

- organic matter and benthic diatoms in strongly acidic Lake Katanuma. *Aquat. Microb. Ecol.* **33**: 87–94.
- , ———, AND S. SHIKANO. 2001. Carbon and nitrogen stable isotope ratios analysis of food sources for *Chironomus acer-biphilus* larvae (Diptera Chironomidae) in strongly acidic Lake Katanuma. *Radioisotopes* **50**: 601–611.
- FORD, P. W., P. I. BOON, AND K. LEE. 2002. Methane and oxygen dynamics in a shallow floodplain lake: the significance of periodic stratification. *Hydrobiologia* **485**: 97–110.
- JELLISON, R., AND J. M. MELACK. 1993. Meromixis in hypersaline Mono Lake, California. 1. Stratification and vertical mixing during the onset, persistence, and breakdown of meromixis. *Limnol. Oceanogr.* **38**: 1008–1019.
- KLING, G. W., AND OTHERS. 1987. The 1986 Lake Nyos gas disaster in Cameroon West Africa. *Science* **236**: 169–175.
- MCMANUS, J., R. W. COLLIER, AND J. DYMOND. 1993. Mixing processes in Crater Lake, Oregon. *J. Geophys. Res.* **98**: 18295–18307.
- OHBA, T., J. HIRABAYASHI, AND K. NOGAMI. 1994. Water, heat and chloride budgets of the crater lake, Yugama at Kusatsu-Shirane volcano, Japan. *Geochem J.* **28**: 217–231.
- PASTERNAK, G. B., AND J. C. VAREKAMP. 1997. Volcanic lake systematics. I. Physical constraints. *Bull. Volcanol.* **58**: 528–538.
- RODRIGO, M. A., E. VICENTE, AND M. R. MIRACLE. 2000. The physical, chemical and biological characteristics of the holomictic sulphated Lake Arcas—2 (Cuenca, Spain). *Hydrobiologia* **418**: 153–168.
- ROWE, G. L., S. L. BRANTLEY, M. FERNANDEZ, J. F. FERNANDEZ, A. BORGIA, AND J. BARQUERO. 1992. Fluid–volcano interaction in an active stratovolcano: The crater lake system of Poás volcano, Costa Rica. *J. Volcanol. Geotherm. Res.* **49**: 23–51.
- SATAKE, K. 1975. Water temperature in Lake Katanuma. *Jpn. J. Limnol.* **36**: 1–5. [In Japanese with English summary.]
- , AND Y. SAJO. 1973. Microbial CO₂ fixation in the anoxic zone in a volcanic acid lake. *Nature* **243**: 99–100.
- , AND ———. 1974. Carbon dioxide content and metabolic activity of microorganisms in some acid lakes in Japan. *Limnol. Oceanogr.* **19**: 331–338.
- , AND ———. 1978. Mechanism of lamination in bottom sediment of the strongly acid Lake Katanuma. *Arch. Hydrobiol.* **83**: 429–442.
- SATO, G. 1995. A formation mechanism of water temperature and water quality in the Lake Katanuma in the Narugo volcano. *J. Jpn. Soc. Water Environ.* **18**: 829–836. [In Japanese with English summary.]
- SIGVALDASON, G. E. 1989. International conference on Lake Nyos disaster, Yaoundé, Cameroon 16–20 March, 1987: Conclusions and recommendations. *J. Volcanol. Geotherm. Res.* **39**: 97–107.
- STRICKLAND, J. D. H., AND T. R. PARSONS. 1972. A practical handbook of seawater analysis, 2nd ed. *Bull. Fish. Res. Board Can.* **167**.
- TAKANO, B., S. OHSAWA, AND R. B. GLOVER. 1994. Surveillance of Ruapehu Crater Lake, New Zealand, by aqueous polythionates. *J. Volcanol. Geotherm. Res.* **60**: 29–57.
- VALLENTYNE, J. R. 1957. Principles of modern limnology. *Am. Sci.* **45**: 218–224.
- WETZEL, R. G. 2001. *Limnology: Lake and river ecosystems*, 3rd ed. Academic Press.

