CONCEPTS & SYNTHESIS
EMPHASIZING NEW IDEAS TO STIMULATE RESEARCH IN ECOLOGY

Tube-dwelling invertebrates: tiny ecosystem engineers have large effects in lake ecosystems

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Abstract. There is ample evidence that tube-dwelling invertebrates such as chironomids significantly alter multiple important ecosystem functions, particularly in shallow lakes. Chironomids pump large water volumes, and associated suspended and dissolved substances, through the sediment and thereby compete with pelagic filter feeders for particulate organic matter. This can exert a high grazing pressure on phytoplankton, microorganisms, and perhaps small zooplankton and thus strengthen benthic-pelagic coupling. Furthermore, intermittent pumping by tube-dwelling invertebrates oxygenates sediments and creates a dynamic, three-dimensional mosaic of redox conditions. This shapes microbial community composition and spatial distribution, and alters microbe-mediated biogeochemical functions, which often depend on redox potential. As a result, extended hotspots of element cycling occur at the oxic-anoxic interfaces, controlling the fate of organic matter and nutrients as well as fluxes of nutrients between sediments and water. Surprisingly, the mechanisms and magnitude of interactions mediated by these organisms are still poorly understood. To provide a synthesis of the importance of tube-dwelling invertebrates, we review existing research and integrate previously disregarded functional traits into an ecosystem model. Based on existing research and our models, we conclude that tube-dwelling invertebrates play a central role in controlling water column nutrient pools, and hence water quality and trophic state. Furthermore, these tiny ecosystem engineers can influence the thresholds that determine shifts between alternate clear and turbid states of shallow lakes. The large effects stand in contrast to the conventional limnological paradigm emphasizing predominantly pelagic food webs. Given the vast number of shallow lakes worldwide, benthic invertebrates are likely to be relevant drivers of biogeochemical processes at regional and global scales, thereby mediating feedback mechanisms linked to climate change.

Key words: biogeochemistry; chironomids; ecosystem modelling; filter-feeding; food web; nutrient cycling; tube-dwelling macrozoobenthos.

INTRODUCTION

Shallow lakes represent the most abundant lake type worldwide. These ecosystems are highly susceptible to global warming and eutrophication, and are of great importance for regional and global element cycles (Wetzel 2001, Downing et al. 2006, Adrian et al.

TABLE 1. Definition of terms based on Jones et al. (1994) and Kristensen et al. (2012).

Term	Definition
Ecosystem engineer	"... organisms that directly or indirectly modulate the availability of resources (other than themselves) to other species, by causing physical state changes in biotic or abiotic materials. In so doing they modify, maintain and/or create habitats." (Jones et al. 1994:374)
Bioturbation	"All transport processes carried out by animals that directly or indirectly affect sediment matrices. These processes include particle reworking and burrow ventilation" (Kristensen et al. 2012:288)
Burrow ventilation	"Rapid exchange of water between the overlying water and subsurface sediment" (Kristensen et al. 2012:293) since "animals flush their open- or blind-ended burrows with overlying water for respiratory and feeding purposes" (p. 285)
Particle reworking	"Faunal displacement and biomixing of particles" including "burrowing, construction and maintenance of galleries as well as ingestion and defecation of particles" (Kristensen et al. 2012:288)
Bioirrigation	Radial molecular diffusion driven or pressure-induced advective pore water "... exchange of solutes between the sediment pore water and the overlying water body." (Kristensen et al. 2012:285)
Excretion	The process by which metabolic waste products and other non-useful materials are eliminated from an organism.

Note: Kristensen et al. (2012) depict the outcome of a broad discussion within the scientific community, especially the Nereis Park research group.

2009). For example, global annual carbon dioxide emissions from inland waters (mainly from shallow lakes) to the atmosphere are similar to carbon dioxide uptake by the oceans, and the global burial of organic carbon in inland water sediments exceeds that in ocean sediments (Tranvik et al. 2009). Small lakes are also disproportionately important in retaining and processing nitrogen (Harrison et al. 2009). Additionally, shallow lakes provide a valuable resource for human use and recreation (Völker and Kistemann 2013). It is therefore important to understand the functioning of these ecosystems, in particular the controls on their metabolism, nutrient cycling, and productivity.

A potentially important driver of lake ecosystem metabolism, benthic invertebrates, has traditionally been disregarded or viewed in a supportive food web context, i.e., as a food source for fish and to a lesser extent as consumers of sedimentary algae and organic matter (Janse et al. 2010, Vander Zanden and Gratton 2011). While the interplay between productivity and the dynamics of shallow lake communities has been documented extensively (Scheffer 1998, Köhler et al. 2005, Huber et al. 2008), the role of benthic invertebrates in regulating biogeochemical cycles and energy flux at the whole-lake scale has received little attention (Covich et al. 1999, Vadeboncoeur et al. 2002). Given the prevalence of small lakes across the globe, as well as the potentially large role of benthic invertebrates, it is essential that we comprehensively evaluate the role of these organisms at multiple scales.

Benthic invertebrates represent a diverse fauna, but tube-dwelling taxa may be especially important because they pump large volumes of water, containing suspended, dissolved, and gaseous substances, through the sediment. Small-scale laboratory studies investigating the pumping activity of tube-dwelling invertebrates (ventilation; see Table 1 for definition of terms) and the subsequent aeration of the sediment (bioirrigation) suggest that tube-dwelling invertebrates play a far more important and diverse ecological role than previously assumed by ecosystem-level analyses. Volumes equiva-

lent to an entire shallow lake can be pumped through the sediment on timescales of days to weeks (Roskosch et al. 2012). This is particularly true for the most widely distributed and frequently the most abundant group of insects in freshwater environments: the family Chironomidae, dipterans in the suborder Nematocera. Most chironomid larvae build tubes composed of silk and various substrate materials, such as detritus, algae, and sediments (Pinder 1986, Armitage et al. 1995). In shallow lakes, chironomids typically occur at densities between 70 and 11 000 individuals/m^2 (Armitage et al. 1995, Mousavi 2002). The sheer number of individuals suggests that tube-dwelling invertebrates are relevant for carbon, nutrient, and energy cycling at the ecosystem level, potentially modulating a feedback with global cycles and climate.

To rigorously assess the ecosystem-level role of tube-dwelling invertebrates, their roles in benthic-pelagic coupling and inducing changes in alternate states needs to be considered. Classical theory on alternative stable states in shallow lakes differentiates macrophyte-dominated (clear) from phytoplankton-dominated (turbid) lakes, and focuses on feedback effects mediated by the impact of fish on phytoplankton through predation on herbivorous zooplankton (trophic cascades) and via bioturbation by fish (Scheffer 1998). Which state prevails under what conditions can be analyzed using long-term records and ecosystem models, and as with any model the predictive power depends on the validity of the model parameters and assumptions. However, existing models of shallow lake ecosystems such as PCLake (Janse 2005, Mooij et al. 2010) or the PEG (Plankton Ecology Group) model (Sommer et al. 1986, 2012, de Senerpont Domis et al. 2013) insufficiently include the benthic-pelagic coupling mediated by tube-dwelling invertebrates and its implications for pelagic food web regulation. There is now ample evidence to suggest that the impacts of these animals on the dynamics of microorganisms, redox gradients, and biogeochemical cycling of nutrients must be taken into account to forecast ecosystem trajectories at the whole-
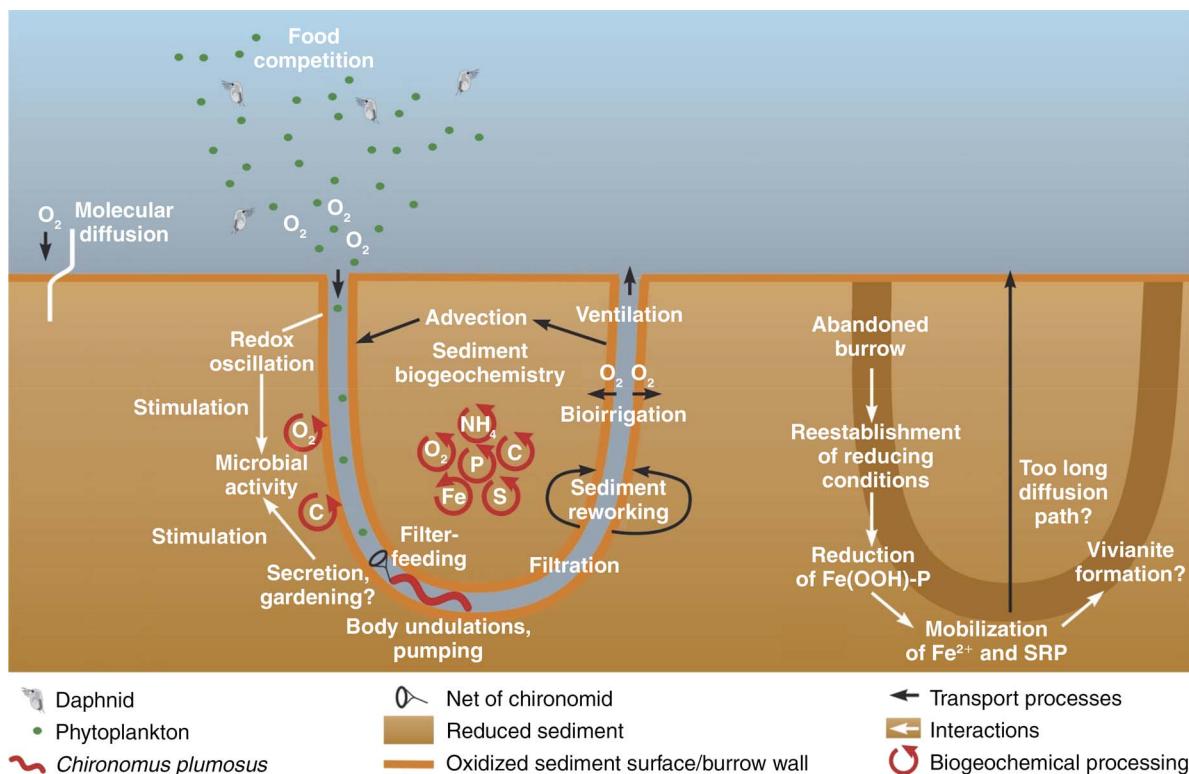
Fig. 1.   Mechanisms by which tube-dwelling invertebrates may control water quality and trophic status (*Chironomus plumosus* larvae used as an example for tube-dwelling invertebrates).

lake scale (e.g., Stief and Hölker 2006, Lewandowski et al. 2007).

