Dams and Downstream Aquatic Biodiversity: Potential Food Web Consequences of Hydrologic and Geomorphic Change

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ABSTRACT / Responses of rivers and river ecosystems to dams are complex and varied, as they depend on local sediment supplies, geomorphic constraints, climate, dam structure and operation, and key attributes of the biota. Therefore, "one-size-fits-all" prescriptions cannot substitute for local knowledge in developing prescriptions for dam structure and operation to protect local biodiversity. One general principle is self-evident: that biodiversity is best protected in rivers where physical regimes are the most natural. A sufficiently natural regime of flow variation is particularly crucial for river biota and food webs. We review our research and that of others to illustrate the ecological importance of alternating periods of low and high flow, of periodic bed scour, and of floodplain inundation and dewatering. These fluctuations regulate both the life cycles of river biota and species interactions in the food webs that sustain them. Even if the focus of biodiversity conservation efforts is on a target species rather than whole ecosystems, a food web perspective is necessary, because populations of any species depend critically on how their resources, prey, and potential predators also respond to environmental change. In regulated rivers, managers must determine how the frequency, magnitude, and timing of hydrologic events interact to constrain or support species and food webs. Simple ecological modeling, tailored to local systems, may provide a framework and some insight into explaining ecosystem response to dams and should give direction to mitigation efforts.

Some effects of dams on rivers and their biota are immediate and obvious, but others are gradual and subtle (Petts 1980, Brookes 1994). Brookes (1994) distinguished between first-order impacts that occur shortly after dam closure, and second-order impacts that arise over time due to geomorphic responses of the channel and floodplain to changes in hydrologic and sediment transport regimes. Downstream impacts of dams on river biota due to migration blockage and altered thermal, nutrient, and sediment loading regimes have been extensively documented (e.g., Ward and Stanford 1979, Lillehammer and Saltveit 1984, Petts 1984, Craig and Kemper 1987). These studies have tended to emphasize impacts on species distributions and life histories, rather than ecological interactions (but see Weisberg and Burton 1993). Here, we will focus on how altered flow regimes, such as those that occur downstream from dams, can affect predator–prey interactions in food webs. Dams have obvious hydrologic impacts when they decrease downstream flow variation, and the frequency of bed scouring flows. Channel incision is another widespread, but more gradual, and in some cases more subtle, downstream impact of dams. Its consequence, the reduction or elimination of access for biota to lateral floodplain habitats may also diminish the resilience, productivity, and biodiversity of river ecosystems.

KEY WORDS: Dams; Food webs; Hydrologic disturbance; Predator–prey dynamics; Succession

Biodiversity in Rivers and Watersheds

"Biodiversity" is a term that is widely used but not yet well defined. It refers to the variety of elements at different levels of biological organization, ranging from genetic through population, community, and ecosystem to landscape levels, that characterize natural ecosystems (Reid and Miller 1989, Noss 1990, Angermeier and Karr 1994). In rivers, for example, biodiversity is diminished if hatchery-raised salmonids are introduced into habitats where different genetic races of the same species evolved. Landscape diversity is particularly important on river floodplains (Sparks 1995), where, for example,

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differences in elevation can differentiate habitats and refuges for plant and animal species that differ in their requirements for soil moisture or water depth. Biodiversity also connotes a goal to preserve global species diversity. Therefore, biodiversity is seen to increase with the number of native species remaining in an ecosystem, but to diminish when exotic species arrive with deliberate or inadvertent human help (Angermeier 1994) because these can lead to the eventual extinction of local species. Dams, then, reduce biodiversity if they exterminate native species or threaten to push these populations towards extinction by facilitating invasions of exotic species or altering the physical habitat.