Received: 13 April 2004

Accepted: 2 June 2004

Amended: 29 July 2004

Limnol. Oceanogr., 49(6), 2004, 2292–2296
© 2004, by the American Society of Limnology and Oceanography, Inc.

Clearance of aquatic hyphomycete spores by a benthic suspension feeder

Abstract—We placed individual *Elliptio complanata* in aerated suspensions of conidia (asexual spores) of aquatic hyphomycetes (Fungi). Mussels actively ingested conidia at an initial rate of over 20,000 h⁻¹. The conidia of the seven most common species were removed at different rates, but there was no consistent correlation between conidial size or shape (tetraradiate, sigmoid, or clove shaped) and removal by *E. complanata*. At the maximum clearance rate, animals ingested the equivalent of 159 ng conidial biomass h⁻¹, corresponding to 4.7 μg d⁻¹ g⁻¹ animal dry mass. At natural densities, *E. complanata* may be able to eliminate a considerable proportion of the conidial production, causing a shift in the proportions of species in the remaining conidia.

In small woodland streams, leaves of riparian trees often dominate the food supply (Allan 1995). They are rapidly colonized by a specialized group of fungi, aquatic hyphomycetes, the growth and activity of which render the substrate more attractive to leaf-eating invertebrates (shredders;

Acknowledgments

We gratefully acknowledge the many helpful suggestions by two anonymous referees and by Dr. J. A. Ackerman. Financial support was provided by NSERC Discovery grants to F.B.

Bärlocher 1985; Suberkropp 1992). Aquatic hyphomycete biomass on decaying leaves may reach 17% of total detrital mass (Gessner 1997), and fungal production per unit area in a small, nutrient-poor stream is of the same order of magnitude as that of bacteria and invertebrates (Suberkropp 1997). Several studies estimated that close to 50% of total fungal production is channeled into conidia (asexual spores; Findlay and Arsuffi 1989; Suberkropp 1991; Sridhar and Bärlocher 2000). Up to eight conidia may be released per microgram of detrital mass per day (Gessner 1997), adding up to a total spore concentration approaching 30,000 L⁻¹ stream water in late fall (Iqbal and Webster 1973). Gessner (1997) estimates that 20 g of conidial mass pass daily through a cross-section of a small stream (discharge of 60 L s⁻¹). Nothing is known about the fate of this component of fine particulate organic matter (FPOM).

The Eastern elliptio, *Elliptio complanata* (Lightfoot), is a freshwater bivalve (Unionidae) found in ponds and streams along the Atlantic seaboard of North America from the Carolinas to the St. Lawrence River Basin and westward to Lake Superior. This benthic suspension feeder occurs in densities of up to 150 animals m⁻² (Fisher and Tevesz 1976). It takes in large volumes of water through an incurrent siphon and clears all particles exceeding 1.6 μm in diameter (Paterson

Table 1. Fungal species evaluated for selective attachment and clearance rates. Size is the largest diameter within space covered by conidial appendages. Number indicates conidia per beaker at beginning of experiment with percentage of total number of conidia in parentheses.

Species	Shape	Size (μm)	Number
<i>Alatospora acuminata</i> Ingold	Tetradiate	46	2,158 (12.4%)
<i>Anguillospora filiformis</i> Greath	Sigmoid	192	6,734 (38.7%)
<i>Articulospora tetracladia</i> Ingold	Tetradiate	73	609 (3.5%)
<i>Clavatospora longibrachiata</i> (Ingold) Marvanová et Nilsson	Tetradiate	26	2,262 (13.0%)
<i>Clavariopsis aquatica</i> de Wild	Tetradiate	77	1,044 (6.0%)
<i>Flagellospora curvula</i> Ingold	Sigmoid	95	2,419 (13.9%)
<i>Heliscus lugdunensis</i> Sacc. et Th�erry	Clove-shaped	33	696 (4.0%)
Totals			15,922 (91.5%)

1986). The uptake of phytoplankton, protozoans, and even bacteria by suspension-feeding bivalves and other collectors is well documented (Madenjian 1995; Kreeger and Newell 1996; Ackerman et al. 2001). Our primary objective was to determine if, and at what rate, *E. complanata* removes suspended conidia from the water. In addition, we wished to determine whether *E. complanata* exhibits differential clearance of aquatic hyphomycete spores given species-specific differences in conidial size and shape (e.g., tetradiate or sigmoidal; Webster 1987). Finally, we estimated the potential contribution of ingested spores to the nutrition of *E. complanata*.

