Global Change and the Biodiversity of Freshwater Ecosystems: Impacts on Linkages between Above-Sediment and Sediment Biota

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Freshwater biota are exposed to a range of natural disturbances varying in strength, frequency, predictability, duration, and spatial scale. Such disturbances can deplete the biota, disrupt ecological processes, and redistribute resources (Giller 1996, Lake 2000). Generally, in both lakes and rivers, recovery from the effects of natural disturbance is relatively rapid, although there are exceptions, such as recovery from catastrophes on the scale of the Mount St. Helens eruption (Niemi et al. 1990, Giller 1996). Human activities are now a major force affecting the ecosystems of the earth (Vitousek et al. 1997, Sala et al. 2000). Human enterprises—agriculture, industry, recreation, and international commerce—are the source of disturbances affecting all ecosystems to varying spatial extents and to varying degrees. The disturbances arise from changes in land use, anthropogenic changes in global biogeochemistry, and biotic additions and losses (Vitousek et al. 1997). These three factors are the principal agents of global environmental change. Furthermore, they interact to give rise to the two large-scale phenomena of climate change and loss of biodiversity (Vitousek et al. 1997).

ALL FORMS OF ANTHROPOGENIC DISTURBANCE—CHANGES IN LAND USE, BIOGEOCHEMICAL PROCESSES, OR BIOTIC ADDITION OR LOSS—NOT ONLY DAMAGE THE BIOTA OF FRESHWATER SEDIMENTS BUT ALSO DISRUPT THE LINKAGES BETWEEN ABOVE-SEDIMENT AND SEDIMENT-DWELLING BIOTA

Freshwater sediment biota are particularly vulnerable to global change because of direct impact on the sediments and on the water over these sediments, and because of the transmission of impacts from adjacent terrestrial ecosystems. Fresh waters are intimately connected to the terrestrial realm through groundwaters and surface waters. Movement of organic matter, nutrients, and sediment among the terrestrial realm, the water column, and aquatic sediments

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tightly connects these three realms. Through the downslope movement of water, freshwater ecosystems are intrinsically linked with their catchments (Hornung and Reynolds 1995).

While studies have addressed the effects of global change on the terrestrial and water column realms (Solbrig et al. 1994, Heywood and Watson 1995), little work has focused on its effects on aquatic sediments, and we know of no work focusing on how the linkages between these realms are affected. Biota living above and in the sediment are abundant and diverse, and each strongly influences ecosystem processes such as primary production and nutrient dynamics (Palmer et al. 1997, Waide et al. 1999). Sediment biota include those organisms (microbes to megafauna) living in, on, or closely associated with aquatic sediments, while above-sediment biota include those organisms inhabiting the water (e.g., fish, plankton, macrophytes) as well as those terrestrial fauna and flora in adjacent habitats in contact with the fresh water (Palmer et al. 2000). Sediment biota interact with above-sediment biota, resulting in changes in biodiversity and ecological processes. The linkages may be persistent, such as the predation by fish on benthos, or intermittent, such as the release of nutrients from flooded sediment into the water of a river in flood.

With the increasing levels of anthropogenic disturbance, it can be expected that one major response will be changes in the linkages between above-sediment and sediment biota. In this review, we examine specifically how the human-generated disturbances driving global environmental change affect linkages between above-sediment and aquatic sediment biota and consequently alter biodiversity and ecological processes. Linkages between the above-sediment and aquatic sediment biota may serve either to dissipate or to magnify the effects of the disturbance. For example, in a eutrophic lake sediment, microbes may break down phytoplankton and macrophytes releasing phosphorus. Under aerobic conditions such phosphorus may become sediment bound, lessening the effects of eutrophication. However, under anoxic conditions the phosphorus may be remobilized into the water column, thus aggravating the eutrophication (Lampert and Sommer 1997).

Assessing the impacts of global change is a difficult exercise given the poor state of knowledge regarding the nature of the linkages and of the effects of disturbance on linkages in freshwater ecosystems. In this examination, we will concentrate on those forms of human disturbance for which there is information on the effects on above-sediment to aquatic sediment linkages in fresh waters.

Global change and freshwater ecosystems

Following the scheme of Vitousek et al. (1997) for global environmental change, there are three primary sources of anthropogenic disturbance that can affect the linkages between above- and below-sediment biota. First, changes in catchment use due to human activities may create a myriad of disturbances in freshwater ecosystems (Hornung and Reynolds 1995, Harding et al. 1998). Disturbances include changes in riparian and catchment vegetation, increased sediment delivery to water bodies, and changes in water body morphology (e.g., channelization). Second, disruptions of biogeochemical processes may occur because of human alteration of flow regimes; alteration of water stores in lakes, rivers, and groundwater; and introduction of pollutants and nutrients into waterways. Changes in catchment land use and global biogeochemistry combine to produce global climate change, notably the greenhouse effect (Vitousek et al. 1997). Third, the loss or addition of biota to fresh waters or biotic exchange may have dramatic and cascading effects that lead to the extinction of native species with subsequent disruption of food webs and ecological processes (Wilcove et al. 1998).

