CHAPTER

3

Understanding the Nexus Between Hydrological Alteration And Biological Invasions

Albert Ruhi*, Jane A. Catford†, Wyatt F. Cross‡,
Daniel Escoriza§, Julian D. Olden¶

*University of California, Berkeley, CA, United States †University of Southampton, Southampton, United Kingdom ‡Montana State University, Bozeman, MT, United States §Institute of Aquatic Ecology, University of Girona, Girona, Spain ¶University of Washington, Seattle, WA, United States

3.1 ALTERED FLOW REGIMES AND BIOLOGICAL INVASIONS: TWO FACETS OF GLOBAL CHANGE IN RIVER ECOSYSTEMS

Throughout history, humans have altered the hydrology or flow regimes of rivers and streams to meet societal needs for transportation, water supply, flood control, irrigation, and hydropower (Ripl, 2003). More than half of the large river systems worldwide are impounded (Nilsson et al., 2005), and a surge of new dams in the developing world threatens some of the world's most biodiverse river systems (Ziv et al., 2012; Zarfl et al., 2015; Winemiller et al., 2016). Dams are a major driver of flow and thermal regime alteration (Carlisle et al., 2010; Olden and Naiman, 2010). This alteration manifests via dampened natural seasonality, but also via artificial signals (e.g., hydropeaking) at management-relevant temporal scales (Bunn and Arthington, 2002; Kennedy et al., 2016).

In addition to changes resulting from dams, increasing hydroclimatic extremes (e.g., supraseasonal droughts) are affecting river ecosystems across large regions (Kirtman et al., 2013; Ruhi et al., 2016). Enhanced evapotranspiration and rainfall variability may shift many rivers from perennial to intermittent flow regimes (Jaeger et al., 2014), and change mean

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annual runoff as well as low and high flows (Döll et al., 2009. The natural flow regime (i.e., the "characteristic pattern of flow quantity, timing, and variability") determines physical habitat availability, longitudinal and lateral ecosystem connectivity, organismal composition, and structure and dynamics in riverine and floodplain wetland ecosystems (Poff et al., 1997; Bunn and Arthington, 2002; Chapter 4). Accordingly, anthropogenically altered flow regimes can affect biodiversity profoundly, across taxonomic groups and levels of biological organization.

Invasion by a nonnative species (understood as a taxa not indigenous to a region) is another prevalent facet of global change in freshwater ecosystems—and, like flow regime alteration, one that poses a major threat to native biota (Sala et al., 2000; Dudgeon et al., 2006). Human activities have increased the rates of intentional and accidental introductions of non-native species in freshwater ecosystems (Kolar and Lodge, 2001), resulting in impacts across multiple taxonomic groups and communities via the establishment of cosmopolitan nonnative species and extirpations of native or endemic ones (Rahel, 2002; Gallardo et al., 2016). Because altered flow regimes may decrease the persistence of native species adapted to historical conditions, while creating opportunities for nonnative species to establish and spread (Bunn and Arthington, 2002; Johnson et al., 2008; Catford et al., 2009), flow regime alteration and invasion are stressors that often co-occur and possibly interact. In this chapter, we will review both the evidence and mechanisms responsible for this alteration-invasion nexus; discuss the ecological consequences at the population, community, and food web levels; and explore scientific challenges and management opportunities in the future.

3.2 THE ALTERATION-INVASION NEXUS

Understanding how altered flow regimes and biological invasions co-occur and potentially interact requires knowledge of the mechanisms that link hydrologic alteration to native biodiversity persistence, as well as the mechanisms that regulate invasions in aquatic ecosystems. Three broad principles explain the dependence of native biodiversity on natural flow regimes (Poff et al., 1997; Bunn and Arthington, 2002). First, scouring floods control channel form, habitat complexity, and patch disturbance, which in turn influence biotic diversity and determine ecological integrity (Naiman et al., 2008; Chapter 4). Second, flow spates trigger dispersal and access of riverine organisms to floodplain habitats, connecting ecosystems via organic matter subsidies and migrating organisms (Junk et al., 1989). Third, "natural" disturbance regimes (i.e., the characteristic magnitude, duration, frequency, and timing of high and low flows) are often coupled with a critical organismal life history with events such as spawning, recruitment, and seed dispersal (Lytle and Poff, 2004; Greet et al., 2012). Thus the maintenance of the characteristic features of a natural flow regime maximizes the persistence of biota with adaptive morphological, behavioral, and life-history traits (Bunn and Arthington, 2002; Lytle and Poff, 2004). These three principles help explain why some nonnative organisms are so successful at colonizing, establishing, and spreading in rivers with modified flow regimes. This tenet, in turn, forms the basis of the *environmental resistance* hypothesis of invasion, which posits that the environmental conditions often constitute a fundamental barrier to the establishment and naturalization of nonnative species in a new range (Moyle and Light, 1996; Catford et al., 2009) (Fig. 3.1; Chapter 5).

