

Relationship between freshwater gastropods and plant communities reflecting various trophic levels

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Abstract

Plant communities were examined in ponds in Brittany (north-west France) and then classified into six types reflecting different trophic levels: oligotrophic, oligodystrophic, mesotrophic, meso-dystrophic, meso-eutrophic and eutrophic. In 45 of these ponds, aquatic snails were sampled in order to determine the relationship between the gastropod species richness and the water trophic levels as indicated by plant community types. The second aim of this study was to determine whether some gastropod species were characteristic of a particular trophic level. The number of plant communities in the ponds was also taken into consideration.

A trophic gradient was found along the F1 axis on the principal plane of the correspondence analyses. The species richnesses low or zero and especially the lymneid, *Lymnaea glabra* were close to the oligo-dystrophic and oligotrophic communities. In contrast, the highest numbers of snail species (5 and above) were found in the most eutrophic ponds where *Hippeutis complanatus*, *Planorbis planorbis*, *Lymnaea stagnalis* and *Planorbarius corneus* were particularly common. The latter species inhabited the ponds including on average the greatest number of macrophyte communities but no significant differences were found between snail species. The ponds which contained the greatest numbers of plant communities included the richest gastropod communities (7 and more) but also the poorest ones (0 or 1 species). Relationships between freshwater snails, macrophytes and trophic levels are discussed.

Introduction

Freshwater gastropod distribution has been studied in relation to many environmental factors including physico-chemical features of water and vegetation. In these field or experimental studies, particular snail-plant relationships have been investigated and distance chemoreception demonstrated (Sterry *et al.*, 1983; Haynes & Taylor, 1984). In contrast, the distribution of some, and particularly of ubiquitous snail species, seems to be independent of vegetational characteristics, e. g. *Lymnaea palustris* (Müller) (Caquet, 1990). Fresh macrophytes are rarely eaten by snails (Reavell, 1980; Thomas, 1987), but they do provide shelter from predators and disturbances (Brönmark,

1985), egg-laying sites and substrates on which snails may crawl, and they support growth of periphyton (algae and bacteria) which is an important food source (Ökland, 1990). Freshwater snail distributions have also been considered to reflect physico-chemical features of water, notably calcium concentration and alkalinity (G. B. G. Dussart, 1976; Meier-Brook *et al.*, 1987). Clarke (1979) and Legendre *et al.* (1984) are among the rare malacologists who have specifically used the term 'trophic stages' in their papers.

Hutchinson (1969) noted that there had been many definitions of the term 'trophic' since its introduction by Weber (1907). According to Codd & Bell (1985): 'the term eutrophication signifies the development of a water body into a state in which the aerobic micro-

bial decomposition of organic matter consumes more oxygen than is introduced into the system, resulting in an increasing oxygen deficit. This definition has been extended beyond the early concept of eutrophication as a natural phenomenon of increasing phytoplankton growth due to enrichment with mineral nutrients'. The enrichment of natural waters can be of natural or/and human origin. In some lakes, organic matter accumulates slowly, and its nature is such that decomposition of breakdown products is slow. These lakes are oligotrophic, but their waters are acid and yellowish-brown due to humic matter. Moreover, the water transparency is relatively low and the lake bottom is covered by a blanket of organic detritus which is only transformed slowly. These lakes have been described as dystrophic lakes (B. Dussart, 1985).

The present study investigates relationships between trophic levels of ponds and snails. Plant communities were used as indicators of the prevailing trophic conditions in the ponds, because the plant communities reflect both vegetation dynamics and trophic levels of water and substrate. Lake macrovegetation is related, to some extent, to the three classical lake types, oligotrophic, eutrophic and dystrophic (Ökland, 1990). According to Spencer & Bowes (1990), the most important environmental factors limiting growth of emergent and floating weeds are temperature, root anoxia and nutrient availability. Papastergiadou & Babalonas (1993) reported that water conductivity together with inorganic nitrogen and phosphorus compounds, are the most important factors affecting macrophyte development. These authors also noted strong relationship between high nitrate and ammonia concentrations and the presence of particular types of plant associations. Few malacologists investigated nutrient states, such as those of phosphorus and nitrogen, an exception being Pip (1987).

