Hydroperiod, predators and the distribution of physid snails across the freshwater habitat gradient

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SUMMARY

1. Studies of species distributions across environmental gradients further our understanding of mechanisms regulating species diversity at the landscape scale. For some freshwater taxa the habitat gradient from small, shallow and temporary ponds to large, deep and permanent lakes has been shown to be an important environmental axis. Freshwater snails are key players in freshwater ecosystems, but there are no comprehensive studies of their distributions across the entire freshwater habitat gradient. Here we test the hypothesis that snail species in the family Physidae are distributed in a non-random manner across the habitat gradient. We sampled the snails, their predators and the abiotic environment of 61 ponds and lakes, spanning a wide range in depth and hydroperiod.

2. Temporary habitats had the lowest biomass of predators. Shallow permanent ponds had the highest biomass of invertebrate predators but an intermediate fish biomass. Deep ponds and lakes had the highest fish biomass and intermediate invertebrate biomass. Five species of physids occurred in the regional species pool and 60 of the 61 ponds and lakes surveyed contained physid snails. Each pond and lake contained an average of just 1.2 physid species, illustrating limited membership in local communities and substantial among-site heterogeneity in species composition.

3. Physids showed strong sorting along the habitat gradient, with Physa vernalis found in the shortest hydroperiod ponds and Aplexa elongata, P. gyrina, P. acuta and P. ancillaria found in habitats of successively greater permanence. When organised into a site-by-species incidence matrix with sites ordered according to their hydroperiods, we found the pattern of incidence to be highly coherent, showing that much of the heterogeneity in species composition from one pond to another is explained by hydroperiod. We also found that the number of species replacements along this gradient was higher than random, showing that replacement is more important than nesting in describing species composition in ponds of different hydroperiod.

4. Discriminant analysis showed that pond depth, invertebrate biomass and fish biomass were the best predictors of species composition. Analysis of these niche dimensions showed that P. vernalis and A. elongata were most successful in shallow, temporary ponds with few predators. P. gyrina and P. acuta were typically found in ponds of intermediate depth and high predator abundance. P. ancillaria was found in the deepest lakes, which had abundant fish predators but few invertebrate predators. Of the five species considered, P. ancillaria, P. vernalis and A. elongata were relatively specialised with regard to key habitat characteristics, P. gyrina was moderately generalised and P. acuta was remarkably generalised, since it alone occurred across the entire freshwater habitat.
The exceptional habitat breadth of *P. acuta* stands in contrast to distributional studies of other freshwater taxa and deserves further attention.

**Keywords:** gastropoda, hydroperiod, predation, species composition, species turnover

**Introduction**

It is widely recognised that species diversity is generated in large part by the process of species replacement along environmental gradients (Whittaker, 1956; Huston, 1994). A key gradient in freshwater is the environmental continuum from small, shallow, temporary ponds to large, deep, permanent lakes (Wellborn, Skelly & Werner, 1996). Studies of the distribution of aquatic organisms suggest that closely related species often sort along the freshwater habitat gradient, with individual species often occupying a relatively narrow portion of the gradient (Zaret, 1980; Cook & Streams, 1984; Spence, 1989; Wellborn, 1994; Skelly, 1996; McPeek, Grace & Richardson, 2001; Stoks & McPeek, 2003; Garcia & Mittelbach, 2008). Thus, in a landscape with lakes and ponds of various sizes, the restricted distributions of individual taxa can generate a level of regional diversity that far exceeds mean local diversity. A leading hypothesis accounting for the restricted distribution of aquatic taxa invokes tradeoffs associated with variation in the predation regime along the habitat gradient (Wellborn et al., 1996; Skelly, 1997; Wissinger et al., 1999). It is important to understand the processes responsible for the limited distribution of taxa, as these are the processes that ultimately maintain high levels of regional biodiversity (Leibold et al., 2004).

The hypothesis of Wellborn et al. (1996), that shifts in species composition are related to changes in predation regime, does not yet have extensive empirical support, as there are few comprehensive studies of species distributions along the freshwater habitat gradient. Previous studies have tended to focus on the fauna of one habitat type (e.g. lakes or ponds or vernal pools) and of those studies that have quantified species distributions across the entire gradient, few have simultaneously measured predator abundance. Thus, the evidence supporting the fundamental tenet of species replacement along the habitat gradient is largely qualitative and anecdotal. One exception is the distributional patterns of amphibians, which has been carefully documented by a number of investigators (e.g. Werner et al., 2007). There is a clear need for similar quantitative studies of how other taxa are distributed across the freshwater habitat gradient, accompanied by measurements of predator abundance.