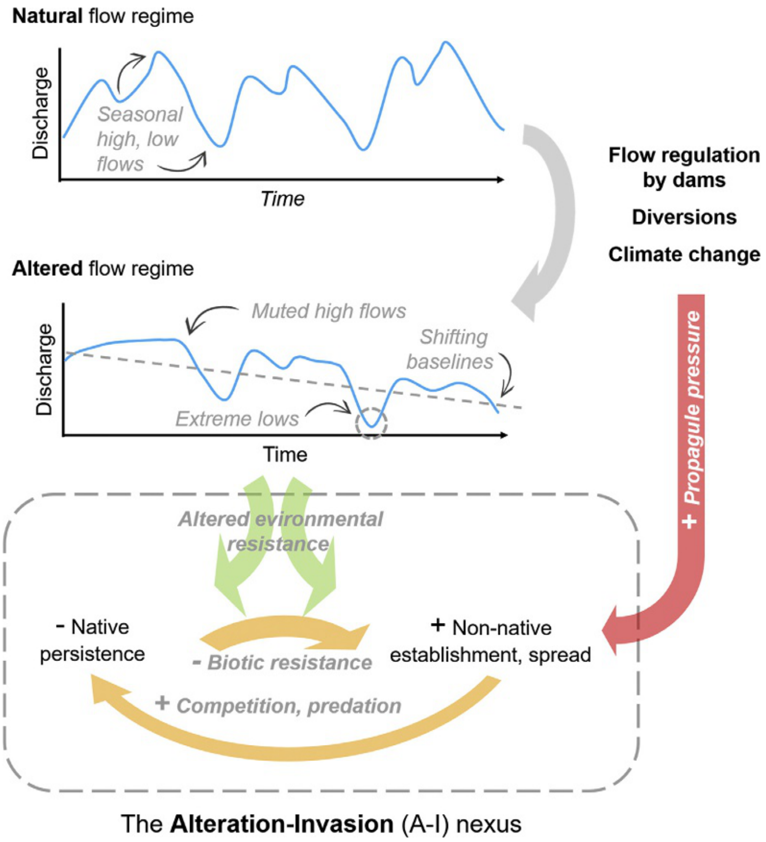

FIG. 3.1 Conceptual diagram showing common features of flow regime alteration driven by dam regulation, diversions, and climate change. Three mechanisms of the alteration-invasion nexus are shown: in green, the environmental resistance mechanism; in orange, the biotic mechanism; in red, the propagule pressure mechanism (see text for more details).

There are a number of additional ways in which flow regime alteration may interact with the species invasion process (Fig. 3.1). First, the *propagule pressure* hypothesis states that the number of introduced individuals and introduction events, along with the spatiotemporal extent of propagule arrival, are key factors limiting invasion success (Simberloff, 2009). Dams promote the deliberate introduction or stocking of nonnative species to establish and maintain recreational fishing opportunities both downstream of dams and in upstream reservoir habitats (Johnson et al., 2008). This represents an important dimension of the alteration-invasion nexus (Table 3.1). Second the direct negative effects of altered flows on native biodiversity imply that nonnative species often naturalize within depauperate communities. According to the biotic resistance hypothesis, diverse and functionally redundant communities tend to repel invaders, slowing down their establishment and spread (Kennedy et al., 2002; Fridley et al., 2007; Escoriza and Ruhí, 2016). Therefore native extirpations may release

TABLE 3.1 Examples of Additive and Synergistic Alteration-Invasion Nexus Across Taxonomic Groups and Climatic Regions

Region	Native Component	Nonnative Component	Alteration	Nexus	References
Mediterranean	Fishes	Fishes	Flow regulation, supraseasonal drought	Mainly additive	Bernardo et al. (2003), Clavero et al. (2004)
S. Africa	Aquatic insects, amphibians, fishes	Water hyacinth, water fern	Flow regulation	Synergistic	Nilsson and Berggren (2000), Gratwicke and Marshall (2001)
SE Australia	Wetland specialist plants	Terrestrial plants	Flow regulation	Additive	Kingsford (2000), Catford et al. (2011, 2014)
American SW	Cottonwood, willow	Salt cedar	Flow regulation	Additive	Nagler et al. (2005), Stromberg et al. (2007a,b)
American SW	Fishes	Fishes	Supraseasonal drought, flow regulation	Mainly additive, suggestion of synergistic	Propst et al. (2008), Gido and Propst (2012), Ruhi et al. (2015), Ruhi et al. (2016)
S. America	Amphibians, invertebrates	African clawed frog	Habitat modification	Synergistic	Lobos and Measey (2002), Lobos and Jaksic (2005)

nonnatives from predation pressure and competition, therefore indirectly assisting them to spread (Fig. 3.1). Finally, given that flow regulation changes the river's ability to store materials and energy, other hypotheses of invasion based on resource availability and heterogeneity (e.g., fluctuating resource availability hypothesis; Davis et al., 2000) could also come into play.

We expect that the alteration-invasion interaction may result in additive, synergistic, or even antagonistic outcomes for native species and ecosystems. In its additive form, flow alteration may primarily serve as a selection regime modification, opening new fundamental niches and modifying realized niches via removal of predators and competitors (Byers, 2002). Although that leads to increased vulnerability to invasion, alteration and invasion are not interacting; instead, invaders are filling empty niches and can be thus considered “passengers of environmental change” (MacDougall and Turkington, 2005). By contrast a synergistic outcome may emerge whenever the environmental-resistance and/or the propagule-pressure mechanisms co-occur with biotic mechanisms (Fig. 3.1). Biotic mechanisms can manifest in both directions; that is, from natives to nonnatives (e.g., native local extirpations decreasing biotic resistance to invasion) or from nonnatives to natives (e.g., nonnatives increasing predation pressure and competition on natives). In order to understand and predict native species responses to global change in the future, it is critical to quantify the relative importance of each mechanism (Ruhi et al., 2015).

The importance of each mechanism may fluctuate in a system, and different mechanisms may even concatenate over space and time depending on the invasion stage. For example, increased propagule pressure driven by international trade that concentrates around urban areas favors nonnative establishment (Francis and Chadwick, 2012); once established, nonnative generalists can use propagule reservoirs in these degraded habitats to “assault” less disturbed habitats (Knops et al., 1999). During this process, some invaders (mainly plants) can even modify the unaltered habitat (from “passenger” to “driver” of ecological change; MacDougall and Turkington, 2005), further facilitating a new wave of alien species (Simberloff and Von Holle, 1999). In Table 3.1, we provide examples of the most common additive and synergistic forms of the alteration-invasion nexus in river ecosystems.

