Assessing the Effects of Climate Change on Aquatic Invasive Species

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Abstract: *Different components of global environmental change are typically studied and managed independently, although there is a growing recognition that multiple drivers often interact in complex and nonadditive ways. We present a conceptual framework and empirical review of the interactive effects of climate change and invasive species in freshwater ecosystems. Climate change is expected to result in warmer water temperatures, shorter duration of ice cover, altered streamflow patterns, increased salinization, and increased demand for water storage and conveyance structures. These changes will alter the pathways by which non-native species enter aquatic systems by expanding fish-culture facilities and water gardens to new areas and by facilitating the spread of species during floods. Climate change will influence the likelihood of new species becoming established by eliminating cold temperatures or winter hypoxia that currently prevent survival and by increasing the construction of reservoirs that serve as hotspots for invasive species. Climate change will modify the ecological impacts of invasive species by enhancing their competitive and predatory effects on native species and by increasing the virulence of some diseases. As a result of climate change, new prevention and control strategies such as barrier construction or removal efforts may be needed to control invasive species that currently have only moderate effects or that are limited by seasonally unfavorable conditions. Although most researchers focus on how climate change will increase the number and severity of invasions, some invasive coldwater species may be unable to persist under the new climate conditions. Our findings highlight the complex interactions between climate change and invasive species that will influence how aquatic ecosystems and their biota will respond to novel environmental conditions.*

Keywords: aquatic systems, climate change, global warming, invasive species

Evaluación de los Efectos del Cambio Climático sobre Especies Acuáticas Invasoras

Resumen: *Los diferentes componentes del cambio ambiental global típicamente son estudiados y manejados independientemente, aunque hay un reconocimiento creciente de que a menudo interactúan múltiples factores de manera compleja y no aditiva. Presentamos un marco conceptual y una revisión empírica de los efectos interactivos del cambio climático y de especies invasoras en ecosistemas dulceacuícolas. Se espera que el cambio climático resulte en temperaturas del agua más cálidas, una menor duración de la cubierta de hielo, alteración de los patrones de flujo, incremento de la salinización y un incremento en la demanda de almacenamiento de agua y estructuras de transportación. Estos cambios alterarán los caminos por los que especies no nativas entran a los sistemas acuáticos por la expansión de instalaciones de cultivo de peces y de jardines acuáticos hacia nuevas áreas y por la facilitación de la dispersión de especies durante inundaciones. El cambio climático influirá en la probabilidad de que se establezcan nuevas especies por eliminación de temperaturas bajas o de hipoxia invernal que actualmente impiden la supervivencia y por el incremento de la construcción de represas que sirven como sitios de importancia para especies invasoras. El cambio climático modificará los impactos ecológicos de especies invasoras mediante el reforzamiento de sus efectos competitivos y depredadores sobre especies nativas y por el incremento de la virulencia de algunas enfermedades. Como un resultado del cambio climático, puede ser necesario desarrollar nuevas estrategias de prevención*

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y control, como la construcción de barreras o esfuerzos de remoción, para controlar especies invasoras que actualmente solo tienen efectos moderados o que están limitados por condiciones estacionales desfavorables. Aunque la mayoría de los investigadores se concentran en cómo incrementará el número y la severidad de las invasiones con el cambio climático, puede que algunas especies invasoras de aguas frías no sean capaces de persistir bajo las condiciones climáticas nuevas. Nuestros resultados resaltan las complejas interacciones entre el cambio climático y las especies invasoras que influirán en cómo responderán los ecosistemas acuáticos y su biota a las nuevas condiciones ambientales.

Palabras Clave: calentamiento global, cambio climático, especies invasoras, sistemas acuáticos

Introduction

Climate change and invasive species are 2 of the most pervasive aspects of global environmental change. Climate change will affect aquatic systems by warming water temperatures, altering stream flow patterns, and increasing storm events (Poff et al. 2002). These changes are expected to have profound effects on the distribution and phenology of species and the productivity of aquatic ecosystems (Parmesan 2006). Humans have greatly facilitated the spread of aquatic invasive species through intentional stocking, aquarium releases, canal construction, and international shipping (Rahel 2007). A rich body of literature documents the widespread invasion of non-native species and their impacts in aquatic systems (e.g., Strayer 1999; Lodge et al. 2006; Stromberg et al. 2007).