The aim of this paper is to review and synthesize existing information in order to articulate the role of tube-dwelling invertebrates in lake ecosystems and to identify knowledge gaps for future research. First we evaluate current knowledge in four areas: (1) biogeochemistry at the scale of individual tubes, (2) nutrient cycling mediated by tube-dwelling invertebrates, (3) filtration and food competition between pelagic zooplankton and tube-dwelling invertebrates, and (4) impacts of predators on tube-dwelling invertebrates and nutrient dynamics. Then we evaluate how the impacts of tube-dwelling invertebrates are expressed at the ecosystem level using two established conceptual models and a dynamical ecosystem model. Based on these theoretical approaches, our final goal is to identify future research domains to overcome current limitations in understanding how tube-dwelling invertebrates affect lake ecosystems.

BIOGEOCHEMISTRY AT THE SCALE OF INDIVIDUAL TUBES

Geochemistry

Oxygen is scarce in the sediment environment, and thus tube-dwelling invertebrates need to pump overlying oxygen-rich water through their U-shaped burrows in the sediment for respiration. Interestingly, given a water flow rate of 60 mL/h (flow velocity 15 mm/s, tube diameter 1.5–2.0 mm, tube depth up to 20 cm), individual *Chironomus plumosus* larvae pump approximately 10 times more water through their burrows than required to meet their oxygen demands (Roskosch et al. 2010b, 2011). Reasons for such high pumping rates are high oxygen consumption by the microbial community of the burrow walls, which reduces oxygen availability to the larvae (Polerecky et al. 2006) and high filter-feeding rates of the larvae, which feed predominantly on particulate matter delivered into the burrow by the water current (Fig. 1; Roskosch et al. 2010b).

Burrow ventilation transports oxygen more rapidly and deeper into the sediment than does molecular diffusion across the sediment–water interface (Meile and Van Cappellen 2003). In addition, the intermittent nature of burrow ventilation affects the temporal distribution of oxygen and redox conditions in sediments surrounding the burrows (Polerecky et al. 2006, Roskosch et al. 2011, Volkenborn et al. 2012). This temporal oscillation in redox can greatly increase the metabolic rates of tube-associated sediment bacteria and stimulate organic matter degradation (Aller 1994).

Pumping activities of tube dwellers can also increase the release of phosphate-P and ammonium-N previously bound in organic detritus to the overlying water column (Fig. 1; Stief and Hölker 2006, Lewandowski et al. 2007, Stief et al. 2010). However, some studies show that

chironomids enhance phosphorus (P) fluxes across the sediment–water interface (e.g., Andersson et al. 1988, Andersen and Jensen 1991, Andersen et al. 2006), while others show the opposite effect (e.g., Lewandowski and Hupfer 2005, Lewandowski et al. 2007). Lewandowski et al. (2007) argue that the apparently contradictory results of chironomids on P flux may illustrate the relative importance of opposing pathways and the importance of variations in sediment type and composition. The classical view of the effects of individual chironomid burrows on P dynamics is that the thin, oxidized layer of sediment surrounding the burrow adsorbs P, due to the presence of oxidized compounds such as Fe-(oxy)hydroxides. This is analogous to the well-known presence of thin oxidized layers at the sediment surface in lakes with oxygenated bottom waters, which are underlain by anoxic sediments (Hupfer and Lewandowski 2008), or seen as iron plaque on plant roots (Christensen et al. 1998, Hupfer and Dollan 2003). The close relation between sedimentary Fe-(oxy)hydroxides and recycled phosphate (known since the early work of Einsele [1938]) has been intensively investigated in various ecosystems and by experimental approaches (e.g., Buffle et al. 1989, Gunnars et al. 2002). P cycling can also be modulated by secondary redox-dependent geochemical reactions (Fig. 1) that may result in ferrous or ferric authigenic P mineral precipitation, such as vivianite or strengite/ tinticite phases (Lijklema 1980, Hyacinthe and Van Cappellen 2004, Walpersdorf et al. 2013, Rothe et al. 2014). As the production of phosphate is tied to organic matter remineralization, organic matter input to sediments is critical in shaping P release. It is also a determining factor in the extent to which dissimilatory iron reduction produces ferrous iron. The fate of that reduced iron in turn depends on the availability of O_2 for rapid reoxidation forming amorphous iron oxides, of sulfide for the precipitation of FeS, and of manganese oxides as an alternate electron acceptor. All of these reactions impact the P cycle (e.g., Giordani et al. 1996, Yao and Millero 1996, Dellwig et al. 2010) and all are potentially affected by tube-dwelling invertebrates.

Redox zonation around tubes can not only establish an "iron curtain" affecting benthic P fluxes, but also governs the transformation of other redox-sensitive elements. For example, oxic halos surrounding tubes likely stimulate nitrification, and the nitrate produced can serve as an electron acceptor for denitrification in nearby anoxic zones. Thus, in the presence of tube-dwelling chironomids, denitrification activity is stimulated mainly because nitrate is efficiently pumped into deep, anoxic, sediment layers where it is readily reduced to molecular nitrogen (Pelegri et al. 1994, Svensson 1998). The ventilation of the tubes thus bypasses the nitrification layer at the sediment surface where nitrate is produced and then slowly diffuses downward into deep, anoxic layers (Thamdrup and Dalsgaard 2008). Bioturbation activities by abundant tube-dwelling inverte-

brates can thus result in a significant net loss of nitrogen from shallow aquatic ecosystems (Jeppesen et al. 1998, Søndergaard et al. 2007), but also in the release of nitrous oxide (a greenhouse gas) from the sediment (Svensson 1998, Stief et al. 2009, Stief 2013). The extent of tube-dweller effects on N cycling depends on the reactivity of organic matter as a source of ammonium for nitrification and as a substrate for denitrification, oxygen as a substrate for nitrification and as an inhibitor of denitrification, and the microbial community carrying out these processes (see *Microbiology*). Direct observational data on the biogeochemical conditions, let alone process rates, are very limited at the scale of tubes. However, new sensor developments such as planar optodes for O_2 (Glud et al. 1996), CO_2 (Zhu and Aller 2010), H_2S (Zhu and Aller 2013), Fe^{2+} (Zhu and Aller 2012), or pH (Zhu et al. 2006) hold promise for quantifying the extent to which tube dwellers alter the biogeochemical conditions in their immediate surroundings. This information will help establish a mechanistic understanding that will ultimately shed light on benthic nutrient fluxes at larger spatial scales, and how they relate to sediment properties.

Most experimental studies of biogeochemical dynamics at the tube scale are short term, lasting only a few days to several weeks. The long-term effects of tube-dwelling invertebrates on biogeochemical cycling are not known, and thus caution is required in extrapolating short-term experiments to longer periods. For example, chironomid-mediated fluxes may be fundamentally different during the initial phase, when they build burrows, than over longer periods. Thus, effects on biogeochemical cycling may depend on the duration of the experiment or whether the initial phase of burrow construction is included. We would expect longer experiments to better reflect dynamics at the lake scale, but long-term effects of chironomids on P fluxes between sediments and water have not been documented. We need long-term sediment core experiments (months or years), with regular addition of organic matter and chironomids, to quantify the net impacts of bioirrigation on whole lake biogeochemistry. The capacity for chironomids to immobilize or remineralize nutrients after reestablishment of anoxic conditions needs to be investigated as a function of initial chironomid density, geochemical sediment composition (e.g., iron and organic matter content), system state (e.g., clear vs. turbid), as well as in the context of the chironomid life cycle. For example, after larvae leave burrows and emerge as adults, solid Fe (III) compounds in the oxidized sediment surrounding the abandoned burrows are rapidly reduced to soluble Fe^{2+} (because of a lack of O_2 supply), and formerly adsorbed P is released to the water. Thus, P sequestration by chironomids may be only a temporary phenomenon, at least for individual burrows (Katsev et al. 2006). In contrast, data from a three-year experiment indicate that P immobilized in chironomid burrow walls remains in the sediment for a

long time (possibly permanently) after larvae emerge (M. Hupfer, S. Jordan, C. Herzog, and J. Lewandowski, *unpublished manuscript*). The underlying mechanism for the phenomenon might be the formation of ferrous Fe-P minerals (e.g., vivianite) due to locally restricted supersaturation by high Fe^{2+} and phosphate concentration near the former walls after reestablishment of anoxic conditions. Furthermore, the upward transport of phosphate from deeper layers to the sediment–water interface is delayed by slow transport processes (diffusion) without chironomid activities.

