shannon's diversity index and equitability varied respectively from 0.7 to 2.1 with a mean of 1.4 ± 0.0 , and from 0.4 to 1.0 with a mean of 0.8 ± 0.0 (Fig. 1c).

The composition of the gastropod community varied greatly over the study period (see occurrence frequency values in Table 1 and Fig. 2). Some species (i.e. *Radix auricularia* (Linné), *R. peregra*, *G. albus*, *Physella acuta* (Draparnaud), *Valvata piscinalis* (Müller) and *V. cristata*) occurred from year to year (occurrence frequency >56.0%) (Fig. 2a). The other species disappeared completely for one or several years (Fig. 2b) although some species sometimes occurred in very large numbers (e.g. *P. planorbis*, the second most abundant species but with an occurrence frequency of 31.9%).

Trematodes in the gastropod community

Eleven morphotypes of cercariae were distinguished in the gastropods sampled. Among them, four were

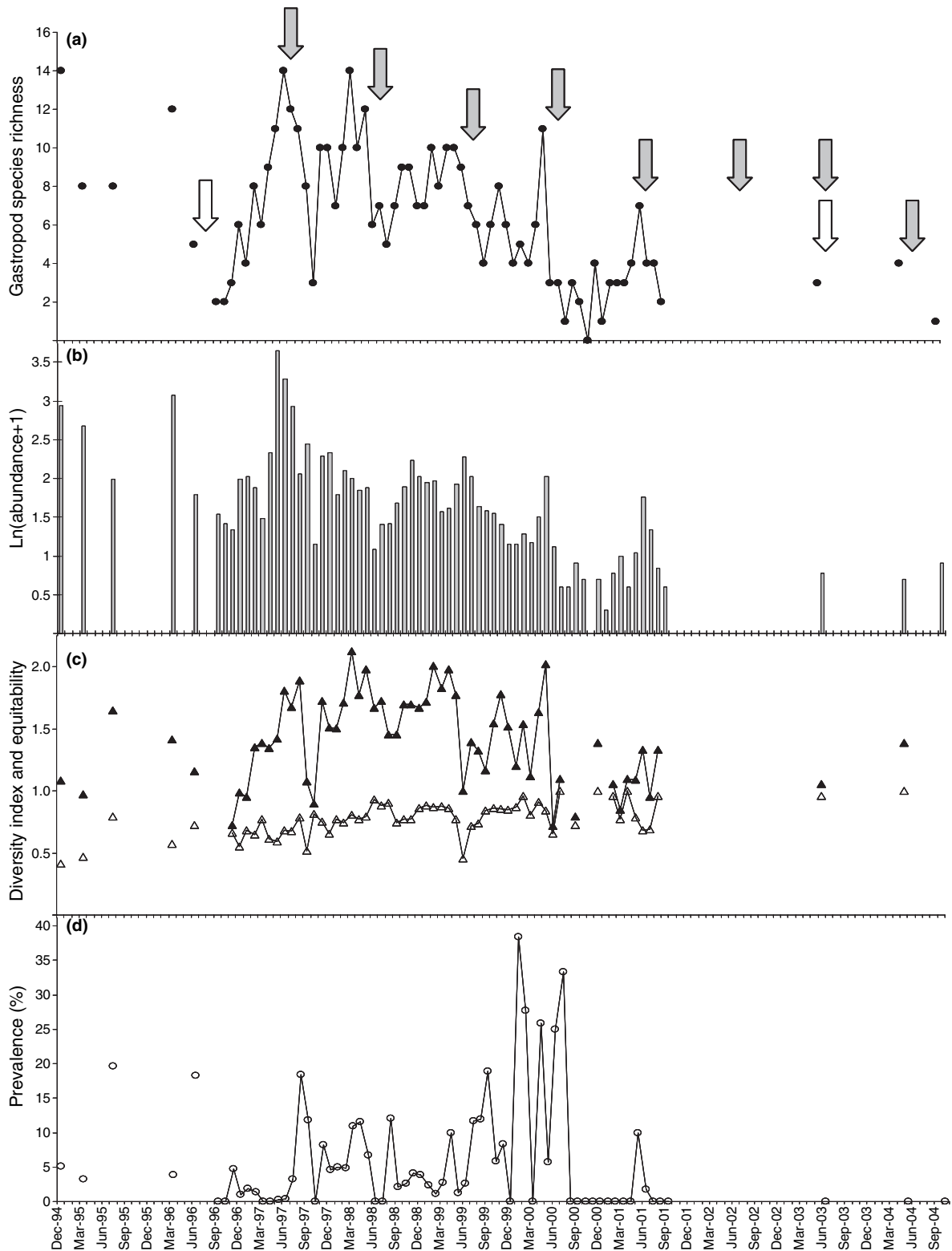


Fig. 1 Temporal fluctuations of (a) gastropod species richness, (b) gastropod abundance, (c) Shannon's diversity index (black triangles) and equitability (white triangles) (not calculated when species richness <3) and (d) trematode prevalence (%) in the Combourg Lake from December 1994 to November 2004. The lake was subject to severe droughts in the summers of 1996 and 2003 (white arrows), and proliferations of cyanobacteria occurred every summer from 1997 to 2004 (grey arrows).