At present, changes in land use appear to be the major driver threatening the biodiversity of streams, whereas for lakes the major driver affecting biodiversity seems to be biotic exchange (Sala et al. 2000). Over the next century, land use and biotic exchange will remain major threats to biodiversity in both lakes and streams, but by the year 2100 climate change will have become a major threat, especially in streams (Poff et al. 2000, Sala et al. 2000).

It is quite rare for a single anthropogenic disturbance to disrupt a freshwater ecosystem. In many (if not most) situations, freshwater ecosystems are exposed to a variety of anthropogenic disturbances acting simultaneously and often synergistically. For example, boreal lakes are under a three-pronged attack from disturbance produced by global warming, acidification, and ozone layer depletion (Gorham 1996, Schindler 1998).

Disturbances arising from catchment use

Human disturbance in a catchment by such activities as agriculture, forestry, mining, and urbanization can generate severe disturbances for water bodies in that catchment (Hornung and Reynolds 1995, Harding et al. 1998). Disturbance to plants and the soil, arising from activities such as grazing by domestic stock, can generate significant sedimentation of water bodies in the catchments (Waters 1995). Land clearance and subsequent changes in vegetation by humans can alter the inputs of dead plant material into water bodies, notably streams that may depend for their metabolism on such inputs.

Sedimentation. Disturbances that alter the abundance or composition of above-sediment plants will alter soils and often lead to the deposition of fine particles on freshwater sediments. This clogs up the interstices between particles (colmation) and significantly alters the range and size of bottom sediment particles (Waters 1995, Boulton 1999). The sedimentation directly affects the diversity of the sediment biota in running waters. By reducing the interstitial spaces, habitat availability is reduced, resulting in decreased diversity and abundance of benthic invertebrates, especially of Ephemeroptera, Plecoptera, and Trichoptera. With large inputs of fine sediments, there is a substantial change in substrate type. In streams, cobble beds may become covered in silt, decreasing the diversity of a normal stream fauna and favoring a limited fauna of burrowing animals, such as oligochaetes and chironomids.

Alterations in the composition of above-sediment plant or animal communities that enhance sedimentation have effects far beyond the sediment invertebrates: normal stream functioning is severely disrupted by colmation (Boulton 1999). Flow into the deeper sediments where surface water and groundwater mix (the hyporheic zone) may be impeded. This zone harbors a distinctive biota from microbes to macroinvertebrates, and it serves as a two-way conduit for the exchange of water, organic matter, nutrients, and biota between aquatic sediments, surface water, groundwater, and adjacent terrestrial soils (Gibert et al. 1997, Boulton et al. 1998, Jones and Mulholland 2000). Upwelling hyporheic water may provide the water column with biota and nutrients, while downwelling surface water provides the hyporheic zone with oxygen, organic matter, and nutrients (Brunke and Gonser 1997, Boulton et al. 1998). These linkages are vital to normal stream functioning and are severely disrupted by colmation (Boulton 1999). With restricted oxygen and organic matter from surface waters, many hyporheic organisms decline or disappear, and the flow of nutrients such as nitrate from the hyporheic zone to the surface may be blocked, limiting surface algal diversity and stream production (Boulton et al. 1998). Thus, human-generated disturbance of the catchment that alters above-sediment biota and generates sedimentation can have profound effects on the biota above and in sediments by altering biodiversity and reducing stream production.

Changes in catchment and riparian zone vegetation. Riparian zones play a critical role in the ecological integrity of freshwater ecosystems. Catchment vegetation, especially that of the riparian zones, performs vital functions for freshwater ecosystems that are described in detail elsewhere in this issue (Palmer et al. 2000). Any disturbances that affect catchment vegetation (above-sediment plants) may lead to reductions in the diversity and abundance of stream detritivores (sediment biota), which in turn may lead to significant alterations in aquatic production. Removal of riparian plants is a major problem in both developed and undeveloped parts of the world. Attempts are being made to mitigate the impacts of this plant loss through restoration and replanting efforts. This is a commendable strategy as long as the goals are to restore diverse, native plant assemblages. In many areas, however, nonnative species are being planted because they grow quickly or are economical to obtain and plant (O'Connor et al. 2000). However, if the sediment biota are not able to process detritus from these plants and/or the plants have allelochemical effects on the microbes or invertebrates, then rates of decomposition will slow (Sweeney 1993, Webster et al. 1995), organic matter will accumulate in aquatic sediments and terrestrial soils, and nutrient regeneration to groundwaters and surface waters will decline. The replacement of native riparian vegetation by exotic species, such as willows in the Southern Hemisphere (Read and Barmuta 1999) and eucalypts in the Northern Hemisphere (Basaguren and Pozo 1994), has been associated with changes in the structure and functional group representation of the benthic invertebrate communities.

