Animal Ecosystem Engineers in Streams

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An impressive array of animals function as ecosystem engineers in streams through a variety of activities, ranging from nest digging by anadromous salmon to benthic foraging by South American fishes, from the burrowing of aquatic insects to the trampling of hippos. These ecosystem engineers have local impacts on benthic habitat and also strongly affect downstream fluxes of nutrients and other resources. The impacts of ecosystem engineers are most likely some function of their behavior, size, and population density, modulated by the abiotic conditions of the stream. In streams, subsidies often control the body size and density of ecosystem engineers, while hydrologic energy controls their distribution, density, and life-history attributes, the habitats they create, and the resources and organisms they affect. Because ecosystem engineers can profoundly affect stream ecosystems, and because they themselves can be significantly affected positively or negatively by human activities, understanding ecosystem engineering in streams is increasingly important for the management of these ecosystems.

Keywords: subsidy, salmon, bioturbation, benthic invertebrates, disturbance

Stream dynamics are controlled by a combination of abiotic and biotic factors. Disturbances such as floods control the characteristics of stream ecosystems and communities, creating a dynamic and complex mosaic of differently aged patches (Resh et al. 1988, Stanford et al. 2005). Streams exhibit high longitudinal connectivity—downstream flows and movements of organisms move nutrients, particles, organisms, and other matter from upland to lowland streams (Hynes 1975, Stanford et al. 2005). Streams often have high lateral connectivity as well: Reciprocal subsidies of matter and organisms connect riparian and stream habitats (Hynes 1975, Naiman and Décamps 1997, Baxter et al. 2005). The activities of animals that physically modify the environment are also critical to stream processes and dynamics.

Beavers build dams; chironomids burrow in sediments; salmon dig nests. In these and many other ways, animals affect stream ecosystems by physically modifying habitats or resources. These animals are ecosystem engineers, broadly defined as "organisms that directly or indirectly control the availability of resources to other organisms" through the "physical modification, maintenance, or creation of habitats" (Jones et al. 1997).

Ecosystem engineers can modify a variety of stream ecosystem attributes. Perhaps most frequently considered (apart from the beaver, *Castor canadensis*) are those that physically modify benthic habitats. However, ecosystem engineers not only have local benthic impacts but also can fundamentally influence a diverse array of stream ecosystem components. For example, ecosystem engineers can impact hydrological dynamics of rivers; specifically, movements of crocodiles (*Crocodylus* spp.), hippos (*Hippopotamus amphibious*), and wildebeests (*Equus burchelli*) can mix the water column of stagnant pools in African rivers, preventing development of anoxic conditions (Gereta and Wolanski 1998). Ecosystem engineers also alter the dynamics of nutrients and particulate matter, key resources for many stream organisms. Thus, it would seem that ecosystem engineers can influence virtually all aspects of stream ecology. For the purposes of this article, I will focus on animals as ecosystem engineers in streams, even though many ecosystem engineers of stream habitats are not animals. For example, riparian trees shade attached algae (i.e., periphyton) in streams (Vannote et al. 1980) and provide large woody debris that serves as structure for stream organisms and changes stream morphology (Gregory et al. 2003).

Although stream ecosystems provide many of the best-appreciated, and potentially the most numerous, examples of ecosystem engineers, there has been virtually no development of a conceptual framework to help understand how, where, and when ecosystem engineers are important to stream ecosystems and communities. Ecosystem engineers have the potential to affect most aspects of stream dynamics, but they are not important in all systems. Thus, a major challenge in understanding the roles of ecosystem engineers in streams (and in all ecosystems, for that matter) is to discern the context dependency of their effects. In this article, I examine the role of ecosystem engineers in streams and propose a frame-

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work to capture the observed variation in where and when ecosystem engineers have large impacts on streams. In particular, I propose that key species attributes (behavior, body size, and density) affect the potential for engineering, and that these are modulated by the abiotic characteristics of streams (namely, hydrologic energy and the importance of cross-habitat subsidies) to determine the importance of any organism in a specific ecosystem.

Understanding variability in the importance of ecosystem engineers

It is likely that ecosystem engineering has a wide range of ecological importance across streams. In some streams, ecosystem engineers may have a few small impacts, but in other streams they may dominate the system. Although classic examples of ecosystem engineers from streams usually focus on strongly interacting species (e.g., beavers), it is likely that many organisms act as ecosystem engineers with weak effects on ecosystems (Jones et al. 1994, 1997). What factors influence whether a species is likely to be a dominant ecosystem engineer?

I propose that the impact an ecosystem engineer has on its environment will be a function of three main aspects of the biology of the ecosystem engineer: behavior, body size, and population density. In addition, these three aspects of the ecology of the ecosystem engineer will be mediated by the abiotic conditions of the ecosystem (figure 1). This conceptual framework is similar to those proposed by Jones and colleagues (1994, 1997) to predict the impacts of ecosystem engineers and by Power and colleagues (1996) to predict community importance of a species. It should be noted that the impact of an ecosystem engineer in this framework is based on the specific impact measured (e.g., displacement of sediments, particulate matter processed).

Behavior. The first factor that will control the impact of an ecosystem engineer on its community is the behavior of the ecosystem engineer. I define ecosystem engineering behavior as the type and frequency of activity that leads to modification of the ecosystem. In other words, what is the behavior that is engineering the ecosystem? Different organisms perform different activities that constitute ecosystem engineering. The impacts that an ecosystem engineer has will depend on the details of this behavior. For example, the impacts that beavers have on streams are driven primarily by their behavior—they build dams that flood riparian forests and change streamflow regimes. Alternatively, benthic-feeding fishes disturb fine sediments, and some benthic insects shred organic matter. While the idiosyncratic nature of ecosystem engineering has been viewed as a challenge to developing predictive frameworks, often simple natural history information will identify the behaviors that are engineering ecosystems (Jones et al. 1994, 1997).

Body size. Ecosystem engineers in streams are represented by a broad range in body sizes, with differences in mass that span at least nine orders of magnitude, from 1 x 10^{-3} gram (g) benthic insects to 4 x 10^{6} g hippopotami. For a specific behavior, larger organisms are likely to have larger impacts on a per capita basis. For example, larger salmon dig larger nests (Steen and Quinn 1999). I predict that the per capita effect of an ecosystem engineer will be a combination of the behavior and body size of the individual.