To elucidate temporal variation in the effects of tube-dwelling invertebrates on P cycling, and hence the net effects on lake water P concentrations, long-term experiments are needed. These experiments should manipulate the abundance of tube-dwelling invertebrates and be combined with smaller-scale studies to ascertain mechanisms and quantify rates. These may include high-resolution pore-water concentration measurements, structural analysis of solid phases (e.g., raster electron microscopy coupled to energy dispersive X-ray spectroscopy, X-ray diffraction) to quantify mineral formation, and measurement of the occurrence and diagenesis of inorganic and organic P forms using sequential extraction (e.g., Psenner et al. 1984, Ruttenberg 1992) or ^{31}P nuclear magnetic resonance (NMR) spectroscopy (e.g., Reitzel et al. 2012).

Microbiology

Metabolic activities, abundance, and community structure of sediment microbes are strongly influenced by steep redox gradients, which can greatly vary in time and space (Frindte et al. 2013), in particular due to bioturbation and feeding activities of benthic invertebrates. The intermittent ventilation of chironomid tubes causes pronounced fluctuations in the concentrations of oxygen, nitrate, and dissolved substrates that affect microbial metabolism in and around the tube (Fig. 1; Stief and de Beer 2006, Stief et al. 2010). Chironomid ingestion of particle-associated microbes leads to the digestion and loss of microbial biomass, but may also induce anaerobic metabolic pathways in the anoxic gut of larvae (Stief et al. 2009). Both bioturbation and feeding activities act simultaneously on planktonic and sediment microbes and thus must be considered jointly.

Bioturbation and feeding activities of tube-dwelling invertebrates change the general community structure of sediment bacteria, as demonstrated with molecular fingerprinting techniques (Hunting et al. 2012, Zeng et al. 2014). In contrast, the total abundance of sediment bacteria remains largely unaffected or increases only slightly in the presence of tube-dwelling invertebrates (Van de Bund et al. 1994, Wieltschnig et al. 2008). Notably, the abundance of certain functional guilds of bacteria may be significantly enhanced by the activities of chironomid larvae. Inside larval tubes, the abundance of methane-oxidizing (Kajan and Frenzel 1999) and iron-oxidizing bacteria (Lagauzere et al. 2011) is significantly

higher than in the surrounding sediment, possibly due to the higher oxygen availability inside ventilated tubes. Also the diversity of certain functional guilds of bacteria (e.g., nitrate-reducing bacteria) is enhanced in the presence of chironomid larvae, either due to metabolic induction of facultative anaerobes in the anoxic gut, or by provision of additional micro-niches and substrates in the sediment (Poulsen et al. 2014).

It has also been hypothesized that tube-dwelling invertebrates cultivate certain bacterial tube communities for food, similar to fungus-farming by ants (Mueller et al. 1998), an effect that goes beyond their impacts via filter feeding or deposit feeding. Such "gardening" activity of tube-dwelling invertebrates creates a suitable microenvironment for specific functional guilds of bacteria on which the larvae feed. Jones and Grey (2011) suggest considering chironomid larvae as "constant gardeners," for example cultivating methane-oxidizing bacteria (MOB) within their tubes. Evidence for the gardening of MOB comes from high ratios of MOB/methanogen DNA around the larval tubes (Gentzel et al. 2012) and ^{13}C-depleted chironomid tissues, resulting from acquisition of methane-derived carbon via methane-cycling microbes (Deines et al. 2007). It has been recently shown for *Tinodes waeneri* caddisflies that larval galleries enhance resource availability and thus play a substantial role in larval nutrition, especially at key times of food shortage (Ings et al. 2012). Thus, gardening activities could affect whole-ecosystem functioning by increasing and selecting the standing crop of algae and other microorganisms as well as biofilm patchiness and activity within lake sediments.

The alteration of microbial communities in sediments inhabited by tube-dwelling invertebrates has significant consequences for microbial metabolism in sediments and for solute exchange between sediments and overlying water. Tube-dwelling invertebrates commonly stimulate microbial organic matter degradation and mineralization through bioturbation and feeding activities. Enhanced mineralization rates in and around the tubes of tube-dwelling invertebrates in concert with pumping activity lead to increased fluxes of CO_2 and DOC from the sediment into the water column (Goedkoop et al. 1997, Hansen et al. 1998, Stief 2007, Hunting et al. 2012). Aside from the carbon cycle, microbial roles in the phosphorus and nitrogen cycles also are greatly affected by tube-dwelling invertebrates. The aforementioned temporal fluctuations of redox conditions inside chironomid tubes can stimulate microbially induced polyphosphate storage (Hupfer et al. 2007). Polyphosphate bacteria have the potential to control a significant portion of the P fluxes between the sediment and the overlying water by redox-dependent changes in their physiology (Khoshmanesh et al. 2002, Hupfer et al. 2008, Diaz et al. 2012). Little is known about the effects of tube-dwelling invertebrates on the role of polyphosphate storing bacteria, and clearly much more research is needed.

Microbes associated with the N cycle are also affected by tube-dwelling invertebrates. For example, the abundance and activity of nitrifying bacteria in sediments is affected by the deposit-feeding activity of chironomids. Grazing at the sediment surface reduces nitrifier abundance, while ventilation of tubes in deeper layers increases nitrifier abundance through supply of oxygen and ammonium (Stief and de Beer 2006). However, the decrease in nitrification activity at the oxygen-rich sediment surface is larger than the concomitant increase in nitrification activity in the oxygen-poor subsurface layers, which results in an overall net decrease of nitrification activity in chironomid-inhabited sediment (Stief and de Beer 2006). This is another example of how the net effect of chironomid larvae (in this case, on nitrifier abundance and overall nitrification rate) can be mediated by interactions with opposing effects.

The overall effects of tube dwellers on changes in abundance of different functional groups of bacteria and the consequent effects on benthic element cycling and element budgets remain largely unknown. Furthermore, data on microbial activity in the vicinity of burrows is even more scarce than data on abundance, and information on the microbial response to fluctuating redox conditions, as well as their potential to buffer fluxes via storage compounds such as polyphosphates, is extremely limited.

Given current knowledge on the relationship between the activities of tube-dwelling invertebrates, their associated microorganisms, and sediment biogeochemistry, it remains elusive to accurately quantify the full suite of effects of tube-dwelling invertebrates on microbial communities and microbially mediated biogeochemical processes.

Tube modelling

An effective way to assess the potential importance of tube construction and associated activities for geochemical, microbial and macrobenthic processes is to integrate them in mechanistic modelling representations. Numerical models are valuable tools to simulate and explain processes at small spatial-temporal scales that are hardly accessible with standard methods. For example, redox shifts by intermittent pumping of chironomids take place in zones that are smaller than the millimeter scale and are thus hard to access even with advanced techniques such as microsensors. In addition, the spatial heterogeneity of the burrow environment may preclude the detection of subtle changes in concentration profiles that may heavily influence fluxes and turnover rates (Brand et al. 2009).

Many models dealing with the influence of ventilation and bioirrigation in the sediment are based on the concept developed by Aller (1980), which describes the ventilated, bioirrigated sediment as a collection of radially symmetrical tubes. Expansions of Aller's seminal work have focused on the effect of coupled geochemical reactions on biologically driven solute exchange (Meile et al. 2005), intermittent pumping (Boudreau and Marinelli 1993, Shull et al. 2009), and how tube abundance and geometry vary with depth (Furukawa et al. 2001). To integrate geochemical, microbial, and macrobenthic processes in a mechanistically adequate representation, small-scale reactive transport models need to be developed that explicitly account for burrow geometry, advective and diffusive transport, and biogeochemical reactions, requiring representations in three dimensions (or two dimensions where symmetries can be exploited; e.g., Koretsky et al. 2005, Na et al. 2008, Volkenborn et al. 2012).

Bioirrigation models for permeable sediments have recently begun to incorporate the effects of pumping on the advection of surrounding sediments (e.g., Timmerman et al. 2002, Meysman et al. 2006). However, in muddy sediments, advection has been neglected so far (e.g., Kristensen et al. 2012). Roskosch et al. (2010a) provided first indications that advection may be relevant close to U-shaped burrows of *C. plumosus* in muddy sediment. By using a three-dimensional model of a chironomid burrow, Brand et al. (2013) showed that this effect indeed plays a role in moderately permeable sediments. Here, advection does not necessarily result in an increased uptake of oxygen in the sediments, since the advective flow into the sediment at the outlet branch is compensated by an advective flow towards the inlet branch, which opposes the diffusive flux into the sediment. The most important consequence of burrow advection is the asymmetry of redox zonations at the inlet and outlet, which defines the reaction space of the various redox-dependent reactions (Brand et al. 2013).

