Homogenous rivers, homogenous faunas

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Habitat change and invasions of alien species are usually listed as the two biggest causes of biodiversity loss. When the two coincide, the results can be devastating, because altered habitat often favors alien species adapted to the changed conditions. This is particularly true in streams and rivers of North America, where homogenization of fish faunas through extinction of native species and invasions of alien species have been widely recorded (1). Although dams that alter flow regimes have been implicated as a causal factor behind this shift in North America, the degree to which flow regimes have been altered is not widely appreciated. The study by Poff *et al.* (2) in this issue of PNAS should help to change this problem. They document that flow alteration by dams in the U.S. is pervasive and that the resulting flow regimes tend to converge on one another, regardless of the original flow regimes of the dammed rivers.

Dams homogenize flows mainly by reducing peak flows and increasing minimum flows, creating more uniform flow conditions. They also change the timing and duration of high and low flows. The exact changes to the flow regime vary from region to region but result in rivers with similar flow regimes and reduced variability in flows. From an aquatic organism's perspective, reduced variability in flows is particularly important, because this results in reduced channel complexity, often with stable channels that have reduced capacity to carry high flows and that are incised at low flows. Less complex channels translate into a lowered diversity of structural features preferred by fish and other aquatic organisms (3). This loss of structure, in turn, results in fewer fish of fewer species. Ironically, these relationships do not change with large hydropower dams that have frequent peaking flows, even though they increase flow variability, because the time scales (often daily) are much shorter than found naturally, whereas other aspects of the flow regime remain similar.

Flow regulation is typically coupled with land-use changes that take advantage of the reductions in flow variability, further homogenizing aquatic habitat. The most prominent of these changes is the construction of close levees, which disconnect the river from its floodplains and reduce or eliminate riparian succession and channel migration. Such restrictions on rivers, of course, are generally perceived as desirable, which is why they are nearly universal.

Likewise, the fishes that invade such regulated rivers are often desirable game and food fishes, such as centrarchid basses (*Micropterus*), catfishes (Ictaluridae), and common carp (*Cyprinus carpio*). In the cold "tail waters" below dams, productive fisheries for various trout (Salmonidae) species develop, usually sustained by fish hatcheries, because flow regulation degrades natural spawning habitat. Thus, homogenized rivers and fish faunas are often regarded as beneficial not only in the U.S. but also in other countries. For example, rivers below dams in the Iberian Peninsula support many of the same North American species (and common carp) found in the homogenized rivers of the U.S. and a reduced diversity of native species (4). This suggests that homogenization of fish faunas in regulated rivers is a worldwide phenomenon and a deliberate policy.

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Most of the large dams that homogenize flows were built in the past 50–60 years with great enthusiasm for their positive economic effects and little appreciation for their negative economic and ecological impacts. Today, the most obvious indication of ecological impact is the loss of native fishes below dams, such as most of the native fish fauna of the Colorado River (5) and species such as the infamous snail darter (*Percina tanasi*) of the Tennessee River. Native invertebrate species, such as unionid clams, also suffer losses in homogenized streams (6). Listing of such species as threatened or endangered under the federal Endangered Species Act of 1973 can result in flow regimes being reregulated to benefit such fishes and their habitats, with mixed results (7).

Minimizing Impacts

What can be done to minimize the impacts of homogenized flow regimes, given the economic importance of dams and reservoirs? Trush *et al.* (8) indicate that if nine key attributes of an alluvial river are maintained, rivers below dams can be managed for ecological integrity without major economic sacrifices. The study of Poff *et al.* (2) indicates that this may be unrealistic, given the high degree of change already in place. We suggest that the following measures are some of the key alternatives for recreating alluvial rivers below dams: dam removal, alteration of flow regimes, protection of tributaries below dams, recreation of floodplains, and active management of channels as habitat. Often these measures must be used in conjunction with one another for successful reestablishment of native biota.