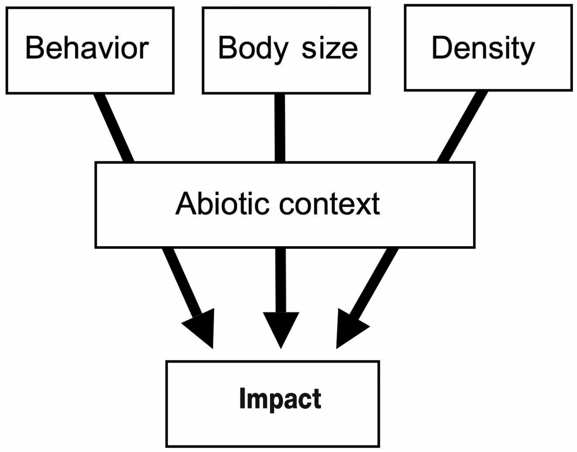

Figure 1. Interacting factors that influence the impacts of a species of ecosystem engineer on streams. The impact of an ecosystem engineer is the extent to which that species changes its habitat, for example, how much sediment it displaces. Behavior is the type and frequency of the activity that is engineering the ecosystem. Body size is the mass of the ecosystem engineer, which should scale the impacts of the specific ecosystem engineering behavior. Density is the relative abundance of the ecosystem engineer. Behavior, body size, and density will all be modulated by the abiotic context. In streams, subsidies often drive large body sizes and densities, and hydrologic energy is the primary abiotic factor.

Population density. The total impact of a species of ecosystem engineers will be a function of its population density as well as the per capita effect described above. Just as different densities of predators will exert different impacts on prey populations, different densities of ecosystem engineers will have different impacts on communities. Specifically, it seems likely that higher densities of ecosystem engineers will have larger impacts, but that this will saturate at some density of ecosystem engineers. Identifying how different densities of ecosystem engineers will affect communities and ecosystems is challenging but crucial to understanding the complexity inherent in nontrophic interactions. Ideally, studies will not only examine the impacts of a single density of ecosystem engineers but examine ecosystem and community impacts across a gradient of densities.

Thus, I propose that ecosystem engineers can have large impacts on streams when they either have behaviors that have large impacts (e.g., beavers), are relatively large given the ecosystem they inhabit (e.g., hippos), reach high densities (e.g., blackflies), or some combination of these factors (e.g., salmon; figure 1). Subsidies often allow organisms to obtain higher densities and larger body sizes then they would be able to on the basis of local production alone (Polis et al. 1997). Subsidies are flows of matter across ecosystem boundaries that increase the productivity of the recipient ecosystem (Polis et al. 1997). Streams are highly subsidized ecosystems (Hynes 1975). These subsidies can substantially increase the body size and population density of a stream's ecosystem engineers. Dense colonies of blackfly larvae are sustained by suspended particulate matter drifting in from upstream habitats. Benthic macroinvertebrates shred the leaves of riparian trees. Hippos and beavers feed almost exclusively on terrestrial vegetation. The biomass of anadromous migratory fishes, such as salmon, in streams is sustained by oceanic production, and these fish obtain population densities out of proportion to the productivity of their freshwater spawning locations. In the sections that follow, virtually all the examples of ecosystem engineers that have large impacts on streams are organisms that receive substantial subsidies.

Abiotic context. In addition to behavior, body size, and population density, the ecological importance of an ecosystem engineer will depend on abiotic conditions (figure 1). This context dependency adds complexity to the challenge of generating conceptual frameworks (Wright and Jones 2006). In streams, the abiotic factor that is an important driver is the hydrologic regime. For example, do floods dominate the stream disturbance regime, thus reducing bioturbation to a minor component of the disturbance regime? It seems likely that in streams with extremely high hydrologic energy, water energy will overshadow any potential impact of ecosystem engineers.

What are the attributes of streams that promote high levels of ecosystem engineering?

To move beyond case studies, it is helpful to have a testable framework for predicting the context dependency of ecosystem engineers. In other words, what are the attributes of streams that promote high levels of ecosystem engineering? According to the conceptual framework outlined above, variation in the importance of ecosystem engineering is driven by the density, size, and behavior of ecosystem engineers, as well as their hydrologic context. Via these four mechanisms, I propose that two main factors control the potential for ecosystem engineering in streams: the intensity of external subsidies and the hydrologic regime (figure 2). Specifically, I predict that ecosystem engineering is more important in streams with heavily subsidized food webs and with low to intermediate hydrologic energy.

Heavy subsidies to stream food webs allow for disproportionate abundances and sizes of ecosystem engineers. As subsidies to ecosystem engineers increase, the impacts of ecosystem engineers will also increase, in parallel with increases in their body size or population density (figure 2). However, it is likely that this effect saturates at some level of subsidization, beyond which further subsidies do not increase the impacts of ecosystem engineers, as their body size or population density is limited by other factors such as physiologic constraints, territoriality, or predation. Even if subsidies continue to increase the total biomass of ecosystem engineers, it is possible that ecosystems have a limited capacity for biological engineering. For example, higher densities of detritivorous web-footed frog tadpoles (*Rana palmipes*) in a Venezuelan stream decreased sediment accumulation in tropical streams up to a point, but this effect saturated at five tadpoles per square meter (m^2) (Flecker et al. 1999). Likewise, there is a finite amount of fine particulate matter in a stream that is available to be dislodged by spawning salmon, and only so much habitat for beavers to flood. If all modifiable habitat has already been modified, the density and body size of ecosystem engineers may increase with no increase in the engineers' impact.

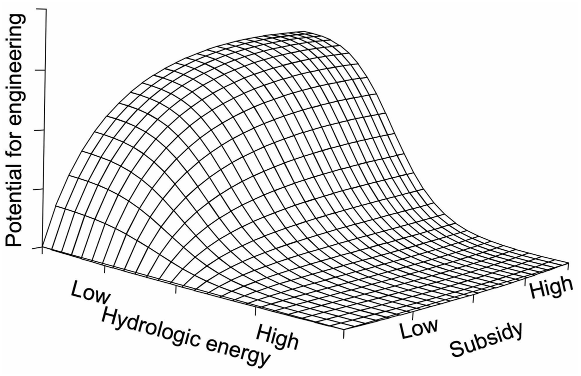

Figure 2. Attributes of streams that control the potential for ecosystem engineering. "Potential for engineering" refers to the relative importance of ecosystem engineers in streams. This potential is influenced by the amount of subsidies to the ecosystem engineers, which can drive increases in body size and density, and by the hydrologic energy of the stream. Hydrologic energy represents the amount of energy in the stream, a combination of flow volume and velocity, and is an indication of the potential for flood disturbance. Hydrologic energy is modeled as a sigmoid function, while subsidies are modeled as a saturating relationship.

