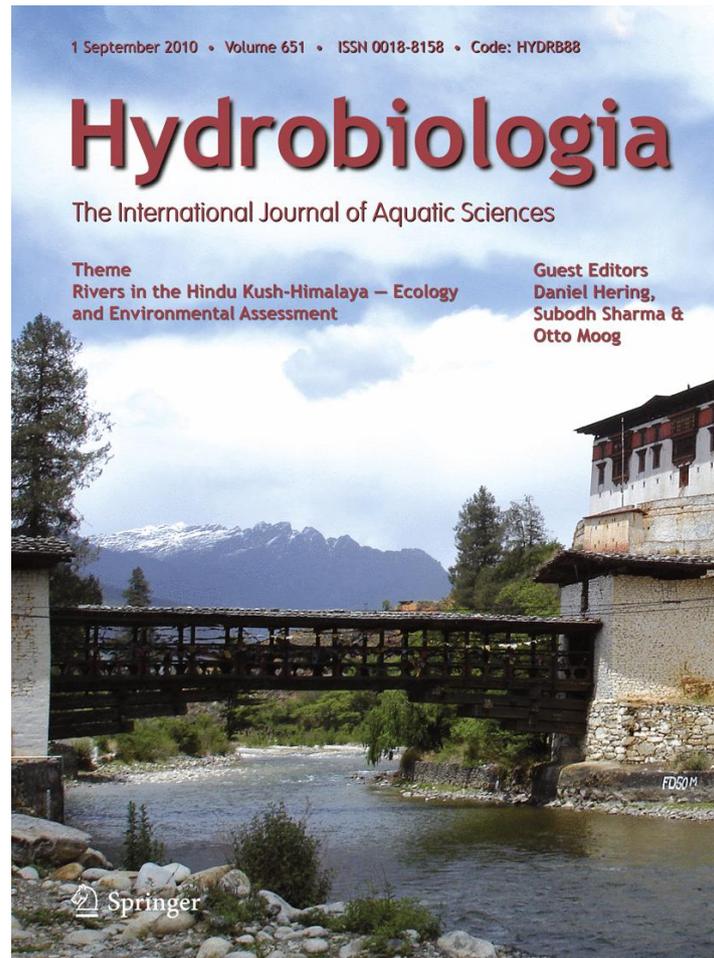


ISSN 0018-8158, Volume 651, Number 1



**This article was published in the above mentioned Springer issue.
The material, including all portions thereof, is protected by copyright;
all rights are held exclusively by Springer Science + Business Media.
The material is for personal use only;
commercial use is not permitted.
Unauthorized reproduction, transfer and/or use
may be a violation of criminal as well as civil law.**

Species-specific effects of gastropods on leaf litter processing in pond mesocosms

Joseph K. Brady · Andrew M. Turner

Received: 23 July 2009 / Revised: 31 March 2010 / Accepted: 12 April 2010 / Published online: 20 May 2010
© Springer Science+Business Media B.V. 2010

Abstract Despite the importance of litter processing in aquatic ecosystems, we have an incomplete knowledge of roles that specific benthic invertebrate taxa play in leaf decomposition. We studied the effect of gastropods on leaf litter decay rates in two outdoor pond mesocosm experiments: one contrasted the individual effects of six gastropod taxa on decomposition of senescent red maple (*Acer rubrum*) leaves and another evaluated the effect of *Stagnicola elodes* on decomposition of senescent leaves from five common deciduous forest tree species. Decay rate of red maple leaves was significantly higher with gastropods present. Rates increased by 14–39% in the presence of the relatively large-bodied pulmonates *S. elodes* and *Helisoma trivolvis*, while the small-bodied pulmonate *Physa gyrina* and the prosobranchs *Goniobasis livescens* and *Bellamya japonica* had smaller, non-significant effects. *S. elodes* significantly increased the decay rates of black cherry (*Prunus serotina*), sugar maple (*Acer saccharum*), red maple,

and red oak (*Quercus rubra*) leaves by 72, 41, 34, and 25%, respectively, relative to no gastropod controls. Our results suggest that some gastropod species may be important players in the processing of allochthonous detritus, particularly in smaller, forest-enclosed lentic systems where leaf litter inputs constitute a large portion of the energy budget.