Disturbance of biogeochemical pathways

Lakes and rivers are linked with their catchments and the air by a range of pathways of vital chemicals. Disturbance can alter the inputs and flux rates of these chemicals and have dramatic effects on the above- and below-sediment biota. As discussed below, river regulation by dams and diversions invariably alters seasonal flows of water and disrupts riverine communities. The input of excessive nutrients into both lakes and rivers can give rise to the undesirable condition of eutrophication. Acid rain falling on catchments and their water bodies can damage lakes and rivers, and toxic contaminants can cause persistent pollution.

Changes in river flows by regulation. Currently humans use 54% of the accessible runoff of the Earth, or 30% of accessible terrestrial fresh water supply, with irrigation using by far the greatest part of the consumed water (Postel 1998). These demands are largely met by damming rivers, with about 40,000 large dams currently in use (McCully 1996). Flow regulation by dams has many disturbing effects on river biota and riparian vegetation (Nilsson et al. 1997), including prevention of the movement of biota, reductions in flow volume, changes in seasonal flow regimes, changes in downstream temperatures and nutrients, reduction in sediments, and changes in downstream channel morphology (Poff et al. 1997, Boulton and Brock 1999).

Flow regulation alters or removes entirely the natural flood regime in fresh waters. The flood pulse is a critical component of the ecology of running waters (Poff et al. 1997). Many rivers have periodic, often seasonal, flooding when rivers break their banks and inundate the wetlands and vegetation of their riparian floodplains. Overbank flows allow ecologically critical exchanges between aquatic sediments and adjacent terrestrial, above-sediment habitats. Overbank flow onto the floodplain allows nutrients and detritus from aquatic sediments to become available to water-column biota; plankton are especially known to bloom after flooding. Floods stimulate a pulse of aquatic and riparian production with rapid increases in biodiversity and abundance (Junk et al. 1989, Nilsson et al. 1997). Many aquatic sediment animals may hatch, move into the water column (above-sediment realm), and feed and disperse. Hence, floods catalyze vital exchanges between the floodplain sediment biota (microbes, plants, and animals) and organisms in the water column (Ward 1989, Boulton and Brock 1999).

Many dams store river discharge and thus prevent or severely attenuate downstream flooding (McCully 1996, Boulton and Brock 1999) and interrupt exchanges between the aquatic sediment and riparian zone. Flood prevention can thus be viewed as a major disturbance that eliminates vital linkages between the floodplain sediments and aquatic sediments, which may severely limit the biodiversity and production of entire rivers and their associated riparian zones.

Eutrophication. Lakes and streams can become eutrophic due to excessive inputs of nutrients (nitrogen and/or phosphorus) from point or non-point sources. Eutrophication has significant impacts on pelagic biota above aquatic sediments because of large increases in phytoplankton density, but not necessarily diversity (Figure 1). Eutrophication may also lead to the loss of macrophytes and their associated flora and fauna (Lampert and Sommer 1997). These above-sediment changes in plankton and macrophytes lead to increased inputs of detritus to aquatic sediments. If oxygen is abundant, sediment microbial activity is stimulated (Tornblom and Bostrom 1995) and there may be an increase in the abundance or species composition of sediment invertebrates (Goedkoop and Johnson 1996). However, with increased detritus inputs to the sediments, deoxygenation can occur; the sediment microbial community responds, and switches the aerobic and diverse invertebrate community to an anoxiatolerant one of low diversity dominated by chironomids and oligochaetes (Lampert and Sommer 1997). Under anoxic conditions, changes in microbial biodiversity occur and reductive microbial processes, such as methanogenesis and nitrate ammonification, may dominate (Storey et al. 1999). Phosphorus may be released from the sediments into the water column, further stimulating primary production and giving rise to self-acceleration of eutrophication (Lampert and Sommer 1997)—a positive feedback between sediment and above-sediment biota. Therefore, the onset of eutrophication is marked by strong links between biota in the water column and sediments, which in turn lead to changes in sediment invertebrate biodiversity and abundance as well as a change in microbial processes. Subsequently the change in microbial processing in the sediments may positively feed back to phytoplankton growth.