Food chain length is one indicator of biodiversity (Reid and Miller 1989, Angermeier and Karr 1994). Food webs are complicated by features such as omnivory, but often chains of energy flow and of strong interactions link certain predators through intermediate consumers to plants or other resources (Paine 1980, Power 1990, 1992a). Chain length (the number of trophic levels in a chain) can be counted by descriptive bottom-up criteria, based on the number of energy transfers inferred from diet analyses (e.g., Cohen 1978) or isotopic fractionation (e.g., Kling and others 1992, Cabana and Rasmussen 1995). Alternatively, the length of functionally significant food chains can be counted by top-down criteria as the number of guilds or populations that are alternately released and suppressed following removal of a top predator. In general, counts of functional trophic levels in food chains, which require potential population regulation (Fretwell 1977, Oksanen and others 1981, Power 1992a), will differ in length from descriptive counts based on energy transfers. For example, juvenile steelhead and large roach (cyprinids) in the Eel River of northern California occurred at the fourth trophic level in functional food chains where experimental manipulations showed that they suppressed small predators, releasing an algivorous midge that was invulnerable to the larger fish, which in turn grazed down algae (Power 1990). Descriptive diet analyses would have placed these larger fish at the third trophic level, however, as algivorous mayflies were the predominant prey found in their guts (Power and others 1992).

Longer functional food chains often occur in more pristine (and desirable) river communities. We will introduce this view with an extreme but not unrealistic example. In arid watersheds in the southwestern United States, water abstraction and overgrazing have virtually eliminated aquatic and riparian vegetation. Nitrogen oxides from polluted air rain down on, but are not taken up by, plants. Instead, they make their way into the groundwater. Near Phoenix, Arizona, these circumstances have led to water wells being shut down because they have accumulated toxic levels of nitrates. According to stream ecologists Stuart Fisher and Nancy Grimm from Arizona State University, residents in the region are literally drinking their own automobile exhaust (personal communication and Koppes 1990). This scenario depicts a river–watershed ecosystem with zero functionally significant trophic levels, i.e., no plants capable of regulating their nitrogen resources. Add plants (one trophic level), and the wells may stay open, but eutrophication problems arise if macrophyte or algal accrual is considered excessive. Add grazers (two trophic levels), and plants may be regulated, but pestiferous outbreaks of insects may occur. Add predatory invertebrates and small fish (three trophic levels) and the situation improves; if these feed larger fish, birds, and wildlife, human anglers, sportsmen, hikers, and naturalists are generally happier. In general, the quality of natural environments for humans increases as food chains lengthen. Values inherent in the notion of biodiversity often correlate positively with the length of functional food chains, unless longer food chains result from the introduction of exotic predators (such as bullfrogs in western US rivers, or Nile perch in Lake Victoria).

Much remains to be learned about how functional food chain length responds to changes in the physical environment. There is presently no secure general theory for predicting the length of descriptive or functional food chains in natural ecosystems. The two most studied hypotheses predict that (1) food chains should lengthen with environmental productivity or the metabolic efficiency of consumers (Elton 1927, Slobodkin 1961), and (2) food chains should shorten with environmental disturbance (Pimm 1982, Pimm and Lawton 1977). While these two hypotheses have been considered as alternatives, it is obvious that disturbance and productivity regimes might interact to influence food chain length.

Effects of Flow Variation on Food Chain Length

Surveys and experiments during drought and flood years in northern California rivers suggest that the lengths of functionally important food chains in rivers generally increase with natural regimes of flow variation. These regimes include bed-scouring floods that qualify as ecological disturbances, because they impose huge mortality on substrate-bound biota. Mechanisms for this result, which does not support the theoretical prediction that disturbance should shorten food chains, involve familiar life history trade-offs between resilience following physical disturbance and resistance to predators for early versus late successional species at lower trophic levels (see Scouring Flows and Succession, below). Flow variation also gives riverine predators periodic access to their prey, while preventing them from overharvesting. In small or incised rivers, prey may enjoy respite from predation during periods of low flow, when shallow in-channel habitats block access for larger predators (see Flow Variation and Predator–Prey Interactions, below). The converse may apply in larger floodplain rivers, where predation may be most intense during low flow periods when predators and prey are concentrated together in channels and permanent off-river waterbodies (Lowe-McConnell 1964). In these systems, prey (including young life stages of cannibalistic predators) may require periodic access to inundated floodplains during high flow periods to rebuild their populations (see Inundation and Dewatering of River Floodplains, below). We will briefly review several case studies from our research and that of others to illustrate these interactions of flow variation with food chain length.