3.3 EFFECTS OF THE ALTERATION-INVASION NEXUS ON RIVERINE POPULATIONS AND COMMUNITIES

Although invasion in freshwater ecosystems can reduce native population abundances, the effects on species diversity are less evident, partly owing to lags between nonnative invasion and native local extirpations (Gallardo et al., 2016). Moreover, many invaders have the capacity to transform habitats; thus nonnatives may affect native organisms not only directly (via biotic interactions), but also indirectly via whole system alterations (e.g., changes in water turbidity, eutrophication; Gallardo et al., 2016). For example, the water hyacinth (Eichhornia crassipes) is a highly invasive aquatic plant native to the Amazon basin that has invaded freshwater ecosystems in North America, Europe, Africa, Asia, and Australasia. High growth rates and dispersal potential (via stolons) allow this plant to rapidly cover large surfaces of water, causing drastic declines in light penetration and dissolved oxygen, as well as fish mortality (Téllez et al., 2008). Increased flow stability due to damming and altered wet-dry cycles have been reported to benefit this species at the expense of native aquatic macrophytes in the Guadiana River (in Spain) and in Australia’s floodplain wetlands (Kingsford, 2000; Bunn and Arthington, 2002; Téllez et al., 2008). A similar case is that of the water fern *Azolla filiculoides*, which is a cosmopolitan invader of modified, lentic riverine habitats. Like the water hyacinth, *Azolla* can fix nitrogen from the air via symbiotic nitrogen-fixing cyanobacteria, which boosts productivity and allows biomass doubling in three days. Thick *Azolla* mats prevent photosynthesis, slow down oxygen diffusion from the air, and suppress both native macrophytes and aquatic macrofauna. In laboratory conditions, *Azolla* suppressed submerged macrophyte growth (Janes et al., 1996), while in the Gwebi River in Zimbabwe, pools with *Azolla* had fewer tadpoles and invertebrate families than pools with no vegetation or with native submerged macrophytes (Gratwicke and Marshall, 2001). Although these invasions of floating macrophytes represent a clear example of the synergistic alteration-invasion nexus, other plant invasions are less drastic. For example the establishment of nonnative helophytes (e.g., *Typha* spp in Australia) is mediated by dam-induced flow stability, but submerged vegetation may disappear with habitat modification, though not due to displacement by *Typha* (Kingsford, 2000; Bunn and Arthington, 2002).

Dams and nonnative species have important negative effects on native faunal communities as well (Fig. 3.2). Mollusks are subject to the combined effects of habitat modification,