Methods—Five specimens of *E. complanata* were collected from the outflow of Silver Lake (Sackville, New Brunswick, Canada) and kept in aquaria with aerated well water (\leq three animals per 30-L aquarium). They were kept without food for 2 d before the experiments, at the acclimation and experimental temperature of 15°C.

Autumn-shed leaves of linden (*Tilia cordata* Mill.) were collected from a single tree, air-dried, and placed in mesh bags (1.6-mm-mesh size). They were incubated in Heinz Brook, a second-order stream near Amherst (Nova Scotia, Canada; pH 6.8, conductivity 178 $\mu\text{S cm}^{-1}$, 18.8 mg L⁻¹ Ca²⁺, 0.1–0.2 m s⁻¹ water velocity, 60 L s⁻¹ base flow). After 4 weeks (21 May–17 June 2003), leaves were taken to the laboratory, rinsed with tap water, and placed in a 250-ml Erlenmeyer flask with 100 ml distilled water. The flask was incubated on a shaker (140 rpm) for 48 h. After 2 d, the contents of the Erlenmeyer flask were poured through a coarse mesh (800 μm) to separate the leaves from fungal spores. The spores, which passed through the sieve, were suspended in 2 liters of Sackville well water. To determine spore concentration in this stock suspension, aliquots of 30 ml were passed through a membrane filter (Millipore, SCWP04700, 8- μm pore size). Retained spores were stained with cotton blue in lactophenol, counted, and identified.

Experiments were performed in 1-liter beakers filled with 1 liter of well water and enriched with an aliquot of the spore suspension to yield a final concentration of 20,000 spores L⁻¹. The beakers were aerated with compressed air introduced through Pasteur pipets. The resulting moderate mixing and small container size minimized settling of the spores and would tend to increase the clearance rate of suspension feeders (Ackerman 1999). To estimate losses due to passive set-

ting, we ran three control beakers without animals but otherwise treated identically.

Animals were introduced into the experimental beakers at time 0 (one animal per beaker), and the experiment was run for a total of 4 h. During the experiment, we checked visually that the mussels had opened their valves and extended their siphons. We measured length, height, and width of the animals (in millimeters) and determined their wet weight (three measurements). No feces or pseudofeces were observed in any of the beakers.

Aliquots of the spore suspensions in control and experimental beakers were taken at times 0, 30 min, 60 min, 120 min, and 240 min. They were passed through membrane filters (8- μm pore size). Retained spores were stained with cotton blue in lactophenol, counted, and identified. The decline in the number of suspended conidia was estimated by nonlinear curve fitting to an exponential decay curve (Levenberg–Marquardt algorithm; Kaleidagraph version 3.6, Synergy Software).

Clearance rates of the mussels were calculated with Gaudl's equation (Gaudl 1951; losses in control beakers were first subtracted) as

$$CR = \frac{V(\ln C_0 - \ln C_t)}{tN}$$

where *CR* = clearance rate in milliliters per animal per hour, *C*₀ = food concentration (=number of spores) at time zero, *C*_{*t*} = food concentration at time *t*, *N* = number of animals, *t* = time in hours, and *V* = volume of food suspension in milliliters.