Ecosystem engineering is more important in streams with low to intermediate hydrologic energy. In streams with overwhelming hydrologic energy, ecosystem engineering is relatively unimportant (figure 2): Disturbance from floods scours out ecosystem engineers, their creations, and the habitats and organisms they affect. At intermediate flows, ecosystem engineers that can have potentially large impacts are organisms that modify the susceptibility of habitats to flows, such as net-spinning caddisflies that stabilize sediments and provide habitat refugia. However, even this modification of the stability of sediments to disturbance will have little effect on a stream that has very severe floods. For example, Cardinale and colleagues (2004) found that the effect of net-spinning caddisflies on stability of sediments was reduced at the highest flow treatment in artificial streams.

The framework I have outlined here should be viewed as a testable hypothesis to be revised, elaborated, and applied to other study systems as a richer understanding of ecosystem engineers is developed. For example, one plausible alternative is that ecosystem engineering might be most important in streams with intermediate hydrology. In these streams, habitat modification by ecosystem engineering may provide resistance to mild scouring. In addition, in streams with intermediate hydrologic energy, water flows may help transport sediments disturbed by bioturbation. Crain and Bertness (2006) provide a more thorough treatment of the importance of different types of ecosystem engineering across stress gradients.

Types of ecological engineering in streams

This section outlines different types of ecosystem engineering in streams and highlights the ways that these examples fit into the conceptual frameworks outlined above.

Habitat creation. Organisms can alter stream habitats by their simple physical presence or by creating new physical structures. *Autogenic* habitat creation is the generation of habitats by the physical structure of the ecosystem engineer. Thus, the physical presence of the ecosystem engineer modifies the abiotic environment. For example, some caddisfly larvae use silk to build armored cases out of gravel and other materials. These cases are biogenic habitats that increase benthic roughness, modifying flow patterns of the boundary layer and particulate depositional patterns (Nowell and Jumars 1984, Cardinale et al. 2002).

Bivalves are another taxon that creates biogenic habitat. Common in some streams, bivalves produce shells that can last for decades after the death of the animal that made them (Gutiérrez et al. 2003). Shells can provide complex hard substrate on soft sediments, altering water flow patterns and particulate deposition. These shells also provide crucial refuge for a variety of organisms and settling habitat for hard-substrate species (Gutiérrez et al. 2003).

Allogenic habitat creation occurs when an organism creates, from materials other than its own structure, a physical construct that subsequently modifies habitats in the absence of the ecosystem engineer. Beavers are the classic example of this type of ecosystem engineer. Through dam building, beavers modify stream morphology, flood existing riparian habitats, alter riparian community succession and diversity (Wright et al. 2002, 2004), modify nutrient and material processing and flows, and provide habitat for fishes (Naiman et al. 1988). These types of habitat creation seem to be more frequent in streams with low to intermediate hydrologic energy. Presumably, in systems with high hydrologic energy, the created habitats would be destroyed by flow.

Bioturbation. Another important type of allogenic ecosystem engineering in streams is bioturbation, the physical perturbation of benthic habitats. Three main types of activities lead to bioturbation in streams: nest digging, foraging, and movement.

Nest digging. Numerous species of freshwater fishes dig nests in which they lay their eggs, producing patches of disturbed substrate (e.g., Carpenter and McCreary 1985, Peterson and Foote 2000). Perhaps the most extensive nest digging in freshwater streams is performed by migratory Pacific salmon (*Oncorhynchus* spp.), which dig large nests and often spawn at high densities (Gottesfeld et al. 2004, Moore et al. 2004). Depending on the species and size of salmon, a female salmon digs a pit up to 0.4 m deep and ranging from 1 to 17 m^2, where she will lay her eggs (Groot and Margolis 1991). This nest digging can disturb large areas in spawning locations. For example, using historical counts of spawning sockeye salmon (*Oncorhynchus nerka*) and previously measured nest sizes, I estimated that salmon have consistently disturbed more than 5000 m^2 of the streambed every summer in two streams in southwestern Alaska over the last 50 years, roughly 30% of the available streambed (figure 3). These estimates assume that each female digs only one nest, and that nests do not overlap because of the extremely territorial behavior of female salmon. In years when salmon populations are high, I estimate that sockeye dug up the entire streambed more than once, being forced to superimpose new nests on top of old nests. In addition, if the commercial fishery had not taken an average of 60% of the returning fish, salmon would consistently disturb more than half of the entire streambed every summer (figure 3).

This nest digging has a variety of impacts on benthic habitats and communities. It displaces fine sediments, subsequently coarsening sediment (Kondolf et al. 1993, Peterson and Foote 2000, Moore et al. 2004). A 5-year study of large sediments in a British Columbia stream found that sockeye salmon nest digging moved more sediment, and buried marked sediments deeper, than many flood events (Gottesfeld et al. 2004). In addition, bioturbation from salmon dislodges fine particulate matter into the stream's water column, driving a pulse in the concentration of suspended particulate matter (figure 4). Concentrations of suspended particulate matter in streamwater during salmon spawning are at least four times higher than before spawning (figure 4). Experimental and observational studies have also shown that nest digging by salmon can drive temporary but dramatic decreases in periphyton biomass (Minakawa and Gara 1999, Moore et al. 2004). Finally, salmon nest digging appears to be a significant source of mortality for benthic invertebrates in stream reaches that have high densities of salmon (Minakawa and Gara 2003). While salmon nest digging is a substantial disturbance to spawning areas, their bioturbation may actually decrease the susceptibility of streams to erosion from floods. Specifically, by sorting sediments into size classes, salmon nest digging may increase critical shear stress (i.e., minimum