Freshwater gastropods are key players in many freshwater food webs, and given suitable abiotic conditions are ubiquitous inhabitants of lakes and ponds of all sizes (Pip, 1986; Jokinen, 1987; Burch, 1988; Dillon, 2000). A number of investigators, dating back nearly 100 years, have described the ecological niche of freshwater gastropod species (e.g. Baker, 1927; Clam-pitt, 1970; Pip, 1986; Jokinen, 1987). Reviews of this literature suggest that habitat permanence and depth play a role in shaping species composition (Lodge et al., 1987; Dillon, 2000; Wethington, 2003), but the distributional studies are qualitative in nature and unsuitable for a rigorous test of the Wellborn et al. (1996) hypothesis. To our knowledge, there are no quantitative studies of the distribution of freshwater snail species and their predators across the entire habitat gradient.

Focusing on the family Physidae, we tested the hypothesis that freshwater gastropod species have a restricted, non-random distribution along the freshwater habitat gradient. We focused on the physids because they are among the most abundant and geographically widespread of North American freshwater invertebrates and they inhabit the entire breadth of the habitat gradient. Based on the results from an extensive survey, we describe the distribution of physid snails in a systematic manner. First, we describe how abiotic factors and predator abundances change across the habitat gradient. Second, we evaluate local and regional diversity. Third, we ask whether species occurrences are random with respect to hydroperiod and whether non-random distributions are produced by turnover or nesting along the hydroperiod-depth gradient. Finally, we describe the realised niche and relative specialisation of each species.

**Methods**

**Study area**

We surveyed 61 freshwater sites (ponds, marshes, swamps and lakes), ranging in surface area from
10 m² to 34.7 km² and with depths up to 19.8 m (Appendix S1). Study sites are situated within the upper Ohio River drainage and in Crawford, Mercer and Erie Counties of northwestern Pennsylvania, U.S.A. This area is on the glaciated Allegheny Plateau and is characterised by moderate relief, elevations between 300 and 400 m, and soils that are calcareous, poorly drained, but relatively fertile. Land use in the region is approximately evenly divided between forest and agriculture. About two-thirds of the study sites are human-made (e.g. constructed by excavation or flooded by dams) and a third are of natural origin. We chose study sites so as to achieve an approximately uniform distribution of habitat sizes from the smallest, most temporary vernal pools to the largest, deepest lakes. The only other selection criteria was ease of access, and sites were not selected or excluded because of presence or absence of physid snails. Nevertheless, all of the 61 sites contained snails, and all but one contained physid snails.

Physical and chemical parameters

For each site we measured pH, conductivity, alkalinity, hydroperiod, depth and surface area. pH was measured in situ with a temperature-compensated pH meter, calibrated daily against buffers. Specific conductivity was likewise measured with a calibrated field meter (values standardised to 25 °C). Total alkalinity was measured by titration with Bromocresol Green color indicator, and is expressed as mg L⁻¹ CaCO₃ equivalents.

Sites were ordered along a hydroperiod-depth gradient from the shallowest and most ephemeral to the deepest and presumably least ephemeral. Temporary habitats were ordered according to hydroperiod, and permanent habitats were ordered according to depth. Hydroperiod of temporary habitats was determined by recording the drying date for each site in the summer of 2006. Sites were classified as temporary or permanent based on our observations over the past 10 years. Even permanent ponds are certain to dry at some longer time scale, so our definition of permanent is a drying frequency of >10 years. Depths of most permanent habitats were measured during a 3-day period in July of 2003. By taking a snapshot in time, we precluded the confounding effects of seasonal dry down in the shallow habitats. The deeper lakes have relatively stable water levels and their depths were measured at other times or drawn from published sources (e.g. Butkas & Ostrofsky, 2006). Pond surface areas were estimated from linear dimensions using a laser range-finder, which was done at the same time that depths were measured. Surface areas of larger lakes (>1 ha) were determined from USGS topographical maps or from Butkas & Ostrofsky (2006).

Based on hydroperiod and depth, sites were divided into three categories: temporary, permanent-shallow and permanent-deep. We categorised permanent sites with a midsummer depth less than 150 cm as shallow and those with a depth greater than 150 cm as deep. We then calculated median pH, conductivity and alkalinity for each habitat type. Differences among habitat types in pH, conductivity and alkalinity were evaluated with the non-parametric Kruskal–Wallis ANOVA.

Predator distribution and abundance

Most of the large predatory invertebrates found in these localities can feed on physid snails to some degree, and some taxa (notably odonates and hemipterans) are very effective and important snail predators (Turner & Chislock, 2007). Therefore, we measured the abundance of invertebrate predators in each of our study ponds and lakes. Invertebrate biomass was sampled with a stove-pipe type sampler, 25-cm in diameter. Large invertebrates were removed from the sampler with a small dip net, identified to the level of family, and wet-mass measured. Taxa retained include all Anisoptera, large Zygoptera, all Hemiptera, large Coleoptera, and the Hirudinea. These large invertebrates function as carnivores and, with the exception of a single taxa (larval Dytiscus verticalis Say), are known snail predators (Turner & Chislock, 2007). We use biomass instead of density as an index of large invertebrate abundance because when combining size classes and taxa, biomass of a predator species is a better predictor of its feeding rate (Peters, 1983). Dytiscus verticalis do not prey on snails, so we performed an additional calculation of biomass with D. verticalis excluded. Small fish were often captured in the sampler and their biomass was measured as well. Stovepipe samplers perform well when sampling the invertebrates of vegetated habitats (Turner & Trexler, 1997). Crayfish, another snail predator, occur in several of our study lakes and
ponds, but are not sampled effectively with the
stovepipe and we did not attempt to estimate their
abundance.