Keywords Allochthonous detritus · Leaf shredder · Benthic food webs · Littoral zone

Introduction

Terrestrially derived leaf litter constitutes an important basal energy source for aquatic habitats within or adjacent to forested environments (Oertli, 1993; Palik et al., 2006). Benthic invertebrate species play an important role in the processing of leaf litter in aquatic systems (Hieber & Gessner, 2002), but our knowledge of the relative contributions of specific benthic taxa to leaf processing remains incomplete (Bjelke & Herrmann, 2005). Considering the importance of leaf litter to the energy budgets of small woodland ponds (e.g., Oertli, 1993), lakes (e.g., Bohman & Herrmann, 2006), and wetlands (e.g., Palik et al., 2006), experiments studying the effects of specific benthic taxa on leaf processing are important for developing a more complete understanding of the processes that mediate ecosystem metabolism and nutrient cycling within these systems.

Handling editor: B. Oertli

J. K. Brady (✉)
Science Department, New Philadelphia High School, 343
Ray Avenue NW, New Philadelphia, OH 44663, USA
e-mail: bradyk@npschools.org

A. M. Turner
Department of Biology, Clarion University, Clarion,
PA 16214, USA

Most inquiries into the relationship between benthic macroinvertebrates and leaf decomposition have focused upon the role of arthropod shredders (Cummins & Klug, 1979; Webster & Benfield, 1986; Bird & Kaushik, 2005; Inkley et al., 2008), which are thought to play a leading role in leaf processing (Cummins et al., 1989). Gastropods are generally considered to be grazers (Cummins et al., 1989). However, a number of studies suggest that some gastropod taxa may also play an important role in leaf processing (Reavell, 1980; Madsen, 1992; Fazi & Rossi, 2000; Lombardo & Cooke, 2002; Proffitt & Devlin, 2005). Because of their nearly ubiquitous geographic distribution, abundance, and persistence in habitats throughout the year, freshwater gastropods could exert a significant influence on leaf processing, particularly in smaller lakes and ponds where leaf litter inputs can constitute a large portion of the energy budget (Oertli, 1993). Most studies have focused on leaf processing in lotic systems but fewer studies have examined leaf processing in lakes and ponds (but see Hanlon, 1982; Oertli, 1993; Ostrofsky, 1997; Pope et al., 1999; Bjelke & Herrmann, 2005; Bohman & Herrmann, 2006) where gastropods can be particularly abundant.

The riparian habitats providing leaf litter to aquatic systems are generally composed of a variety of tree species. Tree leaves are known to exhibit strong species-specific differences in their processing rates (Webster & Benfield, 1986; Ostrofsky, 1997; Abelho, 2001). Similarly, lentic systems typically contain a variety of gastropod species that differ in their feeding morphology (Barnese et al., 1990) and other life history characteristics (Dillon, 2000). Existing studies of detritivory by gastropods have tended to focus on a relatively small number of gastropod and leaf species. Investigations of the leaf processing abilities of gastropods may benefit by incorporating a wider range of gastropod species and leaf substrates. Here we investigate the leaf processing abilities of a range of freshwater gastropod taxa, as well as the effect of one gastropod species on different leaf species, with the goal of evaluating the potential role of gastropods in processing leaf litter in small lakes and ponds.

Methods

We conducted two experiments to evaluate the effect of gastropods on leaf mass loss in aquatic ecosystems:

one contrasted the individual effects of six gastropod taxa on the rate of decomposition of a single leaf species and another evaluated how the decomposition rates of five leaf species were individually affected by a single gastropod species. Both experiments were conducted in pond-like mesocosms placed outdoors at the Pymatuning Laboratory of Ecology in northwestern Pennsylvania, USA.

The leaf processing abilities of six gastropod taxa

We evaluated the leaf processing abilities of six aquatic gastropod taxa: *Stagnicola elodes* (Say 1821) variety 1 (from here on *S. elodes* V1), *Stagnicola elodes* (Say 1821) variety 2 (from here on *S. elodes* V2), *Physa gyrina* (Say 1821), *Helisoma trivolvis* (Say 1817), *Goniobasis livescens* (Menke 1830), and *Bellamya japonica* (von Martens 1861). Species determinations were based on Jokinen (1983) and Burch (1989). *S. elodes* V1 is the more “typical” form of *S. elodes*, having a mean shell width to height ratio of 0.37 ± 0.018 SD, and is found in western Pennsylvania across a range of pond habitats. *S. elodes* V2 is a more robust variety (mean width to height ratio of 0.44 ± 0.026 SD) that may be a different species but has also been described as *S. elodes*. These six taxa were chosen either because they are abundant in local ponds and lakes and thus potentially important players in ecosystem level processes or because pilot studies suggested that they may process leaves.