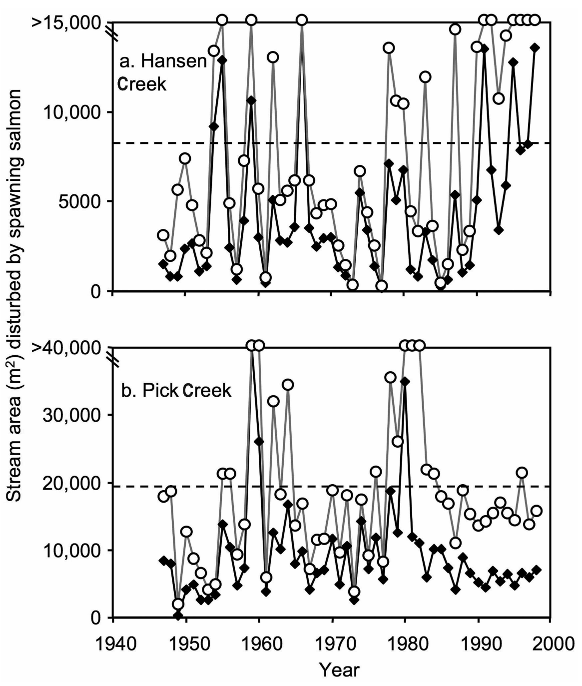

Figure 3. The estimated stream area that was disturbed by spawning salmon in (a) Hansen Creek and (b) Pick Creek, in the Wood River drainage area, Alaska, over the last 50 years. The solid line with black diamonds represents the observed year-specific area disturbed in the two creeks, while the gray line with open circles represents the "plus-harvest" area (theoretical area disturbed in the two creeks if harvest had not occurred). Symbols above the plot areas represent points that were above the scale shown. The dashed horizontal line represents the point at which all available stream area was disturbed by spawning salmon. Thus, any points above this line indicate where salmon churned up the sediments more than once. I calculated the observed area disturbed by multiplying the maximum stream count for that year by a constant average ratio between nest size and sex. I calculated the plus-harvest proportion by multiplying the year-specific proportion disturbed by the ratio of total run to escapement for the fishery for that year. Data used for these calculations are from the Alaska Salmon Project (University of Washington), Steen and Quinn (1999), and Marriott (1964).

flow before bed scouring occurs) of stream bottoms (Montgomery et al. 1996).

In general, nest digging is likely to be important for areas where fishes dig large nests and reach high abundances, and in streams where this biotic disturbance is not overshadowed by frequent and intense flooding. In addition, nest digging seems unlikely to be a common reproductive strategy in streams characterized by extreme disturbance regimes; in these streams, nests would be scoured by floods. Anadromy and other migratory life history strategies allow fishes to achieve sizes and population densities out of proportion to the size and productivity of their freshwater environments (Willson et al. 2004). About 15 families of fish include species that exhibit anadromy, and this life history is especially prevalent in northern mid to high latitudes (Willson et al. 2004). Anadromous fish populations are often controlled by oceanic productivity. For example, salmon returns oscillate on decadal scales linked to cycles of long-term variability in ocean conditions (i.e., Pacific Decadal Oscillation; Mantua et al. 1997). Thus, oceanic climate variability controls coastal disturbance regimes through the population levels of salmon (figure 3). Nest digging, especially by migratory fishes such as Pacific salmon that are subsidized by oceanic productivity, can have substantial impacts on stream ecosystems.

Foraging. Detritivorous and other bottom-feeding taxa can be a key source of bioturbation of stream benthic habitats. These taxa include crayfish (Statzner et al. 2003a), shrimps (Pringle et al. 1993, 1999), tadpoles (Flecker et al. 1999, Ranvestel et al. 2004), and fishes (Flecker 1996, Flecker and Taylor 2004). For example, experimental exclusions of shrimps in tropical rivers have demonstrated that they decrease organic matter accumulation tenfold (Pringle et al. 1999). Shrimps also indirectly increase algal biomass by reducing sediments that otherwise shade periphyton (Pringle et al. 1993).

Moreover, shrimps can both positively and negatively affect benthic insects. By increasing algal abundance, shrimps facilitate mobile invertebrate grazers such as mayfly nymphs (Pringle et al. 1993). However, shrimps negatively affect tube-dwelling chironomids by directly disrupting their tube houses and removing the materials that the chironomids use to build their tubes (Pringle et al. 1993). Pringle and colleagues (1999) scaled up these small experiments to the watershed scale, and discovered that the abundance of shrimps in tropical streams affected interstream variation in levels of benthic organic and inorganic matter.

Benthic fishes are also a source of bioturbation during their foraging. In general, benthic-foraging fishes increase the movement of fine sediments (Statzner et al. 2003b), reducing local sediment accumulation (Power 1990, Flecker 1996). This reduction generally occurs through two mechanisms. First, many bottom-feeding taxa intentionally or accidentally ingest sediments, subsequently digesting them or excreting them into the water column (Ranvestel et al. 2004). Second, benthic species often dislodge fine particulate matter during their search for other benthic food sources such as periphyton or benthic insects (Zanetell and Peckarsky 1996).

Benthic fishes have further impacts on other aspects of the benthic ecosystems. Power (1990) demonstrated that armored catfish (Loricariidae) reduced sedimentation, which decreased the shading of benthic periphyton and led to increased primary productivity. However, severe bioturbation can lead to decreased standing stocks of periphyton (Power 1990). Through perturbation of substrates or accidental ingestion, bioturbation can be a substantial source of disturbance to benthic invertebrates (Flecker and Taylor 2004).

External sources of energy subsidize most of these benthic-foraging ecosystem engineers that dominate stream processes.