Larger ponds and lakes contained fish, most of
which are capable of preying on juvenile pulmonates
(Brown & DeVries, 1985; Lodge et al., 1987; Martin
et al., 1992). The small fish of marshes were ade-
quately sampled with the stovepipe sampler, but fish
in larger lakes required additional sampling. Fish
were sampled from these habitats by repeated hauls
with an 80' bag seine. Captured fish were identified
to species, enumerated and length was measured.
Lengths were then converted into wet biomass based
on published length–weight relationships (Schneider,
Laarman & Gowing, 2000). Differences in the bio-
mass density of fish and invertebrate predators
across pond types were tested with Kruskal–Wallis
ANOVA.

Gastropod survey methods

Snail distributional data are based on 210 sampling
events, for an average of 3.5 samples per site,
conducted between 1998 and 2007. Each site was
sampled at least twice. A D-frame dipnet was repeat-
edly swept through vegetation and bottom debris with
approximately 20 min of sampling effort devoted to a
site for each sampling event. Each site was also
sampled on at least one occasion with a stovepipe
sampler. The stovepipe sampler, 25-cm in diameter,
was firmly seated into the bottom sediments in water
that was between 15 and 30 cm deep, and the contents
were removed by repeated sweeps with a small net.

The taxonomy of the Physidae has been quite
confused (Dillon et al., 2002), in part because variation
in food, predators, temperature, or other environmen-
tal factors can induce shifts in shell morphology
(DeWitt, Robinson & Wilson, 2000). Wethington
(2003); see also Wethington & Lydeard, 2007) recently
revised the classification of species within the Physidae.
Using molecular data, morphological data and breed-
ing experiments, she concluded that the family is
represented in North America by a dozen extant
species. We followed Wethington (2003) in our identi-
fications. Species are most reliably distinguished from
one another by morphology of the penial complex, and
we performed dissections of any questionable speci-
mens in order to confirm identification of difficult
animals.

Analysis of assemblage structure

Survey data yield incidence patterns, with each species
present in a subset of the sites. With respect to any
particular environmental variable, these incidence
patterns may or may not differ from a randomly
generated pattern. Here we examine the survey data
and, focusing on the hydroperiod habitat gradient, ask
whether observed species incidence patterns represent
non-random distributions. Following general practice
in community ecology, we evaluated assemblage
structure in two ways. First, we ranked ponds
according to hydroperiod and constructed a species
by pond incidence matrix. We can then ask whether
the pattern of species incidence across the gradient are
coherent or random. Second, we used the same matrix
to test whether coherent distributions are the result of
“turnover” or “nesting”. Species turnover describes
the degree to which species replace one another along
the habitat gradient. Nestedness is the opposite of high
turnover and describes the degree to which diversity
accumulates along the gradient by addition of new
species without any corresponding species losses. If a
large number of species are found in ponds of some
hydroperiod with subsets of these species occurring at
other hydroperiods, the pattern is described as nested
and turnover is low.

We used the method outlined by Leibold &
Mikkelson (2002) to test whether snail assemblages,
when ordered along the hydroperiod gradient, exhibit
significant coherence and turnover. Coherence of the
incidence matrix was measured by counting the
number of embedded absences along the hydroperiod
gradient. A highly coherent distribution will have few
embedded absences. Conventional approaches ordi-
nate simultaneously along both axis to minimise the
total number of embedded absences. Since we were
interested only in the environmental gradient repre-
sented by hydroperiod, we did not ordinate along the
primary axis. Furthermore, since we did not want our
measure of coherence to depend on the ordering of
physids, we did not count embedded absences occurring along the secondary axis. To test whether
the number of embedded absences contained within
our matrix was significantly fewer than that expected
if species were randomly distributed across the
hydroperiod gradient, we constructed 200 null matri-
ces with the 0's and 1s rearranged randomly so as to
conservate both row and column totals and compared

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the number of observed embedded absences to the null distribution, thereby determining the probability that the observed frequency of embedded absences could be drawn from a random distribution.

To evaluate whether there was significant species turnover, we filled in the embedded absences along the primary axis, and counted the number of times one species was replaced by another between two sites having different hydroperiods. By filling in the embedded absences we insured that we were not simply retesting the hypothesis of coherence. We then created 1000 null matrices in which the species’ ranges were allowed to float randomly along the hydroperiod gradient and measured the turnover. We then compared the observed turnover to that generated within the null matrices.