Dam removal is the most drastic of these options but is increasingly being considered, even for large dams and especially for dams that have lost their economic viability or that are unsafe (9). Dam removal, however, is not just a simple matter of taking out a structure but must consider the downstream effects, for example, of sediment stored behind the dam, changes in water quality (loss of cold water flows from reservoir stratification), and impact of returning high flows to an altered, often miniaturized, channel. Increasingly, it is recognized that dams are rarely isolated from other dams; multiple removals may be needed. For example, an optimal scheme for restoring salmon to Willamette River in Oregon would require the removal of 12 hydropower dams (10).

Alteration of flow regimes is one of the most widely used options because of the perception, often wrong, that large benefits can be achieved at low cost. As a consequence, methodologies have developed worldwide to determine how much water should be left in rivers to maintain ecological function (11). Increasingly, these methodologies focus on restoring a flow regime that mimics in some respects the

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historic flow regime, but that requires much less water. This concept of the natural flow regime (12) is achieving wide acceptance as a useful model for bringing back native organisms adapted to local flows. For example, its application to Putah Creek in California has resulted in a return to the dominance of the native fish faunas to a long reach below a dam (13). In this situation, $\approx$5% of the available water has been used to establish permanent year-round flows and spring spawning flows, with occasional natural spills from the dam relied on for factors requiring high-flow events. In some reaches, active management of the stream channel is also required. In contrast, in the lower Colorado River, attempts to recreate habitats from high-flow events through releases from a major dam have largely failed, and alien fishes continue to dominate the river (5).

The importance of tributaries and their confluences has only recently been recognized as an important organizing phenomenon for the ecology of large rivers (14). In regulated rivers, their potential importance has largely been ignored in favor of the serial discontinuity concept, which states that river ecosystems progressively "reset" themselves as a function of distance below a major dam (15). In reality, tributaries, large and small, can provide a significant input of water, sediment, and other materials to regulated rivers, and their confluences can create complex habitats favored by fishes. In heavily regulated rivers, tributary processes dominate hydrologic and geomorphic conditions. For example, the Yampa River is a large unregulated tributary to the Green River in Utah, which is regulated by Flaming Gorge Dam. Once the Yampa enters the Green, the Green becomes a more complex and variable system, with more native fishes present (16). Protection of tributaries that enter rivers below dams may be one way to counter some of adverse impacts of dams.

A common consequence of flow regulation is the disconnection of floodplains from river channels through a combination of incision, levee construction, and lack of sufficient flood pulses for frequent floodplain inundation. For many species, regular connection to the floodplain at the appropriate time of year is essential for persistence (17). Even partial reconnection of a river to its floodplain through increased flows and levee setbacks can favor native fishes and other organisms. An artificial floodplain along the Sacramento River in California is an important spawning area for the endemic Sacramento splittail (*Pogonichthys macrolepidotus*) and rearing area for juvenile Chinook salmon (*Oncorhynchus tshawytscha*) (18).

Finally, active management of channels of regulated rivers may be necessary to favor desirable organisms, even when a fluctuating flow regime is provided through reservoir reoperation. The trap efficiency of all but a handful of dams significantly reduces recruitment of structural materials such as gravel and large woody debris. Additionally, operational constraints typically limit the size of peak flow releases to levels insufficient to maintain channel function. Active management may involve everything from restructuring a channel with heavy machinery, to adding spawning gravel, to adding large logs and boulders as structure, to removing channel-restricting vegetation (19). Such activity requires a continuous investment of time and money and should be regarded as one of the costs of dam management.

Holistic Management Needed

Unfortunately, even intensive management of a regulated river often cannot prevent invasions by alien species. In fact, in our experience, alien fishes are generally present in low numbers even in "restored" streams with natural flow regimes. The numbers of aliens can quickly increase under favorable conditions, such as prolonged low flows created by drought. Thus, although Poff *et al.* (2) have demonstrated that river regulation is pervasive and results in an increasing homogenization of aquatic faunas, bringing back desirable aquatic communities requires more than just reregulating streams. It requires continuous adaptive management of the waterway and vigilance to prevent new problems from developing, especially the invasion of additional alien species. Increasingly, holistic management of rivers is being demanded, especially for those that are still undammed (20).

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