The independent impacts of climate change and non-native species on aquatic systems are often considered, yet there is a strong likelihood that these primary drivers of global environmental change will also interact in a complex manner (Kolar & Lodge 2000; Stachowicz et al. 2002). For example, global climate change will cause warmer water temperatures in northern-latitude lakes. This may cause seasonally stressful conditions for coldwater-adapted fish species, but may provide suitable thermal conditions to allow non-native warmwater fish species to thrive in these lakes (Sharma et al. 2007). Such species may prey on or compete for food resources with native fishes, leading to the decline or loss of native fish populations (Jackson & Mandrak 2002). In this case, declines in native species and loss of populations would be the result of the synergistic effects of climate warming and non-native species.

Aspects of climate change that may affect aquatic invasive species include altered thermal regimes, reduced ice cover in lakes, altered streamflow regimes, increased salinity, and increased water-development activities in the form of canal and reservoir construction (Poff et al. 2002). These changes may, in turn, alter the pool of potential colonists, influence the chance that non-native species will establish, alter the impact of established invasive species, and require the initiation or expansion of prevention and control efforts (Fig. 1). We illustrate these topics with examples from freshwater and estuary ecosystems from around the world. By highlighting the myriad of potential interactions between climate change and invasive species in aquatic ecosystems, we hope our paper will stimulate increased research emphasis on these issues.

Effects of Altered Thermal Regimes

Climate change is expected to warm much of the Earth's surface. As air temperatures rise, water temperatures will also increase. Most aquatic organisms are ectothermic and therefore temperature is important in their physiology, bioenergetics, behavior, and biogeography (Sweeney et al. 1992; Rahel 2002).

Altered Pathways of Species Introductions

As the climate warms, the geographic areas with suitable temperatures for warmwater aquaculture, tropical fish culture, and outdoor water gardens will expand. For example, optimal temperatures for aquaculture of catfish (*Ictalurus punctatus*) are projected to move 240 km northward in the southeastern United States for every 1 °C increase in mean annual air temperature (McCauley & Beitinger 1992). The aquaculture of other warmwater species such as tilapia (Cichlidae) and some crayfishes would also likely expand to areas currently too cold for outdoor propagation (Lodge et al. 2000; Peterson et al. 2005). Many fishes raised in outdoor facilities for the aquarium trade are tropical species. With climate warming, their culture can expand northward. Water gardens, which are often stocked with non-native species, also could become more widespread as winters become milder (Maki & Galatowitsch 2004). Unfortunately, aquatic organisms often escape captive-breeding facilities and become invasive (e.g., bighead carp [*Hypophthalmichthys nobilis*], walking catfish [*Clarias batrachus*], American bullfrog [*Rana catesbeiana*]; Fuller et al. 1999; Orchard 1999; Padilla & Williams 2004, respectively). Climate warming will therefore likely increase the pool of invasive species by facilitating the spread of fish-culture facilities and water gardens to new areas.