The experiment utilized circular mesocosms (1.5 m diameter, 0.5 m depth) organized into eight rows of seven mesocosms each. On 6 and 7 June 2008 each mesocosm was filled with 400 l of well water, inoculated with 2 l of pond water in order to establish zooplankton, phytoplankton, and periphyton, and covered with shade cloth to prevent colonization by insects. The mesocosms were stocked with 10.00 ± 0.01 SD g of dry red maple (*Acer rubrum* L.) leaves on 16 June 2008, and left to condition for a period of 8 days. Red maple leaves from autumn leaf fall were collected from the forest floor in both autumn and spring and then stored indoors until added to the mesocosms.

Adult gastropods collected from local ponds and lakes were added to the mesocosms on 24 June 2008. The six gastropod treatments and one no gastropod control were randomly assigned to the

seven mesocosms within each row, so rows served as blocks and each treatment was replicated eight times ($n = 8$). Gastropods were stocked at a target biomass of 3 g per tank (wet mass including shell). Realized biomass per tank ranged from 2.7 g to 3.0 g (mean = 2.81 ± 0.09 SD g) except for *B. japonica*, for which we stocked a single individual of the smallest size class available (Range 3.06 to 10.95 g; mean = 7.11 ± 2.60 SD g). Gastropod density ranged from 1 (*B. japonica*) to 46 (*P. gyrina*) individuals per tank. These densities (0.60–26 gastropods m^{-2}) are substantially lower than is typical of ponds (Eisenberg, 1966; Brown, 1982; Dillon, 2000), but we chose to stock a relatively low biomass-density in order to prevent depletion of the periphyton growing in the tanks.

The experiment was terminated on 1 August 2008 after 46 days. Gastropods were removed and enumerated for calculation of survivorship. Leaves were removed on August 1 and 2, rinsed, and placed onto pre-weighed aluminum foil trays. The leaves were left to air dry for 1 week in a protected environment then oven dried at 65°C to constant mass.

The mean instantaneous daily decay rate constant (k) of red maple leaves was calculated for each treatment using the exponential decay model (Petersen & Cummins, 1974). The exponential model is widely used (Benfield, 1996) and was selected to facilitate comparison of results to other studies of leaf processing in aquatic systems. One-way ANOVA was used to evaluate the effect of gastropod treatment (a fixed factor) on decay rate (untransformed) and to compare survivorship of the different gastropod taxa. Inspection of residuals revealed no significant departures from normality or heteroscedasticity. Tukey's post-hoc tests were used to test for pairwise differences between treatment means ($P < 0.05$).

The effect of *Stagnicola elodes* on the decay rates of five species of tree leaves

The leaf processing ability of the gastropod *S. elodes* (V1) was evaluated for five species of tree leaves. The leaf species studied were: American beech (*Fagus grandifolia* Ehrh.), northern red oak (*Quercus rubra* L.), sugar maple (*Acer saccharum* Marsh.), red maple (*Acer rubrum* L.), and black cherry (*Prunus serotina* Ehrh.). These forest trees are typical of the Mixed Mesophytic Forest region (Braun, 1961) that dominates the

terrestrial environment surrounding the habitats where our gastropod specimens were collected.

The experiment used forty 130 l mesocosms (1.32 m \times 0.78 m \times 0.30 m depth) arranged into five rows of eight. We employed a 5 \times 2 factorial completely randomized design in which the five leaf treatments were randomly assigned to the mesocosms, then gastropod or no gastropod treatments were randomly assigned to each leaf treatment ($n = 4$ for each treatment combination).

Following methods similar to those employed in the first experiment, the mesocosms were filled with 100 l of well water, inoculated with 1 l of pond water, and covered with shade cloth on 26 June 2008. Mesocosms were stocked with 8.05 ± 0.04 SD g of dry leaf material. Gastropods were stocked at a target biomass of 2.5 g (wet mass including shell) per tank. Realized biomass ranged from 2.45 to 2.77 g (2.63 ± 0.10 SD g) per tank. Gastropod density was held constant at six individuals per tank (6.0 gastropods m^{-2}). This density of *S. elodes* is lower than that reported from field surveys of this species (Eisenberg, 1966; Brown, 1982).

The experiment was terminated on 28 July 2008 after 32 days. Adult gastropods were removed from the mesocosms and enumerated. Juveniles were sampled with a time constrained search (10 min per mesocosm). Leaves were removed, rinsed, placed onto pre-weighed aluminum foil trays, and oven dried at 65°C to constant mass.