Acidification. Acidification of fresh waters due to acid rain inputs can have serious impacts on terrestrial and freshwater systems and on exchanges between the two systems. Acid rain enhances the movement of toxic metals, such as aluminum, from catchment soils to water bodies (Hornung and Reynolds 1995). Reductions in the abundance and diversity of sediment biota may result from direct toxic effects, or from indirect effects exerted by disruption of ecosystem processes. In the acidification of lakes, two linkages are disrupted. The major disruption is the reduction in processing of detritus from above-sediment plants by aquatic sediment biota

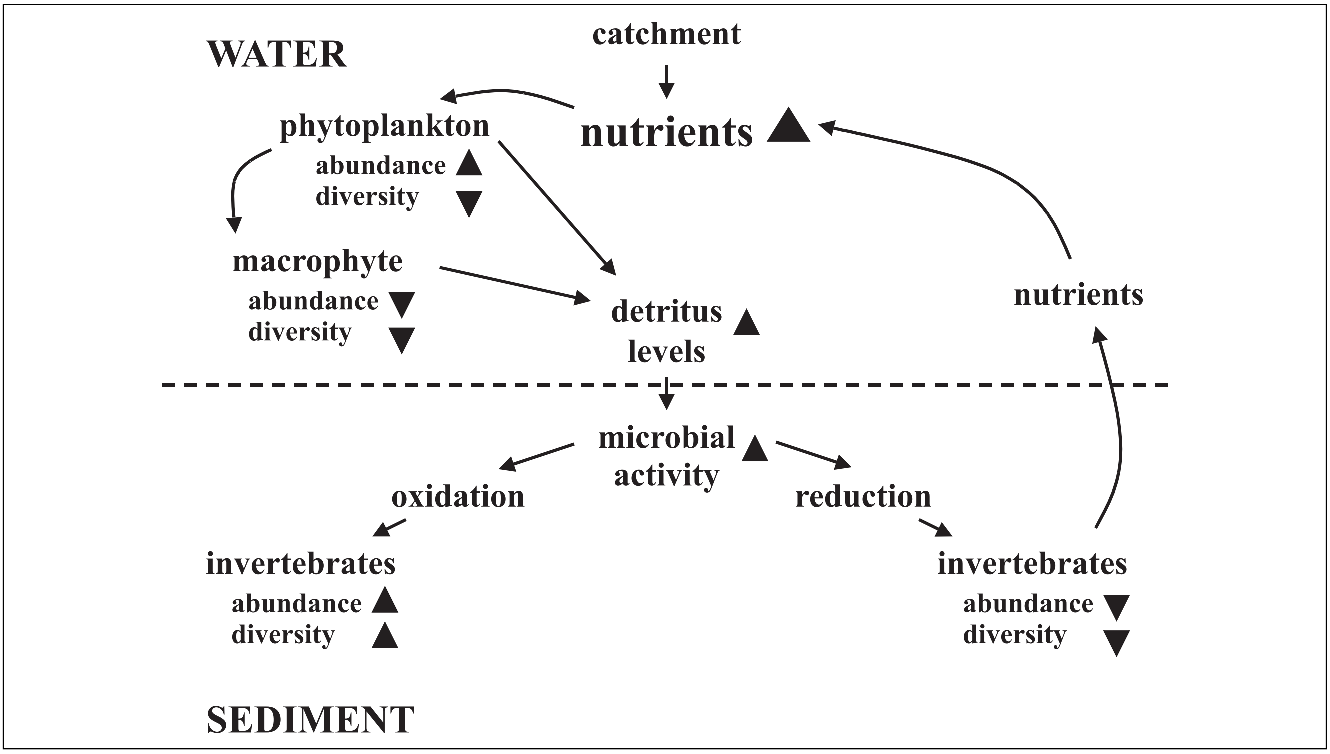

Figure 1. Linkages between above-sediment and sediment components and processes in lacustrine ecosystems that are affected by eutrophication. Upright triangles denote components or processes that increase in amount; inverted triangles denote components or processes that decrease in amount. With an increase in nutrient concentrations in the water column, there is an increase in phytoplankton abundance and a decline in macrophytes, increasing detritus inputs to the sediments. Microbial activity (decomposition) is stimulated. When oxygen is available, sediment invertebrate abundance and diversity increase. If oxygen is not available, reduction occurs. The anoxic conditions in the sediments lower sediment invertebrate abundance and diversity and facilitate the mobilization of nutrients back into the water column, further augmenting the eutrophication.