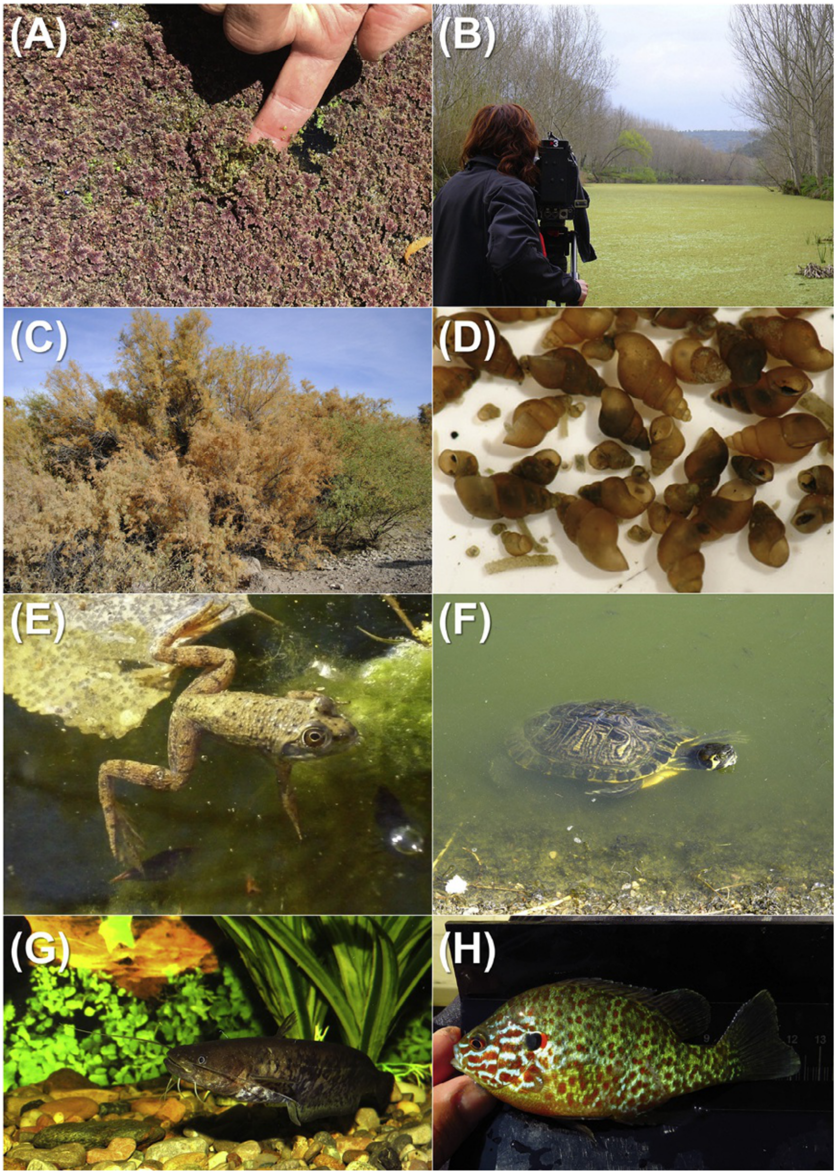

FIG. 3.2 (A) Closeup of a thick floating layer of water fern (Azolla sp.) [credit: A. Ruhi], (B) covering the Ter River (Catalonia, Spain) after intense water diversion activities upstream [credit: L. Sala]. (C) Salt cedar (Tamarix spp.) in the Salt River, Arizona, US, where it has been progressively replacing native cottonwoods due to decreasing water tables [credit: E. Moody]. (D) Shells of New Zealand mudsnails (Potamopyrgus antipodarum), a nonnative invertebrate that often thrives and fuels river food webs in dam tailwaters [credit: P.J. Bryant]. (E) American bullfrog (Rana catesbeiana) [credit: R. Greene] and (F) pond slider (Trachemys scripta) [credit: G. Pascual], two invasive herptiles that benefit from lentification and habitat modification. (G) wels catfish (Silurus glanis) and (H) pumpkin seed sunfish (Lepomis gibbosus), two invasive fishes favored by reservoirs, in the highly regulated Ebro River basin (Catalonia, Spain) [credit: R. Merciai].

increased predation pressure, and competition with nonnative counterparts (e.g., *Dreissena, Corbicula, Potamopyrgus*), which in North America caused the decline of several freshwater mussel species (Ricciardi et al., 1998; Strayer, 1999). Altered flow regimes have reduced native fish populations and increased nonnative establishment in many regions, particularly in water-scarce basins (e.g., Mediterranean, US Southwest, and Australia), where freshwater allocations for ecosystems and agriculture are increasingly at odds (e.g., Bernardo et al., 2003; Pusey et al., 2006; Propst et al., 2008). In the Colorado and Rio Grande basins of the American Southwest, current hydrologic change is increasing the risk of quasiextinction for native fishes (+8.5% risk) while ameliorating such risk for nonnative fishes (−5.9% risk; Ruhi et al., 2016). Over the past 150 years, species with low fecundity and high investment in juvenile survivorship have spread the fastest in that area (Olden et al., 2006). Although these traits should not be favored under highly variable (i.e., flashy hydrographs with frequent high-flow pulses) flow regimes, these features that typified arid land rivers in the past are becoming increasingly rare. Despite the primacy of the environmental-resistance mechanism, direct and indirect biotic mechanisms often contribute to accelerate the replacement of native ichthyofauna. Piscivore fish invasions can have strong deleterious effects on nonnative populations, while nonnatives that are parasite vectors can secondarily decimate local fish communities via parasite infection (Cucherousset and Olden, 2011). For instance, the Stone moroko (*Pseudorasbora parva*) has become a highly invasive fish in Europe after being introduced from Asia. Besides competing with native cyprinids, this species is a reservoir of the intracellular parasite *Sphaerothecum destruens*, a threat for many freshwater fishes (Britton et al., 2008; Andreou et al., 2012).

The importance of the alteration-invasion nexus is less clear for amphibians and aquatic reptiles. The African clawed frog (*Xenopus laevis*) occupies modified freshwater habitats in Chile, California, France, and Portugal, with weirs and irrigation networks likely enhancing its expansion (McCoid and Fritts, 1993; Lobos and Jaksic, 2005; Rebelo et al., 2010). More remarkably the American bullfrog (*Rana catesbeiana*) is now present in South America, Southeast Asia, and Europe. In the 1920s it was introduced in northern California, where its spread was facilitated by an abundance of disturbed streams and livestock ponds (Nussbaum et al., 1983). The bullfrog occupies permanent freshwater habitats, where it coexists with predatory fish; nonnative fish often further assist their spread by accelerating native frog (though not bullfrog) decline (Lawler et al., 1999). In addition, some of these invasive fishes (e.g., *Lepomis macrochirus*) may reduce the abundance of large arthropods, releasing bullfrog larvae of predators (Adams et al., 2003). Because nonnative bullfrogs require stable flows and deep permanent reaches to complete their long larval development, in Mediterranean climate and arid land rivers the impact of this species could be reduced by restoring flow intermittency.

Turtles also provide examples of alteration-assisted invasion in rivers. The pond slider *Trachemys scripta* was introduced in the Sacramento River Basin (California), but it was only established in highly disturbed reaches, where the native western pond turtle *Actinemys marmorata* was not able to maintain large populations (Thomson et al., 2010). In Singapore and Italy, *Trachemys scripta* is also associated with artificial lakes and waterways that serve as propagule reservoirs to its colonization to natural habitats (Yong et al., 2014; Grano and Cattaneo, 2015). As a general rule, a nonnative long-term establishment is more likely if alteration is permanent (Bunn and Arthington, 2002); thus the potential for strong biotic mechanisms will be higher in impoundments than in downstream habitats with temporarily altered regimes.

Finally, although most examples of the alteration-invasion nexus show additive and synergistic effects of alteration and nonnatives on natives, in some cases this interaction may be antagonistic. For example, in the Manuherikia River in New Zealand, nonnative brown trout (*Salmo trutta*) were more susceptible to water abstraction than native roundhead galaxias (*Galaxias anomalus*), and human-induced low flows favored galaxiid populations by preventing trout establishment (Leprieur et al., 2006). This kind of antagonistic alteration-invasion nexus may occur when the flow alteration enhances some natural feature of the hydrograph, particularly flow intermittence (Acuña et al., 2017).