The present study used a classification of Breton wetlands including ponds, based on phytosociological analysis (Clement, 1986; Clement & Touffet, 1988). The number of macrophyte communities in the ponds was also of interest because a large number reflects a diversified ecosystem. This study describes:

- gastropod species richness in relation to both the number of plant communities present, and the trophic levels indicated by these plant communities;
- associations between 13 gastropod species and both the number of plant communities and the trophic levels indicated by these.

Materials and methods

Study sites

The 45 ponds studied were located in eastern Brittany, North-Western France: latitudes 48°4'–47°44' north; longitudes 2°14'–1°08' west. All ponds were more than a hundred years old. The underlying geological formations were granitic and metamorphic or pre-cambrian and paleozoic rocks (schists and sandstones) in the Armorican massif. Pond bottoms were usually covered by mud, and surface areas ranged from 1 to 97 hectares (Costil, 1993).

Plants community type in relation to trophic levels

Plant communities, as defined by phytosociological analysis using the sigmatis method (Braun-Blanquet & Pavillard, 1928; Gehu & Rivas-Martinez, 1981), provide reliable indexes of phytocenotic diversity. Plant communities as opposed to plant species, provide fuller information about environmental conditions. Phytoecological analyses can be derived from the fact that given plant community types behave similarly under similar environmental conditions (Clement & Touffet, 1988). Some macrophyte communities in the sampled ponds were indeed associated with particular trophic levels (Table 1). Ponds were allocated to one or other of the following groups on the basis of their macrophyte community type: oligo-dystrophic (8 ponds), oligomesotrophic (5), meso-dystrophic (7), mesotrophic (10), meso-eutrophic (1) and eutrophic (14).

Snail sampling

The study took place from April 28 to May 20, 1988, before recruitment of young snails to any adult populations. Temperatures ranged from 14 °C to 20 °C. Snails were collected with a square hand-net (50 × 50 cm) in the littoral area (depth: 0–1.2 m). Six 30-second sweeps were made giving a total sampling time of 3 minutes. The number of samples taken from qualitatively different areas in ponds was a function of the surface areas occupied by these zones. All material collected (detritus, vegetation, substratum, snails) was brought back to the laboratory. The samples were then filtered using a 1 mm-grid sieve, and the snails then sorted and examined under a binocular microscope.

Table 1. Macrophyte communities recorded in the 45 studied ponds in relation to various trophic levels indicated by plant communities (named according to the dominant characteristic species).

Trophic levels	Macrophyte communities reflecting the trophic level	Abbrev.
Oligo-dystrophic	<i>Ranunculus ololeucus</i> Ll.	ROL
	<i>Juncus heterophyllus</i> L. Duf.	JHE
	<i>Pilularia globulifera</i> L.	PGL
	<i>Eleocharis multicaulis</i> Smith & <i>Helodes palustris</i> Spach	EHP
	<i>Carex panicea</i> L. & <i>Carex dernissa</i> Horn	CCD
	<i>Potamogeton polygonifolius</i> Pourr. & <i>Helodes palustris</i>	PHP
	<i>Juncus acutiflorus</i> Ehrh. & <i>Sphagnum apiculatum</i> Limdb.	JSA
	<i>Scirpus fluitans</i> L.	SFL
	<i>Juncus bulbosus</i> L.	JBU
	<i>Potentilla palustris</i> Scop. & <i>Menyanthes trifoliata</i> L.	PMT
Oligotrophic	<i>Littorella uniflora</i> (L.) Asch.	LUN
	<i>Littorella uniflora</i> & <i>Eleocharis palustris</i>	LEP
	<i>Eleocharis acicularis</i> Roem. & Schult.	EAC
Meso-dystrophic	<i>Carex paniculata</i> L.	CPA
	<i>Carex vesicaria</i> L.	CVE
	<i>Carex elata</i> All.	CEL
Mesotrophic	<i>Phalaris arundinacea</i> L.	PAR
	<i>Myriophyllum alterniflorum</i> & <i>Nymphaea alba</i> L.	MNA
Meso-eutrophic	<i>Typha latifolia</i> L.	TLA
	<i>Typha angustifolia</i> L.	TAN
	<i>Scirpus lacustris</i> L.	SLA
	<i>Phragmites australis</i> (Cav.) Trin. ex Steud	PAU
Eutrophic	<i>Glyceria maxima</i> Holmb	GMA
	<i>Carex riparia</i> Curt	CRI
	<i>Carex pseudocyperus</i> L.	CPS
	<i>Rumex hydrolapathum</i> Huds.	RHY
	<i>Rorripa amphibia</i> L. & <i>Oenanthe aquatica</i> Poir.	ROA
	<i>Eleocharis palustris</i> & <i>Oenanthe fistulosa</i> L.	EOF
	<i>Potamogeton</i> spp.	POT
	<i>Hydrocharis morsus-ranae</i> L.	HMR
	<i>Ceratophyllum demersum</i> L.	CDE
	<i>Hottonia palustris</i> L.	HPA
	<i>Elodea canadensis</i> Mich.	ECA
	<i>Lemna minor</i> L.	LMI
	<i>Utricularia neglecta</i> Lehm.	UNE