**Analysis of realised niche and relative specialisation**

The analysis of assemblage structure showed high coherence with significant turnover. Therefore, as a final analysis we sought to describe the abiotic and biotic environment of ponds occupied by each species, i.e. a multivariate description of the species’ realised niche. We first constructed a dominance matrix (as opposed to a occurrence matrix) listing the physid species that was numerically dominant in each pond along with pond habitat variables. We then determined which habitat variables were most useful in predicting the dominant species by performing stepwise discriminant analysis. Using backward stepwise elimination, the discriminant analysis retained or rejected abiotic and biotic habitat variables according to their ability to predict species identity. The analysis also tested for multivariate differences in the habitat variables of ponds dominated by each species (i.e. the realised niche). Discriminant analysis assumes that predictive variables are not highly correlated so we screened habitat variables for correlations and retained depth, alkalinity, pH, conductivity, invertebrate biomass, and fish biomass. One of the physids, *Physa acuta* Draparnaud, occupied the entire range of habitats, which resulted in a violation of the homogenous variance requirement and made any analysis of niche differentiation relatively meaningless (James & Mcculloch, 1990). Thus, we excluded sites dominated by *P. acuta* from the discriminant analysis.

Discriminant analysis yielded a subset of habitat variables that were most useful in predicting the dominant physid, so we described the realised niche of each species with a focus on these habitat dimensions. We grouped sites by physid species and calculated median parameter values for abiotic habitat variables (depth, surface area, alkalinity, pH and conductivity) and mean predator abundance (invertebrate biomass, fish biomass, total predator biomass). Niche breadth of each species was examined by calculating the number of sites dominated, mean CV of abiotic variables of sites dominated, and mean CV of biotic variables for sites dominated.

**Results**

**Site characteristics**

Our study ponds and lakes (Appendix S1) spanned a large gradient of surface area, depth, and hydroperiod. Midsummer surface areas ranged from 0 to 3470 ha and midsummer depths ranged from 0 to 19.6 m. Twenty of the 61 study systems were observed to dry at some point during the period of observation and are hereafter categorised as temporary habitats. There were few systematic changes in abiotic parameters along the habitat gradient, other than depth and permanence (Table 1). Alkalinity and conductivity were consistently high, reflecting the

<table>
<thead>
<tr>
<th>Abiotic variables</th>
<th>Temporary</th>
<th>Shallow</th>
<th>Deep</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number surveyed</td>
<td>20</td>
<td>25</td>
<td>16</td>
</tr>
<tr>
<td>Maximum Depth (cm)</td>
<td>9.5</td>
<td>60</td>
<td>430</td>
</tr>
<tr>
<td>Area (m²)</td>
<td>130</td>
<td>360</td>
<td>283,000</td>
</tr>
<tr>
<td>Alkalinity (mg L⁻¹)</td>
<td>72</td>
<td>72</td>
<td>78</td>
</tr>
<tr>
<td>pH</td>
<td>7.1</td>
<td>7.1</td>
<td>8.0</td>
</tr>
<tr>
<td>Conductivity (µS cm⁻¹)</td>
<td>234</td>
<td>167</td>
<td>210</td>
</tr>
</tbody>
</table>

**Predator biomass**

| Fish biomass (g m⁻²)               | 0.8 (2.2) | 0.6 (1.2) | 21.2 (17.9) |
| Invertebrate biomass (g m⁻²)       | 1.3 (2.2) | 4.0 (5.7) | 2.1 (3.0)   |
| Invertebrate biomass (g m⁻²)*      | 0.6 (1.0) | 3.9 (5.7) | 2.1 (3.0)   |
| Total predator biomass (g m⁻²)     | 2.1 (3.2) | 4.6 (5.7) | 23.3 (17.5) |

Median values are shown for abiotic variables. Predator biomass density values are means with standard deviations in parentheses. All four measures of predator biomass differed significantly among habitat types (*P* < 0.05).

*Invertebrate biomass density calculated after excluding *Dytiscus verticalis.*
hard water characteristic of the region, and did not differ among habitat types ($P > 0.05$). pH was also generally high, although deep habitats tended to have a slightly higher pH than did shallow and temporary habitats ($P < 0.05$, Table 1).

**Predator abundance**

Our survey results support the hypothesis that predator abundance changes in a systematic and predictable manner along the hydroperiod-depth gradient. Biomass of predatory invertebrates was lowest in temporary habitats, highest in shallow habitats and intermediate in deep habitats (habitat type effect: $P = 0.04$; Fig. 1 top). Differences among habitat types were stronger when *D. verticalis*, an ineffectual predator of snails (Turner & Chislock, 2007), was excluded from the analysis ($P < 0.01$; Table 1), as most of the predatory invertebrates biomass in temporary habitats was attributable to the presence of larval *D. verticalis*.