FLOW ALTERATION AND PLANT COMMUNITIES IN THE MURRAY RIVER WETLANDS, AUSTRALIA

In an example of invasion as a "passenger" of environmental change, the regulation of the Murray River in southeastern Australia has resulted in a reduction in diversity and abundance of native vegetation in the floodplain wetlands and a subsequent increase in exotic, largely terrestrial-adapted species (Fig. 3.3). The Murray River has been regulated since the late 1800s through instream impoundments, interbasin transfers, water diversions, and extraction. The mean annual flow has decreased from 12,300 to 4900 hm^3, with an overall reduction in winter and spring flows and an increase in summer and autumn flows (Maheshwari et al., 1995). Because floods are generally now smaller, shorter, less frequent, and aseasonal, the flooding patterns of the thousands of wetlands that occur in the Murray River floodplain have been altered. Consistent with other parts of the basin, such hydrologic changes have been met with declines in native vegetation and an increased dominance of exotic plants. Specifically, wetlands that experienced the greatest reductions in 10-to-20-year recurrence floods had reduced the cover of amphibious (wetland specialist) native vegetation and increased the cover of terrestrial nonnative vegetation (Catford et al., 2011). It is interesting to note that the occupancy and abundance of terrestrial native species also declined with flow regulation (Catford et al., 2014). These findings suggested that both terrestrial and amphibious native plants are adapted to the historical (but not the modified) flood regime and that the nonnative increase was the symptom (not the cause) of native abundance decline. Therefore invasion in these wetlands could be managed by facilitating native species through the reinstatement of mid-range floods. The reinstatement of historical floods has helped restore native wetland vegetation and discourage nonnatives in the Macquarie Marshes, also in SE Australia (Dawson et al. 2017).

3.4 EFFECTS OF THE ALTERATION-INVASION NEXUS ON RIVERINE FOOD WEBS

The alteration-invasion nexus may also change the ecological functioning of rivers by influencing the structure and stability of food webs (Cross et al., 2013; Gallardo et al., 2016). To date, research focusing on the impacts of alteration-mediated invasions on riverine food webs remains limited. However, two general principles depicting the independent effects of flow alteration and invasion on riverine food webs can help to provide insight. First, flow regimes represent a major control on the riverine food-web structure, controlling it both

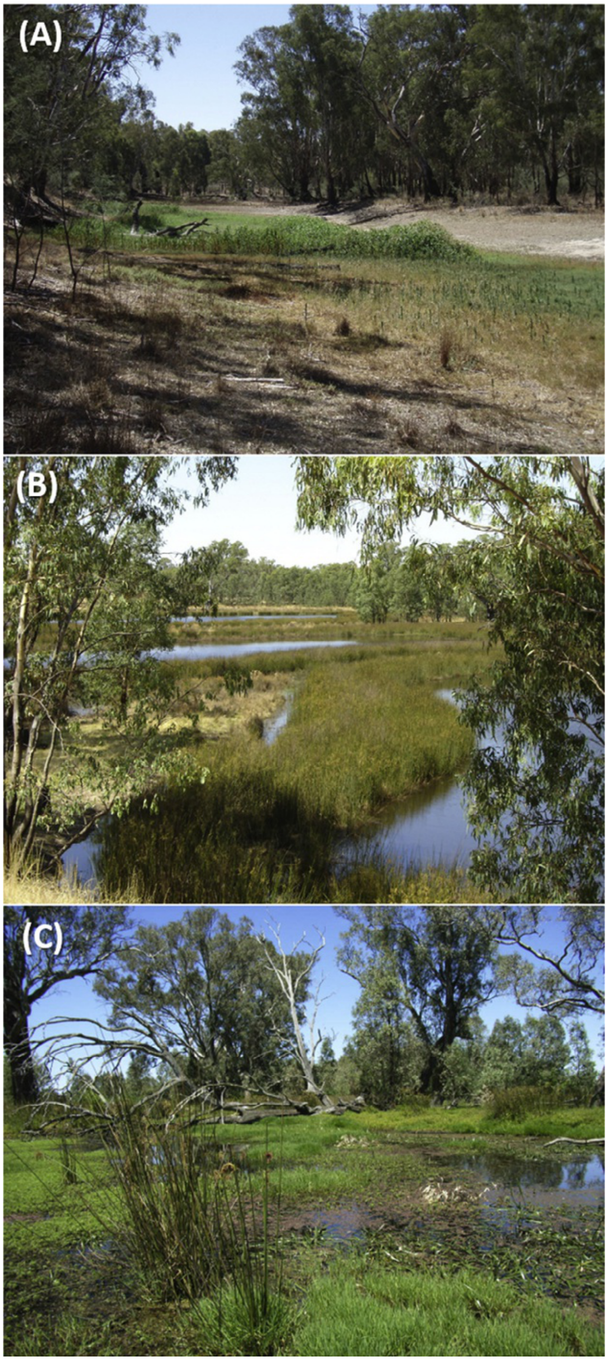

FIG. 3.3 Floodplain wetlands along the River Murray, Australia, showing (A) a dry wetland dominated by exotic vegetation, and (B) and (C) inundated wetlands dominated by native wetland plants. Photos by J. Catford. Wetlands located near Tocumwal (A), Corowa (B) and Albury (C).

ultimately (via changes in productivity, disturbance, and ecosystem size) and proximately (by allowing or preventing food-web reassembly) (Post and Takimoto, 2007; McHugh et al., 2010; Sabo et al., 2010). Second, aquatic food webs are particularly sensitive to changes in food-web topology or network structure, thus species additions and replacements may have strong impacts on food-web dynamics and stability (Carpenter et al., 1985; Pace et al., 1999). Here, we discuss evidence supporting these two principles and then connect them in the context of the alteration-invasion nexus.