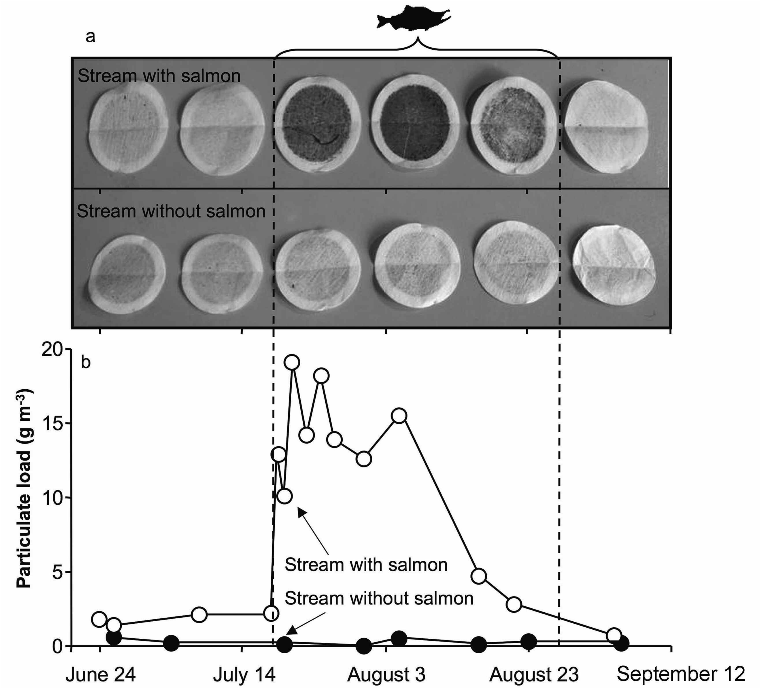

Figure 4. The impact of bioturbation by spawning salmon on the concentrations of total suspended particulate matter in the outflows of two Alaskan creeks. Shown here are the seasonal dynamics of particulate load of water throughout the open-water summer period from a stream with high densities of salmon and a reference stream without salmon. The dashed vertical lines enclose the period of salmon spawning in the stream with salmon. (a) Picture of the seasonal progression of particulate load. Pictured are GF/F filters (pore size = 0.7 micrometers) that had 2 liters (L) of water filtered onto them throughout the 2002 summer from Pick Creek (top), which has high densities of spawning sockeye salmon during midsummer, and Cottonwood Creek (bottom), a nearby stream without salmon. (b) Seasonal dynamics of concentrations of suspended particulate matter in the same two streams in 2003. Points represent the mean of two replicate grab samples of 2 L of water from stream outflows that were filtered onto GF/F filters, dried, and weighed. There were no substantial changes in discharge during the period of salmon spawning. Photograph: Jonathan W. Moore.

For example, populations of many detritivorous fishes in South America (e.g., *Prochilodus*) are subsidized by annual migrations to productive downstream floodplains (Winemiller and Jepsen 2004). In addition, many of the shrimps that are important ecosystem engineers are subsidized by migrations from the ocean (March et al. 2003). Thus, the aforementioned studies are further support for the hypothesis that ecologically important ecosystem engineers are often highly subsized (figure 2).

Movements. Movements of benthic taxa also can be a source of bioturbation. Benthic invertebrates such as crayfish (Statzner et al. 2003a) or stoneflies (Zanetell and Peckarsky 1996) dislodge fine sediments and reduce sediment accumulation. Moreover, movements of hippos between rivers and terrestrial feeding grounds carve new channels and prevent existing stream channels from becoming clogged with sediments and vegetation (Naiman and Rogers 1997). As the contrast between the crayfish and hippos might suggest, the magnitude and severity of this type of bioturbation depends on the size, abundance, and behavior of the ecosystem engineer (figure 1; Jones et al. 1997, Naiman and Rogers 1997, Statzner et al. 2003b).

These examples demonstrate that bioturbation can be caused by a wide range of activities and can be a substantial source of disturbance to benthic habitats. It appears that bioturbation is not commonly observed in streams with high hydrologic energy (figure 2). In slow-moving streams, as in marine ecosystems with soft sediments, bioturbation can be an important source of soft-sediment mixing (Peterson 1979). This bioturbation aerates sediments, changes sediment nutrient cycling, increases nutrient recycling to the water column, and changes benthic community composition (Covich et al. 1999). In addition to the local impacts discussed in the previous sections, bioturbation can also alter flow dynamics, nutrient processing, and downstream transport of organic matter and nutrients in stream ecosystems (Gutiérrez et al. 2006). These larger-scale and downstream impacts are less well described.

Bioconsolidation. Some animals physically modify habitats by consolidating benthic sediments. These activities immobilize sediments, rendering them less susceptible to future erosion. For example, caddisflies' silk filtration nets, which anchor sediments, add complexity to benthic habitats. Experiments in artificial stream channels have demonstrated that caddisflies decrease sediment erodibility, increasing critical shear stress (Statzner et al. 1999, Cardinale et al. 2004). Extrapolation of these results to natural streams suggests that caddisflies can decrease the probability of streambed scour per year by 17% (Cardinale et al. 2004). However, during extreme flow events, floods are likely to scour streambeds regardless of bioconsolidation by caddisflies (figure 2). Thus, through modification of the local habitat, bioconsolidators increase the resistance of stream ecosystems to moderate, but not to severe, abiotic disturbances.

Particulate matter processing. Some ecosystem engineers drive particulate matter processing in streams by physically modifying the size and location of particulate matter. This ecosystem engineering is a physical process, a by-product of consumption, that is not captured by principles of typical trophic ecology. Suspension-feeding invertebrates such as bivalves or blackfly larvae can transform vast quantities of seston (suspended living and nonliving matter) into fecal pellets, thus changing the location (suspended versus benthic) and size (small versus large) of organic matter in streams (Wotton et al. 1998). Benthic invertebrates known as shredders rip apart large pieces of organic matter, such as leaves, into smaller pieces. This processing of particulate matter increases the relative surface area available for microbial colonization, increasing the availability and palatability of the particulate matter for downstream collectors or scrapers (Cummins 1974). The experimental application of insecticides to streams dramatically decreases leaf processing rates and subsequent downstream transport of this particulate organic matter (figure 5; Wallace et al. 1982, 1991). Thus, ecosystem engineers are crucial to processing and downstream fluxes of matter. Key stream ecology concepts such as the river continuum concept (Vannotte et al. 1980) either implicitly or explicitly depend on this ecosystem engineering of particulate organic matter.

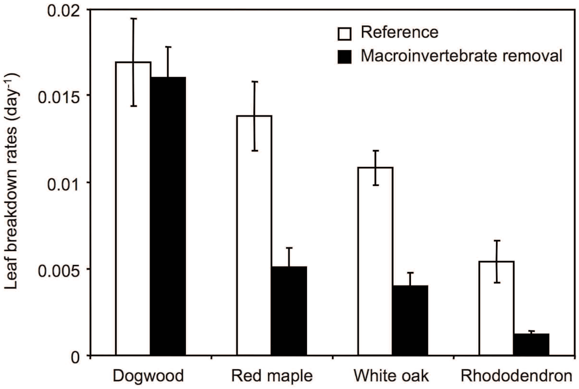

Figure 5. The impact of macroinvertebrates on processing rates of leaves. Mean exponential breakdown rates per day (± 95% confidence interval) of four leaf species in two North Carolina streams: one stream that had macroinvertebrate consumers removed via the application of an insecticide, and an adjacent reference stream with an intact macroinvertebrate assemblage. Data are from Wallace et al. 1982, table 2.