To test whether conidial species varied in attachment rates in control beakers or were consumed (cleared) at different rates in treatment beakers, we compared initial conidial counts (time 0) and counts after 30 min (time 30). Numbers of consumed conidia were corrected by subtracting losses from control beakers. Feeding preferences were expressed by the selection index (values >1 indicating preference, and values <1 indicating avoidance; Krebs 1999) and by Manly's α index (assuming variable prey populations, varies between 0 and 1; Krebs 1999). Because the accuracy of the test varies with sample size and requires positive values, we evaluated only the seven most common conidial types, which collectively accounted for 91.5% of initial numbers (Table 1). Sample sizes to estimate conidial counts varied between 60 and 700. Conidial shapes of the seven species

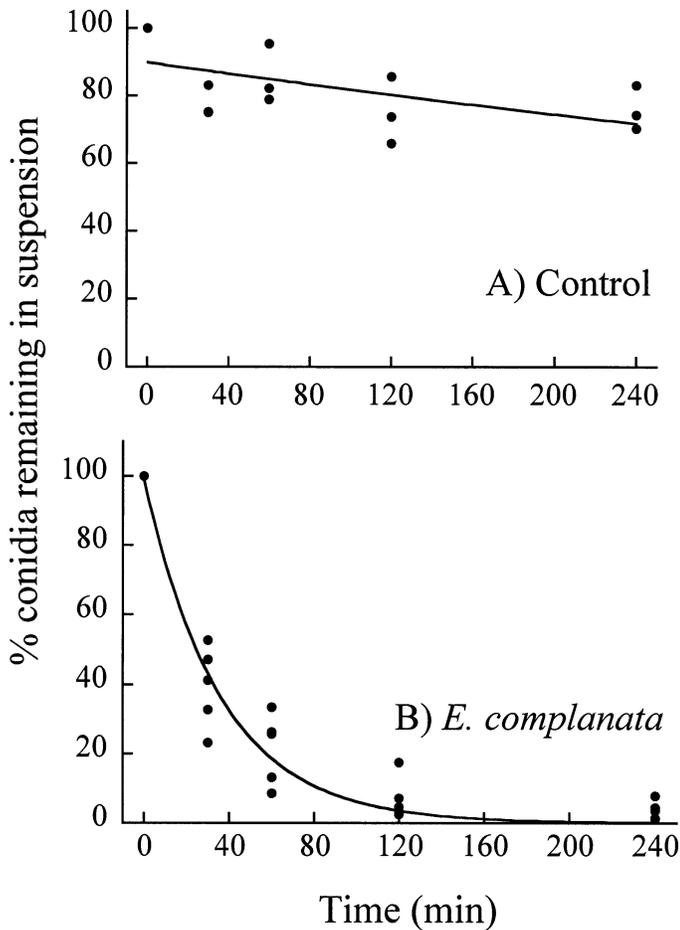


Fig. 1. Loss of suspended conidia in (A) three controls (no animals), and (B) five treatment beakers (each containing one *E. complanata*).

were classified as sigmoid (elongated, s-shaped), tetra radiate (four appendages emerging from a common point), and clove shaped (Webster 1987). As a crude measure of size, we determined the longest axis within the space described by all appendages of a conidium. In sigmoid and clove-shaped conidia, this corresponds to their length; in tetra radiate conidia, it corresponds to the combined length of the two longest appendages.

Results—Initial conidium concentrations were $18,700 \pm 2,700 \text{ L}^{-1}$ (mean \pm SD) in control (without animals) and

$16,100 \pm 3,300 \text{ L}^{-1}$ in experimental (with animals) beakers (difference was not significant, $t = 1.14$, 6 degrees of freedom, $p = 0.30$). Loss rates clearly increased in the presence of *E. complanata* (Fig. 1; exponential loss rates $k = 0.00094$ for control and 0.028 for treatment, respectively). Overall, we identified 21 species of aquatic hyphomycetes.

Body length of the five mussels varied between 62 and 89 mm and wet mass between 18.6 and 52.9 g (Table 2), and their individual soft-body dry mass varied between 0.8 and 2.3 g (based on formula by Balfour and Smock 1995).

As spore removal was highest during the first 30 min of the experiment (cf. Fig. 1), we used this initial period to calculate clearance rates. Clearance rates varied between 900 and 1,800 ml individual⁻¹ h⁻¹, corresponding with specific clearance rates of between 600 and 1,300 ml g⁻¹ h⁻¹ (Table 2). In general, absolute clearance rates increased and size-specific clearance rates decreased with body length and body mass of the mussels. This is in agreement with animal physiological expectations (Schmidt-Nielsen 1997).