There was a strong concordance between mid-summer water depth and the presence of well developed fish communities. With just two exceptions, ponds and lakes deeper than 150 cm contained multiple species of fish and had a biomass density >5.0 g $\text{m}^{-2}$, whereas ponds shallower than 150 cm lacked fish entirely, or contained two or fewer fish species and <5.0 g $\text{m}^{-2}$ fish biomass (Fig. 1 bottom). Differences in fish biomass among habitat types were highly significant ($P < 0.001$). Because both invertebrate and fish predators were least abundant in temporary habitats, total predator biomass depended strongly on habitat type, with deep habitats having the highest total biomass and temporary habitats the lowest total biomass ($P < 0.001$, Table 1).

**Regional and local diversity**

Our surveys show that northwest Pennsylvania is home to five species of physid snail: *Physa acuta*, *Physa ancillaria* (Say), *Physa gyrina* (Say), *Physa vernalis* (Taylor and Jokinen), and *Aplexa elongata* (Say). Local diversity averaged 1.2 physid species per site, and thus beta diversity (ratio of regional to local diversity) was 4.1, illustrating limited community membership at local scales and substantial heterogeneity in species composition. The level of local diversity was very similar across habitat types, as mean local diversity of temporary habitats was equal to 1.15 species per pond, shallow permanent habitats averaged 1.20 species, and deep habitats averaged 1.25 snail species per pond.

**Assemblage coherence and turnover**

An examination of the distribution of the five physids across the 61 ponds and lakes shows that there were clear patterns of restricted distribution and species replacement along the habitat gradient (Fig. 2). Our analysis confirmed that species distributional patterns were non-random with respect to hydroperiod. When the data are organised into a species-by-site incidence matrix (e.g. Fig. 2) and sites are ordered according to
their hydroperiods, the resulting pattern of incidence is highly coherent \((P < 0.005)\). The observed matrix (Fig. 2) contains 53 embedded absences, whereas null matrices conserving row and column totals contained an average of 128 ± 22 (±1 SD) embedded absences. Thus, much of the variation in assemblage structure from one pond or lake to another is explained by hydroperiod. We also found that the number of species replacements along this gradient was higher than would be expected from a random distribution of species \((P = 0.035)\). Thus species replacement is more important than nesting in describing the incidence of species along the habitat gradient.

**Realised niches and specialisation**

Discriminate analysis showed significant multivariate habitat differentiation among species (Wilk’s Lambda = 0.020, \(F_{9,36} = 15.9, P < 0.001\)). With backward elimination, patterns of physid dominance was best modelled with three habitat variables: maximum depth, invertebrate biomass and fish biomass. The reduced model successfully predicted the dominant physid species for 62% of the 21 ponds included in the analysis.

Focusing on those niche dimensions identified in the discriminate analysis as the best predictors of physid species composition, a simple description of niche differentiation emerges. *Physa vernalis* was dominant in sites with the shortest hydroperiod, a low abundance of invertebrate predators and no fish predators (Table 2). *Aplexa elongata* sites were on average slightly deeper and more persistent than those dominated by *P. vernalis*. *Aplexa* sites had the lowest invertebrate biomass and also lacked fish (Table 2). Sites dominated by *P. gyrina* were intermediate with respect to depth and fish biomass, but biomass of invertebrate predators was highest in *P. gyrina* sites. *Physa ancillaria* was found only in the deepest and largest of the lakes surveyed. These lakes are characterised by very high fish biomass and intermediate invertebrate biomass (Table 2). *Physa acuta* occupied a niche with mean values intermediate to the other species, but it was so ubiquitous as to make analysis of niche centroids relatively uninformative.

With regard to relative habitat breadth, all metrics (analysis of frequency of occurrence, C.V. of abiotic variables, and C.V. of predator biomass) yielded the same rank-ordering of specialisation. *Physa ancillaria* had the narrowest habitat distribution, followed by *P. vernalis*, *A. elongata*, and *P. gyrina* (Table 3). *P. acuta* had by far the broadest habitat distribution, as it was the dominant species in 39 of the 60 sites studied, and it occupied every habitat from highly ephemeral pools to deep permanent lakes (Table 3).