Frontiers in studies of ecosystem engineers in streams

The previous sections demonstrate that a diverse array of activities and organisms can physically modify stream habitats in different ways. Across this diversity, it appears that ecosystem engineers have the largest impacts in streams with intermediate to low hydrologic energy, and that the ecosystem engineers that cause these largest impacts are often highly subsidized to obtain high densities and body sizes. Although these case studies generally support the predictions illustrated in figure 2, future comparisons of the importance of ecosystem engineering across habitats may reveal valuable insights into the factors that modulate ecosystem engineering. In addition to developing and testing conceptual frameworks such as those described above, there are several potentially fruitful research directions for the study of ecosystem engineers in streams.

Feedbacks to future populations. Given that ecosystem engineers modify their habitat, and that habitat quality often influences population survival, there are many likely circumstances in which the current population of ecosystem engineers will influence its future population viability. If habitat modification by an ecosystem engineer promotes its own success, there will be feedback between generations. For example, salmon nest digging decreases substrate mobility by sorting substrate, reduces the shear stress of streambeds, and thus decreases the risk that incubating eggs and young will be dislodged and killed during floods (Montgomery et al. 1996). In addition, salmon nest digging decreases local levels of fine sediment that otherwise can clog interstitial water movement and smother incubating eggs. Thus, a critical question is whether the recovery of small salmon populations is inhibited by the lack of habitat maintenance by ecosystem-engineering salmon. These types of population feedback loops are potentially important, but have not been well described.

Understanding impacts across time and space. Most research has focused on short-term impacts of ecosystem engineers on relatively small spatial and temporal extents. One of the frontiers in studies of ecosystem engineers is to understand how they impact streams on larger scales, both in space and time. For example, salmon populations are highly variable from year to year and are frequently heavily targeted by commercial fisheries (figure 3). Because of their population variability, the impacts that salmon have on streams will vary among years, oceanic climate regimes, and fishing harvest policies.

In addition, because streams are linked by downstream water flow, ecosystem engineers in stream ecosystems will often not only have local impacts but also affect fluxes of nutrients and materials, with subsequent downstream impacts. For example, materials dislodged through bioturbation and particulate matter processing by shredder invertebrates may modify potential food availability for collecting or filter-feeding benthic insects downstream. Despite observations that ecosystem engineers can dramatically alter downstream fluxes of resources, with likely consequences for downstream communities, most research has focused on their local effects. Downstream impacts are likely to be more difficult to identify than localized impacts, and potentially more diffuse, but not necessarily less important.

In addition to having high longitudinal connectivity, streams often exhibit high lateral connectivity, with tight coupling between stream and riparian ecosystems (Hynes 1975, Naiman and Décamps 1997, Baxter et al. 2005). With the exception of beavers, and to a lesser extent hippos, the role of stream ecosystem engineers in influencing riparian habitats is not well known (Naiman and Rogers 1997). Stream ecosystem engineers may affect riparian communities through a multitude of pathways, and many questions about these pathways remain unanswered. For example, do salmon that dig nests adjacent to stream banks lead to undercutting and subsequent bank erosion? Do ecosystem engineers such as grizzly bears that create paths through riparian vegetation increase stream–riparian coupling (Naiman and Rogers 1997)?

The impacts of ecosystem engineers on an evolutionary scale are also poorly understood. Through time, organisms evolve in response to different selection pressures from their environment. Given that ecosystem engineers modify their environment, and that organisms evolve in response to their environment, ecosystem engineers will drive the evolution of cohabitating organisms. For example, severe, predictable, and frequent disturbances can drive the life history evolution of stream organisms (Lytle and Poff 2004). Benthic insects emerge before predictable and severe floods, thus avoiding the potentially risky flood period (Lytle 2002). Given that ecosystem engineers can also be a severe and predictable source of disturbance to fresh waters, it is possible that stream organisms have evolved life histories to minimize their mortality risk. For example, in streams in Canada and Alaska, salmon nest digging consistently disturbs spawning reaches at the same time every year (Gottesfeld et al. 2004). This nest digging has been hypothesized to drive the phenology of aquatic insects' life history, as aquatic insects in these systems emerge immediately before salmon spawning (Moore et al. 2004). In addition, by modifying habitats, ecosystem engineers may influence their own evolutionary trajectory (Odling-Smee et al. 2003). Investigating these evolutionary effects will be another fruitful direction in studies of ecosystem engineers.

Conservation implications

Human activities modify stream ecosystem engineers by way of two main mechanisms. First, human activities modify the abundances and subsequent impacts of ecosystem engineers. Second, humans themselves act as ecosystem engineers. Both mechanisms have small- and large-scale impacts that are poorly understood.

The loss of native ecosystem engineers and the introduction of nonnative ecosystem engineers as a result of human actions may have unforeseen consequences that extend beyond expectations based simply on trophic dynamics. Ecosystem engineers that have large impacts on streams may be particularly vulnerable to human impacts for several reasons. First, these organisms are likely to be large or abundant as a result of subsidies that are frequently disrupted by human activities such as dams or deforestation of riparian forests (see Naiman and Décamps 1997). In addition, dominant ecosystem engineers in streams may be more likely targets for fisheries, because these taxa are often large-bodied and abundant (Coleman and Williams 2002). *Prochilodus*, a dominant migratory detritivore fish in South American streams, is intensely fished (see Flecker 1996). Last, dominant ecosystem engineers often obtain large sizes and high population densities through subsidies they obtain during migrations. These migrations are often blocked by dams (March et al. 2003). For example, Atlantic and Pacific salmon populations have undergone drastic declines and extinctions in many regions of Europe and the United States due to a combination of human activities. Loss of these and other ecosystem engineers can lead to dramatic changes in ecosystem function, but we do not yet fully understand what these changes may be. The effects of introducing nonnative ecosystem engineers can also have potentially dramatic impacts that are not well understood (Crooks 2002).

Even as humans add or subtract ecosystem engineers, humans themselves act as ecosystem engineers in streams—perhaps the most important ecosystem engineers the world has encountered. For example, over half the large river systems in the world are affected by dams (Nilsson et al. 2005), which reduce the global flux of sediments and carbon to the ocean by impounding more than 1 billion metric tons of carbon and 100 billion metric tons of sediments in reservoirs every year (Syvitski et al. 2005). Humans are one of the only ecosystem engineers that can have direct impacts even on streams that have extremely high hydrologic energy, being an important exception to the framework illustrated in figure 2. However, humans achieve this extraordinary level of environmental modification by using extreme energy subsidies such as fossil fuels (Crowder et al. 1996). Through changing global flow regimes (Lytle and Poff 2004, Nilsson et al. 2005), humans are also changing the abiotic context for ecosystem engineering. In ways that scientists don't fully understand, the loss or addition of ecosystem engineers may affect the numerous goods and services humans obtain from streams (Postel and Carpenter 1997).