NUTRIENT CYCLING MEDIATED BY TUBE-DWELLING INVERTEBRATES

Tube-dwelling invertebrates alter nutrient cycles through a variety of processes. In addition to altering sediment biogeochemistry, they modulate benthic-pelagic exchange of organic matter and nutrients and increase sedimentation rates due to their filter-feeding activity and the entrapment of particulate organic matter (and hence nutrients) inside their burrows (Fig. 1). Lewandowski and Hupfer (2005) highlight further possible impacts of tube-dwelling chironomids on organic matter and nutrient fluxes by resuspension, ingestion, and defecation of organic particles. Furthermore, chironomids excrete nutrients into the water column in dissolved inorganic forms (i.e., NH_4^+ and PO_4^{3+}) that are available to primary producers and heterotrophic bacteria. Finally, effects on bacterial communities can further alter nutrient cycling. One notable effect of altered metabolic activity of nitrifying and denitrifying gut bacteria is the emission of the greenhouse gas nitrous oxide from oxic/anoxic burrows and from anoxic guts of *C. plumosus* (Svensson 1998, Stief et al. 2009). The net effect of all these processes on nutrient fluxes between sediments and water is difficult to predict and may differ between compounds, because

some of the aforementioned processes affect flux rates in opposing directions. For example, aeration of the sediment by chironomids may increase N flux (Stief and Hölker 2006) and at the same time decrease P flux (Lewandowski and Hupfer 2005) from sediments, while excretion will increase both P and N fluxes.

Over the past 10–15 years, the number of field studies quantifying nutrient excretion rates of freshwater animals has increased considerably, stimulated to a large extent by the development of ecological stoichiometry theory (Sterner and Elser 2002). Ecological stoichiometry theory seeks to understand the coupled cycling of multiple elements (e.g., N and P) and often focuses on elemental ratios. Of particular interest is how the ratio of nutrients released by consumers relates to nutrient ratios in their bodies and their food sources. While numerous studies on fish, zooplankton, and stream invertebrates have explored various components of ecological stoichiometry, such studies are much less common for lake benthic invertebrates, with the exception of a few taxa, such as the zebra mussel *Dreissena polymorpha* (e.g., Naddafi et al. 2008).

Only a few studies have separated metabolic nutrient excretion from other effects of tube dwellers on nutrient cycling. In fact, studies on nutrient excretion rates of chironomids in lakes are relatively scarce, especially considering their widespread distributions and high densities. A literature review revealed only six papers reporting on N and/or P excretion rates of lake chironomids, and all of these were conducted for eutrophic lakes (Table 2). Mass-specific excretion rates varied considerably among studies, especially for N. Only four of these studies measured both N and P excretion rates, and mean N:P excretion ratios vary by more than a factor of 10 among the studies (Table 2). Furthermore, none of these studies attempted to relate rates or ratios to nutrient contents or ratios in animal bodies or their food sources, which are goals central to ecological stoichiometry theory. Given the complex and potentially large effects of chironomids on N and P cycling, it is imperative that future studies quantify N and P fluxes due to bioturbation, aeration, excretion by benthic invertebrates to determine net impacts on nutrient cycles, and place chironomid-mediated nutrient cycling in a more explicit stoichiometric framework. Such an approach will aid in developing predictive models of the role of benthic invertebrates in biogeochemical cycles and ascertain whether we can predict nutrient cycling effects of benthic invertebrates using ecological stoichiometry as a conceptual framework. For example, several of the parameters we use to model whole-lake effects of chironomids (see *Integrative ecosystem modelling*) have relevance to nutrient excretion, such as N and P contents of sediments, the soluble nutrient fraction of egested food, and others (Appendix: Table A2).

Bioirrigation and ventilation may affect the oxygen concentration in the overlying water because sedimentary oxygen uptake is strongly enhanced by these processes (Meile and Van Cappellen 2003: Fig. 1). This is particularly important during thermal stratification, when vertical mixing of water and dissolved compounds is suppressed. Water column oxygen concentration is further affected by the release of reduced species such as H_2S (e.g., Giordani et al. 1996) from the sediment into the overlying water column when the buffering capacity of, e.g., metal oxides in surface sediments is exhausted (Lewandowski and Hupfer 2005). Because variation in oxygen distributions at the sediment–water interface can affect many redox-dependent reactions involving N and P, changes in oxygen mediated by tube-dwellers can influence the direction and flux of elements between sediments and water, and can thus have effects on whole-lake nutrient cycling.

Tube-dwelling invertebrates also may play a key role in the carbon cycle in lakes, particularly in regard to methane fluxes. It has been only recently recognized that methane-oxidizing bacteria, which convert methane produced in anoxic sediments to microbial biomass, provide a potentially important energy source for lake food webs (Sanseverino et al. 2012), largely because they are consumed by chironomid larvae (Jones and Grey 2011). It can be hypothesized that active burrow ventilation enhances total methane oxidation to carbon dioxide within the sediment and therewith strongly decreases the global warming potential of the carbon gas if it is eventually emitted to the atmosphere at the lake surface (Bastviken et al. 2011).

Finally, it should be noted that tube-dwelling aquatic insects can modulate fluxes of carbon and nutrients across the land–water interface. Emerging insects such as chironomids leave aquatic systems, thereby exporting carbon and other nutrients to the terrestrial landscape (e.g., Scharnweber et al. 2014). Vander Zanden and Gratton (2011) suggest that emergent insect flux to land increases as a function of lake size, while deposition of terrestrial particulate organic carbon from land to lakes decreases as a function of lake size (Mehner et al. 2005, Vander Zanden and Gratton 2011). So it may be predicted that net C and nutrient burial rate, as mediated by aquatic insects, might be reduced with increasing lake size.

In summary, tube-dwelling invertebrates can modulate nutrient fluxes in many ways. The overall changes in nutrient availability and stoichiometry can in turn control primary production and thus, the structure of the phyto- and zooplankton community.

FILTRATION AND FOOD COMPETITION BETWEEN PELAGIC ZOOPLANKTON AND TUBE-DWELLING INVERTEBRATES

Many tube-dwelling chironomids pump water through their U-shaped burrows to obtain oxygen and planktonic food particles (Walshe 1947). Pumping periods are regularly interrupted by non-pumping periods. During non-pumping periods, chironomids such as *C. plumosus* larvae spin conical nets of mucus in their burrows (Roskosch et al. 2011). After a period

TABLE 2. N and P excretion rates of lake-dwelling chironomids from field-based studies. Table 2 continues on the next page.

Source	No. observations†	Mass-specific excretion rate	
		N (µg N·g dry mass^{-1}·h^{-1})‡	P (µg P·g dry mass^{-1}·h^{-1})‡
Devine and Vanni (2002)	21	262.42 (53.07)	33.08 (7.34)
Fukuhara (1985), Yasuda (1989)#	16	112.55 (20.20)	11.18 (3.05)
Henry and Santos (2008)	55	72.09 (8.25)	68.56 (9.43)
Fukuhara (1985), Yasuda (1989)#	11	84.44 (15.54)	23.13 (2.45)
Tátrai (1982)	37	1281.79 (63.38)	no data
Ji et al. (2011)	29	no data	20.77 (2.17)
Ji et al. (2011)	15	no data	26.66 (4.96)

Note: na, not applicable.

† Number of replicate excretion rate measurements. Each replicate usually contains several individuals, placed together in one container.

‡ Mean with SE in parentheses.

§ Mean and range (in parentheses), if available.

¶ Dry mass estimated by multiplying wet mass times 0.167 (Waters 1977).

Fukuhara and Yasuda (1985) report data on P excretion, while Fukuhara and Yasuda (1989) report N excretion data, from the same study.

of pumping, the nets with all entrapped particles are eaten. As a result, chironomids can be very efficient filter feeders, transporting significant amounts of particulate organic matter and nutrients into the sediment. Chironomids drastically reduce particle densities in the burrow outlet fluid compared to the inlet fluid (Morad et al. 2010). Based on known pumping rates, filtration effects at the lake-wide scale might be comparable to the increased water clarity and shifts in phytoplankton communities associated with expanding dreissenid mussels (Strayer 2009). A few studies on marine tube-dwelling invertebrates report size-specific and particle-type-specific retention efficiencies. For example, Christensen et al. (2000) reported that the polychaete, *Hediste diversicolor*, has a capacity to retain phytoplankton at a rate of 139 mmol C·m^{-2}·d^{-1}. Riisgård (1991) found that for *H. diversicolor*, retention efficiency was 100% for particles >7.5 µm, 86% for 6.3-µm particles, and 30% for 3-µm particles. Similarly, Griffen et al. (2004) found 90% retention efficiency for particles >7.5 µm for the mud shrimp *Upogebia pugettensis*.

In contrast to data on marine benthic animals, surprisingly, there is no systematic study of the filtration efficiency of chironomids that allows quantification of their grazing impacts on phytoplankton, microorganisms, and small zooplankton communities. It is essential to experimentally quantify retention efficiencies of chironomids for different particle qualities and sizes under different environmental conditions. Particle settlement and adhesion within burrows also causes an unknown fraction of phytoplankton retention (Griffen et al. 2004). Experiments might be conducted by adding chironomids to microcosms filled with lake sediment and overlying water. Particle image velocimetry (PIV), particle tracking velocimetry (PTV), and laser-induced fluorescence (LIF) might be applied to determine flow velocities above burrow openings and to characterize different natural and artificial particles entering and leaving the burrows. Additionally, laser in situ scattering

and transmissometry (LISST) sensors could be used to quantify filtration performance for different particles.