Flow Variation and Predator–Prey Interactions

Brier Creek, in south central Oklahoma, is a small incised stream. During low-flow periods, pools are well isolated from each other by long shallow riffles. Some pools are filled with filamentous green algae (predominantly *Rhizoclonium*), while others are barren. Green pools contain bass (*Micropterus salmoides* and *M. punctatus*); barren pools lack bass and contain schools of the grazing minnow, *Campostoma anomalum,* which are absent in bass pools. Redistribution of bass and *Campostoma* among pools, by floods or experimentalists, can change green bass pools to barren *Campostoma* pools (from three to two trophic levels) within weeks. Dynamics in the opposite direction are equally rapid (Power and others 1985). When bass are added to *Campostoma* pools, some minnows are eaten, but others (in some trials, up to half of the original population) emigrate to avoid bass. Minnows cross shallow riffles to swim to bass-free pools (Power and others 1985). At low flow, bass are too deep-bodied to follow them. If flows were chronically low, bass trapped in pools without minnows would starve. If flows in Brier Creek were chronically high enough so that riffles were corridors rather than barriers for bass, bass might overeat their minnow prey throughout the entire stream and then starve. Methods that only evaluated habitat availability for particular taxa [e.g., instream flow incremental methodology (IFIM) models (Orth and Maugham 1982, 1986)] would not predict or explain population declines for bass or minnows if these arose due to the lack of the variable flow regimes required to sustain the predator–prey dynamics.

Inundation and Dewatering of River Floodplains

In larger, lowland rivers, floodplain habitats are extremely important as feeding areas, nurseries, and overwintering habitats for riverine fishes and other biota (Welcomme 1985, Bayley 1995, Sparks 1995, Junk and others 1989). Reduced access to floodplains can greatly diminish the productivity and, in some cases, the viability of these populations (Sparks and others 1990).

River floodplains are spatially, hydrologically, and biologically complex and dynamic (Junk and others 1989, Welcomme 1985). Ecologists have long recognized that spatial heterogeneity and temporal fluctuation can play strong roles in maintaining the richness and complexity of ecological communities. In heterogeneous, fluctuating environments, consumers are less likely to overeat and exterminate their prey (Hastings 1977, Huffaker 1958). Competitors that dominate under particular conditions are likely to lose their performance advantage before they can exclude lesser competitors (Connell 1978, Hutchinson 1961, Tilman 1994). Therefore, the hydrologic fluctuations that impose huge stranding mortality on river biota (Bonnetto, cited in Welcomme 1985) may, paradoxically, enhance the persistence of ecological communities by reducing the chances that their constituent populations will go extinct (Sparks 1992, Welcomme 1985). These views are supported by our preliminary simulation studies of simplified floodplain river food chains. In hydraulic food chain models, river food chains could sustain top predators only when the river biota had periodic access to floodplains. When flow diversions or levees prevented spillover, only two, or in some simulations one, trophic level(s) persisted (Power and others 1995a).

Hydraulic food chains constitute a modeling approach that links the relatively well understood responses of river width, depth, and velocity to changes in discharge to the poorly understood responses of river biota to these hydraulic parameters (Power and others 1995a,b). The food webs are modeled as modified Lotka-Volterra equations for food chains with three or four trophic levels and two energy sources, detritus and vegetation. Strengths of interaction between or among trophic levels are modulated by hydrologic changes in two ways. First, mobile or drifting components of the food web are concentrated within the channel during low flow and diluted over floodplains when these are inundated after spillover. Second, certain biological parameters (e.g., growth, feeding, or mortality rates) in the coupled biomass balance equations are written as explicit functions of hydraulic variables (flow width, depth, velocity, or interactions of these terms). These hydraulic food chain models are not intended as predictive tools, but as conceptual frameworks to guide field observations and measurements when tailored to specific ecosystems.