The number of spores removed from suspension was from 10,300 to 17,100 per hour and mussel, representing a bio-volume of 136,000–318,000 μm^3 individual⁻¹ h⁻¹ (Table 2).

Using species-specific spore volumes given by Bärlocher and Schweizer (1983) and Chauvet and Suberkropp (1998) and assuming an average biomass of 500 fg μm^{-3} of spore volume (Gessner 1997), the conidial biomass ingested per individual *E. complanata* was from 68 ng to 159 ng h⁻¹.

For the control beakers, selection indices indicated the same relative tendency to settle and/or attach to the beaker walls as did Manly's α ($p < 0.0001$), with *Alatospora acuminata* (ALAC) disappearing from suspension the fastest (Fig. 2A). There was no obvious pattern relating these rates to conidial shape, and a linear regression between selection indices and conidial size was not significant ($p = 0.6$).

As indicated by the selection indices, mussels preferred *Articulospora tetracladia*, *Clavariopsis aquatica*, and *Anguillospora filiformis* over conidia from all other taxa (Fig. 2B; $p < 0.0001$), a pattern that differed profoundly from the controls. Again, there was no obvious pattern relating indices to conidial shapes, and a linear regression between selection indices and size was not significant ($p = 0.11$).

Discussion—In temperate deciduous forests, between 70% and 90% of leaves entering a stream do so during a relatively brief period of 4–8 weeks in autumn (Bray and Gorham 1964; Allan 1995). They represent the major source of energy for aquatic hyphomycetes; not surprisingly, there

Table 2. Clearance rates and uptake of conidial volume and biomass by five individual *E. complanata*. Soft-body dry mass calculated as in Balfour and Smock (1995); for spore mass, a value of 500 fg μm^{-3} spore volume was assumed (Findlay and Arsuffi 1989).

	Body length (mm)	Wet mass (g)	Soft-body dry mass (g)	Clearance rate (ml ind ⁻¹ h ⁻¹)	Specific clearance rate (ml g ⁻¹ h ⁻¹)	Volume of captured spores (μm^3 ind ⁻¹ h ⁻¹)	Mass of captured spores (ng ind ⁻¹ h ⁻¹)
1	62	18.6	0.75	1,000	1,300	296,000	148
2	67	25.3	0.95	900	1,000	136,000	68
3	73	29.5	1.24	1,500	1,200	213,000	106
4	85	48.8	2.01	1,800	900	169,000	85
5	89	52.9	2.28	1,300	600	318,000	159