Laboratory experiments not only allow for controlled environmental conditions, but also enable easy access to the inlet and outlet of individual burrows. Additionally, medium-scale mesocosm or enclosure experiments mimicking more natural conditions and complementing the small-scale experiments should be used as well. Such experiments might be conducted, for example, with different densities of tube-dwelling invertebrates under realistic temperature and light regimes with varying sediment compositions. Experiments should be run from spring (when cladocerans dominate zooplankton assemblages) until late summer (when copepods dominate) to account for seasonal fluctuations in zooplankton grazing pressure.

Because tube-dwelling invertebrates compete for food resources with filter-feeding pelagic zooplankton, it is essential to determine the relative grazing impact of chironomids on plankton communities compared to the pelagic zooplankton. In shallow polymictic Müggelsee, a well-studied lake with respect to the impacts of environmental change on plankton communities (Adrian et al. 2006, Wagner and Adrian 2009), the filtration capacity of chironomids was on the same order of magnitude as that of daphnids, which are traditionally thought to be the grazers that exert the strongest effects on phytoplankton. These estimates were based on observed chironomid densities in the sediment of the lake in 2005 (mean 700 individuals/m^2 [Roskosch et al. 2010b]), long-term average (1980–2010) daphnid abundances in the pelagic zone (mean 1980–1994, 37.48 individuals/L; mean 1995–2010, 23.8 individuals/L [Gerten and Adrian 2000; R. Adrian, *unpublished data*]), average chironomid pumping rates of 60 mL/h, and average *Daphnia* filtration rates of 400 µL·individual^{-1}·h^{-1}. The estimates show that chironomids are capable of filtering the entire volume of the lake once every 5 days (~1 m^3·m^{-2}·d^{-1}) whereas daphnids clear the lake volume every 5–15 days (~0.3–1.0 m^3·m^{-2}·d^{-1}; R.

TABLE 2. Extended.

N:P excretion ratio molar	Abundance (no./m²)§	Biomass (g wet mass/m²)§	Biomass (g dry mass/m²)§	Species investigated
19.75 (4.01)	513 (0–4348)		0.036 (0–4.92)	unidentified, mixed species (probably Chironomini and Tanytarsini)
42.35 (7.62)	no data	3.10	0.52¶	Chironomus plumosus
3.36 (0.41)	1398 (9–12907)		0.034 (0.000001–424)	mostly Chironomus sp.
7.95 (0.66)	no data	9.31	1.55¶	Tokunagayusurika akamusi
na	no data	no data	no data	Chironomus sp.
na	no data		(<0.1–84)	Chironomus sp.
na	no data		(<0.1–84)	Tanypus sp.

Adrian, *unpublished data*). Clearance rates of pelagic *Dreissena* veligers are within the range of those reported for cladocerans (MacIsaac et al. 1992). In Müggelsee, cladocerans and *Dreissena* larvae had similar abundances during summer, but their abundances were negatively correlated (Wilhelm and Adrian 2007). Thus, the relative proportion of chironomid filtration efficiency on phytoplankton remained equally important in strong or weak cladoceran years. Although the grazing impact of settled adult *Dreissena* mussels can be >1000 times greater than that that of veligers, their effects are likely restricted to hard substrates above nearshore *Dreissena* beds (MacIsaac et al. 1992). Tube-dwelling chironomids filter water from layers close to sediments and thus affect the whole water column only in well-mixed water bodies. In contrast, filter-feeding daphnids often affect the entire upper water column of shallow lakes. Thus, information on filtration rates alone may not necessarily predict the relative whole-lake effects of these different suspension feeder groups. In addition, we need information on the spatial scales over which they exert effects.

Given their high filtering rates, chironomids may compete with the filtering zooplankton for the same food resources, although vertical habitat segregation of the two groups may lessen these competitive interactions (Fig. 1). Moreover, the grazing pressure exerted by chironomids is much more constant across seasons compared to that of the pelagic zooplankton, whose abundances show stronger seasonal fluctuations (Fig. 2). The grazing impact of tube-dwelling chironomids on pelagic phytoplankton and small zooplankton has been neglected in pelagic food web models (Sommer et al. 2012), but may account for some of the unexplained interannual variability of plankton communities in productive lakes. Clearly, competitive interactions between tube-dwelling invertebrates and zooplankton are possible and need to be explored experimentally.

IMPACTS OF PREDATORS ON TUBE-DWELLING
INVERTEBRATES AND NUTRIENT DYNAMICS

The larvae and pupae of tube-dwelling invertebrates are important food items for many fish, amphibians, crayfish, amphipods, and insects such as stoneflies, dragonflies, true bugs, and beetles (e.g., Armitage et al. 1995). Of the different predator groups, benthivorous fish

are believed to be the most important in shallow lakes. Lammens et al. (1985) calculated, for example, that, when conditions for bream (*Abramis brama*) are optimal, these fish can consume ~10% of chironomid standing biomass per day. During an extensive analysis of the phosphorus flows within in the Loosdrecht lakes (the Netherlands), the feeding pressure of fish on benthos was estimated to be 1.4 mg $P \cdot m^{-2} \cdot d^{-1}$ (or 0.06 g $C \cdot m^{-2} \cdot d^{-1}$) while the concentration of soluble reactive phosphorus was very low (2 μg/L; Van Liere and Janse 1992). This consumptive removal of biomass and nutrients can result in trophic cascades in both benthic and pelagic food chains, depending on the consumptive impact of chironomids in these chains. Furthermore, the consumption and release of nutrients by predators of chironomids can represent an important flux of nutrients within the benthic habitat and/or an important translocation of nutrients from the benthos to the water column (Vanni 2002). There is also evidence that a substantial portion of pupal mortalities is caused by predation. Wagner et al. (2012) reported temporary coupling of the benthic and pelagic food webs by pelagic fish feeding on ascending chironomid pupae. Finally, the C:N:P content of the benthos community as well as the rates (and ratios) by which benthic inverte-
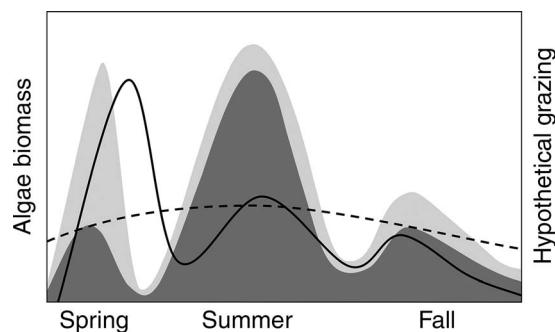

FIG. 2. Hypothetical grazing of filter feeders and biomasses of edible (zooplankton; light gray) and non-edible (tube-dwelling invertebrates; dark gray) algae in a eutrophic lake (modified version of the PEG model of Sommer et al. [1986]). The grazing pressure exerted by tube-dwelling invertebrates (dashed line) is much more constant across seasons compared to that of the pelagic zooplankton (solid line), whose abundances show strong seasonal fluctuations causing, e.g., a clear-water phase caused in combination with nutrient limitation and sedimentation.

CONCEPTS & SYNTHESIS

brates transport and release nutrients can be altered via size-selective predation on benthic invertebrates (Carpenter et al. 1992, Vanni 2002).

Predators can also exert non-consumptive effects on benthic communities, i.e., by eliciting antipredator responses in prey, including habitat shifts that provide refuge from predators and associated diet shifts that balance trade-offs between foraging and risk avoidance (Schmitz et al. 2010). This in turn can alter ecosystem processes related to nutrient cycling (Stief and Hölker 2006, Premo and Tyler 2013). Like many other benthic organisms, tube-dwelling chironomids can detect chemicals from fish and can respond with distinctive avoidance behaviors. For example, *Chironomus riparius* responds to predators by decreasing both the duration of excursions outside their tubes and the lengths of their bodies exposed to predators (Hölker and Stief 2005). This predator-avoidance behavior significantly increases the exposure of freshly deposited organic particles to oxygen, by reducing their burial in subsurface layers and by enhancing the aeration of subsurface layers via burrow ventilation, conditions that together increase the rate of organic matter mineralization (Stief and Hölker 2006). This is related to non-consumptive effects of predators that decrease zebra mussel clearance rate and thus the impact of zebra mussels on phytoplankton (Naddafi et al. 2008).

Both consumptive and non-consumptive predator effects potentially lead to changes in the spatial distributions of organic matter in sediments. The relative importance of non-consumptive vs. consumptive effects remains a matter of debate, even though recent studies on other predator–prey systems have clearly shown that non-consumptive effects can be as strong as, or even more than an order of magnitude stronger than, consumptive effects (Peacor and Werner 2001, Schmitz et al. 2004, Hölker and Mehner 2005). Schmitz et al. (2010) suggest that consumptive effects may have little net effect on organic matter decomposition and redistribution between sediments and overlying water. Instead, non-consumptive effects cause redistribution of organic matter because the variation in predation risk may alter the spatial availability of nutrients in the water column. Tracking non-consumptive effects is a challenging task, but an important one, if we are to gain a better understanding of the functional role of predators for carbon flow and nutrient cycling in aquatic systems. Experiments are urgently needed, in which consumptive vs. non-consumptive effects are quantitatively evaluated.