Data analysis

Only the data for species collected in at least 4 ponds were considered for statistical analysis. When the abundance of a species was equal to one in a given

pond, this species was only considered further if it had already been collected during one of the several prospective studies. The data for species richnesses from 7 to 9 were pooled because of the low number of occurrences. Data sets were compared using non-

Table 2. The most frequent gastropod species collected in the 45 ponds studied. N is the number of ponds with the species.

Family	Species	Abbreviations	N	Frequency (%)
Lymneidae	<i>Lymnaea peregra</i> (Müller)	PER	37	82.2
	<i>Lymnaea palustris</i> (Müller)	PAL	20	44.4
	<i>Lymnaea glabra</i> (Müller)	GLA	11	24.4
	<i>Lymnaea stagnalis</i> (L.)	STA	6	13.3
Physidae	<i>Physa acuta</i> (Draparnaud)	ACU	23	51.1
Planorbidae	<i>Gyraulus albus</i> (Müller)	ALB	16	35.5
	<i>Planorbarius corneus</i> (L.)	COR	8	17.8
	<i>Anisus spirorbis</i> (L.)	SPI	8	17.8
	<i>Planorbis planorbis</i> (L.)	PLA	5	11.1
	<i>Bathyomphalus contortus</i> (L.)	CON	5	11.1
	<i>Segmentina nitida</i> (Müller)	NIT	4	8.9
	<i>Hippeutis complanatus</i> (L.)	COM	4	8.9
Bithyniidae	<i>Bithynia tentaculata</i> (L.)	TEN	8	17.8

Table 3. Gastropod species richness (R), number of occurrences of each species richness value (N) and mean number of plant communities ($N_{pc} \pm S.D.$)

R	0	1	2	3	4	5	6	7 and +
N	3	2	12	6	4	6	5	7
$N_{pc} \pm$	$11.7 \pm$	$13.0 \pm$	$7.2 \pm$	$6.3 \pm$	$4.25 \pm$	$8.0 \pm$	$12.4 \pm$	$15.6 \pm$
S.D.	10.3	4.2	4.3	4.2	3.59	5.3	9.4	5.1

Table 4. Mean ($\pm S.D.$), minimum (Min) and maximum (Max) numbers of macrophyte communities present in the ponds sampled for the various gastropod species (the numbers in brackets are the numbers of occurrences of each species).

Species	Mean	Min	Max
<i>Lymnaea peregra</i> (37)	9.3 ± 6.4	1	25
<i>Lymnaea palustris</i> (20)	10.5 ± 7.5	1	25
<i>Lymnaea glabra</i> (11)	11.9 ± 5.8	5	19
<i>Lymnaea stagnalis</i> (6)	13.2 ± 6.2	5	19
<i>Physa acuta</i> (23)	10.1 ± 5.3	1	19
<i>Gyraulus albus</i> (16)	12.0 ± 7.7	1	25
<i>Planorbarius corneus</i> (8)	14.0 ± 5.8	5	19
<i>Anisus spirorbis</i> (8)	10.4 ± 6.7	1	21
<i>Planorbis planorbis</i> (5)	7.3 ± 7.2	1	19
<i>Bathyomphalus contortus</i> (5)	8.8 ± 8.3	1	21
<i>Segmentina nitida</i> (4)	10.2 ± 6.5	1	18
<i>Hippeutis complanatus</i> (4)	9.8 ± 3.5	6	11
<i>Bithynia tentaculata</i> (8)	10.6 ± 8.6	1	25

parametric tests (Kendall correlation and the Kruskal-Wallis test). Multivariate analysis (Factorial Correspondence Analysis) provided two distributions in the F1 F2 planes, for plant communities in relation to both gastropod species richness and species composition. All calculations were performed with STATVIEW (1988) or STAT-ITCF (1988) programs.