The mean instantaneous daily decay rate constant was calculated for the leaf litter of each tank using the exponential model described above. Two-way ANOVA was used to evaluate effects of leaf species and gastropod presence/absence on daily decay rate. Leaf species and gastropods had interactive effects, and we explored the nature of the interaction with t tests separately testing for each leaf species whether gastropods had an effect on decay rates. One-way ANOVA was used to evaluate the effect of leaf species on gastropod survivorship and juvenile biomass.

Results

The leaf processing abilities of six gastropod taxa

Gastropods had a highly significant effect on the decay rate of red maple leaves, but individual

gastropod taxa varied in their effect on mass loss (Fig. 1). Mean leaf decay rates ranged from 0.0142 day⁻¹ (no gastropod treatment) to 0.0196 day⁻¹ (*S. elodes* V2). *S. elodes* V2 and *Helisoma trivolvis* were the most effective leaf processing taxa, increasing mean decay rates of red maple leaves by 39 and 27%, respectively, over no gastropod treatments. *S. elodes* V1 had a smaller but significant effect on mean decay rate (Fig. 1). *Physa gyrina*, *Goniobasis livescens*, and *Bellamyia japonica* had no significant effects on leaf decay rate (Fig. 1).

Gastropod survivorship, averaged across taxa, was 75.0 ± 3.7 SE%. Survivorship differed significantly among taxa (one-way ANOVA, $F_{5,42} = 18.15$, $P < 0.001$, $R^2 = 0.68$). Tukey's post-hoc tests revealed that *S. elodes* V1, which had a mean survivorship of 35.8%, differed significantly from all other taxa, which had mean survivorship >60% ($P < 0.01$).

The effect of *Stagnicola elodes* on the decay rates of five species of tree leaves

Averaged across all leaf treatments, *S. elodes* had a significant positive effect on leaf decay rate (two-way ANOVA: gastropod effect: $F_{1,30} = 75.37$, $P < 0.001$, model $R^2 = 0.91$), but the effect of *S. elodes* depended on leaf species (Fig. 2). Significant effects of *S. elodes* on mass loss were observed for black cherry, sugar maple, red maple, and red oak

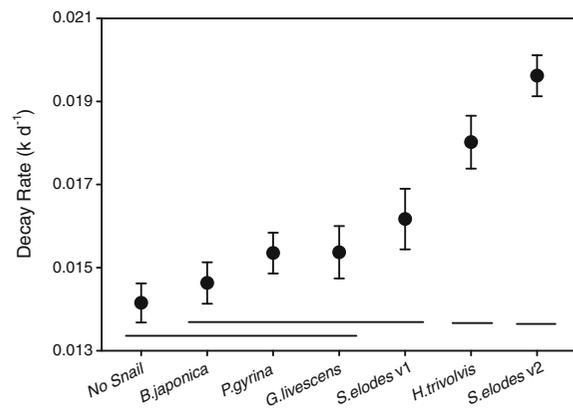


Fig. 1 Decay rates of leaves with six snail taxa and a no-snail control treatment (one-way ANOVA: $F_{6,42} = 21.30$, $P < 0.001$, model $R^2 = 0.81$). Error bars represent treatment means ± 1 standard error ($n = 8$ replicate mesocosms per treatment). Horizontal lines show treatments not significantly different from one another (Tukey's post-hoc test, $P < 0.05$)

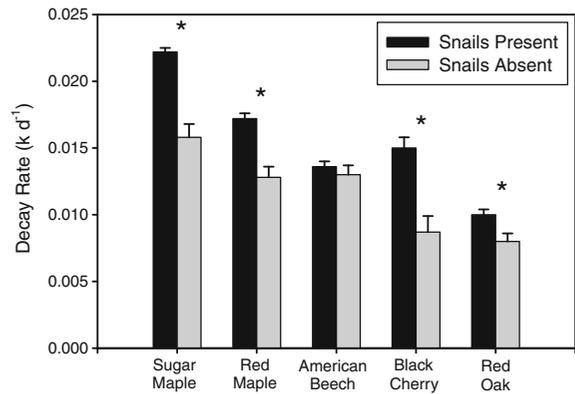


Fig. 2 Comparison of decay rates for five leaf species with *S. elodes* present or absent (two-way ANOVA: snail × leaf species effect, $F_{4,30} = 6.43$, $P < 0.001$, model $R^2 = 0.91$). Error bars represent treatment means ± 1 standard error ($n = 4$ for each treatment combination). Stars denote leaf species for which *S. elodes* had a significant effect on decay rate (t test, $P < 0.05$)

leaves ($P < 0.05$), with *S. elodes* increasing mean leaf decay rate by 72, 41, 34, and 25%, respectively, over no gastropod controls. *S. elodes* did not significantly alter the decay rate of American beech ($P = 0.47$). Leaf species varied in their decay rates when averaged across gastropod and no gastropod treatments (two-way ANOVA: leaf species effect: $F_{4,30} = 54.28$, $P < 0.001$), ranging from 0.0090 day⁻¹ (red oak) to 0.0190 day⁻¹ (sugar maple).