(microbes and shredders, Muniz 1991), and the second is the change in predation rates of above-sediment biota on aquatic sediment benthos (Bendell and McNicol 1995).

Phytoplankton and zooplankton diversity decline but productivity may not change (Figure 2; Schindler 1994). Macrophytes usually decline in diversity and abundance, but filamentous algae (e.g., *Mougeotia, Zygnema*) can increase (Schindler 1994). Sphagnum moss may also increase and exacerbate the acidification, adding hydrogen ions to the system (a positive feedback) (Muniz 1991). Inputs of detritus from the littoral zone to bottom sediments may rise but this may not benefit the sediment biota because in acid waters microbial detritus decomposition is greatly reduced (Schindler 1994). Benthic macroinvertebrates (such as crustaceans and mollusks) that are strongly dependent on calcium availability are very sensitive to the effects of increased acidity (Muniz 1991). Hence, acidified systems may lose their large-bodied detritus processors (shredders) and sediment bioturbators, such as crayfish and mussels, with consequential effects on benthic processes. Increasing acidity reduces benthic diversity, with insects generally being the most tolerant (Bendell and McNicol 1995). Many acidified lakes lose their predatory fish, which may be replaced by increased densities of insect predators such as benthic odonatans (Bendell and McNicol 1995).

Toxic pollution. Pollution of fresh waters is caused by thermal inputs, inputs of biodegradable material, and inputs of persistent inorganic and organic chemicals (e.g., heavy metals and chlorinated hydrocarbons). These inputs have direct toxic effects on both above-sediment and sediment biota and, for some persistent chemicals, linkages between biota in the above-sediment and sediment realms may exacerbate and prolong the pollution. For example, metals and pesticides come to reside in aquatic sediments where they may be remobilized through the activities of sediment biota and become bioavailable to above-sediment flora and fauna (Chapman et al. 1998). Thus, sediment biota may be responsible for maintaining persistent chronic toxicity of recalcitrant pollutants. Mercury offers a seminal example. In anoxic sediments, bacteria may convert inorganic mercury into methyl mercury, which then may be readily taken up by sediment invertebrates and transferred into the pelagic food chain (bioaccumulation and bioconcentration) (Connell and Miller 1984, Chapman et al. 1998). Chlorinated hydrocarbons, such as polychlorinated biphenyls, can be bioaccumulated by sediment dwellers, such as chironomids and bivalves, then transferred via the food chain to other invertebrates (Bruner et al. 1994), to fish (Kidd et al. 1995), and ultimately to waterfowl (Mazak et al. 1997).