Results

Gastropod species collected most frequently in the 45 ponds belonged to three pulmonate families and to one prosobranch family (Bithyniidae) (Table 2). *L. peregra* collected in more than 80% of the ponds was the most frequent species, whereas the planorbids, *H. complanatus* and *S. nitida*, were found in only four ponds.

Plant communities and gastropod species richness

The number of plant communities varied from one pond to another, ranging from 1 to 25 (mean 9.4; SD=6.4) and differed significantly in relation to snail species richness ($H=12.33$; $p=0.05$; Kruskal-Wallis test). Highest mean number of plant communities (15.6) was recorded for ponds from which seven or more gastropod species were sampled, whereas the lowest mean number (4.25) was recorded from ponds with only four species (Table 3). Gastropod species richness was significantly and positively correlated with the number of plant communities present: $t=0.204$ ($Z=1.903$; $N=42$; $p<0.05$; Kendall correlation). A contingency table which recorded gastropod species richness and plant community type (Table 1) was used as matrix for correspondence analysis. The first two axes included 57% of the total inertia of the point plot, of which 40.4% for F1 and 16.2% for F2 (Fig. 1). The macrophyte communities characteristic of oligo-dystrophic environments contributed most to F1 (the relative contribution to inertia of this axis, named CTR, was of 45.2%), and species richness equal to zero (R0; CTR=34.5%) was close to them. Plant communities which reflect the most eutrophic conditions (meso-eutrophic and eutrophic) and greatest species richnesses (R5, R6 and R7+) were located on the opposite side of the factorial space. There was therefore a trophic gradient along F1. Species richness R6 made the greatest contribution to F2 (47.5%) which also isolated the plant communities related exclusively (ROA, EOF) or preferentially (ECA, TLA) to R6. This axis also appeared to separate the communities of emergent plants (HPA, PAU, TLA) from communities of hydrophytes (LMI, CDE).

Plant communities and gastropod species

P. corneus inhabited ponds in which the number of plant communities was, on average, the highest (14.0), in contrast to *P. planorbis* which was associated with ponds having an average plant community number of only 7.3 (Table 4). Nevertheless, no significant differences were found among species ($H=7.194$; $p=0.85$; Kruskal-Wallis test).

In Fig. 2, the F1 and F2 axes accounted for 58.9% of the overall inertia on the principal plane of the correspondence analysis based on the plant communities and the 13 gastropod species. The first axis (40% of the inertia) reflected a trophic gradient (as for species richness). The eutrophic and the meso-eutrophic commu-

nities (respectively, the relative contributions to inertia of this axis, CTR=19.7% and CTR=5.6%) were thus found at the opposite extreme to the oligo-dystrophic communities (CTR=55.2%). Species located close to the oligo-dystrophic macrophyte communities were: *L. peregra* (PER; CTR=10.7%), *P. acuta* (ACU; CTR=24.5%), *L. glabra* (GLA; CTR=18.6%) and *A. spirorbis* (SPI; CTR=0.7%). The first two snail species were found in every plant community (with the exception of *P. acuta* which was not sampled with *Utricularia neglecta*) and they can be considered ubiquitous. The distribution of *L. glabra*, a rarer species, was more closely associated with oligotrophic conditions, even when these had a somewhat dystrophic character. *A. spirorbis* was similar, but to a slighter extent, and the finding must be treated with caution because of its poor projection on the plane. This planorbis, like *B. contortus*, inhabited ponds for which an average of only one eutrophic plant community was recorded. When the distributions of *P. corneus* (COR) and *L. stagnalis* (STA) were considered, the number of eutrophic plant communities in ponds reached a mean of 3.5 and these snails were located on the F1 F2 plane close to the most eutrophic communities such as *P. planorbis* (PLA) and *H. complanatus* (COM). The F2 axis (18.7% of the inertia) separated the three oligotrophic communities (for EAC, CTR=6.4%) from the oligo-dystrophic communities, except for *Scirpus fluitans*, which is sometimes regarded as a pioneer species in disturbed sites, even if these are meso or eutrophic ponds (Szymeja & Clement, 1990).

Discussion

Number of plant communities

An increase in number of plant communities in a pond generally corresponds to an increase in number of plant species. This is a general but not invariable feature because macrophyte communities are characterized by variable species number, aquatic communities usually including fewer species than amphibious ones (Felzines, 1983). While number of plant species could not then be used, the number of plant communities does seem to provide useful information on phytoecological conditions.