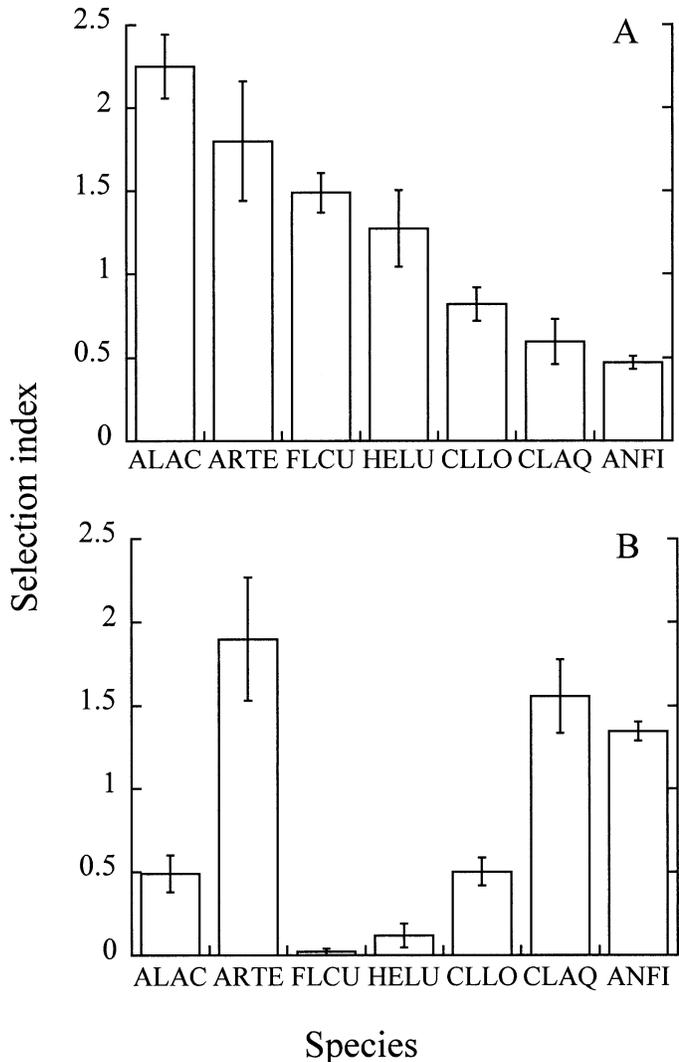


Fig. 2. Selection indices (Krebs 1999) for seven most common conidial species, $\pm 95\%$ confidence limits. Values >1 indicate disproportionately high attachment/consumption. (A) Attachment rates in control beakers. (B) Clearance rates in treatment beakers. ALAC, *Alatospora acuminata*; ARTE, *Articulospora tetracladia*; FLCU, *Flagellospora curvula*; HELU, *Heliscus lugdunensis*; CLLO, *Clavatospora longibrachiata*; CLAQ, *Clavariopsis aquatica*; ANFI, *Anguillospora filiformis*.

is a huge surge in conidia released a few weeks after leaf fall. Large tetra- and sigmoidal conidia readily settle on surfaces, and the average downstream displacement by spores is relatively modest (Webster 1987). Various authors estimated the half distance (distance to remove 50% of the suspended spores from the water column) to be a few hundred meters (Thomas et al. 1991; Bärlocher 1992a,b). Spores might passively settle on the streambed or associated substrates, where they will eventually be decomposed by bacteria or ingested by collectors. Or conidia in the water column may be captured by suspension feeders. Our study demonstrates for the first time that at least one common benthic consumer removes suspended conidia. Similar clearance rates were found in preliminary experiments with the brown

mystery snail, *Campeloma decisum* (Viviparidae, Mollusca): snails of 18.6 g wet mass showed a clearance rate of 1,200 ml h^{-1} and an uptake of 126 ng h^{-1} spore mass (unpubl. obs.).

Our clearance rates are comparable with those for algae consumed by *E. complanata* (Paterson 1986) or *Hyridella menziesi*, a closely related species of the same family (Roper and Hickey 1995). Based on initial particle concentrations of 84–142 ng L^{-1} , our mussels were likely feeding at maximum rates (Walker et al. 2001). If similar clearance rates apply to field conditions, the influence of mussels on conidia can be substantial. As a first approximation, *E. complanata* may clear between 2% and 100% of the water in a 500-m-long \times 3-m-wide \times 0.2-m-deep stream reach with a base flow of 60 $L s^{-1}$, given reported mussel densities that range from 2.5 to 150 individuals m^{-2} (Fisher and Tevesz 1976; Balfour and Smock 1995), a clearance rate of 1 L individual $^{-1} h^{-1}$ (Table 2), and a large number of assumptions, including a simple well-mixed reactor model. The loss of conidia due to invertebrate consumption may be important, especially if the potential effects of other suspension feeders are considered (Wotton 2003). Moreover, the selective clearance of conidia (*Articulospora tetracladia* $>$ *Clavariopsis aquatica* $>$ *Anguillospora filiformis*; Fig. 2B) may influence stream foodwebs.