Scouring Flows and Succession

As mentioned above, our surveys and experiments suggest that, in contrast to the theoretical prediction that disturbance should lead to shorter food chains, bed scouring floods can lengthen functionally important food chains in northern California rivers. In California's Mediterranean climate regime, rivers normally experience flooding during winter months and a period of low flow during summer. After scouring floods, primary consumer (grazer) guilds in northern California rivers are initially dominated by mobile, unarmored (e.g., mayfly nymphs) or lightly armored invertebrate taxa. Over time, these early successional taxa, which are vulnerable to predators, are replaced by more heavily armored or sessile forms that are less vulnerable. Allocations to defense (armor, silk for retreats, and/or a sessile life-style) rather than to protoplasm and offspring slow the somatic and population growth as a population rebounds from flood scour, but such traits confer immunity from predators in our system. Consequently, defended late successional taxa come to dominate grazer guilds when flood-free periods last more than one year: during prolonged drought or in channels with artificially regulated flow (Power 1992b, 1995, Power and others 1995c). Selective predation is sufficient to explain these changes, but there is also evidence that sessile (late successional) grazers may outcompete mobile (early successional) taxa (e.g., McAuliffe 1984). Comparisons of these successional trends in a sunny river with higher primary productivity and a darker tributary with lower primary productivity suggest that late-successional, predator resistant taxa may dominate lower trophic levels sooner after disturbance in more productive habitats. An explanation is that these resistant taxa can recover from disturbance and take over space and algal resources more quickly following disturbances if local rates of food renewal are high.

Succession from more to less edible species following floods can also occur at the first trophic level among primary producers. In Brier Creek, Oklahoma, epilithic diatoms, followed by the green alga *Rhizoclonium*, dominated stream substrates after a flood. Within 26 days, however, *Rhizoclonium* was replaced by the green alga *Spirogyra* at many sites (Power and Stewart 1987). Diatoms are among the most edible and nutritious of algae for stream grazers (e.g., Kupferberg and others 1994). Epilithic diatoms were overgrown by *Rhizoclonium*, but this rough-skinned macro-alga supports high densities of epiphytic diatoms. When epiphytized, *Rhizoclonium* is greatly preferred by grazers to *Spirogyra*, which has a mucousy surface to which diatoms cannot adhere. *Spirogyra*'s ability to slough epiphytes and to grow as floating masses that can shade the rock-bound *Rhizoclonium* allow this less palatable alga to become increasingly dominant during later stages of succession following flood scour (Power and Stewart 1987).

These successional changes in primary producers in Brier Creek and in primary consumers in northern California rivers both imply that energy transfer from lower to higher trophic levels (e.g., fish) may attenuate in the absence of annual flood scour, a prediction we are currently investigating in regulated and unregulated northern California streams. Periodic rejuvenation of the food web supporting fish and other higher trophic levels is one of several reasons to maintain an adequate frequency of bed scouring flows. Another well-documented ecosystem service of flushing flows is the cleansing and resupply of spawning gravels for salmonids (e.g., Mundie 1979, Kondolf and others 1991, 1993, Ligon and others 1995, Milhouse in preparation). In addition, in western US rivers, flushing flows often suppress invading alien riverine species. Many alien animal species that threaten native species in western US rivers today are introductions from more lentic aquatic habitats [e.g., bullfrogs (Hayes and Jennings 1986), large-mouth bass and other piscivorous centrarchids (Moyle 1976, Moyle and others 1986); and mosquitofish (*Gambusia affinis*) (Meffe 1984, Meffe and Minckley 1987)]. These taxa tend to move upstream into steeper parts of watersheds during periods of low flow but are displaced downstream to a much greater degree than are natives during floods (Meffe 1984, Kupferberg 1996, Power and Roberts, unpublished data). In addition, alien plants, such as tamarisk, an aggressive spreader with high rates of evapotranspiration that can severely lower water tables, are also commonly more vulnerable to flood scour than is native vegetation (Stromberg 1993, Stromberg and others 1993, personal observations). Periodic flushing may generally enhance biodiversity by differentially clearing channels of encroaching plant or animal alien species. In some cases, flushing flows also serve to clear native vegetation as well, which, in the prolonged absence of scouring flows, can encroach to an extent that diminishes local biodiversity.