Table 1 Details on gastropod species sampled in the Combourg Lake from December 1994 to October 2004: family, scientific and abbreviated names, abundance, frequency of occurrence (percentage of months a species was collected in 69 months) and prevalence (percentage of snails harbouring trematodes)

Family	Species	Abbreviation	Abundance	Occurrence frequency (%)	Prevalence (%)
Valvatidae	<i>Valvata cristata</i> Müller	Vcr	1393	56.52	2.30
	<i>Valvata pulchella</i> Studer	Vpu	377	20.29	2.65
	<i>Valvata piscinalis</i> (Müller)	Vpi	276	63.77	6.52
Lymnaeidae	<i>Lymnaea truncatula</i> (Müller)	Ltr	43	4.35	2.33
	<i>Stagnicola palustris</i> (Müller)	Spa	210	28.99	4.76
	<i>Radix peregra</i> (Müller)	Rpe	1749	73.91	2.57
	<i>Radix auricularia</i> (Linné)	Rau	1218	76.81	9.03
	<i>Lymnaea stagnalis</i> (Linné)	Lst	33	18.84	21.21
Planorbidae	<i>Gyraulus albus</i> (Müller)	Gal	3757	68.12	2.24
	<i>Gyraulus acronicus</i> (Férussac)	Gac	12	2.90	0.00
	<i>Planorbis planorbis</i> (Linné)	Ppl	2119	31.88	2.45
	<i>Planorbarius corneus</i> (Linné)	Pco	75	18.84	12.00
	<i>Armiger crista</i> (Linné)	Acr	598	36.23	0.50
	<i>Segmentina nitida</i> (Müller)	Sni	66	4.35	1.52
	<i>Hippeutis complanatus</i> (Linné)	Hco	69	28.99	2.90
Acroloxiidae	<i>Acroloxus lacustris</i> (Linné)	Ala	110	42.03	4.55
Physidae	<i>Physella acuta</i> (Draparnaud)	Pac	1175	66.67	0.00

identified to genus, three to family and four remained undetermined (Table 2). Of the total parasitic fauna, the cercariaeum *Asymphylogora* sp. (Monorchiiidae) was the most abundant (42.5% of the patent infrapopulations) and the most frequent (occurrence frequency of 52.2%), followed by the furcocercaria *Tylodelphys* sp. (Diplostomidae) (18.0% and 33.3% respectively). Three other types of furcocercariae, three xiphidiocercariae, two echinostomes and one notocotyle were also recorded. The cercariaeum *Asymphylogora* sp. was a permanent resident with its entire life cycle within the lake (autogenic). Its regular distribution among the snail hosts (Table 3) was better explained by the abundance of gastropods than by any physiological characteristics (the four host species that were the most highly infected by *Asymphylogora* sp. were also the four most abundant species). The other trematode morphotypes had aggregated distributions among the snail hosts (Table 3) and were temporary residents (mean occurrence frequency of $12.0 \pm 3.6\%$) (allogenic).

Trematode larvae (sporocysts/rediae, cercariae) had a total prevalence of 2.9% and were detected in 15 of the 17 species of gastropods (Table 1). The 395 trematode infrapopulations were unequally distributed among the gastropod community and had prevalences ranging from 0.5% for *Armiger crista* (Linné) to 21.2% for *Lymnaea stagnalis* (Linné) (Table 1).

Depending on the gastropod species, the richness of trematode component communities (Table 3) varied

from a single digenean morphotype for *Valvata pulchella* Studer, *Lymnaea truncatula* (Müller), *Stagnicola palustris* (Müller), *L. stagnalis*, *Planorbarius corneus* (Linné), *Segmentina nitida* (Müller) and *Acroloxus lacustris* (Linné), to seven for *G. albus* and *R. auricularia* (mean of 2.3 ± 0.6 morphotypes per host species). Species richness of trematode infracommunities (in one host individual) was very low: 1.0 ± 0.0 on average with a maximum of two digenean morphotypes per host. In addition, only six double parasite infections were detected (1.5% of infected snails).

Two gastropod species were not found infected. The first was *P. acuta*, a North American physid introduced to Europe and probably not an intermediate host species in its European range, given the absence of infected individuals among the 1175 collected for 10 years. The second was *Gyraulus acronicus* (Férussac), a planorbid too rare in the lake (only 12 specimens sampled) to determine whether or not it is a potential snail host.