In this study, gastropod species richness was significantly correlated with the number of plant communities and this, in particular, reflected increase in snail species richness with increase in habitat diversi-

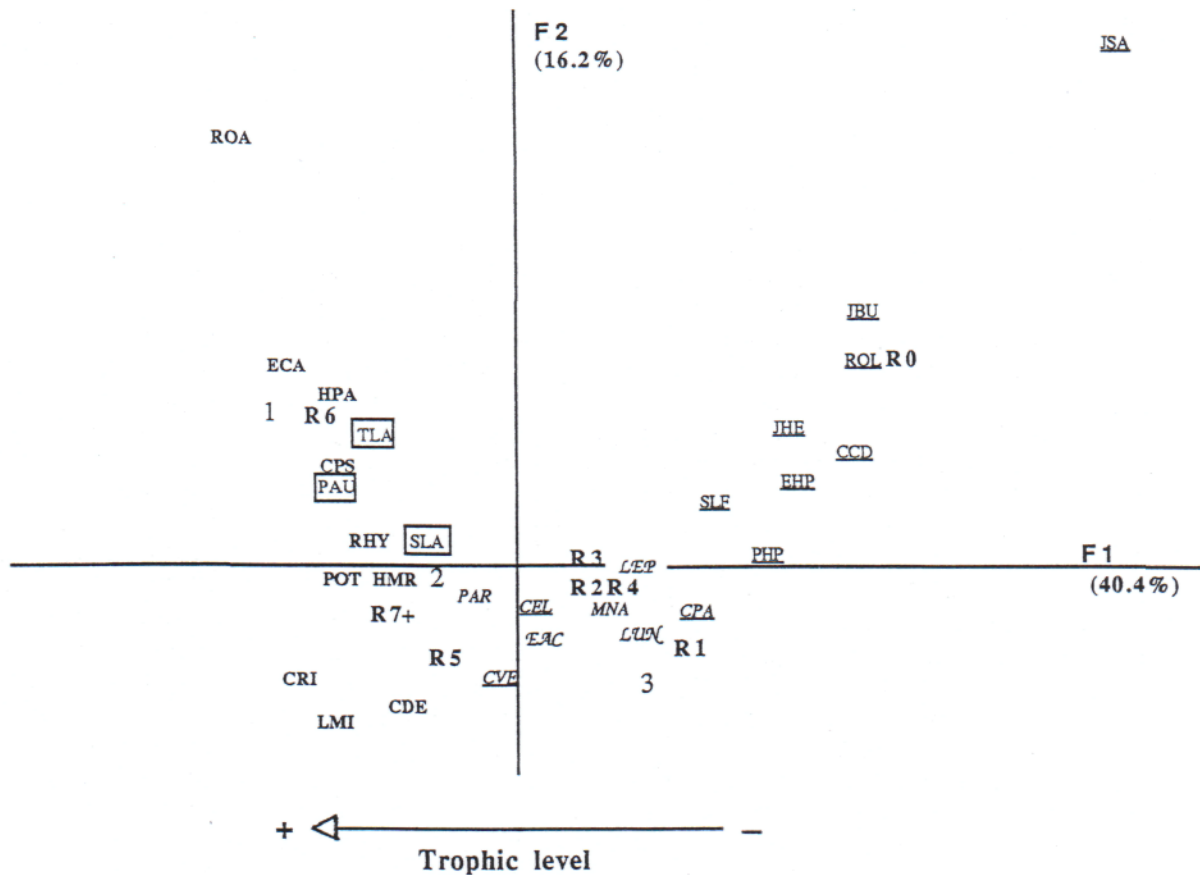


Fig. 1. Representation of the 8 values of gastropod species richness (from R0 to R7+) and the macrophyte communities (reflecting various trophic levels) on the principal plane of the correspondence analysis. R7+ represents the species richnesses equal to 7 and above. For the community abbreviations, see Table 1. The numbers represent the communities showing the same coordinates: 1 corresponds to EOF and UNE; 2 to TAN and GMA; 3 to PGL and PMT. The trophic levels of the macrophyte communities (MCO) (see Table 1) are indicated as follows: - oligo-dystrophic: MCO; oligotrophic: MCO; meso-dystrophic: MCO; mesotrophic: MCO; meso-eutrophic: MCO; eutrophic: MCO.