It should be noted that effects of benthic invertebrates on bioturbation, redistribution of organic matter, and nutrient cycling must be evaluated in comparison to other organisms that may have similar kinds of effects, such as fish. The feeding activity of benthivorous fish may directly cause bioturbation and resuspension of the sediment and mobilization of nutrients (Persson and Nilsson 2007, Adámek and Maršálek 2013). In addition, it has been shown that benthivorous fish affect the sediment structure in a way that facilitates wave resuspension of sediment (Scheffer et al. 2003). However, these fish can also alter the abundance and distribution of benthic invertebrates. Based on an empirical relationship and a minimal model, Persson and Nilsson (2007) conclude that shallow lake systems should be more resistant to switches from a clear to a turbid state when (1) benthic invertebrate biomass, maximum size of benthivorous fish, and giving up density (the amount of benthic food left behind by foragers) are high, and (2) biomass of benthivorous fish is low. Thus, shifts between alternate states likely depend on the activities of predators and benthic invertebrates, as well as interactions between these two groups (for further details, see also *Alternative stable states*).

IMPACTS AT THE LAKE-WIDE SCALE

Although there is ample evidence that tube-dwelling invertebrates act as tiny ecosystem engineers that significantly alter multiple important ecosystem functions, it is difficult to assess their importance at a lake-wide scale. Many of the processes we have discussed interact and their combined effects are therefore difficult to quantify. Models can be useful tools for assessing the propagation of processes to the ecosystem level. However, we feel that existing conceptual and numerical models of shallow lake ecosystems, such as the PEG model or PCLake, insufficiently account for the presence of tube-dwelling invertebrates and their interactions within the food web (Mooij et al. 2010, Sommer et al. 2012). Here, we consider how tube-dwelling invertebrates can be better integrated into two conceptual models that address two of the most influential concepts in lake ecology, seasonal succession, and alternative stable states. Then we modify an established dynamical ecosystem model to assess how tube-dwelling invertebrates influence lakes at the ecosystem level.

Seasonal succession: the PEG model

Lake phytoplankton and zooplankton communities undergo an annual seasonal succession in relation to nutrient availability, predation, and competition (Brönmark and Hansson 2005, Sommer et al. 2012). To explain these dynamics, the PEG model was proposed, and later revised, by Sommer et al. (1986, 2012; Fig. 2). A prominent feature of the model is the clear-water phase, a period of low phytoplankton biomass and hence high water transparency, which is explained by a combination of zooplankton grazing, nutrient limitation, and sedimentation. Strong fluctuations in the population density of pelagic zooplankton and density-mediated grazing dynamics are regarded as the main top-down effects influencing phytoplankton, including the clear-water period. However, these interactions are likely heavily influenced by filter-feeding benthic invertebrates. Based on impacts of dreissenids (e.g., Strayer 2009), the filter-feeding activity of other benthic invertebrates can be expected to exert a relevant feeding

pressure on the phytoplankton community, and perhaps small zooplankton, and hence affect the entire planktonic community.

Roskosch et al. (2012) showed the existence of seasonal and temperature-dependent variation in chironomid metabolism and filter-feeding activity, resulting in somewhat higher ventilation rates during summer. However, in contrast to zooplankton, for which the overall feeding activity is dependent on both temperature and population density, the feeding pressure by benthic invertebrates is less dynamic throughout the year because there is usually less seasonal variation in population density due to overlapping generations and species (e.g., Armitage et al. 1995, Hölker and Breckling 2002, Roskosch et al. 2010b; Fig. 2). Thus, food-web impacts of tube-dwelling invertebrates might be especially relevant during periods of relatively low zooplankton abundances. In many temperate lakes, zooplankton biomass is high enough to exert strong top-down effects on phytoplankton only for a few weeks, i.e., during the clear water phase. Thus, it is possible that tube-dwelling filter feeders are more important grazers than zooplankton during most of the year. Quantifying the relative importance of the more constant grazing impact of tube-dwelling filter feeders across seasons, as opposed to temporally fluctuating grazing pressure of cladoceran-dominated (spring) vs. copepod-dominated (summer) zooplankton communities, is an urgent need, and may help to understand some of the unexplained variability in phytoplankton succession still confronting ecologists (Cottingham et al. 2001).

If tube-dwelling filter feeders exert significant grazing on phytoplankton and small zooplankton, this implies that they may also exert a competitive pressure on pelagic zooplankton for food resources (Fig. 1). For example, tube-dwelling filter feeders might contribute to the collapse of zooplankton communities when food resources become scarce after a peak in zooplankton biomass. Because tube-dwelling filter feeders are capable of utilizing alternative food resources (e.g., detritus), their pressure on the phytoplankton community may remain high, and therefore they may postpone or dampen subsequent growth peaks of phyto- and zooplankton. These hypotheses need to be tested with field experiments.

Alternative stable states

The concept of ecosystem state plays an important role in lake ecology and management. Classical theory on alternative stable states predicts that shallow lakes can exist in one of two contrasting states, clear or turbid, which are resilient to changes in external pressures (Scheffer 1998). Indeed, while many vegetated clear lakes have become turbid and eutrophic because of excessive nutrient input, restoration efforts to restore the clear state have shown to be less effective than expected, as lakes tend to linger in a turbid state. Apparently, over a substantial range of external nutrient loading rates,

lakes can occur in either contrasting state, at a given nutrient input rate (Scheffer 1998).

An important factor delaying the ecosystem response to reduced external nutrient loading is the persistent internal nutrient loading from nutrient-rich sediments. In addition, several positive feedback loops in the food web and the abiotic environment act as self-stabilizing buffering mechanisms. For example, at high phytoplankton concentrations, macrophytes are suppressed by shading. As a result, the nutrients that were formerly sequestered by macrophytes become available for phytoplankton, causing a further increase in phytoplankton and decrease in transparency. In addition, with fewer plant roots to stabilize the sediment, wind-driven resuspension and bioturbation by fish leads to even more turbidity. As plants are generally better competitors for nutrients than phytoplankton are when light is abundant, the same feedback loops, but in the opposite direction, stabilize the clear-water state once it is attained. Such positive feedbacks are the key ingredients for the emergence of alternative stable states, whereby the strength of feedback loops is important for determining the resilience of the contrasting states. Scheffer et al. (1993) presented a conceptual model summarizing the prevailing feedback mechanisms (Fig. 3). A simple way of evaluating whether the overall effect of a set of indirect interactions is positive or negative is to multiply the signs along the path of that loop (Fig. 3).

Filter-feeding invertebrates influence many of the processes and groups that are part of known stabilizing feedback loops (Fig. 3). Therefore, their abundance and functioning are probably important for determining the nonlinear response of lakes to external pressures. For example, by influencing the biogeochemistry in sediments, tube-dwelling invertebrates have the potential to induce a net influx or net outflux of nutrients from the sediment, which will strengthen or dampen the competition for nutrients between phytoplankton and macrophytes (see *Nutrient cycling mediated by tube-dwelling invertebrates*). Chironomid species can also modulate the nutrient-related feedbacks by extracting nutrients when they hatch and fly away, which will favor the clear water condition (see *Nutrient cycling mediated by tube-dwelling invertebrates*). Via their high grazing pressure on phytoplankton, filter-feeding benthos may exert a negative feedback by depleting algal resources (see *Filtration and food competition between pelagic zooplankton and tube-dwelling invertebrates*). Yet, by clearing the water column tube-dwelling benthos can relieve aquatic plants from their competition with phytoplankton for light and nutrients, which stimulates the clear-water state. In a similar way, the trapping of particulate organic matter is important in keeping the water clear. Also the consumer–resource interaction with benthivorous fish, which influences the turbidity via bioturbation, is in itself a negative feedback (see *Impacts of predators on tube-dwelling invertebrates and nutrient dynamics*). However, phytoplankton can benefit from the bioturbation, whereby the turbidity is
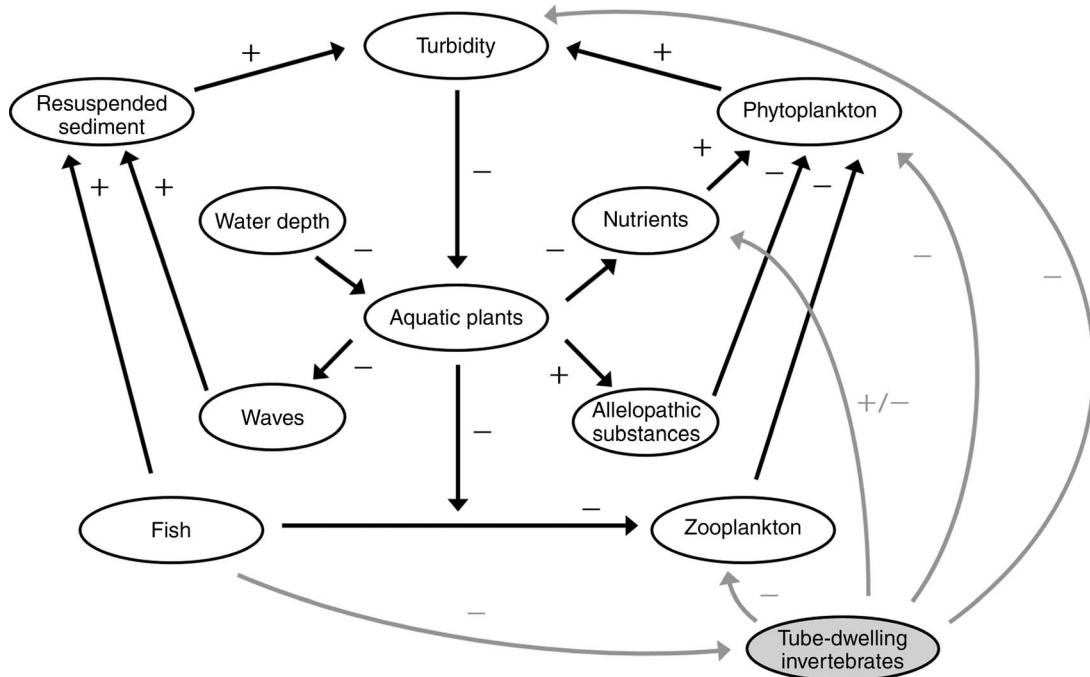
Fig. 3. Interactions and feedbacks in a lake ecosystem concerning water turbidity, including the (partly unknown) effects of tube-dwelling invertebrates (in gray) that may cause alternative equilibria. Both turbidity and aquatic plants have a positive effect on themselves through different feedback loops, of which several are influenced by tube-dwelling invertebrates (figure modified from Scheffer et al. [1993]).

further enhanced. Lammens et al. (1985) showed that omnivorous fish can use chironomids as an alternative food source, allowing them to maintain high biomass and hence a high predation pressure on zooplankton, which is a more favorable food source. Phytoplankton benefit from this apparent competition, which thus stimulates the turbid state.