Gastropod survivorship did not differ among leaf treatments (one-way ANOVA, $F_{4,15} = 0.53$, $P = 0.71$, model $R^2 = 0.12$), and averaged 48 ± 4 SE%. Juvenile gastropods were present in all gastropod addition treatments, but juvenile biomass did not differ among leaf treatments (one-way ANOVA, $F_{4,15} = 0.51$, $P = 0.73$).

Discussion

Although it is known that benthic invertebrates, as a group, are important in the processing of leaf litter in aquatic systems (Graça, 2001; Hieber & Gessner, 2002), our understanding of the relative contributions of individual benthic species is incomplete (Covich et al., 1999). Thus, while the categorization of species into functional groups (i.e., shredders and grazers) is instrumental in the study of key ecological processes such as nutrient cycling in aquatic systems, current

functional categorizations do not capture the full complexity of trophic habits (Jonsson et al., 2001; Bjelke & Herrmann, 2005; Tanaka et al., 2006). Gastropods have been traditionally categorized as scrapers and grazers (Cummins & Klug, 1979; Cummins et al., 1989), but our results show that some gastropods can function as leaf processing species in lakes and ponds.

The leaf processing abilities of six gastropod taxa

Our study revealed that *S. elodes* V2, *H. trivolvis*, and *S. elodes* V1 had a significant influence on the decay rate of red maple leaves. Other studies also suggest that these taxa can process leaves. *H. trivolvis* has been reported to include decaying leaves in its diet (Brown, 1982; Lombardo & Cooke, 2002), and *S. elodes* has been described as a generalist that feeds on leaf litter (Jokinen, 1983). Taken together, these results support the hypothesis that *S. elodes* and *H. trivolvis* are effective leaf processors.

Nutrient enrichment has been shown to have a positive effect on leaf decay rate (Meyer & Johnson, 1983; Grattan & Suberkropp, 2000; Gulis & Suberkropp, 2003; Spanhoff et al., 2007). Snails grazing on periphyton remineralize nutrients and can have a significant positive influence on concentrations of dissolved nitrogen and phosphorus (Hunter, 1980; Underwood, 1991). Because microbial activity is often dependent on dissolved nutrient concentrations, it is possible that the gastropods in our study could have had an indirect positive effect on leaf decay rate by making limiting nutrients more available. Although this mechanism could potentially explain a portion of the elevated decay rates, it fails to explain the observed gastropod species-specific differences in leaf decay rates. For example, *S. elodes* V2 accelerated leaf processing 8.0-fold more than did *P. gyrina*, even though the two species share a similar life history, body size, and physiology (Dillon, 2000) and were stocked at the same biomass. It is quite unlikely that nutrient remineralization rates varied greatly between these two species, so such strong differences in their effects on leaf decay suggest additional species-specific mechanisms.

Differences in radular structure and tooth morphology between species are related to observed effects on leaf decay rate, consistent with a direct processing mechanism. *Stagnicola* and *Helisoma* tend

to have large, bicuspid or tricuspid teeth, whereas *Physa* tend to have small teeth with fine, elongate cusps (Barnese et al., 1990). It is likely that the small radular teeth of *Physa gyrina* are poor tools for processing leaf tissue, whereas the bipartite and tripartite edges of the teeth of *Stagnicola* and *Helisoma* are more effective at abrading the surfaces of leaves. Thus, the correspondence between tooth morphology and effects on leaf mass loss support the hypothesis that the observed increases in leaf decay rates in the presence of *S. elodes* V2, *H. trivolvis*, and *S. elodes* V1 treatments were the result of direct feeding by the gastropods.