According to overall prevalence, the two most parasitized species, *L. stagnalis* (21.2%) and *P. corneus* (12.0%), were very rare gastropod species (respectively 0.3 and 0.6% of the total abundance of gastropods; occurrence frequency of 18.8%), whereas the four most abundant gastropod species had fewer infections (2.2% for *G. albus*, 2.5% for *P. planorbis*, 2.6% for *R. peregra* and 2.3% for *V. cristata*; Table 1). The most frequent gastropod species, *R. auricularia*

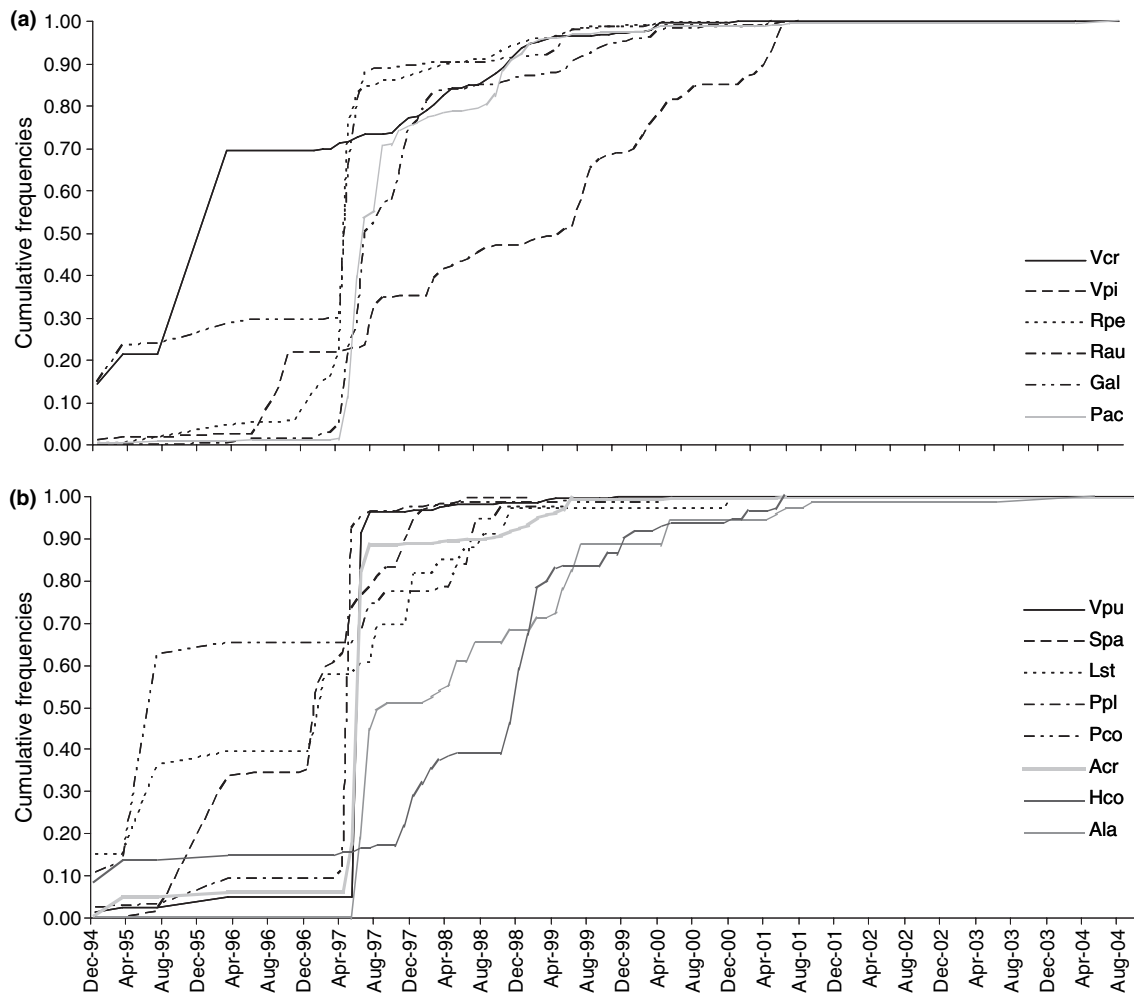


Fig. 2 Cumulative frequencies of gastropod species in the Combourg Lake from December 1994 to November 2004 (see the text for details on sampling dates): (a) species with occurrence frequency $\geq 50\%$, (b) species with occurrence frequencies of 5–50%. Full names of gastropods are given in Table 1.

(overall prevalence of 9.0%), represented 28.3% of all infected gastropods (first rank, Table 1) and was the main first intermediate host for five trematodes (versus 0.4 ± 0.2 trematode on average for the 14 other host gastropod species; Table 3). The monthly prevalence of trematodes in the host species could be as high as 100% for some species at some times (e.g. *L. stagnalis*, *R. peregra*, *R. auricularia*, *G. albus* and *V. pulchella*), with an average of $8.0 \pm 0.9\%$ (Appendix 1).