The flow regime is linked directly or indirectly to three major controls of food-web structure in running waters: disturbance, productivity, and ecosystem size (Post, 2002; McHugh et al., 2010; Sabo et al., 2010). Food chain length describes the number of trophic transfers that occur between basal resources and top predators, and it is an important component of food-web structure because it influences trophic dynamics and nutrient cycling (Schindler et al., 1997; Post, 2002; McIntyre et al., 2007). The widely supported disturbance hypothesis of food chain length is directly linked to flow regimes; this hypothesis builds on the observation that in model systems, longer food chains are less stable and take longer to recover than shorter chains (Pimm and Lawton, 1977). These observations suggest that flow stability should lengthen food chains, a prediction that has been met in both large-scale studies comparing riverine food webs across broad hydroclimatic and biogeographic gradients and in smaller-scale studies examining local effects of river regulation. For instance, Sabo et al. (2010) found that food-chain length in rivers across the United States decreased with stochastic variability in flow and intermittency, which were in turn mediated by drainage area; the larger the drainage area, the more stable the flow regime. In another study focusing on food-web responses to a dam in the Ebro River basin (Catalonia, Spain), Ruhi et al. (2016) found that flow stability resulting from regulation led to an increased food chain length. In this case, food chain lengthening was driven by a diet shift of a dominant fish species towards prey items that occupied a higher trophic position (i.e., omnivory mechanisms; Post and Takimoto, 2007).

Flow regime alteration may also influence food-web structure via bottom-up effects through changes in primary production or ecosystem size or via an interaction between disturbance and bottom-up effects. In the long-studied Eel River (California, US), blooms of *Cladophora* and associated epiphytic diatoms appear after winters with scouring floods that displace predator-resistant caddisflies that would otherwise prevent energy from flowing to higher trophic levels (Power et al., 2008). This postflood food web can sustain salmonids and other predators via a prey base built of epilithic and epiphytic algal carbon, but only if hyporheic exchange during summer base flow is sufficient. Drought or water abstraction during summer may cause warm, stagnant conditions that kill salmonids; in this case, previously complex food webs may be replaced by a one-link food chain consisting of cyanobacteria, some of which are toxic to vertebrates (Power et al., 2015). Although this example comes from a dynamic, unregulated river, Wootton et al. (1996) showed that food webs in regulated sections of northern California rivers strongly resembled those in unregulated rivers during the anomalous years without large winter floods. Thus, research in dynamic, unregulated rivers may provide a mechanistic understanding of how riverine food webs respond to high- and low-flow anomalies (whether these are management- or climate-driven). Controlled field experiments may also increase understanding of the mechanisms by which higher levels of organization respond to altered disturbance regimes. In a mesocosm-based dewatering study, Ledger et al. (2013) found that supraseasonal drought caused important losses of species and interactions particularly among predators, even though network-level properties were preserved. In a similar study, Walters and Post (2008) found that the maximum trophic position did not respond to a low-flow disturbance (instead, fishes survived in isolated deeper pools), but size structure did, with larger organisms being relatively more sensitive to drought (as in Ledger et al., 2013). Overall, a clear link exists between flow regime alteration and the vertical dimension of riverine food webs, with flow stabilization generally lengthening, and drying disturbance shortening (or shifting size spectra of) riverine food chains.

In addition to rewiring or extirpating the native components of a food web, flow regime alteration may also affect food-web structure and dynamics via the facilitation of nonnative species. An invader may ‘replace” a native taxon or may represent a net addition to the community. In addition, invasive taxa may affect the extant nodes via novel trophic links, thus altering topology. Because aquatic food webs are often characterized by strong links, these invasion-induced changes in topology can have pervasive effects on food-web dynamics (e.g., trophic cascades or “downward dominance through the food chain;” Strong, 1992). For example, the introduction of zooplanktivorous fishes in reservoirs can release phytoplankton from predation pressure; in this way the trophic position of the invader can determine the responses of other food-web components (Gallardo et al., 2016). Although many invasions in rivers concern top trophic positions, they can also occur at or near the base of the food web (e.g., macrophytes and invertebrate grazers; Téllez et al., 2008; Cross et al., 2010), or within detrital pathways (e.g., crayfish; Moody and Sabo, 2013). Overall, understanding whether flow-induced species gains, losses, and replacements lengthen or shorten the food chain and whether they contribute to a particular energy pathway is key to anticipating the effects of invasions on food-web dynamics (Table 3.2).

THE ALTERATION-INVASION NEXUS IN THE COLORADO RIVER FOOD WEB

The Colorado River in the Grand Canyon provides an insightful case of the effects of the alteration-invasion nexus on food-web structure and dynamics. Glen Canyon dam operations have altered downstream flow and thermal regimes and geomorphological processes, which together with introductions of non-native taxa, profoundly influence the food web (Stevens et al., 1997; Cross et al., 2011, 2013; Kennedy et al., 2016). In river segments close to the dam, the invertebrate assemblage is dominated (~70% of total invertebrate production) by only two nonnative taxa that were either introduced inadvertently (i.e., the New Zealand mudsnails Potamopyrgus antipodarum (Cross et al., 2010) or purposefully to support a recreational trout fishery (i.e., scuds, Gammarus lacustris). At the top of the food web, a nonnative predator (e.g., the rainbow trout Oncorhynchus mykiss) dominates fish production (>98%). Energy flows at this site are highly inefficient (i.e., there is a considerable amount of production that does not support production at higher trophic levels, therefore becoming a trophic “dead end”). Additionally, the relatively few links per species and the dominance of strong interaction strengths suggest this is an instable food web (Cross et al., 2013). However, with increasing distance from the dam the physical template starts to recover (e.g., warmer temperatures and elevated turbidity). The food web gains complexity as other native taxa are represented at all trophic positions, while other invertebrate taxa (e.g., midges and blackflies) as well as native fish dominate secondary production. These downstream food webs are more complex, energy flows are more efficient, and food-web topology is more consistent with theoretically "stable" food webs (i.e., more trophic links per species, incorporation of detrital pathways, and abundance of weak trophic interactions, Fig. 3.4). An experimental flood conducted by the Glen Canyon Adaptive Management Program (Melis et al., 2012) confirmed that the simplified food webs close to the dam were much less resistant to flood disturbance than the more complex downstream food webs. It is interesting to note that the flood had a strong negative effect on the production of nonnative mudsnails, though it had a positive effect on nonnative rainbow trout. Together, these observations suggest that riverine food webs affected by the alteration-invasion nexus may be relatively more sensitive to disturbance.