Decay rates for red maple leaves in our mesocosms were within the range reported in the literature (Petersen & Cummins, 1974; Webster et al., 1995; Ostrofsky, 1997; Abelho, 2001). Comparison of leaf processing rates in the presence of gastropods to decay rates reported for other invertebrate taxa can be problematic, since other variables known to influence leaf decay (e.g., leaf species, pH, temperature, dissolved oxygen, nutrient concentration, water depth, etc.) are not standardized across experiments. In a mesocosm experiment somewhat similar to ours, Fazi and Rossi (2000) found that processing rates of *Alnus glutinosa* leaves in tanks containing four macroinvertebrate species (two shredders and two scrapers) stocked at densities of 2–8 individuals g⁻¹ leaf litter were 50% higher than in control tanks over the course of 77 days. Our gastropod densities were roughly 10-fold lower than the median densities used by Fazi and Rossi (2000), but we observed slightly larger effects on leaf decay rates. The gastropod densities that we used were lower than is typical of lakes and ponds (Eisenberg, 1966; Brown, 1982; Dillon, 2000), suggesting that at field densities some gastropod species could have effects on the rate of leaf decomposition as important as those species typically classified as shredders. Further studies comparing leaf decomposition rates of typical arthropod shredders with leaf processing gastropods are necessary to fully appreciate the relative importance of snails in leaf decomposition within benthic communities.

The effect of *Stagnicola elodes* on the decay rates of five species of tree leaves

The effects of *S. elodes* on leaf decay rate depended on leaf species. *S. elodes* had the largest effects on decay

rates of black cherry, sugar maple, red maple, and red oak leaves and had a small effect on the decay rate of American beech. Leaf processing invertebrates are known to preferentially feed on leaves with higher decomposition rates, which are more readily colonized by aquatic fungi and other microorganisms (Cummins & Klug, 1979; Graça, 2001). This “conditioning” by microorganisms is important, since most macro-detritivore species lack the ability to digest cellulose and other recalcitrant compounds that make up a large portion of leaf tissue and because microbial colonization increases the nutritional content of the leaves (Graça, 2001). Most studies of leaf processing by macroinvertebrates incorporate pre-conditioning periods of 2–3 weeks (e.g., Lombardo & Cooke, 2002; Aßmann et al., 2009). Abelho (2001) suggests 2 weeks are generally necessary for full microbial colonization of leaf tissue in streams, and conditioning in lentic habitats probably proceeds even more slowly (Baldy et al., 2002). Thus, it is likely that our leaves were only minimally colonized at the onset of our experiment, making the effect of gastropods on leaf decay even more striking. Gut extracts from gastropods have been shown to hydrolyze cellulose (Calow & Calow, 1975; Kesler, 1983), and cellulase activity has been shown to be higher in gastropods than in insects (Monk, 2006). Thus, it seems plausible that gastropods have adaptations enabling them to utilize cellulose-rich leaf litter directly and bypass the extensive microbial conditioning required by many benthic macroinvertebrate consumers. Although we suspect that a more typical pre-conditioning approach (e.g., Lombardo & Cooke, 2002) would have yielded even stronger effects on leaf decay rate, experiments studying how the degree of microbial colonization influences leaf processing by gastropods could yield interesting results and would further clarify the role of gastropods in leaf decomposition.

Mortality of *S. elodes* (V1) was high in both experiments, but in this experiment we noted that neither mortality nor reproductive output correlated with leaf species. It is unlikely that the observed mortality resulted from starvation, since our mesocosms contained abundant periphyton in addition to leaves. Forbes & Crampton (1942) studied a population of *S. elodes* and found that the adults died in midsummer following a bout of oviposition. Thus, we feel it is likely that the observed mortality of *S. elodes* V1 is attributable to the phenology typical of this taxon.

Conclusions regarding gastropods and leaves

In ponds and small lakes that receive substantial inputs of senescent leaf litter from riparian production, leaf processing is a key energetic flux supporting secondary production in food webs (Oertli, 1993; Bohman & Herrmann, 2006). Additionally, leaf processing by the benthic community could strongly affect lake-wide food webs by regulating primary productivity through the remineralization of nutrients confined within leaf material (Moore et al., 2004). Together, these observations demonstrate that leaf processing is an important ecosystem function in ponds and small lakes. Since gastropods are common and persistent members of the benthic communities of lentic systems, our finding that gastropods accelerate leaf processing rates suggests that they may have substantial effects on nutrient cycling, organic matter dynamics, and other ecosystem processes. A better understanding of the role of gastropods in leaf processing will provide important insights into factors regulating the productivity of lentic ecosystems.

Acknowledgments We thank Emily Cholak for her help with the setup, maintenance, and data collection for this experiment. We also thank Judy Cholak, Corrie Laughlin, Deonna Soergel, Owen Brady, Elliot Brady, and Jody Brady for their assistance with field work and two anonymous reviewers whose comments greatly improved this manuscript. This study was supported by the National Science Foundation via a Research Experience for Teachers award to A. M. Turner and J. K. Brady and is a contribution of the Pymatuning Laboratory of Ecology.