Considering the potentially large impacts of tube-dwelling invertebrates on system processes and the importance of feedbacks in governing the dynamics of shallow lake ecosystems, it is essential that we learn more about feedbacks that are influenced or established by this group of consumers. As such, it is important to gain more insight into how omnivorous feeding by chironomids and fish, and the resulting apparent competition, influences the negative feedback in consumer–resource interactions. Also, we identify the need to investigate how changes in the abiotic environment feedback to the tube-dwelling invertebrate abundance, such as anoxia and the consolidation of the sediment by plant roots and wind-induced sediment resuspension.

Integrative ecosystem modelling

Integrative dynamical models can be useful tools to elucidate the relative importance of hypothesized processes for ecosystem functioning under different environmental conditions and various management scenarios. They allow for upscaling the aforementioned direct and indirect effects of tube-dwelling filter feeders on phytoplankton productivity (due to grazing and changes in nutrient availability and stoichiometry), on zooplankton (due to food competition and grazing pressure), and on biogeochemical cycles. Also, the importance of the relatively constant grazing of tube-dwelling filter feeders across seasons, compared to the more temporally dynamic grazing capacity of zooplankton, can be evaluated (Fig. 2). Finally, and importantly the models allow us to explore feedback loops that may be altered by these important consumers (Fig. 3).

Due to its extensive coverage of the aquatic food web, and by embracing several more key concepts such as nutrient cycles, stoichiometry, and benthic-pelagic coupling, the ecosystem model PCLake is particularly suited for studying the impacts of tube-dwelling filter feeders, and assessing their importance for self-stabilizing mechanisms within the framework of alternative stable states (Mooij et al. 2010). This model describes the dynamics of nutrients, phytoplankton, macrophytes, and upper trophic levels within the framework of closed cycles of nutrients and organic matter (Janse 2005, Janse et al. 2010; Fig. 4). PCLake has been calibrated against data from >40 lakes, resulting in lake characteristics resembling an "average" shallow lake in the temperate zone (i.e., mean depth = 2 m, areal hydraulic loading = 20 mm/d, fetch = 1000 m, slightly clayish sediment, no surrounding wetland zone [Janse et al. 2010: Appendix]). We used PCLake to analyze the importance of tube dwelling filter feeders for water quality and trophic state
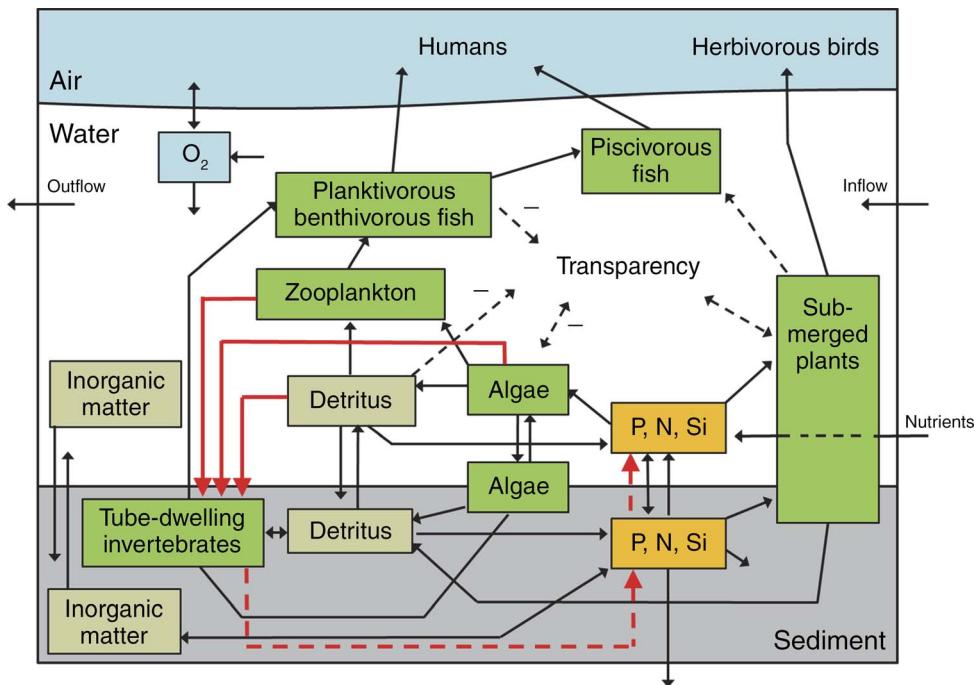
Fig. 4. Structure of the ecosystem model PCLake, including the role of tube-dwelling invertebrates (modified from Janse [2005]). Black arrows with solid lines denote mass fluxes (e.g., food relations), black arrows with dotted lines denote other interactions. Red arrows with solid lines denote mass fluxes and red arrows with dotted lines denote other interactions that should be considered in future studies. Minus sign denotes negative influence (otherwise positive influence).

in the context of alternative stable states. We tested two working hypothesis (scenarios) for a typical temperate shallow lake (as defined by Janse et al. 2010). Bifurcation analysis was used to explore effects for ecosystem-level parameters, along with manual inspection of individual process rates (for details, see Appendix).

Scenario 1.—As a first step, we analyzed how the default implementation of benthic invertebrates affects ecosystem functioning by varying the density of the zoobenthos. As in the original model, the benthic invertebrates feed on sediment phytoplankton and

detritus only (not on phytoplankton in the water column). Thus the top-down control of pelagic phytoplankton is of less importance in this scenario. Rather, this first analysis assesses the importance of the trophic interactions with benthivorous fish; specifically, an increase in benthic invertebrates sustains a larger population of benthivorous fish, which stimulates fish-mediated resuspension of inorganic matter and nutrients, and enhances the resilience of the turbid state via these mechanisms (Fig. 5). This mechanism is further discussed by Lischke et al. (2014). Conversely, when

Fig. 5. PCLake simulations of chlorophyll *a* (mean of summer half-year after 20 years) as a function of phosphorus loading for a default lake (medium zoobenthos abundances), a lake with high zoobenthos abundances, and a zoobenthos-free lake. Simulations based on two initial states: a clear-water state and step-wise increase of P load and a turbid state with phytoplankton dominance and step-wise decrease of P load. Other settings were identical with the shallow (2 m depth) default lake (default PCLake settings) and no filter-feeding of zoobenthos. The nitrogen loading was assumed to be always 10 times that of the phosphorus loading. Arrows denote the direction of the hysteresis loop.
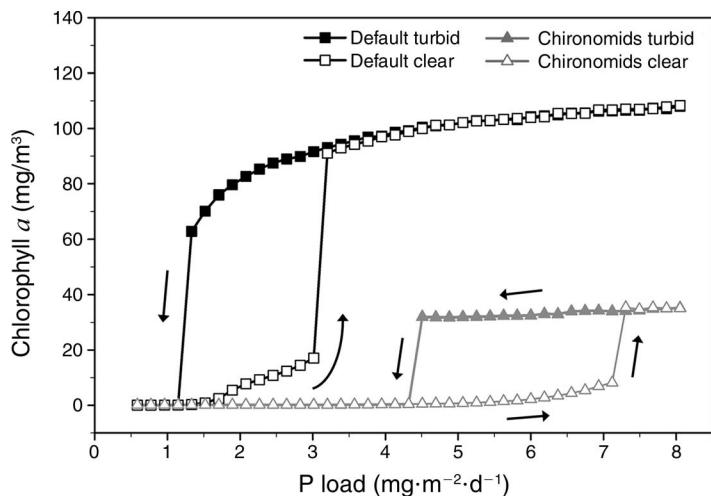

CONCEPTS & SYNTHESIS
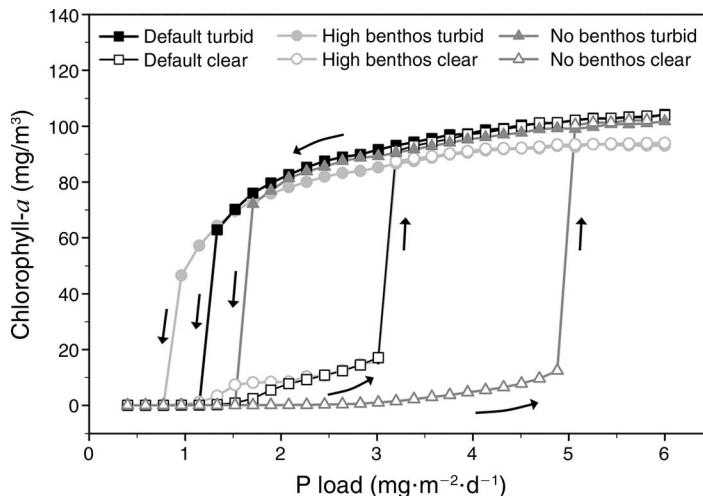
Fig. 6. PCLake simulations of chlorophyll *a* concentrations (mean of summer half-year after 20 years) as a function of phosphorus loading, for default PCLake settings, and for the inclusion of a filter-feeding invertebrate group (e.g., chironomids). Arrows denote the direction of the hysteresis loop. Note: compared to Fig. 5, the *x*-axis has a different range.

benthic invertebrates are removed from the system, the population of benthivorous fish collapses and the system becomes less sensitive to nutrient loading.