The complementary question is how relevant ingested conidia are to the nutrition of invertebrates. To our knowledge, H. B. N. Hynes was the first to observe small, star-shaped structures (almost certainly tetra- and sigmoidal conidia) in the guts of stonefly larvae (unpubl. obs., quoted in Bärlocher 1992a), and conidia, most of them no longer viable, were reported from the feces of the amphipod *Gammarus pulex* (Bärlocher 1981). The data presented here represent the first quantitative estimate of total intake for a suspension-feeding invertebrate. Considering the fact that the maintenance ration of a mussel of 1 g soft-body dry mass is 1.5% of its mass per day (Winter 1978), the amount of hyphomycete conidia filtered here corresponds to only between 0.01% and 0.03% of the maintenance ration (i.e., 1.0–4.7 $\mu g g^{-1} d^{-1}$; see Table 2). Even if we assume a temporarily higher concentration of hyphomycete spores—values of up to 30,000 conidia L^{-1} were reported in the literature (Iqbal and Webster 1973)—the contribution of spores to the nutrition of *E. complanata* remains negligible. The possibility remains that spores may be rich in micronutrients, such as vitamins, trace elements, or essential fatty acids or that spores may contribute significantly to the diets of other stream invertebrates (Suberkropp 1992).

Without considering the wide range of other suspension-feeding invertebrates, we were able to show that benthic mussels at natural densities have the potential to significantly depress numbers of fungal conidia suspended in streams and modify their species make-up. This, in turn, may affect detritus processing—when spore concentrations are significantly depressed, fungal colonization and degradation of detritus may be delayed. By reducing the traveling distance of conidia, suspension feeders potentially act as within-stream barriers and may limit dispersal of fungi. Conidial biomass, however, seems insufficient to contribute substantially to the mussels' nutritional requirements.

Felix Bärlocher

Department of Biology
Mt. Allison University
63B York Street
Sackville, New Brunswick E4L1G7, Canada

Heinz Brendelberger

Zoologisches Institut der
Christian-Albrechts-Universität zu Kiel
Abteilung Limnologie
Olshausenstrasse 40
D-24098 Kiel, Germany