References

- Abelho, M., 2001. From litterfall to breakdown in streams: a review. *The Scientific World* 1: 656–680.
- Aßmann, C., E. von Elert & R. Gergs, 2009. Effects of leaf litter and its fungal colonization on the diet of *Limnomysis benedeni* (Crustacea: Mysida). *Hydrobiologia* 636: 439–447.
- Baldy, V., E. Chauvet, J. Charcosset & M. O. Gessner, 2002. Microbial dynamics associated with leaves decomposing in the mainstem and floodplain pond of a large river. *Aquatic Microbial Ecology* 28: 25–36.
- Barnese, L. E., R. L. Lowe & R. D. Hunter, 1990. Comparative grazing efficiency of pulmonate and prosobranch snails. *Journal of the North American Benthological Society* 9: 35–44.
- Benfield, E. F., 1996. Leaf breakdown in stream ecosystems. In Hauer, F. R. & G. A. Lamberti (eds), *Methods in Stream Ecology*. Academic Press, San Diego.

- Bird, G. A. & N. K. Kaushik, 2005. Processing of elm and maple leaf discs by collectors and shredders in laboratory feeding studies. *Hydrobiologia* 126: 109–120.
- Bjelke, U. & J. Herrmann, 2005. Processing of two detritus types by lake-dwelling shredders: species-specific impacts and effects of species richness. *Journal of Animal Ecology* 74: 92–98.
- Bohman, I. M. & J. Herrmann, 2006. The timing of winter-growing shredder species and leaf litter turnover rate in an oligotrophic lake, SE Sweden. *Hydrobiologia* 556: 99–108.
- Braun, E. L., 1961. *The Woody Plants of Ohio*. Ohio State University Press, Columbus.
- Brown, K. M., 1982. Resource overlap and competition in pond snails: an experimental analysis. *Ecology* 63: 412–422.
- Burch, J. B., 1989. *North American Freshwater Snails*. Malacological Publications, Hamburg, Michigan: 365.
- Calow, P. & L. J. Calow, 1975. Cellulase activity and niche separation in freshwater gastropods. *Nature* 255: 478–480.
- Covich, A. P., M. A. Palmer & T. A. Cowl, 1999. The role of benthic invertebrate species in freshwater ecosystems: zoobenthic species influence energy flows and nutrient cycling. *BioScience* 49: 119–127.
- Cummins, K. W. & M. J. Klug, 1979. Feeding ecology of stream invertebrates. *Annual Review of Ecology and Systematics* 10: 147–172.
- Cummins, K. W., M. A. Wilzbach, D. M. Gates, J. B. Perry & W. B. Taliaferro, 1989. Shredders and riparian vegetation. *BioScience* 39: 24–30.
- Dillon, R. T. Jr., 2000. *The Ecology of Freshwater Molluscs*. Cambridge University Press, Cambridge.
- Eisenberg, R. M., 1966. The regulation of density in a natural population of the pond snail, *Lymnaea elodes*. *Ecology* 47: 889–906.
- Fazi, S. & L. Rossi, 2000. Effects of macro-detritivores density on leaf detritus processing rate: a macrocosm experiment. *Hydrobiologia* 435: 127–134.
- Forbes, G. S. & H. E. Crampton, 1942. The differentiation of geographical groups in *Lymnaea palustris*. *Biological Bulletin* 82: 26–46.
- Graça, M. A. S., 2001. The role of invertebrates in leaf litter decomposition in streams – a review. *International Review of Hydrobiology* 86: 383–393.
- Grattan II, R. M. & K. Suberkropp, 2000. Effects of nutrient enrichment on yellow poplar leaf decomposition and fungal activity in streams. *Journal of the North American Benthological Society* 20: 33–43.
- Gulis, V. & K. Suberkropp, 2003. Leaf litter decomposition and microbial activity in nutrient-enriched and unaltered reaches of a headwater stream. *Freshwater Biology* 48: 123–134.
- Hanlon, R. D. G., 1982. The breakdown and decomposition of allochthonous and autochthonous plant litter in an oligotrophic lake (Llyn Frongoch). *Hydrobiologia* 88: 281–288.
- Hieber, M. & M. O. Gessner, 2002. Contribution of stream detritivores, fungi, and bacteria to leaf breakdown based on biomass estimates. *Ecology* 83: 1026–1038.
- Hunter, R. D., 1980. Effects of grazing on the quantity and quality of freshwater aufwuchs. *Hydrobiologia* 69: 251–259.