Conclusions

The concept of ecosystem engineering has proved useful to stream ecologists by reinforcing the knowledge that many animals have impacts on streams that cannot be explained simply by food web relationships. These impacts often drive community dynamics, ecosystem processes, disturbance regimes, and flows of nutrients and other resources, and can modify local as well as downstream habitats. I propose that key characteristics of ecosystem engineers and the streams they inhabit may allow for prediction of when and where ecosystem engineers will be important in influencing stream dynamics. These hypotheses should be tested and revised, with studies in streams as well as other systems. Studies in streams have provided many of the classic examples of how ecosystem engineers can have profound impacts on their habitats and communities. It is possible that ecosystem engineers are especially important in streams because these habitats are highly subsidized ecosystems, allowing ecosystem engineers to reach the high biomasses often associated with having large impacts. Given that ecosystem engineers can have large effects on fundamental characteristics of stream ecosystems, and given that they may be particularly susceptible to human impacts, understanding the role of ecosystem engineers in streams is critical for developing reasonable strategies for managing lotic ecosystems.

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References cited

Baxter CV, Fausch KD, Saunders WC. 2005. Tangled webs: Reciprocal flows of invertebrate prey link streams and riparian zones. Freshwater Biology 50: 201–220.

Cardinale BJ, Palmer MA, Collins SL. 2002. Species diversity enhances ecosystem functioning through interspecific facilitation. Nature 415: 426–429.

Cardinale BJ, Gelmann ER, Palmer MA. 2004. Net spinning caddisflies as stream ecosystem engineers: The influence of *Hydropsyche* on benthic substrate stability. Functional Ecology 18: 381–387.

Carpenter S, McCreary NJ. 1985. Effects of fish nests on pattern and zonation of submersed macrophytes in a softwater lake. Aquatic Botany 22: 21–32.

Coleman FC, Williams SL. 2002. Overexploiting marine ecosystem engineers: Potential consequences for biodiversity. Trends in Ecology and Evolution 17: 40–44.

Covich AP, Palmer MA, Crowl TA. 1999. The role of benthic invertebrate species in freshwater ecosystems. BioScience 49: 119–126.

Crain CM, Bertness MD. 2006. Ecosystem engineering across environmental gradients: Implications for conservation and management. BioScience 56: 211–218.

Crooks JA. 2002. Characterizing ecosystem-level consequences of biological invasions: The role of ecosystem engineers. Oikos 97: 153–166.

Crowder LB, Reagan DP, Freckman DW. 1996. Food web dynamics and applied problems. Pages 327–336 in Polis GA, Winemiller KO, eds. Food Webs: Integration of Patterns and Dynamics. New York: Chapman and Hall.

Cummins KW. 1974. Structure and function of stream ecosystems. BioScience 24: 631–642.

Flecker AS. 1996. Ecosystem engineering by a dominant detritivore in a diverse tropical stream. Ecology 77: 1845–1854.

Flecker AS, Taylor BW. 2004. Tropical fishes as biological bulldozers: Density effects on resource heterogeneity and species diversity. Ecology 85: 2267–2278.

Flecker AS, Feifarek BP, Taylor BW. 1999. Ecosystem engineering by a tropical tadpole: Density-dependent effects on habitat structure and larval growth rates. Copeia 1999: 495–500.

Gereta E, Wolanski E. 1998. Wildlife–water quality interactions in the Serengeti National Park, Tanzania. African Journal of Ecology 36: 1–14.

Gottesfeld AS, Hassan MA, Tunnicliffe JF, Poirier RW. 2004. Sediment dispersion in salmon spawning streams: The influence of floods and salmon redd construction. Journal of the American Water Resources Association 40: 1071–1086.

Gregory SV, Boyer KL, Gurnell AM, eds. 2003. The Ecology and Management of Wood in World Rivers. Bethesda (MD): American Fisheries Society. American Fisheries Society Symposium 37.

Groot C, Margolis L, eds. 1991. Pacific Salmon Life Histories. Vancouver (Canada): University of British Columbia Press.

Gutiérrez JL, Jones CL. 2006. Physical ecosystem engineers as agents of oxygen in aquatic systems. BioScience 56: 227–236.

Gutiérrez JL, Jones CG, Strayer DL, Iribarne OO. 2003. Mollusks as ecosystem engineers: The role of shell production in aquatic habitats. Oikos 101: 79–90.

Hynes HBN. 1975. The stream and its valley. Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie 19: 1–15.

Jones CG, Lawton JH, Shackak M. 1994. Organisms as ecosystem engineers. Oikos 69: 373–386.

———. 1997. Positive and negative effects of organisms as physical ecosystem engineers. Ecology 78: 1946–1957.

Kondolf GM, Sale MJ, Wolman MG. 1993. Modification of fluvial gravel size by spawning salmonids. Water Resources Research 29: 2265–2274.

Lytle DA. 2002. Flash floods and aquatic insect life-history evolution: Evaluation of multiple models. Ecology 83: 370–385.

Lytle DA, Poff NL. 2004. Adaptation to natural flow regimes. Trends in Ecology and Evolution 19: 94–100.

Mantua NJ, Hare SR, Zhang Y, Wallace JM, Francis RC. 1997. A Pacific interdecadal climate oscillation with impacts on salmon production. Bulletin of the American Meteorological Society 78: 1069–1079.

March JG, Benstead JP, Pringle CM, Scatena FN. 2003. Damming tropical island streams: Problems, solutions, and alternatives. BioScience 53: 1069–1078.

Marriott RA. 1964. Stream Catalog of the Wood River Lake System, Bristol Bay, Alaska. Washington (DC): US Fish and Wildlife Service. Special Scientific Report—Fisheries no. 494.

Minakawa N, Gara RI. 1999. Ecological effects of a chum salmon (*Oncorhynchus keta*) spawning run in a small stream of the Pacific Northwest. Journal of Freshwater Ecology 4: 327–335.

———. 2003. Effects of chum salmon redd excavation on benthic communities in a stream in the Pacific Northwest. Transactions of the American Fisheries Society 132: 598–604.

Montgomery DR, Buffington JM, Peterson NP, Schuett-Hames D, Quinn TP. 1996. Stream-bed scour, egg burial depth, and the influence of salmonid spawning on bed surface mobility and embryo survival. Canadian Journal of Fisheries and Aquatic Sciences 53: 1061–1070.