ty. The importance of a diversified plant environment for snails has been long stressed by many authors, for example Boycott (1936) and Brönmark (1985). Aho (1966) studied gastropod population density and found this to be highest in lakes with the highest plant productivity. The lowest plant community number was recorded for a snail species richness of 4. The relative scarcity of gastropod species from 2 to 4 could have been due to the low macrophyte community diversity. The number of plant communities increases as a pond matures. It is likely that the ponds concerned, despite their age, nevertheless were still at an early stage of development. The correlation between gastropod species richness and plant community number was not linear since ponds without snails (R0) or with only one species (R1) had an average of more than 11.5 plant

communities. Here, macrophyte community number cannot explain low snail species number. An explanation is more likely to be found in the qualitative characteristics of the vegetation, since plant morphology and its fine structure may be more significant (Calow, 1973). Moreover, the fact that plants are submerged or emergent is of great importance for snails (Lamarche *et al.*, 1982; Lodge *et al.*, 1987) and another aspect of quality is trophic level as reflected by plant communities. There were no differences in snail species distribution in relation to number of plant communities recorded in the ponds they inhabited. The snails lived in ponds which included on average 10.6 macrophyte communities (SD=1.8; N=13). To our knowledge, no gastropod species have been reported as actively avoiding vegetation. Irrespective of species, the snails