- Inkley, M. D., S. A. Wissinger & B. L. Baros, 2008. Effects of drying regime on microbial colonization and shredder preference in seasonal woodland wetlands. *Freshwater Biology* 53: 435–445.
- Jokinen, E. H., 1983. *The Freshwater Snails of Connecticut*. State Geological and Natural History Survey of Connecticut: Bulletin 109.
- Jonsson, M., B. Malmqvist & P. Hoffsten, 2001. Leaf litter breakdown rates in boreal streams: does shredder species richness matter? *Freshwater Biology* 46: 161–171.
- Kesler, D. H., 1983. Cellulase activity in gastropods: should it be used in niche separation? *Freshwater Invertebrate Biology* 2: 173–179.
- Lombardo, P. & G. D. Cooke, 2002. Consumption and preference of selected food types by two freshwater gastropod species. *Archiv für Hydrobiologie* 155: 667–685.
- Madsen, H., 1992. Food selection by freshwater snails in the Gezira irrigation canals, Sudan. *Hydrobiologia* 228: 203–217.
- Meyer, J. L. & C. Johnson, 1983. The influence of elevated nitrate concentration on rate of leaf decomposition in a stream. *Freshwater Biology* 13: 177–183.
- Monk, D. C., 2006. The distribution of cellulase in freshwater invertebrates of different feeding habits. *Freshwater Biology* 6: 471–475.
- Moore, J. C., E. L. Berlow, D. C. Coleman, P. C. de Ruiter, Q. Dong, A. Hastings, N. Collins Johnson, K. S. McCann, K. Melville, P. J. Morin, K. Nadelhoffer, A. D. Rosemond, D. M. Post, J. L. Sabo, K. M. Scow, M. J. Vanni & D. H. Wall, 2004. Detritus, tropic dynamics, and biodiversity. *Ecology Letters* 7: 584–600.
- Oertli, B., 1993. Leaf litter processing and energy flow through macroinvertebrates in a woodland pond (Switzerland). *Oecologia* 96: 466–477.
- Ostrofsky, M. L., 1997. Relationship between chemical characteristics of autumn-shed leaves and aquatic processing rates. *Journal of the North American Benthological Society* 16: 750–759.
- Palik, B., D. P. Batzer & C. Kern, 2006. Upland forest linkages to seasonal wetlands: litter flux, processing, and food quality. *Ecosystems* 9: 142–151.
- Petersen, R. C. & K. W. Cummins, 1974. Leaf processing in a woodland stream. *Freshwater Biology* 4: 343–368.
- Pope, R. J., A. M. Gordon & N. K. Kaushik, 1999. Leaf litter colonization by invertebrates in the littoral zone of a small oligotrophic lake. *Hydrobiologia* 392: 99–112.
- Proffitt, C. E. & D. J. Devlin, 2005. Grazing by the intertidal gastropod *Melampus coffeus* greatly increases mangrove leaf litter degradation rates. *Marine Ecology Progress Series* 296: 209–218.
- Reavell, P. E., 1980. A study of the diets of some British freshwater gastropods. *Journal of Conchology* 30: 253–271.
- Spanhoff, B., R. Bischof, A. Bohme, S. Lorenz, K. Neumeister, A. Nothlich & K. Kusel, 2007. Assessing the impact of effluents from a modern wastewater treatment plant on breakdown of coarse particulate organic matter and benthic macroinvertebrates in a lowland river. *Water, Air, and Soil Pollution* 180: 119–129.
- Tanaka, M. O., A. C. A. Ribas & A. L. T. de Souza, 2006. Macroinvertebrate succession during leaf litter breakdown

- in a perennial karstic river in Western Brazil. *Hydrobiologia* 568: 493–498.
- Underwood, G. J. C., 1991. Growth enhancement of the macrophyte *Ceratophyllum demersum* in the presence of the snail *Planorbis planorbis*: the effect of grazing and chemical conditioning. *Freshwater Biology* 26: 325–334.
- Webster, J. R. & E. F. Benfield, 1986. Vascular Plant Breakdown in Freshwater Ecosystems. *Annual Review of Ecology and Systematics* 17: 567–594.
- Webster, J. R., J. B. Wallace & E. F. Benfield, 1995. Organic processes in streams of the eastern United States. In Cushing, C. E., K. W. Cummins & G. W. Minshall (eds), *Ecosystems of the World. Volume 22. River and Stream Ecosystems*. Elsevier, Amsterdam, The Netherlands: 117–187.