Moore JW, Schindler DE, Scheuerell MD. 2004. Disturbance of freshwater habitats by anadromous salmon in Alaska. Oecologia 139: 298–308.

Naiman RJ, Décamps H. 1997. The ecology of interfaces: Riparian zones. Annual Review of Ecology and Systematics 28: 621–658.

Naiman RJ, Rogers KH. 1997. Large animals and system-level characteristics in river corridors. BioScience 47: 521–529.

Naiman RJ, Johnston CA, Kelley JC. 1988. Alteration of North American streams by beaver. BioScience 38: 753–762.

Nilsson C, Reidy CA, Dynesius M, Revenga C. 2005. Fragmentation and flow regulation of the world's large river systems. Science 308: 405–408.

Nowell ARM, Jumars PA. 1984. Flow environments of aquatic benthos. Annual Review of Ecology and Systematics 15: 303–328.

Odling-Smee FJ, Laland KN, Feldman MW. 2003. Niche Construction: The Neglected Process in Evolution. Princeton (NJ): Princeton University Press.

Peterson CH. 1979. Predation, competitive exclusion, and diversity in the soft-sediment benthic communities of estuaries and lagoons. Pages 233–264 in Livingston RG, ed. Ecological Processes in Coastal and Marine Systems. New York: Lenum.

Peterson DP, Foote CJ. 2000. Disturbance of small-stream habitat by spawning sockeye salmon in Alaska. Transactions of the American Fisheries Society 129: 924–934.

Polis GA, Anderson WB, Holt RD. 1997. Toward an integration of landscape and food web ecology: The dynamics of spatially subsidized food webs. Annual Review of Ecology and Systematics 28: 289–316.

Postel SL, Carpenter SR. 1997. Freshwater ecosystem services. Pages 195–214 in Daily G, ed. Nature's Services. Washington (DC): Island Press.

Power ME. 1990. Resource enhancement by indirect effects of grazers: Armored catfish, algae, and sediment. Ecology 71: 897–904.

Power ME, Tilman D, Estes JA, Menge BA, Bond WJ, Mills LS, Daily G, Castilla JC, Lubchenco J, Paine RT. 1996. Challenges in the quest for keystones. BioScience 46: 609–620.

Pringle CM, Blake GA, Covich AP, Buzby KM, Finley A. 1993. Effects of omnivorous shrimp in a montane tropical stream: Sediment removal, disturbance of sessile invertebrates and enhancement of understory algal biomass. Oecologia 93: 1–11.

Pringle CM, Hemphill N, McDowell WH, Bednarek A, March JG. 1999. Linking species and ecosystems: Different biotic assemblages cause interstream differences in organic matter. Ecology 1999: 1860–1872.

Ranvestel AW, Lips KR, Pringle CM, Whiles MR, Bixby RJ. 2004. Neotropical tadpoles influence stream benthos: Evidence for the ecological consequences of decline in amphibian populations. Freshwater Biology 49: 274–285.

Resh VH, Brown AV, Covich AP, Gurtz ME, Li HW, Minshall GW, Reice SR, Sheldon AL, Wallace JB, Wissmar RC. 1988. The role of disturbance in stream ecology. Journal of the North American Benthological Society 7: 433–455.

Stanford JA, Lorange MS, Hauer FR. 2005. The shifting habitat mosaic of river ecosystems. Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie 29: 123–136.

Statzner B, Arens MF, Champagne JY, Morel R, Herouin E. 1999. Silk-producing stream insects and gravel erosion: Significant biological effects on critical shear stress. Water Resources Research 35: 3495–3506.

Statzner B, Peltret O, Tomanova S. 2003a. Crayfish as geomorphic agents and ecosystem engineers: Effect of a biomass gradient on baseflow and flood-induced transport of gravel and sand in experimental streams. Freshwater Biology 48: 147–163.

Statzner B, Sagnes P, Champagne J-Y, Viboud S. 2003b. Contribution of benthic fish to the patch dynamics of gravel and sand transport in streams. Water Resources Research 39: 1–17.

Steen RP, Quinn TP. 1999. Egg burial depth by sockeye salmon (*Oncorhynchus nerka*): Implications for survival of embryos and natural selection on female body size. Canadian Journal of Zoology 77: 836–841.

Syvitski JPM, Vörösmarty CJ, Kettner AJ, Green P. 2005. Impact of humans on the flux of terrestrial sediment to the global coastal ocean. Science 308: 376–380.

Vannote RL, Minshall GW, Cummins KW, Sedell JR, Cushing CE. 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Sciences 37: 130–137.

Wallace JB, Webster JR, Cuffney TF. 1982. Stream detritus dynamics: Regulation by invertebrate consumers. Oecologia 53: 197–200.

Wallace JB, Cuffney TF, Webster JR, Lugthart GJ, Chung K, Goldowitz BS. 1991. Export of fine organic particles from headwater streams: Effects of season, extreme discharges, and invertebrate manipulation. Limnology and Oceanography 36: 670–682.

Willson MF, Gende SM, Bisson PA. 2004. Anadromous fishes as ecological links between ocean, fresh water, and land. Pages 284–300 in Polis GA, Power ME, Huxel GR, eds. Food Webs at the Landscape Level. Chicago: University of Chicago Press.

Winemiller KO, Jepsen DB. 2004. Migratory neotropical fishes subsidize food webs of oligotrophic blackwater rivers. Pages 115–132 in Polis GA, Power ME, Huxel GR, eds. Food Webs at the Landscape Level. Chicago: University of Chicago Press.

Wotton RS, Malmqvist B, Muotka T, Larsson K. 1998. Fecal pellets from a dense aggregation of suspension-feeders in a stream: An example of ecosystem engineering. Limnology and Oceanography 43: 719–725.

Wright JP, Jones CG. 2006. The concept of organisms as ecosystem engineers ten years on: Progress, limitations, and challenges. BioScience 56: 203–209.

Wright JP, Jones CG, Flecker AS. 2002. An ecosystem engineer, the beaver, increases species richness at the landscape scale. Oecologia 132: 96–101.

Wright JP, Gurney WSC, Jones CG. 2004. Patch dynamics in a landscape modified by ecosystem engineers. Oikos 105: 336–348.

Zanetell BA, Peckarsky BL. 1996. Stoneflies as ecological engineers—hungry predators reduce fine sediments in stream beds. Freshwater Biology 36: 569–577.