Trends in the gastropod community and environmental stressors

The severe drought in the summer of 1996 resulted in the disappearance of nearly all gastropods (Fig. 1a,b). After the drought, diversity increased gradually up to

1.8 in June 1997, whereas equitability was unchanged with a mean of 0.7 ± 0.0 from November 1996 to June 1997 (Fig. 1c). The successful recolonization of the lake by gastropods observed in 1997 was due to reproductive effort, characterized by a substantial population explosion in spring (May and June 1997: 4456 and 1899 individuals collected belonging to 11 and 14 species in the 2 months, respectively) and two moderate breeding events during the summer (July, August and September 1997: 841, 114 and 278 individuals belonging to 12, 11 and 8 species, respectively) and the autumn (November and December 1997: 194 and 215 individuals both belonging to 10 species; Fig. 1a,b). This high reproductive effort in 1997 was seen in no other year of the study period. Indeed, visual examination shows a monotonous

Table 2 Details on larval trematodes sampled in the Combourg Lake from December 1994 to October 2004 (395 infrapopulations of which 22 prepatent infections not included here): cercarial morphotypes and abbreviations, intramolluscan stages, identification, number of patent trematode infrapopulations (NTI), frequency of trematode occurrence (FTO), and specificity (number of first intermediate host species, NGH)

Cercariae	Abbreviation	Intramolluscan stages	Identification	NTI	FTO (%)	NGH
Cercariaeum	Cer	Rediae	<i>Asymphyiodora</i> sp.	168	52.17	13
Furcocercaria 1	Fur1	Sporocysts	<i>Tylodelphys</i> sp.	71	33.33	5
Echinostome 1	Ech1	Rediae	Echinostomatidae	34	24.64	3
Notocotyle	Not	Rediae	<i>Notocotylus</i> sp.	30	14.49	3
Xiphidiocercaria 2	Xip2	Sporocysts	Unknown	28	8.70	2
Furcocercaria 2	Fur2	Sporocysts	Strigeoidea	20	13.04	3
Xiphidiocercaria 1	Xip1	Sporocysts	Unknown	14	17.39	2
Furcocercaria 3	Fur3	Sporocysts	<i>Trichobilharzia</i> sp.	5	4.35	2
Furcocercaria 4	Fur4	Sporocysts	Unknown	1	1.45	1
Echinostome 2	Ech2	Rediae	Echinostomatidae	1	1.45	1
Xiphidiocercaria 3	Xip3	Sporocysts	Unknown	1	1.45	1

Table 3 Number of trematode infrapopulations in each first intermediate host species in the gastropod community of the Combourg Lake from December 1994 to October 2004 (prepatent infections are not included; abbreviations of gastropod species are in Table 1)

Cercariae	Vcr	Vpu	Vpi	Ltr	Spa	Rpe	Rau	Lst	Gal	Ppl	Pco	Acr	Sni	Hco	Ala
Cercariaeum	26	9	16	1	9	17	13		50	20		1	1	1	5
Furcocercaria 1						14	41	6	9			1			
Echinostome 1						5	22		2	4					
Notocotyle						3	6		14	7					
Xiphidiocercaria 2									2	18	8				
Furcocercaria 2						4	13		3						
Xiphidiocercaria 1						5	9								
Furcocercaria 3							4		1						
Furcocercaria 4	1														
Echinostome 2														1	
Xiphidiocercaria 3			1												

decline in gastropod abundance and species richness (Fig. 1a,b). This trend was confirmed by fitting a linear regression to the June 1997–June 2001 series [$y = 5.54x - 0.08$, $P < 0.05$ for abundance (Fig. 3a), and $y = 11.01x - 0.17$, $P < 0.05$ for species richness (Fig. 3e)].

The decline of the gastropod community coincided with the recurrent proliferations of cyanobacteria from June to September in the years 1997–2004. Gastropod abundance and species richness were extremely low from June 2000 to the end of the survey (October 2004): on average, 8.6 ± 2.9 individuals belonging to 2.9 ± 0.4 species compared to 262.3 ± 98.0 individuals belonging to 7.8 ± 0.4 species from December 1994 to May 2000. In 2003, the decline was probably accentuated by the simultaneous severe drought and cyanobacterial proliferations. Intoxication of the gastropods by the cyanotoxins was clear, all gastropods (collected in May

and October 2004) harbouring MC-LR in their tissues, both before and after the cyanobacterial proliferations. The values ranged respectively from 8 to 98 ng g^{-1} fresh weight (1 to 13 ng g^{-1} dry weight) in May and from 168 to 24268 ng g^{-1} (22 to 3249 ng g^{-1} dry weight) in October.

The autocorrelation function showed no seasonal components for gastropod abundance (only a significant autocorrelation coefficient at lag 1; Fig. 3b) or for species richness (Fig. 3f), despite evident annual peaks in abundance that did not occur exactly at the same time each year (Fig. 1b). Indeed, the spring is the main period of reproduction, resulting in a peak in gastropod abundance, but depending on the year and the species, one, two or three breeding periods may occur.