Vegetation Encroachment into Channels

Although riparian and aquatic plants are crucial to the structure and function of ecological communities in streams, reduced flows can allow vegetation to encroach into river channels to an extent that leads to practical problems, such as reduced flood conveyance (Wade 1994), and to ecological concerns. On the Trinity River of northern California, vegetation encroachment downstream from a dam has greatly reduced the cobble bar habitat that yellow-legged frogs (*Rana boylii*) require for oviposition (Lind and others 1996). Another dramatic example comes from the work of South African scientists. The Sabie-Sand River is one of six formerly perennial rivers draining from the west into Kruger National Park (Davies and others 1994). The pools of this bedrock-bedded river are required as habitat for hippopotomi and crocodiles, as well as for surface water used by elephants, giraffes, and other terrestrial megafauna. Upstream from Kruger Park, water abstraction for silviculture (of exotic eucalyptus and pines), commercial agriculture, and drinking water supplies to rural settlements in the former homelands caused the Sabie to stop flowing for the first time in 1989 and again in 1992 (Davies and others 1994). Carter and Rogers (1989) document a worrisome transition in the Sabie within Kruger National Park, from bedrock water pools to sand to reed beds to woody riparian vegetation. This successional sequence involves a positive feedback that makes it difficult to reverse. Reeds (*Phragmites mauritianus*) establish extensive beds when sediments are deposited by low flows. Established reeds trap more sediment and evapotranspire off more water, creating conditions that further enhance their spread until the surface water is gone. Flow releases from two proposed dams that will be built on the Sabie must be extremely carefully planned if they are not to cause serious further degradation to what Davies and others (1994) have called "this major lifeline to the premier wildlife conservation area in South Africa."

Management Considerations and Research Priorities

If dams are to be redesigned and managed to better protect biodiversity, we need to implement our existing understanding and develop better understanding in three areas. Listed in increasing order of their complexity and our uncertainty, these are the geomorphic, ecological, and socioeconomic factors that respond to and constrain dam and river management.

Geomorphic Considerations

As Ligon and others (1995) stated, if the physical foundation of a river's ecosystem is pulled out from under the biota, even the most insightful biological research and management program will fail to preserve biodiversity. Given the limited time, money, and knowledge available for mitigating dam effects of biodiversity, they recommend emphasis on maintaining the dynamic physical regimes that, over the long term, maintain the habitat's essential predam geomorphology. We understand in general how the frequency and magnitude of channel discharge and sediment transport events determine channel and floodplain morphology (e.g., Wolman and Miller 1960, Leopold and others 1964). Challenges remain, however. While dominant discharge concepts in geomorphology recommend the maintenance of predam bankfull flow levels, rarer events may be crucial to generating habitat diversity [e.g., topographic variation on floodplains (Sparks 1995)] essential to the biota. Rare superfloods, for example, may be needed to clear reedbeds from pools of the Sabie River, but geomorphologists may not be able to predict the required frequency and magnitude, because we know too little about flow-through vegetation. In general, site-specific research will be necessary because local geomorphic responses of rivers to dams are varied and complex and depend on sediment supply, local geomorphic constraints, and dam structure and operation. Riverbeds may incise or aggrade, affecting floodplain inundation; bed sediments may coarsen or fine (Williams and Wolman 1984); channel patterns may change (e.g., from braided to single thread) (Stanford and Ward 1993, Ligon and others 1995).