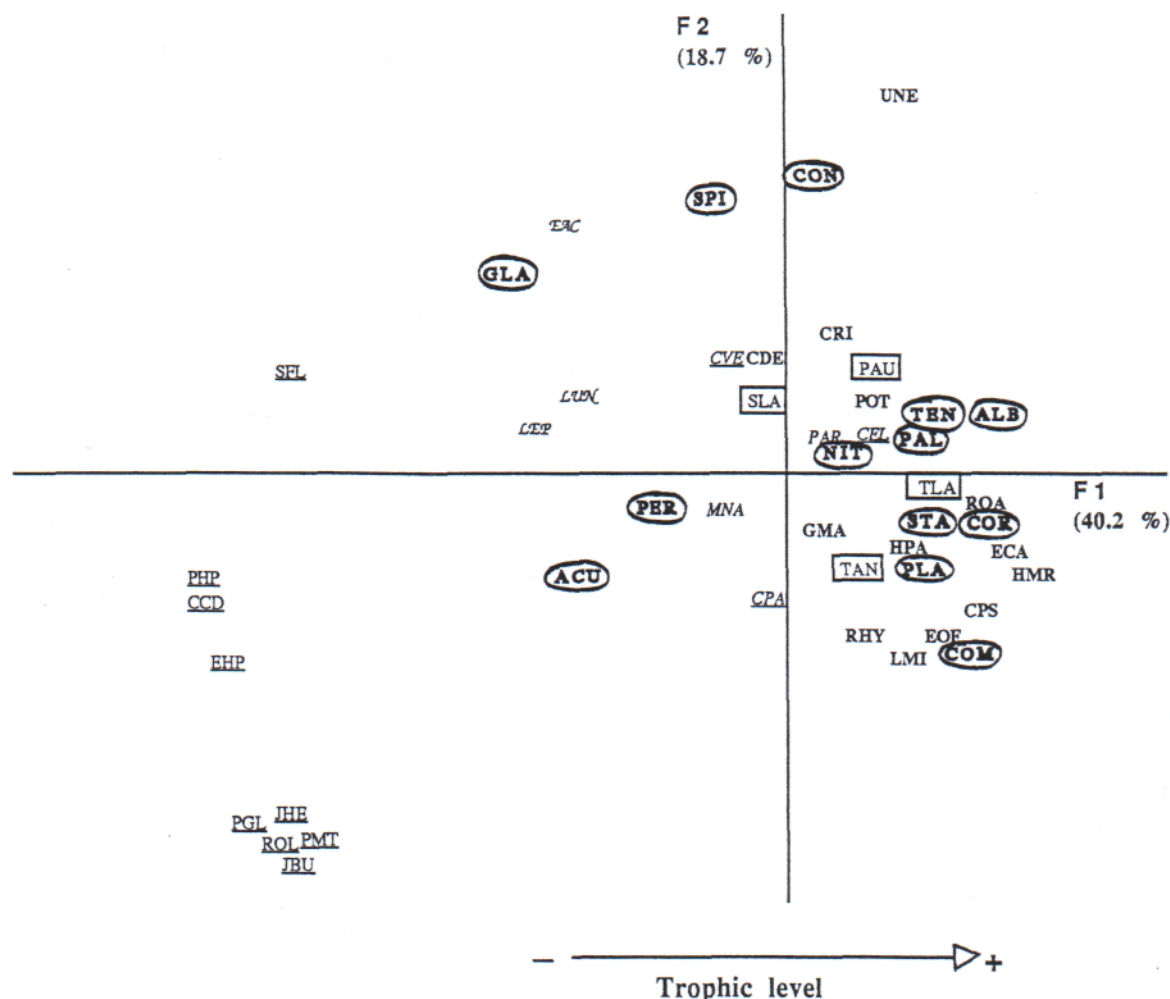


Fig. 2. Distribution of the 13 gastropod species and the macrophyte communities (reflecting various trophic levels) in the FIF2 plane of the correspondence analysis. For abbreviations, see the Tables 1 and 2. The communities around **ROL** have the same coordinates. The trophic levels of the macrophyte communities (MCO) (see Table 1) are indicated as follows: – oligo-dystrophic: **MCO**; oligotrophic: **MCØ**; meso-dystrophic: **MCO**; mesotrophic: **MCO**; meso-eutrophic: **MCO**; eutrophic: **MCO**. The snail species: **SPE**.

favoured the ponds where the number of plant communities tended to be high. Despite an apparent similarity in ecological requirements, gastropod species differ from each other in many respects (Aho *et al.*, 1981). The mean number of plant communities in the 45 ponds was 9.4 (SD = 6.4). The mean number was lower than this for three snail species, *P. planorbis*, *B. contortus* and *L. peregra*, when plant community number was calculated for snail species. Ökland (1990) did not give details about *P. planorbis*, rarely collected, but he reported that the two other species were significantly associated with quantitatively and qualitatively rich vegetation (category A) and with quantitatively rich vegetation (category B), but to a

much lesser extent than most other species. According to Mouthon (1986), these two species are commonly found on stones. The lack of significant between-species differences suggested that qualitative features even more than the quantitative features of plant communities should be considered when factors affecting snail species distributions are being studied.

Trophic conditions

Trophic conditions for most authors who have considered the question have only meant quantity of food available for the snails. They have emphasized the close relationships between the macroveg-

etation (therefore habitat productivity) and the biology and dynamics of specific populations (Russell-Hunter, 1961; Legendre *et al.*, 1984; Brown & De Vries, 1985). Growth of *Potamopyrgus jenkinsi* (Smith) was faster in the environment (water and substrate) of a more eutrophic lake, regardless of whether snails were from meso-oligotrophic or eutrophic lakes (Dorgelo, 1988).

The trophic conditions recorded in the present study, and thus the results, must be considered in relation to the fact that almost all Brittany ponds would be considered as eutrophic by hydrobiologists, if compared with the unproductive lakes of Scotland and Canada, or with the mountainous lakes of Scandinavia. In both correspondence analyses the F1 axis reflected a trophic gradient which represented an appreciable proportion of the overall inertia (40.4% and 40.2%, respectively for gastropod species richness and for the different species). In the F1 F2 factorial plane, greatest species richnesses (5 or more) were located near the meso-eutrophic and eutrophic communities, while the lowest values and notably zero were located in the opposite group. It might be thought that the high habitat productivity would result in high snail biomass but not necessarily high snail species richness. The present analysis has shown that an environment with high trophic level, reflected in the presence of eutrophic plant communities, provides favourable conditions for the coexistence of many species. Ökland (1990) has expressed this idea as follows: 'For most species, sites with a quantitatively and qualitatively rich vegetation (type A) were obviously much more favourable than sites where only the quantitative aspect is significant (type B); the major distinction between these two types of vegetation was the presence of eutrophic plant species in the first category, and their absence in the second'. If calcium is adequate for snail survival, then lake productivity and habitat diversity may determine snail density and species richness within a region (Russell-Hunter, 1978). Pip (1987) found that gastropod species richness, when pooled for all her study sites, was significantly and positively correlated with (molybdenum reactive) phosphorus, total dissolved solids and total alkalinity, and negatively correlated with dissolved organic matter. Browne (1981) found a positive, but non-significant relationship between mollusc species richness and eutrophication level in New York lakes.