The monthly prevalence of trematodes in the gastropod community varied from 0 to a maximum of 38.5% in January 2000 (Fig. 1d) with an average of

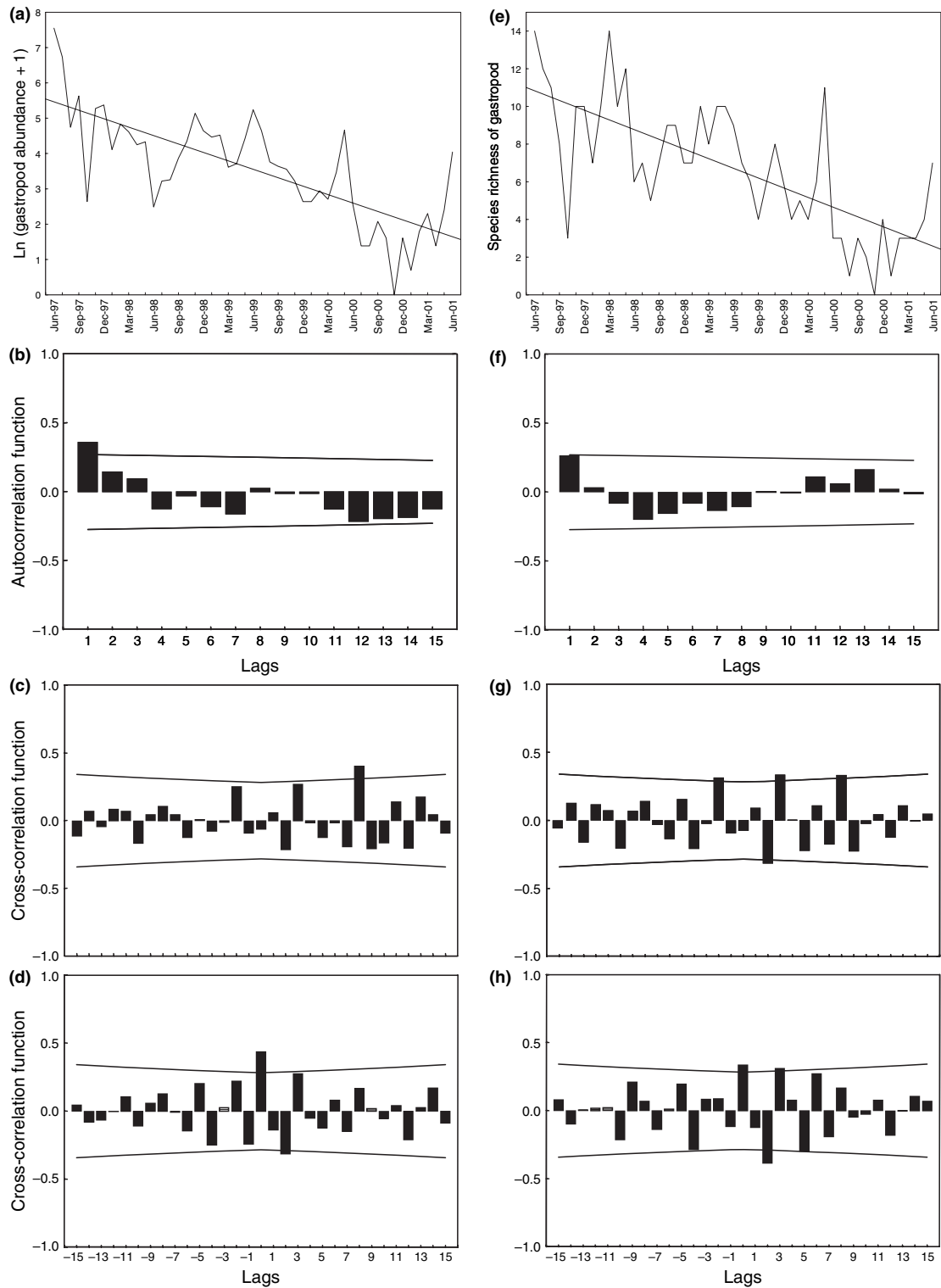


Fig. 3 Data series analyses of gastropod and parasitism descriptors in Combourg Lake over the June 1997–June 2001 period. Trends in gastropod abundance (a) and gastropod species richness (e), autocorrelation function of gastropod abundance (b) and gastropod species richness (f), cross-correlation function between residuals of gastropod abundance and residuals of prevalence (c) and residuals of trematode species richness (d) and cross-correlation function between residuals of gastropod species richness and residuals of prevalence (g) and residuals of trematode species richness (h).

6.1 ± 1.0%. From July 2001 to the end of the study period (October 2004), no trematode was found in gastropods, and during the 10-year survey, the abundance of infected gastropods decreased mainly in conjunction with a decrease in total gastropod abundance. The cross-correlation function between residuals of gastropod abundance and residuals of prevalence did not show a strong relationship, with only a positive correlation at lag 8 [in series differenced that is lag 7 ($t-1$, see Methods) in the original data series] being significant (Fig. 3c). Only two significant correlations were found in the cross-correlation function between gastropod abundance and species richness of trematodes: a positive one at lag -1 and a negative one at lag 1 in the original data series (Fig. 3d). The cross-correlation function performed between species richness of gastropods and trematode descriptors also showed some significant correlations (Fig. 3g,h).

Discussion

Long-term investigations of the dynamics of natural animal communities combining both parasites and other environmental stressors remain scarce (Esch *et al.*, 1975; Morley *et al.*, 2003, 2006; Jokela *et al.*, 2005). In this paper, the main goal was to test whether parasitism by larval trematodes, and punctuated or recurrent severe environmental perturbations (drought and toxic cyanobacteria) significantly affect the abundance and species composition of gastropods. According to the kind of environmental stressor, various responses of the gastropod community have been distinguished.