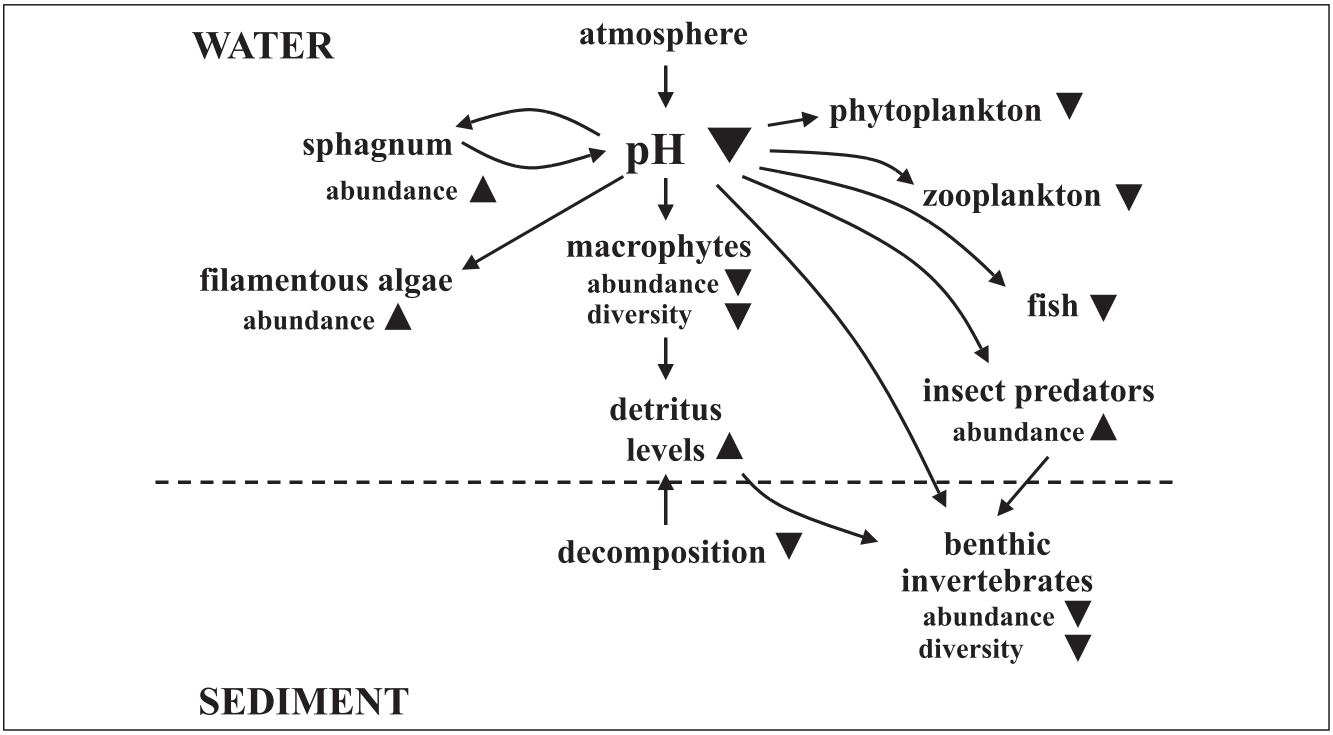

Figure 2. Linkages between above-sediment and sediment components and processes in lakes affected by acidification. Upright triangles denote components or processes that increase in amount; inverted triangles denote components or processes that decrease in amount. Acidification caused by atmospheric inputs may increase the abundance of both sphagnum moss and filamentous algae but reduce macrophyte abundance. These changes may, in turn, elevate detritus levels. Because detritus is not decomposed, it is not readily consumed by benthic invertebrates of the sediments. Thus, this linkage is weakened. Acidification directly depletes diversity and abundance of phytoplankton, zooplankton, and fish in the water column as well as that of sediment invertebrates. With acidification, the abundance of insect predators may rise.

Direct additions or losses of biota

While loss of species by exploitation from freshwater ecosystems has occurred, it is a relatively minor threat to biodiversity in comparison with the impacts of introduced species (Richter et al. 1997). Introduced species may deplete, if not eliminate, native species by predation, competition, habitat alteration, and hybridization (Richter et al. 1997, Ricciardi and Rasmussen 1998).

Many species of organisms have been moved by humans from their natural localities to other freshwater systems either deliberately or accidentally (Allan 1995, Lodge 2000). Introduced plants, and fish in particular, have done extensive damage to native freshwater ecosystems, including their bottom sediments. Trout have been deliberately introduced around the world. In many Australian and New Zealand waters, trout have replaced the native galaxiids that feed mainly on animals in the water column. Consequently, with galaxiids the benthic grazers are abundant and with high grazing pressure from them algal biomass is low. The introduced trout replacing the galaxiids consume almost all the benthic invertebrate production and greatly reduce grazing pressure; as a result, algal biomass may be high (Huryn 1998). Thus, through the introduction of nonnative fish, a strong linkage is developed between above-sediment and sediment biota. The new food web is an example of a trophic cascade, whereby the effects of strong top-down control (here, fish predators) cascade down the food chain. This example underscores the point that many introductions, especially of animals, give rise to major reconfigurations of the trophic structure of the affected ecosystem.

A dramatic example of the major and multiple changes in freshwater ecosystems caused by the introduction of a single species is provided by the impacts of the zebra mussel, *Dreissena polymorpha*, in North America, especially in the Great Lakes and the Hudson River (Strayer et al. 1999). The mussels, which have undergone phenomenal increases in abundance, have densely colonized extensive sections of the bottom and built up to such levels that they may filter 70–125% of the water column per day in summer (Strayer et al. 1999). Primarily because of this very high filtration rate and the consequent removal of particles from the water, zebra mussels have created major changes in the water column and its biota, including dramatic decreases in phytoplankton, zooplankton, and silt in the water column. Nutrients that were previously used by the phytoplankton now become concentrated in the water, and combined with greater light penetration may lead to increased macrophyte abundance. Populations of native bivalves drop sharply after zebra mussel invasion, either because zebra mussels kill native bivalves by settling on them or because the zebra mussels deplete food supply (phytoplankton).

While many of these events may seem localized to the water column, there are also major effects on aquatic sediments. First, many native bivalves are important bioturbators and this function is not performed by the invading zebra mussels. Second, because zebra mussels provide structurally complex habitat and biodeposit material, invertebrates living on the mussel beds and in the surrounding sediments may actually increase (Botts et al. 1996, Ricciardi et al. 1997). Third, an increase in benthos may lead to an increase in fish production. Thus, *Dreissena* has altered ecosystem structure by strengthening the linkage between above-sediment and sediment biota (*Dreissen*–phytoplankton) that in turn depletes zooplankton and elevates nutrient levels in the water column. As stressed by Strayer et al. (1999), zebra mussels have changed the structure of ecosystems they have invaded and have come to exert key control over ecosystem structure and dynamics.