![Fig. 2 Distributions of five species of physid snails along the hydroperiod and depth gradient. Vertical dashed lines represent the permanence and predator transitions.](image-url)

**Table 2** Abiotic and biotic characteristics of ponds dominated by each of the five physid species, with species ranked by depth of the ponds and lakes in which they are found

<table>
<thead>
<tr>
<th></th>
<th><em>P. vernalis</em></th>
<th><em>A. elongata</em></th>
<th><em>P. gyrina</em></th>
<th><em>P. acuta</em></th>
<th><em>P. ancillaria</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Mid-summer depth (cm)</td>
<td>3.0</td>
<td>4.5</td>
<td>40</td>
<td>60</td>
<td>1140</td>
</tr>
<tr>
<td>Area (m²)</td>
<td>725</td>
<td>300</td>
<td>770</td>
<td>360</td>
<td>278,500</td>
</tr>
<tr>
<td>Alkalinity (mg L⁻¹)</td>
<td>131</td>
<td>62.5</td>
<td>84</td>
<td>72.5</td>
<td>164</td>
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<tr>
<td>pH</td>
<td>6.8</td>
<td>6.8</td>
<td>7.1</td>
<td>7.7</td>
<td>8.1</td>
</tr>
<tr>
<td>Conductivity (µS cm⁻¹)</td>
<td>264</td>
<td>260</td>
<td>160</td>
<td>197</td>
<td>260</td>
</tr>
<tr>
<td>Invertebrate biomass (g m⁻²)</td>
<td>1.40</td>
<td>0.33</td>
<td>2.4</td>
<td>2.06</td>
<td>0.50</td>
</tr>
<tr>
<td>Fish biomass (g m⁻²)</td>
<td>0</td>
<td>0</td>
<td>5.5</td>
<td>6.03</td>
<td>32.6</td>
</tr>
<tr>
<td>Total predators (g m⁻²)</td>
<td>1.40</td>
<td>0.33</td>
<td>7.9</td>
<td>8.09</td>
<td>33.1</td>
</tr>
</tbody>
</table>

Median values are shown for abiotic variables and means for predator biomass values. Niche dimensions in bold are those identified by stepwise discriminate analysis as the best predictors of physid species composition.

Further development of a theory of lacustrine community structure depends on a detailed knowledge of species replacement patterns, but comprehensive studies of species turnover along the entire freshwater habitat gradient, including quantitative estimates of predator abundances, are largely lacking. Here we show that species belonging to a single freshwater gastropod family occur across the entire habitat gradient, but individual species have a restricted and non-random distribution with respect to hydroperiod (with one important exception). As a result, there is substantial turnover of gastropod species, and regional diversity is much higher than mean local diversity.

Descriptive studies aimed at detecting broad-scale patterns in the species composition of freshwater snail assemblages have traditionally focused on pH and alkalinity (Okland, 1983; Bronmark, 1985; Pip, 1986; Jokinen, 1987; Carlsson, 2000). Lodge et al. (1987) reviewed this work and concluded that calcium availability likely limits snails at a regional scale, but hypothesised that competition, predation and pond drying were important at a local scale. As a result, there is substantial turnover of gastropod species, and regional diversity is much higher than mean local diversity.

Descriptive studies aimed at detecting broad-scale patterns in the species composition of freshwater snail assemblages have traditionally focused on pH and alkalinity (Okland, 1983; Bronmark, 1985; Pip, 1986; Jokinen, 1987; Carlsson, 2000). Lodge et al. (1987) reviewed this work and concluded that calcium availability likely limits snails at a regional scale, but hypothesised that competition, predation and pond drying were important at a local scale. The patterns described in this study are consistent with the predictions of Lodge et al. (1987), as we found that variation in pH, conductivity and alkalinity was not related to local species composition, but depth and predator biomass did successfully predict species composition. However, the specific mechanisms responsible for the restricted distribution of freshwater gastropods are still poorly understood, and we turn here to a brief evaluation of the evidence for two processes: predation and stress tolerance.

Several studies of aquatic invertebrates suggest that species replacement along the habitat gradient is driven by shifts in the abundance and identity of the top predators (Cook & Streams, 1984; McPeek, 1990, 1998; Wellborn, 2002). Wellborn et al. (1996) formulated a model which asserts that species turnover is driven by fitness tradeoffs associated with predation. Physiological, morphological or behavioural traits that confer protection against the predators of larger ponds and lakes often incur costs that put the bearer of those traits at a disadvantage in ponds lacking predators or with different sorts of predators (e.g. Werner & McPeek, 1994; Wissinger et al., 1999; Wellborn, 2002; McPeek, 2004; Werner et al., 2007). Consistent with the Wellborn hypothesis, we found that turnover in physid species composition coincided with shifts in the type and abundance of snail predators. Also consistent with the predation hypothesis, a number of experimental field studies have shown that both fish and invertebrate predators influence gastropod abundance (Kesler & Munns, 1989; Bronmark, 1992; Bronmark, Klosiewski & Stein, 1992; Martin et al., 1992; Osenberg, Mittelbach & Wainwright, 1992; Lodge et al., 1994; Nystrom & Perez, 1998; Chase, 2003; Turner & Chislock, 2007), but these studies have focused on population regulation within lakes, not patterns of replacement among lakes. Ultimately, predation experiments involving snail species from across the habitat gradient are necessary in order to evaluate the full role of predators in structuring species composition of freshwater snail assemblages.