Stress induced by trematode parasitism

Trematode parasitism is a continuous stressor for gastropods, where potentially large temporal fluctuations might be partly explained by differences in the prevalences of both autogenic (permanent with entire life cycle within the lake, e.g. *Asymphylodora* sp. with freshwater fish as definitive host) and allogenic trematodes (temporary, e.g. *Tylodelphys* sp., *Notocotylus* sp., *Trichobilharzia* sp. and most echinostomatids and strigeids with migrant waterfowl as definitive hosts). High prevalences may result in decreased intrinsic growth rates of the gastropod populations, through the detrimental effects induced by larval

trematodes on their first intermediate host (parasitic castration and mortality), as suggested by some authors (Lafferty, 1993; Gérard, 1997, 2001a). Moreover, larval trematodes could modify the competitive interactions between closely related species gastropods such as *R. auricularia* and *R. peregra*. These two lymneids have numerous physiological and ecological similarities and do not usually coexist (Adam & Lewis, 1992) but they were found together with inverse population abundances in this study. One can suppose that differences in parasitism patterns may partly explain the differences in the abundance of *R. auricularia* and *R. peregra*.

However, despite the potentially strong impact of parasites on some host species, we demonstrated that trematode parasitism did not affect the gastropod community as a whole. Indeed, there was strong resistance of the gastropod community when faced with trematode parasitism.

The absence of an effect of the trematode stressor on the gastropod community may be due to other significant environmental stressors. As survival of parasites and hosts are interlinked, the decline of trematodes during the later years of the survey may be explained by the concomitant decline of gastropod populations (and perhaps the other hosts in the life cycle such as freshwater macroinvertebrates, fish and waterfowl). Indeed, trematode infection levels may depend on intermediate host densities, as suggested by Hanson & Poulin (2006). A second explanation for the decline of trematodes involves their own sensitivity to environmental perturbations, in particular for free larval stages (miracidium, cercariae). Helminths with a heteroxenous life cycle are supposed to be sensitive bioindicators of environmental changes in aquatic ecosystems (Lafferty, 1997; Lafferty & Kuris, 1999; Morley *et al.*, 2003, 2006), and field investigations have shown that the prevalence of digeneans in their intermediate and definitive hosts are inversely related to the degree of pollution (Siddall, Pike & MacVicar, 1993; Valtonen, Holmes & Koskivaara, 1997).

Drought episodes

Punctuated droughts were responsible for the disappearance of nearly all gastropod species, and thus represent a severe environmental stressor for gastropods and their associated parasites (Gérard, 2001b). Nevertheless, the extent of this stressor was limited

because of the resilience of the gastropod community, responding rapidly after the drought in 1996: the community was restored after only 9 months (May 1997). In contrast to the prosobranch species (only represented by Valvatidae), pulmonates dominated the gastropod community. This may be attributable to their broader physiological and ecological tolerances (see for reviews: Aldridge, 1983; MacMahon, 1983; Dillon, 2000). Indeed, pulmonates are well adapted to abiotic and punctuated stressors such as large water level variations and seasonal drought episodes that are common in the littoral zone of hydrosystems, due to their pulmonary respiration and their greater genetic and phenotypic plasticity, allowing them to vary trait expression in response to environmental changes. The extremely high reproductive effort recorded in May 1997 after the unusual drought episode in summer 1996 may be an adaptive response of freshwater gastropods to environmental fluctuations. The maintenance of life-history variation in response to fluctuating conditions in freshwater systems has also been reported for other aquatic invertebrates experiencing similar year-to-year variation of factors such as drought (e.g. Dudgeon, 1983; Brendonck & Riddoch, 1999).

Cyanobacterial toxins

Although blooms are a natural phenomenon in fertile freshwaters worldwide, anthropogenic eutrophication increases the frequency and severity of cyanobacterial blooms. Microcystin concentrations commonly exceed $5 \mu\text{g L}^{-1}$ in eutrophic waters during summer in temperate areas (Chorus & Bartram, 1999) and in the region of our study site (Brittany, France) 70% of monitored lakes support cyanobacterial densities that reach between 100 000 and five millions cells mL^{-1} during summer (L. Brient, unpubl. data). Bioaccumulation of microcystins in gastropods has been demonstrated in the field (e.g. Zurawell, Kotak & Prepas, 1999) as well as in laboratory experiments after exposure to dissolved microcystins (Gérard *et al.*, 2005) or ingestion of toxic cyanobacteria (Lance *et al.*, 2006). Cyanotoxin intoxication *in situ* had detrimental effects on performance of the snails (e.g. strong decrease of fecundity) (Gérard *et al.*, 2005; Gérard & Poullain, 2005; Lance *et al.*, 2007), indicating a negative impact of toxic cyanobacteria on the gastropod populations. As a consequence, the noted proliferations of

harmful cyanobacteria in the Combourg Lake might largely explain the decline of the gastropod community observed during the later years of the study.