The trophic stage of a given habitat is a synthetic parameter which is correlated with other factors including water chemistry, vegetation, pond substra-

tum and the geological formations of the drainage basin. Species, for example, might respond not directly but indirectly to nutrient concentrations through the effects of these on oxygen content, predators and plant cover (Legendre *et al.*, 1984). The trophic stage is also related to the pond surface, small ponds tending to be more eutrophic than larger ponds. A complicating factor in the present study was that the size of the studied ponds ranged between 1 and 97 hectares, yet no significant correlation was found between the pond area and gastropod species richness (Costil, 1993). Eutrophication affects snail communities but a reverse effect also exists, and could be quite important for lake management. In experimental studies, Van Vierssen *et al.* (1993) showed that well-developed snail communities can to some extent remove spring periphyton accumulations, so offsetting eutrophication.

Species could be classified according to their position along the F1 axis as follows:

- Eutrophic conditions: *H. complanatus*;
- Meso-eutrophic conditions: *P. corneus*, *L. stagnalis*, *P. planorbis*;
- Mesotrophic conditions: *L. palustris*, *B. tentaculata*, *S. nitida*, *G. albus*;
- Oligotrophic conditions: *L. glabra*, *A. spirorbis*, *B. contortus*;
- All types of environments: *L. peregra*, *P. acuta*.

In this tentative classification, *H. complanatus* emerges the most eutrophic species. It was collected by Mouthon (1981) in a pond area polluted by sewage, where green algae and the snails thrived. It is of course more difficult to classify the intermediate species, e.g. *G. albus*, which was collected in a wider variety of habitats than the three other species of its category. A significant positive correlation has been recorded between the distribution of this planorbid and nitrates, and a significant negative correlation with phosphates (G. B. J. Dussart, 1976). According to Legendre *et al.* (1984), some benthic species seem to be good indicators of the eutrophic level of the ecosystem. These authors noted that some species are limited to eutrophic waters, and most of the species which are tolerant of oligotrophic waters could live in environments richer in nutrients. The latter species are ubiquitous and sometimes collected from snail communities with few species, where interspecific competition is low (Costil, 1994). In North America, Clarke (1979) attempted to use freshwater gastropods as indicators of progressive trophic stages in lakes. He reported from qualitative records that most species and subspecies were eurytrophic, but a few were both common and entirely,

or nearly, restricted to lakes of particular trophic levels. These latter species – e.g. *Stagnicola catascopium* (Say) and *Planorbula armigera* (Say) – with the exception of *Lymnaea stagnalis*, which Clarke found in eutrophic lakes as we did, are not found in Europe. The following species, present in our study area and ‘recently’ introduced or very rare in North America, were only collected in eutrophic lakes: *Armiger crista* (L.), *Lymnaea auricularia* (L.) and *L. peregra*. We cannot draw conclusions about the first two species because they were found, respectively, on only one and two occasions in the ponds we studied. On the other hand, we found *L. peregra* in all kinds of ponds, and it is probable that the species, when introduced, requires a special type of habitat (in the present case a richer one). In the second factorial analysis of the present study, the F2 axis appeared to separate the oligotrophic communities from the oligo-dystrophic communities. This axis also classified the gastropod species into two categories: the species which tolerated dystrophy (*L. peregra*, *P. acuta*), and those which tolerated this but with more difficulty (*L. glabra*, *A. spirorbis*). Dystrophic conditions have been reported to be unfavourable for freshwater animals (Tucker, 1958; G. B. J. Dussart, 1976; Petersen *et al.*, 1986) including snails (Aho, 1966; Ökland, 1990). The colour of water is primarily of value as an indicator of humic content, and also correlates strongly with lake water pH (Aho *et al.*, 1981). These authors found a significant negative correlation between the colour of the water and snail species richness.

In the future, it would be interesting to investigate the relationships between trophic stages and snail distributions, measured in terms both of their abundance and biomass. Some authors have reported that vegetation is a good indicator of trophic conditions. No publications appear to have dealt with the relationships between freshwater snail distributions and trophic levels as reflected by plant community types. The present study does, however, suggest that this could be relevant and further work would be required to examine these questions in more detail and confirm these first conclusions (for example by obtaining further records of snail species occurrences). This paper has examined snail distributions in relation to trophic conditions as indicated by vegetation communities. A forthcoming paper will examine the relations between snail distributions and trophic conditions as determined by chemical analyses of water.

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