TABLE 3.2 Hypothesized Mechanisms Linking Dam-Induced Flow Regime Alteration to Food-Web Responses via Nonnative Species in Reservoirs and Downstream Habitats

Cause(s)	Consequence(s)	Mechanism	Food Web Theory
Dampened disturbance regimes (downstream)	Food chain lengthening	Dam-induced flow stabilization may allow food webs to support extra trophic levels, favoring establishment of nonnative top predators (e.g., piscivore fishes)	Dynamic stability or "disturbance" hypothesis of food-chain length (Pimm and Lawton, 1977)
	Food web rewiring	Generalist nonnative primary and secondary consumers may be able to track resources relatively faster via dietary shifts. Nonnative taxa without effective predators may lead to high productivity and trophic dead ends.	Omnivory and insertion mechanisms (Post and Takimoto, 2007)
	Food web simplification	Novel flow and thermal regimes tend to favor nonnative taxa that can fill open fundamental niches; by filling them, nonnatives may further constrain native realized niches via antagonistic interactions, leading to loss of nodes and links.	Food web niche model (Thompson et al., 2012)
Lentic conditions (in the reservoir)	Food chain lengthening	Increased residence time allows for higher storage and processing rates of organic matter, potentially increasing productivity and allowing extra (nonnative) trophic levels	"Productivity" or resource availability hypothesis of food-chain length (Pimm, 1982; Schoener, 1989) R* rule or resource-ratio hypothesis (Tilman, 2004)
	Top-down effects	Lentic conditions and keystone herbivores may favor strong effects of nonnative top predators on the lower trophic levels	Trophic cascades (Strong, 1992)
Increased habitat capacity (in the reservoir, tailwaters)	Food chain lengthening	Expanded flooded area and longer hydroperiods increase the absolute size of productive aquatic ecosystem, allowing extra (nonnative) trophic levels	Productive space and ecosystem size hypotheses of food chain length (Schoener, 1989; Post et al., 2000)