Scenario 2.—Next we expanded the PCLake model to include a filter-feeding chironomid group. Based on the many ways that chironomids can interact with other ecosystem components, we established several interactions, including filtering of the water column, the consumption of phytoplankton and detritus (leading to direct competition for food with zooplankton), sequestration of carbon and nutrients in sediments, excretion of nutrients into the water column (both altering nutrient dynamics and stoichiometry), predation by benthivorous fish, and extraction of matter during emergence. The bifurcation analysis reveals a clear impact of chironomids on the system; phytoplankton biomass (chlorophyll) is lowered in the presence of chironomids, at virtually all P loading rates. Furthermore, the critical P loading rate needed to induce a catastrophic regime shift increases greatly (Fig. 6). Thus, the models suggest that chironomids confer resilience to shallow lakes in terms of maintaining the clear-water state. The results of this scenario should be interpreted with care because the parameter values we used are still uncertain, the expanded model was not recalibrated to real lakes, and a connection with a more detailed model of individual tubes has not been made. However, the results clearly indicate that the ecosystem-level effects of tube-dwelling invertebrates are potentially very significant (Fig. 6). This potential importance of tube-dwelling invertebrates has long been overlooked, and their filtration rate has probably been by mistake incorporated into that of zooplankton during earlier model calibrations (Janse et al. 2010). We thus conclude that the inclusion of tube-dwelling filter-feeders is likely to increase model validity and predictive power, potentially leading to more complete understanding of shallow lake food webs and successful applications of the model for water quality management.

CONCLUSIONS

Our evaluation of the current state of knowledge on the ecological roles and importance of tube-dwelling invertebrates identified five major research domains that are insufficiently studied, and thus limit our understanding of the role of tube-dwelling invertebrates in lake ecosystems (Table 3). Major gaps in knowledge include our understanding of how small ecosystem engineers impact redox zonation, the microbial sediment community, organic matter and nutrient turnover, nutrient excretion and stoichiometry, filtration and food competition, and feedback mechanisms that influence other organisms and even whole ecosystems. To overcome these scientific knowledge gaps we need integrated research programs incorporating physical, biogeochemical and trophic processes, and their interactions, mediated by tube-dwelling invertebrates.

Taxa such as the abundant and widespread chironomid larvae may significantly shape their habitat and impact the biogeochemical cycling of nutrients limiting lake primary production. Within a food web context, tube-dwelling macrozoobenthos are probably more important players than previously assumed, with far reaching ecosystem consequences. We suggest investigating the manifold impacts of model organisms such as *C. plumosus*. The central hypothesis of future studies could be that tiny but abundant ecosystem engineers, in particular tube-dwelling invertebrates, exert high filter-feeding pressure and affect biogeochemical cycles in shallow lake ecosystems. Given the abundance of shallow lake ecosystems, the cumulative effects of these animals may be substantial at the global or at least regional scale.

Experimental investigations should incorporate many spatial scales, from the burrow (filtration capacity, tube microbiology, and sediment geochemistry) to large mesocosms (phytoplankton filtration, competition with pelagic filter feeders, and nutrient cycling), preferably as complementary approaches within the same set of lakes. The experimental findings need to be integrated into lake

TABLE 3.   Five main general research domains that deserve more attention in studies of how tube-dwelling invertebrates affect shallow lake ecosystems.

Small-scale tube biogeochemistry	Impacts of tube-dwelling invertebrates on nutrient cycling	Filtration and food competition	Impacts of predators on tube-dwelling invertebrates and nutrient dynamics	Impacts at the lake-wide scale
How is the capacity of P immobilization and remobilization impacted by tube-dwelling invertebrate density, geochemical sediment composition (e.g., iron and organic content), and system state (e.g., clear vs. turbid)?	Do tube-dwelling invertebrates alter the availability of P, N, and organic C in the water column (water quality) and thus influences algal growth due to altered biogeochemical turnover?	What is the filtration efficiency of dominant tube-dwelling invertebrates?	Do top predators (e.g., benthivorous fish) regulate nutrient cycling in aquatic systems via predator induced changes of tube-dwelling invertebrates to a relevant extent?	Are benthic filter-feeders able to impact pelagic phyto- and zooplankton communities?
Is there a long-term impact of tube-dwelling invertebrates on P burial rates?	How do the various mechanisms by which tube-dwelling inverts mediate nutrient cycling (bioturbation, aeration, excretion, etc.) interact and impact on nutrient cycles?	How is the filter rate of tube-dwelling invertebrates impacted by particle properties and environmental conditions?	Do consumptive effects may have little net effect on organic matter decomposition and redistribution between sediments and overlying water, whereas non-consumptive effects cause redistribution of organic matter?	How does the physical environment feedback to benthic filter-feeders in terms of anoxia and sediment structure?
Do tube-dwelling invertebrates severely impact the microbial community of burrow walls?	Does the change in nutrient availability and stoichiometry control primary production and thus, the structure of the phyto- and zooplankton community?	How does omnivory influence the consumer resource interactions and the filter rate?	To what extent does the feeding activity of benthivorous fish cause resuspension of the sediment?	Can small but abundant tube-dwelling invertebrates significantly affect the state of shallow lake ecosystems?
How do tube-dwelling invertebrates effect the subtle change in abundance of nitrifiers and maybe other bacteria on benthic element cycling?	Can we predict nutrient cycling effects of tube-dwelling inverts using ecological stoichiometry as a conceptual framework?	Do tube-dwelling tube-dwelling invertebrates exert a relevant feeding pressure on small zooplankton?		How does the relative importance of benthic versus pelagic zooplankton grazing change especially in the context of global warming?
Are tube-dwelling invertebrates cultivating certain bacterial tube communities for food?	Can aquatic insect larvae modulate fluxes of organic matter and nutrient also across the water-terrestrial interface?	Do tube-dwelling tube-dwelling invertebrates exert a relevant feeding pressure on the phytoplankton community? Do competitive interactions between planktonic and benthic filter feeders exist?		Which relevant functional traits have to be integrated in future ecosystem models?

CONCEPTS & SYNTHESIS

ecosystem models by including nutrient cycling and food web interactions mediated by benthic invertebrates. The models can be used to reassess the role of these tiny ecosystem engineers for the trophic state of shallow lakes and to better predict how lake restoration measures such as lake aeration or destratification might alter habitat distribution of redox zones. Such measures may result in increased habitats for tube-dwelling invertebrates and, because of their ventilation activity, in a more permanent P removal that stabilizes a lower trophic state.

Climate change is altering the global cycles of water, C, N, and P (e.g., Tranvik et al. 2009). At the same time,

compensatory mechanisms can reconfigure food webs such that they maintain ecosystem functioning in the face of disturbance. It can be hypothesized that the relative importance of tube-dwelling invertebrates vs. zooplankton grazing might change in the context of global warming. Climate scenarios predict shifts from dimictic to monomictic thermal regimes in many lakes by the end of the 21st century (Kirillin 2010), i.e., winter stratification will completely disappear in many lakes. In summer, climate warming produces an opposite, stabilizing effect, i.e., lakes that are already dimictic may stratify more stably or for longer durations, and shallow polymictic

lakes may become dimictic (Adrian et al. 2009). The ecological consequences of this latter regime shift are likely to be more drastic than dimictic-to-monomictic transitions, because the abrupt detachment of the nutrient-rich hypolimnion from the euphotic zone and the increase in hypoxic sediment area is likely to trigger stronger competition between autotrophs and a change in the relative proportions of pelagic zooplankton vs. benthic macroinvertebrates. Future projections of the fluxes of matter and greenhouse gases to and from aquatic ecosystems, related to natural or anthropogenic environmental changes, are greatly limited by our ability to characterize the driving forces and in particular the key players in aquatic food webs. A better understanding of the role of tiny ecosystem engineers in modulating overall ecosystem functioning will help in predicting future changes in shallow lake ecosystems and the implications for global matter fluxes. The sheer number of small lakes suggests that benthic invertebrates are relevant in driving small-scale processes that add up to global importance.

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CONCEPTS & SYNTHESIS

SUPPLEMENTAL MATERIAL

Ecological Archives

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