Alternatively, snail species turnover along the freshwater habitat gradient may be caused by shifts in the type and severity of abiotic stress, independent of predation. Survival in temporary ponds demands the ability to aestivate and tolerate desiccation and high soil temperatures. Survival in shallow ponds likely requires an ability to tolerate low winter oxygen concentrations and high sulphide concentrations in summer. Deep ponds are relatively benign environments, and tradeoffs associated with adaptations aimed at dealing with desiccation and anoxia may put the animal at a disadvantage in benign environments. The “stress-tolerance” model has received

Table 3 Relative specialisation of the five physid species, measured as the mean variation in abiotic characteristics and mean variation in predator biomass of the habitats in which each species is dominant. Abiotic variance is the mean of the coefficient of variation (standard deviation/mean) for depth, surface area, alkalinity, pH, and conductivity. Predator variance is the mean of the coefficient of variation for biomass of predatory invertebrates and fish.

<table>
<thead>
<tr>
<th>Species</th>
<th>Number of ponds dominated</th>
<th>Mean C.V. – Abiotic variables</th>
<th>Mean C.V. – Predator biomass</th>
</tr>
</thead>
<tbody>
<tr>
<td>P. vernalis</td>
<td>2</td>
<td>0.41</td>
<td>1.18</td>
</tr>
<tr>
<td>A. elongata</td>
<td>4</td>
<td>0.58</td>
<td>1.21</td>
</tr>
<tr>
<td>P. gyrina</td>
<td>13</td>
<td>1.09</td>
<td>1.55</td>
</tr>
<tr>
<td>P. acuta</td>
<td>39</td>
<td>1.33</td>
<td>1.72</td>
</tr>
<tr>
<td>P. ancillaria</td>
<td>2</td>
<td>0.18</td>
<td>0.62</td>
</tr>
</tbody>
</table>
substantial empirical support for other ecosystems (Grime, 1977; Menge & Sutherland, 1987), but has not been extensively tested in freshwater ecosystems. There is some evidence that *P. gyrina* dominates in ponds that suffer from low winter oxygen concentrations, suggesting that *P. gyrina* can better tolerate the hypoxia of these ponds (A. M. Turner, unpubl. data). Other environmental stressors that limit gastropod species distributions may include parasitism or blooms of toxic algae (Bernot & Lamberti, 2008; Gerard, Carpentier & Pallisson, 2008). Future studies could address relative tolerance of snail species to environmental stress and integrate the predation and stress tolerance models by investigating potential tradeoffs between stress tolerance and anti-predator defences. The patterns of species composition shown here are probably shaped by both predation and stress tolerance, so manipulative approaches will be necessary in order to elucidate the underlying mechanisms.

Some studies have found that abundance of predatory invertebrates across the habitat gradient is lowest in temporary ponds and reaches its peak in long-hydropoierid fishless ponds (Wiggins, MacKay & Smith, 1980; Schneider & Frost, 1996; Wellborn et al., 1996), but others assert that temporary ponds have a high density of predators (Lake, Bayly & Morton, 1989). Our quantitative survey showed that there were significant differences among pond types in biomass of predatory invertebrates. Average invertebrate biomass in shallow ponds was about two-fold that of deep ponds and lakes and three-fold that of temporary habitats.

Deep ponds and lakes had a mean fish biomass about 30-fold higher than that of shallow and temporary ponds. Water depth was an excellent predictor of whether a pond would contain a well developed fish community, as all but one of the ponds with a midsummer depth >150 cm contained a well developed fish community (>2 species and biomass density >5 g m$^{-2}$), and all but one of the ponds with a midsummer depth <150 cm had a poorly developed fish community or no fish at all. These shallow ponds often contained mudminnows, fathead minnows or sticklebacks, all of which are tolerant of the winter anoxia that restricts the development of fish communities. The “fish” transition was fairly abrupt, as ponds with a midsummer depth >150 cm had a much higher fish biomass than ponds only slightly shallower (Fig. 1).

Batzé & Wissinger (1996) proposed a two-state model in which temporary habitats are dominated by insect predators and permanent habitats are dominated by fish. In contrast, Wellborn *et al.* (1996) developed a model with three habitat types: temporary ponds characterised by low predator density; permanent, fishless ponds with high invertebrate density; and fish ponds with low invertebrate but high fish density. Our predator data show that shallow, permanent ponds have low fish biomass relative to deeper ponds and lakes, but a high biomass of predatory invertebrates relative to temporary ponds, a pattern consistent with the three-state model of Wellborn *et al.* The success of predatory insects and fish in short hydropoierid ponds may vary with latitude. At high latitudes, summer drying and a short growing season excludes many insects from temporary ponds, and winter anoxia excludes fish from shallow permanent ponds, allowing insects to dominate. Thus, the two-state model proposed by Batzer and Wissinger may well apply to lower latitude wetlands, especially those that experience their wet season in summer.