Global climate change and the greenhouse effect

As humans alter the landscape and exploit earth's natural resources, the flux of gases between land, water, and the atmosphere has been radically altered. Increases in the atmosphere of greenhouse gases, mainly carbon dioxide and methane, have caused climate change, and decreases in stratospheric ozone have led to increases in ultraviolet (UV) radiation. UV radiation may damage freshwater biota (Vinebrooke and Leavitt 1999), as do the changes in water temperature and flow regimes that are expected under climate change scenarios (Poff et al. 2000).

With the increasing levels of greenhouse gases in the atmosphere, it is projected that there will be a steady rise in surface temperatures, both on land and in water. For freshwater ecosystems, there will be increases in water temperature, changes in regional climate and hydrology, shifts in streamflow, changes in lake volumes and thermal structure, alterations in catchment inputs (e.g., detritus, nutrients into lakes and rivers), and a marked increase in the frequency and intensity of extreme events such as droughts and floods (Arnell et al. 1996, Lodge 2000, Poff et al. 2000).

Changes in temperature may alter above-sediment biota and hence through linkages affect sediment biota. As suggested by Meyer and Pulliam (1992), regional warming may lead to changes in the plant species composition of riparian zones. In turn, it can be expected that this will result in changes in the quality and quantity of detrital inputs, which may alter the life history dynamics, biodiversity, and species composition of the resident sediment detritivores. Increased atmospheric carbon dioxide concentrations may lead to increases in carbon:nitrogen and lignin:nitrogen ratios in catchment plants, which in turn will slow down litter decomposition in soil (Ineson and Cotrufo 1997). Such chemical changes may also slow down breakdown rates of leaf litter by sediment detritivores in streams (Ostrofsky 1997) and reduce their abundance and diversity (Palmer et al. 2000).

Increased temperatures may also have dramatic consequences on pelagic biota, which in turn may have cascading effects on the sediment biota. Fish as predators can exert strong effects on the abundance and productivity of bottom-dwelling invertebrates in streams, lakes, and ponds (Power 1990, McDonald et al. 1996, Scheffer 1998). In temperate and arctic latitudes and in alpine areas, fish species, especially those in isolated lakes and in fragmented stream systems, may be eliminated (Carpenter et al. 1992, Keleher and Rahel 1996, Lodge 2000). The impacts of the loss of predatory fish on sediment biodiversity depends on web structure; the loss of top predators in a three trophic-level system may increase sediment invertebrate biodiversity, but loss of the top predator in a four trophic-level system may lead to a loss of biodiversity in sediment invertebrates (Power 1990, 1995).

Global climate change is predicted to increase the frequency and intensity of extreme events (Arnell et al. 1996, Poff et al. 2000). If flood or drought severity or frequency increases, important linkages between above-sediment and sediment biota could be disrupted. For example, in northern California streams, the normal winter floods deplete the populations of grazing invertebrates to such an extent that in spring the filamentous alga *Cladophora* can grow unchecked by grazing invertebrates. The *Cladophora* may then bloom and produce clumps that slough off and form floating mats, all of which favor sediment invertebrates that consume the algae and its detritus. The system thus supports four trophic levels: algae, algal consumers (e.g., chironomids), small predators (e.g., odonatans, young fish), and large predators (e.g., trout) (Power 1995). However, in abnormal drought years, algal grazers are not kept in check by small predators. Thus, the *Cladophora* experiences high herbivory, and without a standing crop of algae the system may support only two trophic levels, algae and grazers. Therefore, changes in the hydrological regime through altering linkages between sediment and above-sediment biota directly shape trophic structure in freshwater systems.

Droughts may also intensify interactions between pelagic predators and sediment biota in streams because droughts reduce habitat and fragment the continuity of running-water systems. When water levels drop, pools become more isolated and predation by fish, lentic invaders (e.g., Hemiptera) and birds (all above-sediment biota) on sediment fauna is intensified (Lake 2000). Overall, both sediment and above-sediment biota, such as fish, may be greatly depleted (Stanley et al. 1997, Gasith and Resh 1999). It seems that in general, drought may exert more dramatic and lasting effects than floods on sediment biota, both directly and by altering interactive linkages (Lake 2000).