To conclude, the response of the gastropod community to environmental stressors depends not only on the ecological and physiological characteristics of the gastropod species (Russel-Hunter, 1961), but also on the proportion of gastropod populations affected by the perturbations. In the case of parasitism, only some host populations were infected by larval trematodes (from 0.5% to 21.2% depending on species) and equilibrium would not be expected to be disrupted until parasite prevalence reaches a threshold value, specific to each gastropod population and to each host-parasite association. Disruption of equilibrium due to trematode parasitism is likely to be rarely observed in the gastropod community because of the generally low overall prevalence (2.9% of the snails in this study). Fluctuations in the gastropod community are more strongly related to environmental stressors such as desiccation or cyanotoxins that affect all the gastropods, than to parasitism by larval digenetic trematodes, which are themselves also susceptible to various pollution sources. Whereas drought is a stress historically observed in stagnant freshwaters, and resulting in resiliency of the gastropod community, the degradation of water quality related to increasing proliferations of toxic cyanobacteria is a more recent stressor and might explain the disruption of a stable equilibrium and the observed decline of the gastropod community.

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Appendix 1 Trematode prevalence in gastropod species from December 1994 to October 2004 in the Comboung Lake (69 samples). Absence of gastropod species in samples is indicated by ‘-’

	Vcr	Vpu	Vpi	Ltr	Spa	Rpe	Rau	Lst	Gal	Ppl	Pco	Acr	Sni	Hco	Ala
Dec-94	0.99	33.33	66.67	0.00	-	66.67	-	80.00	0.90	46.00	25.00	0.00	0.00	-	0.00
Mar-95	0.00	0.00	50.00	-	-	-	-	-	3.37	18.18	50.00	0.00	-	-	0.00
Jul-95	-	-	-	-	0.00	36.36	0.00	28.57	20.00	10.00	13.51	-	-	-	-
Mar-96	1.34	11.11	0.00	-	5.88	7.84	0.00	0.00	10.98	5.56	0.00	0.00	1.67	-	0.00
Jun-96	-	-	-	-	0.00	14.29	35.71	-	13.33	-	-	-	-	-	-
Sep-96	-	-	0.00	-	-	0.00	-	-	-	-	-	-	-	-	-
Oct-96	-	-	0.00	-	-	0.00	-	-	-	-	-	-	-	-	-
Nov-96	-	-	-	6.67	-	0.00	-	-	0.00	-	-	-	-	-	-
Dec-96	0.00	-	-	0.00	0.00	1.61	-	-	0.00	0.00	-	-	-	-	-
Jan-97	-	-	-	-	2.63	1.72	-	0.00	0.00	-	-	-	-	-	-
Feb-97	-	-	-	-	0.00	0.00	8.33	0.00	0.00	0.00	-	-	-	-	-
Mar-97	-	-	-	-	0.00	0.00	0.00	-	0.00	0.00	-	-	-	-	-
Apr-97	0.00	-	-	-	0.00	0.00	0.00	-	0.00	0.00	-	-	-	-	0.00
May-97	0.00	-	0.00	-	0.00	0.00	0.44	-	0.00	0.70	-	0.00	-	-	-
Jun-97	0.00	0.00	0.00	-	0.00	0.81	1.47	0.00	0.36	5.00	0.00	0.26	-	0.00	0.00
Jul-97	10.00	5.26	0.00	-	0.00	7.14	2.30	-	4.69	10.53	0.00	5.56	-	0.00	-
Aug-97	0.00	-	0.00	-	0.00	-	60.00	0.00	19.05	16.67	-	-	-	33.33	0.00
Sep-97	-	-	20.00	-	0.00	16.00	45.76	-	0.00	-	50.00	-	-	0.00	-
Oct-97	-	-	-	-	-	-	0.00	-	-	-	-	-	-	-	-
Nov-97	-	-	-	-	30.77	44.44	2.41	-	12.50	0.00	-	0.00	-	-	-
Dec-97	3.85	0.00	-	-	0.00	0.00	6.45	0.00	8.33	0.00	-	-	-	-	0.00
Jan-98	0.00	-	-	-	25.00	5.56	0.00	-	100.00	-	-	-	-	-	0.00
Feb-98	10.53	-	-	-	0.00	0.00	5.36	-	0.00	-	-	0.00	-	0.00	25.00
Mar-98	0.00	100.00	0.00	-	0.00	10.0	13.64	0.00	20.00	-	0.00	0.00	-	0.00	0.00
Apr-98	16.13	0.00	0.00	-	-	33.33	0.00	-	20.00	-	-	0.00	-	0.00	0.00
May-98	12.50	0.00	50.00	-	0.00	0.00	0.00	-	0.00	0.00	0.00	-	-	25.00	0.00
Jun-98	-	-	0.00	-	0.00	0.00	-	0.00	0.00	-	-	0.00	-	-	-
Jul-98	0.00	-	0.00	-	-	0.00	-	-	-	-	0.00	-	-	0.00	-
Aug-98	-	-	0.00	-	-	0.00	-	100.00	-	-	-	-	-	-	-
Sep-98	0.00	-	33.33	-	-	0.00	0.00	-	0.00	-	-	0.00	-	-	-
Oct-98	0.00	50.00	50.00	-	-	0.00	0.00	-	0.00	-	0.00	0.00	-	-	-
Nov-98	0.00	-	-	-	-	11.11	28.57	0.00	0.00	-	-	0.00	-	0.00	25.00
Dec-98	2.70	-	-	-	-	10.00	11.11	-	25.00	-	-	0.00	-	-	0.00
Jan-99	0.00	-	-	-	-	0.00	0.00	-	0.00	-	-	0.00	-	-	22.22
Feb-99	0.00	-	0.00	-	0.00	0.00	33.33	-	0.00	-	-	0.00	-	0.00	0.00
Mar-99	0.00	50.00	0.00	-	-	0.00	-	-	0.00	-	-	0.00	-	-	0.00
Apr-99	0.00	0.00	0.00	-	-	100.00	20.00	-	22.22	-	-	0.00	-	0.00	0.00
May-99	0.00	100.00	-	-	-	0.00	0.00	-	0.00	0.00	-	0.00	-	0.00	0.00
Jun-99	-	-	0.00	-	-	16.67	25.00	-	0.70	0.00	0.00	0.00	-	0.00	-
Jul-99	-	-	0.00	-	-	8.33	23.08	-	10.00	-	-	0.00	-	0.00	-
Aug-99	-	-	10.53	-	-	0.00	23.08	-	0.00	0.00	-	-	-	-	-
Sep-99	-	-	10.53	-	-	0.00	40.00	-	20.00	-	-	-	-	-	-
Oct-99	0.00	-	0.00	-	-	-	13.33	-	0.00	-	-	-	-	-	0.00
Nov-99	0.00	0.00	33.33	-	-	0.00	12.50	-	0.00	0.00	-	-	-	-	-
Dec-99	0.00	-	0.00	-	-	0.00	0.00	-	0.00	-	-	-	-	-	0.00
Jan-00	0.00	-	-	-	-	0.00	83.33	-	-	-	-	-	-	-	0.00
Feb-00	0.00	-	0.00	-	-	33.33	66.67	-	-	-	-	-	-	-	-
Mar-00	-	-	0.00	-	-	0.00	0.00	-	0.00	-	-	-	-	-	-
Apr-00	0.00	-	25.00	-	-	-	33.33	-	55.56	-	-	-	-	-	0.00
May-00	11.11	-	28.57	-	-	0.00	4.35	-	0.00	0.00	0.00	0.00	-	0.00	0.00
Jun-00	-	-	11.11	-	-	-	100.00	-	-	-	-	-	-	-	-
Jul-00	-	-	-	-	-	100.00	0.00	-	0.00	-	-	-	-	-	-
Aug-00	-	-	0.00	-	-	-	-	-	-	-	-	-	-	-	-
Sep-00	-	-	0.00	-	-	-	-	-	0.00	-	-	-	-	-	-