Wellborn *et al.* (1996) asserted that virtually every type of animal inhabiting freshwater has a limited distribution across the lentic permanence – predation gradient. Our data show that three of the physids are highly specialised and have narrow habitat distributions (*P. vernalis*, *A. elongata*, and *P. ancillaria*). One has a moderately broad distribution (*P. gyrina*), and one, *Physa acuta*, has an exceptionally broad habitat distribution. *Physa acuta* occupied more than three quarters of the ponds studied and were found in the shallowest, most temporary ponds as well as the deepest, largest lakes. Further, *Physa acuta* is not even restricted to the range of systems studied here; it can be abundant in streams and rivers (Jokinen, 1992), and is also abundant in the benthos of the Laurentian Great Lakes (Stewart, Miner & Lowe, 1998). Several other studies of aquatic invertebrates have identified species with a broad habitat distribution (Hanson & Swanson, 1989; Muthukrishnan & Palavesam, 1992). Thus, it is clear that in some cases aquatic taxa break the rule of limited distributions and that the ubiquity of specialisation in freshwater may have been overstated.

On a broader geographic scale, it appears that habitat breadth is related to geographic range. *Physa vernalis* and *P. ancillaria*, both habitat specialists,
occur only in northeastern North America and have each been reported from only a limited number of localities (Jokinen, 1983, 1992; Taylor & Jokinen, 1984). *Aplexa elongata* and *P. gyrina*, found in this study to be moderately generalised species, both occupy a broad range across North America (Harman & Berg, 1971; Burch, 1988; Martin, 1999). *Physa acuta*, a super-generalist, is found on every continent of the world and is abundant nearly everywhere it occurs (Dillon *et al.*, 2002). Evidence suggests that *Physa acuta* is native to North America and has spread around the world in just the past 200 years (Dillon *et al.*, 2002; Bousset *et al.*, 2004). Considering the staggering breadth of its geographic distribution and the high densities typically achieved by *Physa acuta* populations, this species is surely among the most successful of all freshwater animals. It is important to know how frequent such super-generalists are, as they lower diversity and tend to be invasive.

There have been several studies of phenotypic plasticity of *Physa acuta* (Crowl & Covich, 1990; DeWitt *et al.*, 2000; Turner & Montgomery, 2003; Turner, Turner & Lappi, 2006). These show that *P. acuta* adjusts its behaviour, morphology and life-history in response to environmental factors, including predators. We hypothesise that the degree of plasticity in behaviour and morphology facilitates *P. acuta*’s wide breadth in habitat and geography. Comparative studies, evaluating the relative plasticity of physid species and relating plasticity to habitat breadth, have not yet been conducted. Mower & Turner (2004) did compare the morphological traits and behavioural plasticity of *P. acuta* and *Stagnicola elodes*, a habitat specialist, and found that the degree of shell development failed to correctly predict habitat distributions, but that a consideration of behavioural plasticity did. By viewing the degree of plasticity as a species trait, we were able to gain insight into patterns of species replacement that would not otherwise have been possible.

In sum, our results show that predator abundance and identity change in a predictable manner across the freshwater habitat gradient. The distribution of physid snails supports the contention that, with respect to the freshwater habitat gradient, most lentic species have limited distributions and substantial species turnover, but it also provides an interesting example of a striking exception. The mechanisms responsible for limiting the distribution of physids remain unclear, with both differential vulnerability to predators and differential tolerance of abiotic stress likely playing a role in producing species turnover. Pulmonate snails provide a powerful model system with which to evaluate questions regarding the mechanisms responsible for regulation of community structure.

**Acknowledgments**

A number of colleagues helped with the survey work, often under adverse conditions. Field assistants include Randy Bernot, Christy Mower, Beth Brokaw, Cheri LaFlamme, Rachel Martin, Heidi Lappi, Sarah Turner, Scott Ray, Mike Chislock, Rebekah Turner, and Martin Heben. Jon Chase, Julia Butzler, Jason Hoverman, and Nancy Schoeppner helped find additional ponds. This study was supported by the National Science Foundation (Grant No. 0444939) and is a contribution of the Pymatuning Laboratory of Ecology.

**References**


**Supporting Information**

Additional Supporting Information may be found in the online version of this article:

**Appendix S1.** Abiotic and biotic data for the 61 study ponds and lakes. T, S, and D denote temporary, shallow, and deep ponds and lakes. Latitude and longitude are degrees and minutes. Species codes are as follows: A = *Physa acuta*, E = *Aplexa elongata*, V = *Physa vernalis*, G = *Physa gyrina*, and Anc = *Physa ancillaria*. “TPred” is total predator biomass, “Inv Pred” is biomass of invertebrate predators.

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(Manuscript accepted 2 January 2009)