Wetlands will also be greatly affected by increased temperatures and altered hydrology associated with climate. Wetlands currently are responsible for about 40% of the annual methane flux to the atmosphere (Carpenter et al. 1992). Most of this methane production occurs in wetlands above 40° north. Because temperature increases are expected to be greatest at high latitudes, these wetlands may experience permafrost melting and increased availability of free water. Under these conditions, changes in microbial activities are expected to lead to the emission of large quantities of either carbon dioxide or methane into the atmosphere (Gorham 1991). This increased emission will further elevate temperatures and stimulate more plant growth, producing more detritus for microbial decomposition. Thus, a positive feedback loop of global proportions linking above-sediment to sediment processes may be set up.

Summary and conclusions

Volumes have been written about the expected effects of global change. There is also a fairly extensive, albeit rather recent, literature on the effects of global change on terrestrial, pelagic, and sediment-dwelling biota. To date, however, with respect to these biota, global change has been examined largely in terms of its direct and separate effects on above-sediment and sediment biota. Because linkages between above-sediment and aquatic sediment biota have not been extensively explored in freshwater ecosystems (Palmer et al. 2000), our focus on the effects of global environmental change on linkages between above-sediments and sediments has required some speculation. While global environmental change suggests a large-scale, single phenomenon, it is actually due to the effects of many forms of disturbances of different types, modes of action, and ecological outcomes. We have attempted to examine those disturbances most likely to affect linkages between above-sediment and sediment biota.

Those linkages most affected by global change appear to be in the direction of above-sediment biota (particularly pelagic fauna and terrestrial plants) to sediment biota rather than in the opposite direction. Because of their hydrological and geomorphological settings, freshwater ecosystems are extremely dependent on inputs from their catchments and the air. Many disturbances act through effects on terrestrial flora (e.g., altered catchment vegetation), on pelagic biota (e.g., altered plankton or fish assemblages), and on the sediment biota of running waters that depend on upstream inputs and processes (e.g., biota isolated or lost due to river regulation). Hence, disturbances acting in these ways are more likely to affect above-sediment biota before below-sediment biota, and this directionality of the effects of disturbance on above-sediment and sediment linkages is also found in terrestrial and marine systems (Smith et al. 2000, Wolters et al. 2000).

The linkages most altered by global change disturbances are those linkages involving the transfer of consumable resources, such as nutrients and detritus, or those involving biotic interactions, such as predation. For example, alterations in the transfer of detritus from above-sediment biota (e.g., due to eutrophication or changes in riparian vegetation) and the loss of key pelagic predators (e.g., due to acidification or displacement by exotic species) can both exert strong effects on the sediment biota. In some instances, the effects of disturbance may ripple across several trophic levels and fundamentally alter ecological patterns and processes in entire freshwater ecosystems.

The degree and extent to which global environmental change disturbances weaken or disrupt linkages vary, as do the effects on the biota. For example, weakening of the linkage between the pelagic realm and hyporheic sediment biota due to sedimentation may have only small-scale and minor effects, whereas the elimination of floods by river regulation completely breaks the linkage between pelagic riverine biota and the sediment biota of floodplains. Changes in the species involved in linkages, by disturbances such as invasion by exotics, can weaken or break linkages. The replacement of native catchment vegetation by exotic plant species could alter or perhaps entirely change the species composition of detritivorous sediment biota in streams. Far more research is needed to make definitive predictions.

Interestingly, human disturbance can in some cases strengthen linkages between above-sediment and aquatic sediment biota, which may exacerbate the effects of disturbance. For example, the switching of fish predators by the deliberate introduction of new species may result in dramatic increases in both consumptive and nonconsumptive effects on sediment prey. Changes in the supply of detritus from the photic zone to bottom sediments provides another example of how linkages may be strengthened. The delivery of excessive detritus to bottom sediments may lead to oxygen depletion there, which in turn may stimulate anaerobic microbial processes, ultimately resulting in the release of more nutrients from the sediments back into the water column (Figure 1). These added nutrients may then stimulate phytoplankton production in the photic zone, further increasing the delivery of organic matter to bottom sediments. A final and much larger scale example of strengthened linkages due to global environmental change is that increased temperatures may accelerate the emission of greenhouse gases from temperate and boreal wetlands (due to microbial activities in aquatic sediments), which will further add to the greenhouse effect.

For all forms of human disturbance producing global environmental change, there are immense gaps in our knowledge. Given that all the forms of disturbance dealt with in this paper are likely to increase in extent and strength, there is clearly a strong imperative to carry out well-targeted research in freshwater ecosystems on the nature and strengths of linkages between above-sediment biota and sediment biota and how different disturbances affect these vital linkages.

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