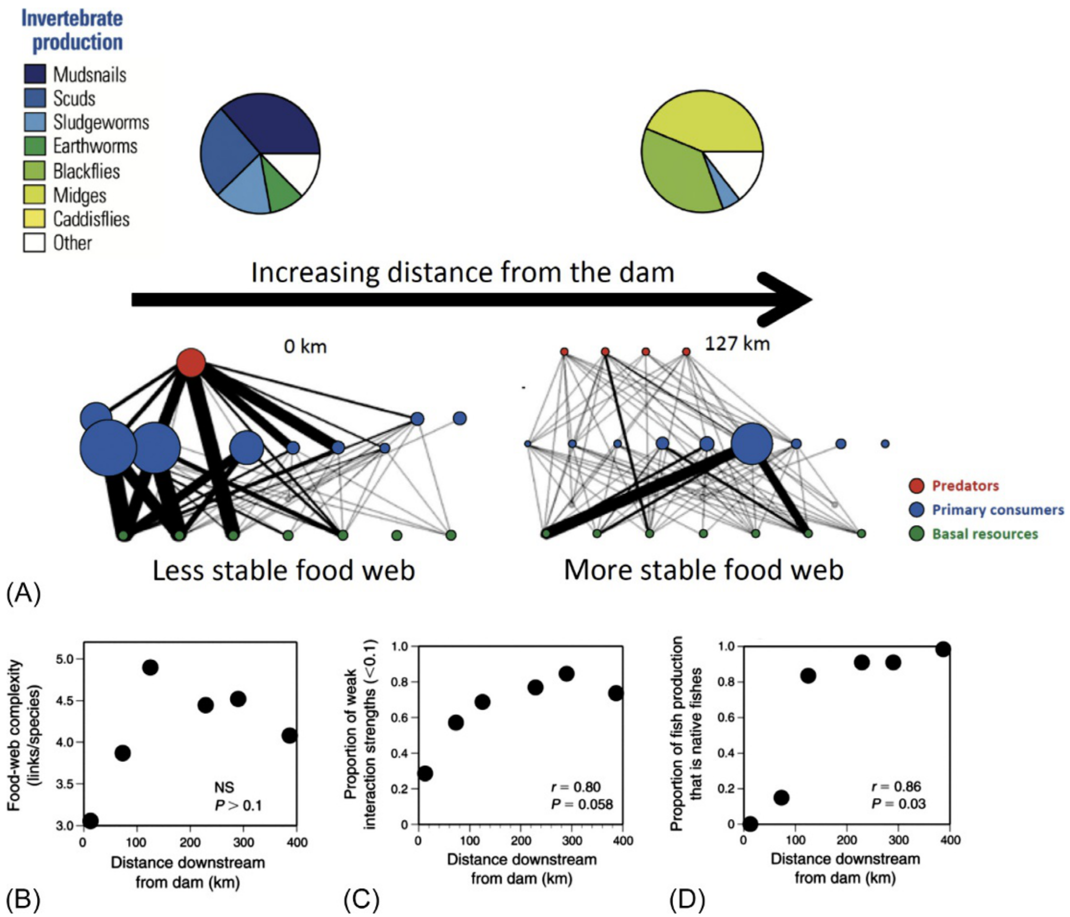

FIG. 3.4 Changes in food-web structure, function, and stability in the Colorado River, U.S.A. (adapted from Cross et al., 2013; Kennedy et al., 2013). (A) With increasing distance from the dam, invertebrate secondary production shifted from being dominated by non-native mudsnails and scuds, to blackflies and midges. Example energy flow food webs below the dam (0 km) and 127 km downstream show increasing complexity and prevalence of weak links. Food web complexity (B), the proportion of potentially-stabilizing weak trophic interactions (C), and proportional native fish production (D), increased with distance from the dam (0–386 km).

3.5 THE ALTERATION-INVASION NEXUS AS A FRESHWATER CONSERVATION CHALLENGE

Given the global prevalence of modified and managed rivers, where a return to the natural flow regime is no longer feasible, the adaptive management of dams and other existing infrastructure may help to achieve desirable ecological outcomes (Acreman et al., 2014; Poff et al., 2016). In recent decades, heightened efforts have focused on manipulated flow releases from dams with the goal of simultaneously benefiting native and disfavoring nonnative components of biodiversity. In the Tallapoosa River (Alabama, US), Travnichek et al.

(1995) demonstrated an increased species richness and abundance of native fluvial-specialist fishes relative to nonnative habitat generalists in response to increased minimum flows below Thurlow Dam. In the San Juan River (Southwest US), native fish densities increased in response to elevated releases from the Navajo Dam in the spring to mimic snowmelt runoff; however, nonnative fish density increased in response to the lowering of summer flows, which also reflected unregulated flow patterns (Propst and Gido, 2004). An experimental flood below Alamo Dam on the Bill Williams River had relatively weak effects on nonnative fishes; these taxa recovered to preflood numbers just days after the release (Pool and Olden, 2015). Finally, the reoperation of other infrastructure (e.g., wastewater treatment plants) could be useful in some cases to mitigate supraseasonal drought (via flow augmentation) or to preserve intermittency (and promote native intermittent specialists) in small streams (Halaburka et al., 2013; Acuña et al., 2017).

On the other hand, the aging and rising costs of the world's dams, coupled with an increasing awareness of their environmental consequences, has often elevated dam removal as a viable restoration strategy. Dam removal can minimize several problems associated with downstream environmental effects that promote nonnative species. Dam removal can restore migratory and movement routes for fishes; however, these barriers can also isolate and protect native species from aggressive downstream invasive species. This challenge is especially acute in inland western North America, where remnant populations of native trout (e.g., cutthroat and bull trout) have been invaded by nonnative brook, brown, and rainbow trout while simultaneously encountering countless impassable small and large dams, diversions, and road culverts. Biologists charged with conserving native salmonids often disagree over the relative merits of building new barriers or converting temporary barriers such as impassable culverts into permanent structures to limit upstream invasions versus removing barriers to allow recolonization, demographic support, or movement to complementary habitats to enhance population persistence (Fausch et al., 2009). This invasion-isolation dilemma clearly illustrates that dam removal is not a panacea for fish conservation; managers face a clear trade-off because the barriers designed to protect native populations from invasions (i.e., purposeful small dam construction for conservation) may also hasten their extinction by creating small populations isolated in habitat fragments (Rahel, 2013). Dam removal also eliminates upstream reservoirs that often function as invasion "hubs" for freshwater invaders (Havel et al., 2005). Indeed, Johnson et al. (2008) found reservoirs were up to eight times more likely than natural lakes to have established populations for five widespread aquatic invaders, and species introductions in reservoirs can spread to upstream rivers (Gido et al., 2004). The replacement of reservoir fish assemblages by more typical riverine species can occur relatively quickly after the dam is removed. For example, nonnative fishes adapted to slow-moving water and fine sediments gave way to native riverine fishes within a year of removal of a Wisconsin dam (Kanehl et al., 1997).

Although much research is focusing on the intersection between water resource engineering and river conservation ecology (Acreman et al., 2014; Poff et al., 2016; Poff and Schmidt, 2016), important challenges for managing the alteration-invasion nexus remain. Disentangling the relative importance of the different mechanisms operating in the nexus (Fig. 3.1) is essential but often difficult, especially without additional field experiments and/or long-term data analyses. Additionally, the effects of operation-induced and climate-driven flow alteration are often conflated, but it is important to quantify climate-driven uncertainty because it constrains freshwater resources management, thus inducing further alteration. Predicting effects of an alteration-driven invasion at the higher levels of organization (e.g., communities and food webs) is another key challenge, in this case arising from food web rewiring and feedbacks that are difficult to predict and may affect the native and nonnative components of biodiversity differently. Finally, more research is needed to determine optimal management strategies to mitigate impacts when these are interactive, or when the native and nonnative components of biodiversity do not negatively covary—in those cases, alteration (and thus potential restoration) is not a zero-sum game, and trade-offs likely need to account for values other than native species conservation. On the bright side, however, the notion of "designer flows" (hydrographs that represent an optimal trade-off between socioeconomic and ecological outcomes) is gaining attention (Chapter 19; Acreman et al., 2014), and experimental flow releases from dams will offer increasing opportunities to test and inform restoration science via whole-system manipulation.

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