Appendix 1 (Continued)

	Vcr	Vpu	Vpi	Ltr	Spa	Rpe	Rau	Lst	Gal	Ppl	Pco	Acr	Sni	Hco	Ala
Oct-00	-	-	0.00	-	-	-	0.00	-	-	-	-	-	-	-	-
Nov-00	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dec-00	-	-	-	-	-	0.00	0.00	0.00	-	-	-	-	-	-	0.00
Jan-01	-	-	-	-	-	0.00	-	-	-	-	-	-	-	-	-
Feb-01	0.00	-	-	-	-	0.00	-	-	-	-	-	-	-	-	0.00
Mar-01	0.00	-	0.00	-	-	-	0.00	-	-	-	-	-	-	-	-
Apr-01	0.00	-	0.00	-	-	-	0.00	-	-	-	-	-	-	-	-
May-01	-	-	16.67	-	-	-	0.00	-	-	-	-	-	-	0.00	0.00
Jun-01	-	-	0.00	-	-	-	0.00	-	3.13	-	-	0.00	-	0.00	0.00
Jul-01	-	-	0.00	-	-	-	0.00	-	0.00	-	-	-	-	-	-
Aug-01	-	-	0.00	-	-	0.00	0.00	-	-	-	-	-	-	-	-
Sep-01	-	-	0.00	-	-	-	-	-	-	-	-	-	-	0.00	-
Jun-03	-	-	-	-	-	0.00	0.00	-	-	-	-	-	-	-	-
May-04	-	-	-	-	-	-	0.00	-	-	-	-	0.00	-	0.00	-
Oct-04	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Vcr: *Valvata cristata*, Vpu: *Valvata pulchella*, Vpi: *Valvata piscinalis*, Ltr: *Lymnaea truncatula*, Spa: *Stagnicola palustris*, Rpe: *Radix peregra*, Rau: *Radix auricularia*, Lst: *Lymnaea stagnalis*, Gal: *Gyraulus albus*, Ppl: *Planorbis planorbis*, Pco: *Planorbis cornutus*, Acr: *Armiger crista*, Sni: *Segmentina nitida*, Hco: *Hippeutis complanatus*, Ala: *Acroloxus lacustris*.