While some physical changes caused by dams are immediate and obvious, others are so gradual that they may go unrecognized by humans using the river for many years and by biological teams focused on local habitat assessment. This may be the case with gradual channel incision downstream from dams (Ligon and others 1995). Causes of downstream incision are well understood. Large dams can trap virtually all of the incoming sediment (Williams and Wolman 1984). Channels downstream are cut off from replenishing supplies of sediment and, as a consequence, commonly degrade (Leopold and others 1964). Channel degradation or incision may persist for tens to hundreds of kilometers downstream from high dams (Williams and Wolman 1984). What may be more difficult to recognize, particularly where incision is subtle and historical topographic surveys are lacking, is that even slight incision of channels may have strong ecological effects. Channel incision will lower water tables around the river, with consequences for riparian vegetation that feed back to affect river communities (e.g., Stromberg 1993, Murphy and Koski 1989). In addition, channel incision will reduce the number and duration of overbank flows, reducing access to floodplains for river biota. Dam-protected human developments on floodplains can make this loss for biodiversity seemingly permanent, but repeated flooding during 1993 and afterwards is causing humans to rethink their land-use practices along rivers like the Mississippi and the Russian River of

California. Floodplain restoration for biodiversity is a particularly promising area for future research in ecological engineering (Sparks 1995, Bain and Boltz 1989).

Channel incision effects could be reduced or possibly prevented by dams designed to periodically pass stored sediments. This feature would have also great practical importance, as it would maintain the upstream water-storage capacity of reservoirs. Engineering research is needed here, as regular passage of sediment is presently feasible only for relatively small reservoirs (Ligon and others 1995). Alternatively, perhaps this consideration should constrain the size of future dams that are built.

Ecological Considerations

Previously, ecological impacts of regulated flow regimes have been largely assessed by evaluating their effect on the availability of habitat units within certain ranges of physical parameters (e.g., depth, velocity). These methods, of which the instream flow incremental method (IFIM) is the best known, point out the linkage between flow regulation, physical habitat availability, and fish (Orth and Maughan 1982, 1986) or invertebrates (Gore and others 1989). While these methods provide information of value linking land use to habitat dynamics of focal species, they are not sufficient because they ignore vital ecological linkages, such as those among focal species and their food or predators (e.g., Mathur and others 1985). Even if the focus of biodiversity conservation efforts is on a target species rather than whole ecosystems, a food web perspective is necessary, because the population dynamics of any species depend critically on how their resources, prey, and potential predators also respond to environmental change (e.g., Weisberg and Burton 1993). In addition, these methods are too "close-focus," time-consuming, and costly to apply when practical problems require a larger-scale, more holistic overview (King and Tharme 1993, cited in Davies and others 1994).

To conserve native species, we must understand how flow regimes influence the key interactions in the food webs supporting them. Our hydraulic food chain models (Power and others 1995a,b) are examples of such approaches, although our efforts are still quite preliminary. Such approaches should be more macroscopic than IFIM assessments. To apply such methods, we would first determine the large-scale geomorphic features of a river system that affect how water and sediment are routed through it (average downstream slope, whether the bed is alluvial or bedrock, pool frequency and volume, bankfull depths, positions of major tributaries, etc.). Next, we would construct an interaction web representing our best guess at the crucial ecological processes that regulate abundances of focal species. These species may be singled out for attention because they are strong interactors in food webs (Paine 1980), because they are threatened or endangered, or because they have commercial or cultural value (e.g., Ligon and others 1995). We would attempt to determine and model those life history stages that are bottlenecks for these species. Expert systems models that interrogate people with knowledge of local ecology may be useful at this stage (O'Keefe and Davies 1991, Starfield and others 1989). When interaction webs have been drawn up, they should be trimmed to be as parsimonious as possible (representing only interactions hypothesized to be crucial). At this stage, we would consider how channel hydraulics and hydrology, under various flow regimes, would influence the key species interactions represented. In our hydraulic food chain approach (as described above), these influences are mediated both by the dilution and concentration of biota as river stage rises and falls and by the effects of discharge-related parameters (flow velocity, depth, width, or derived variables such as turbidity) on the rates of ecological processes (birth, growth, mortality, feeding, movements, etc.). The model at this stage should motivate focused field work to calibrate relationships that appear poorly defined but important. Once partially calibrated, the model may (tentatively) suggest how to manage flow regimes to preserve the ecological functions needed to sustain species and food webs. An adaptive management approach (Walters 1986) should be adopted that treats the model predictions and recommendations as hypotheses. The actual behavior of the system under specified managed flow regimes should be closely monitored, and data and insights from this monitoring program should feed back to improve the model that motivates the management. This iteration should be prolonged.