References

- ACKERMAN, J. D. 1999. Effect of velocity on the filter feeding of dreissenid mussels (*Dreissena polymorpha* and *Dreissena bugensis*): Implications for trophic dynamics. *Can. J. Fish. Aquat. Sci.* **56**: 1551–1561.
- , M. R. LOEWEN, AND P. F. HAMBLIN. 2001. Benthic-pelagic coupling over a zebra mussel reef in western Lake Erie. *Limnol. Oceanogr.* **46**: 892–904.
- ALLAN, J. D. 1995. *Stream ecology*. Chapman and Hall.
- BALFOUR, D. L., AND L. A. SMOCK. 1995. Distribution, age structure, and movements of the freshwater mussel *Elliptio complanata* (Mollusca: Unionidae) in a headwater stream. *J. Freshw. Ecol.* **10**: 255–268.
- BÄRLOCHER, F. 1981. Fungi on the food and in the faeces of *Gammarus pulex*. *Tr. Br. Mycol. Soc.* **76**: 14–19.
- . 1985. The role of fungi in the nutrition of stream invertebrates. *Bot. J. Linn. Soc.* **91**: 83–94.
- . 1992a. Research on aquatic hyphomycetes: Historical background and overview, p. 1–15. *In* F. Bärlocher [ed.], *The ecology of aquatic hyphomycetes*. *Ecol. Stud.* 94. Springer.
- . 1992b. Recent developments in stream ecology and their relevance to aquatic mycology, p. 16–37. *In* F. Bärlocher [ed.], *The ecology of aquatic hyphomycetes*. *Ecol. Stud.* 94. Springer.
- , AND M. SCHWEIZER. 1983. Effects of leaf size and decay rate on colonization by aquatic hyphomycetes. *Oikos* **41**: 205–210.
- BRAY, J. R., AND E. GORHAM. 1964. Litter production in forests of the worlds. *Adv. Ecol. Res.* **2**: 101–157.
- CHAUVET, E., AND K. SUBERKROPP. 1998. Temperature and sporulation of aquatic hyphomycetes. *Appl. Environ. Microbiol.* **64**: 1522–1525.
- FINDLAY, S. E. G., AND T. L. ARSUFFI. 1989. Microbial growth and detritus transformation during decomposition of leaf litter in a stream. *Freshw. Biol.* **21**: 261–269.
- FISHER, J., AND M. TEVESZ. 1976. Distribution and population density of *Elliptio complanata* in Lake Pocotopaug, Connecticut. *Veliger* **18**: 332–338.
- GAULD, D. T. 1951. The grazing rate of planktonic copepods. *J. Mar. Biol. Assoc. U.K.* **29**: 695–706.
- GESSNER, M. O. 1997. Fungal biomass, production and sporulation associated with particulate organic matter in streams. *Limnologia* **13**: 33–44.
- IQBAL, S. H., AND J. WEBSTER. 1973. Aquatic hyphomycete spora of the River Exe and its tributaries. *Trans. Br. Mycol. Soc.* **61**: 331–346.
- KREBS, C. J. 1999. *Ecological methodology*. Benjamin/Cummings.
- KREEGER, D. A., AND R. I. E. NEWELL. 1996. Ingestion and assimilation of carbon from cellulolytic bacteria and heterotrophic flagellates by the mussels *Geukensia demissa* and *Mytilus edulis* (Bivalves, Mollusca). *Aquat. Microb. Ecol.* **11**: 205–214.
- MADENJIAN, C. P. 1995. Removal of algae by the zebra mussel (*Dreissena polymorpha*) population in western Lake Erie: A bioenergetics approach. *Can. J. Fish. Aquat. Sci.* **52**: 381–390.
- PATERSON, C. G. 1986. Particle size selectivity in the freshwater bivalve *Elliptio complanata*. *Veliger* **29**: 235–237.
- ROPER, D. S., AND C. W. HICKEY. 1995. Effects of food and silt on filtration, respiration and condition of the freshwater mussel *Hyridella menziesi* (Unionacea: Hyriidae): Implications for bioaccumulation. *Hydrobiologia* **312**: 17–25.
- SCHMIDT-NIELSEN, K. 1997. *Animal physiology*. Cambridge Univ. Press.
- SRIDHAR, K. R., AND F. BÄRLOCHER. 2000. Initial colonization, nutrient supply, and fungal activity on leaves decaying in streams. *Appl. Environ. Microbiol.* **66**: 1112–1119.
- SUBERKROPP, K. 1991. Relationships between growth and sporulation of aquatic hyphomycetes on decomposing leaf litter. *Mycol. Res.* **95**: 843–850.
- . 1992. Interactions with invertebrates, p. 729–747. *In* F. Bärlocher [ed.], *The ecology of aquatic hyphomycetes*. *Ecol. Stud.* 94. Springer.
- . 1997. Annual production of leaf decaying fungi in a woodland stream. *Freshw. Biol.* **38**: 169–178.
- THOMAS, K., G. A. CHILVERS, AND R. H. NORRIS. 1991. A dynamic model of fungal spora in a freshwater stream. *Mycol. Res.* **95**: 184–188.
- WALKER, K. F., M. BYRNE, C. W. HICKEY, AND D. S. ROPER. 2001. Freshwater mussels of Australasia, p. 5–31. *In* G. Bauer and K. Wächtler [eds.], *Ecology and evolution of the freshwater mussels Unionoida*. *Ecol. Stud.* 145. Springer.
- WEBSTER, J. 1987. Convergent evolution and the functional significance of spore shape in aquatic and semi-aquatic fungi, p. 191–201. *In* A. D. M. Rayner, C. M. Brasier, and D. Moore [eds.], *Evolutionary biology of the fungi*. Cambridge Univ. Press.
- WINTER, J. E. 1978. A review on the knowledge of suspension-feeding in lamellibranchiate bivalves, with special reference to artificial aquaculture systems. *Aquaculture* **13**: 1–33.
- WOTTON, R. S., B. MALMQUIST, AND K. LEONARDSON. 2003. Expanding traditional views on suspension feeders—quantifying their role as ecosystem engineers. *Oikos* **101**: 441–443.

Received: 1 March 2004

Accepted: 4 June 2004

Amended: 6 July 2004