Models that address the ecological effects of flow and sediment transport must consider the timing of major events as well as their frequency and magnitude. The required regimes may involve periodically deepening riffles between pools so predators have access (but not continual access) to prey (e.g., Brier Creek); periodically inundating floodplains long enough so that prey populations and young life history stages have sufficient time to grow in numbers or body size before they lose these refuges from predators after reconfinement of floodplain rivers, and periodically stirring the beds of gravel-bedded rivers so that early successional prey taxa can rejuvenate food chains, facilitating the flow of energy to higher trophic levels (e.g., northern California rivers). In many situations, there will be magnitude–frequency trade-offs for managers to consider. For example, the longer the interval between flows that scour out vegetation encroaching downstream from dams, the larger will be the magnitude of the discharge required to uproot larger, denser, better established vegetation.

Above, we have stressed the importance of providing some minimum frequency of flow variation in regulated rivers, but commonly flow variation is too frequent for the biology. Effects on invertebrates and fish of hydroelectric power-peaking regimes that fluctuate with artificially high frequencies have been reviewed by Gore (1994). If flood pulses can be delivered with more natural frequencies, the timing of flow releases can be managed to benefit, rather than harm, biodiversity. Potamodromous fish in the Zambezi River were able to spawn downstream from Kariba dam, provided that peak flows were discharged during the correct season (Kenmuir 1976, cited in Davies 1979). Managers can also time flow releases to favor native species and disfavor alien invaders. For example, in western US rivers, scouring flows should not be released when vulnerable life history stages of salmonids or native frogs (eggs, larvae) are present (Lind and others 1996). In some cases, however, spring or summer pulses might be useful as a management strategy, e.g., to flush out alien bullfrog eggs or to discourage invasive alien vegetation. Determining what range of flow conditions is acceptable for life stages and species of special concern and how capable species are of tracking these conditions within watersheds should also be priority for research. Kupferberg's (1996) study of how the geomorphic characteristics of oviposition sites of foothills yellow-legged frogs (*Rana boylii*) affect the survivorship of their egg masses during spring runoff exemplifies the type of study needed to understand how physical regimes in natural and altered rivers will affect species population dynamics. Simple modeling approaches, like our hydraulic food chain models, can organize our thinking about the relevant time scales for these processes and interactions and suggest which areas of uncertainty (about interactions, relationships or parameter values) would be most useful to further investigate.

Socioeconomic Considerations

Although there are practical benefits for some of the management goals outlined above, in general they will not be cheap to implement. As the electric power industry experiences deregulation, pressures increase to produce energy as cheaply as possible. Deregulation, however, may also give local utilities increased access to a growing national market marked by "green consumerism." If environmental scientists and dam managers can comprehend and clarify how managed and natural flow regimes affect river ecosystems in a sufficiently timely fashion, utilities will be in a position to inform their customers and stockholders when specific decisions arise that require trade-offs between production efficiency and environmental protection. If such choices are made clear and explicit, utilities may discover, and help to expand, a viable national market that can support energy produced in an environmentally sound manner.

Vaclav Havel, in his 1990 New Year's address to the Czech people as their newly elected president, commented that they had inherited "... the most contaminated environment in Europe," in part because "The previous regime—armed with its arrogant and intolerant ideology—reduced man to a force of production, and nature to a tool of production" (Havel 1995). He was speaking, of course, of the previous communist totalitarian regime that ruled Czechoslovakia. It remains to be seen whether a democracy, with an economy that currently is increasingly structured by free market forces, will, in the long run, do better.

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