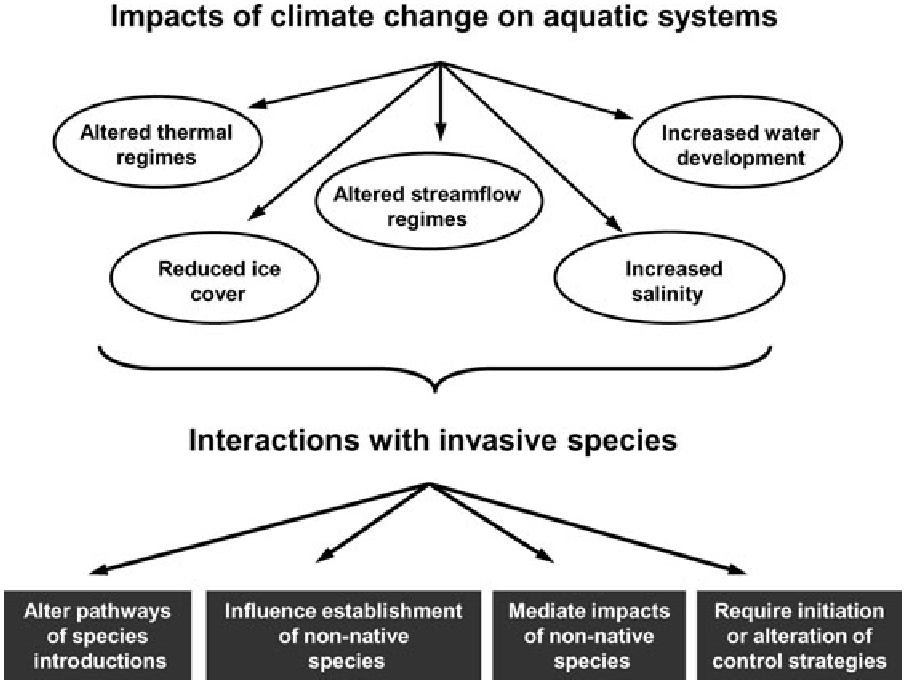

Figure 1. Characteristics of aquatic systems that will be altered by climate change and how these changes will affect invasive species.

Changes in Likelihood That Non-Native Species Will Become Established

Fish are often classified into thermal guilds based on temperature tolerance: coldwater species have physiological optimums <20 °C; coolwater species have physiological optimums between 20 and 28 °C, and warmwater species have physiological optimums >28 °C (Magnuson et al. 1997). On this basis, coldwater temperatures can be viewed as a filter that prevents warmwater-adapted species from establishing self-sustaining populations (Fig. 2). As water temperatures warm with climate change, the effectiveness of this filter will diminish, and warmwater species could spread to new areas and become established.

Biologists have attempted to predict range expansions of aquatic species by projecting current species temperature limits onto maps of future temperature conditions. Mohseni et al. (2003) predict that the number of stream stations with suitable thermal habitat for warmwater fishes will increase by 31% across the coterminous United States. Sharma et al. (2007) estimate the distribution of smallmouth bass (*Micropterus dolomieu*) in Canada will advance northward to encompass much of the country by the year 2100, and a similar scenario is envisioned for the highly invasive common carp (*Cyprinus carpio*) (Minns & Moore 1995). Mandrak (1989) predicts that with climate warming, 19 warmwater fish species from the Mississippi or Atlantic Coastal basins may invade the lower Laurentian Great Lakes (Ontario, Erie, and Michigan) and that 8 warmwater fish species currently present in the lower Great Lakes could invade the upper Great Lakes (Huron and Superior). These 27 fish species would bring with them 83 species of parasites that do not currently exist in the Great Lakes, opening the door for epizootic outbreaks of pathogens in immunologically naïve native fishes (Marcogliese 2001). In Europe the ranges of 16 warmwater fish species are expected to expand and the ranges of 11 coldwater species are expected to shrink (Lehtonen 1996). Finally, some human diseases with water-dependent vectors may expand to new areas with climate warming (e.g., malaria; Martin & Lefebvre 1995).

Although most studies of range expansion involve warmwater species, climate warming could allow the expansion of invasive coldwater species into new areas. For example, native bull trout (*Salvelinus confluentus*) appear to have a competitive advantage over non-native brook trout (*S. fontinalis*) in the coldest streams in the Rocky Mountains (Rieman et al. 1997). As these streams warm, brook trout are expected to achieve competitive superiority and thus displace native bull trout from one of their last remaining refuges from invasive species.

There is evidence that some aquatic species have already responded to climate change. Shifts in the distribution of marine species have been documented (Perry et al. 2005). In freshwater systems climate change is associated with earlier breeding in amphibians (Beebee 1995), earlier emergence of dragonflies (Odonata) (Hassall et al. 2007), and compositional shifts of entire insect communities (Burgmer et al. 2007). There is speculation that the recent establishment of 2 species of tropical dragonflies in Florida represents a natural invasion from Cuba and the Bahamas that is related to climate change (Paulson 2001). In Great Britain the distribution of 20 species of odonates, 14 species of aquatic hemiptera, and 15 species of fish has shifted northward over a 25-year period (Hickling

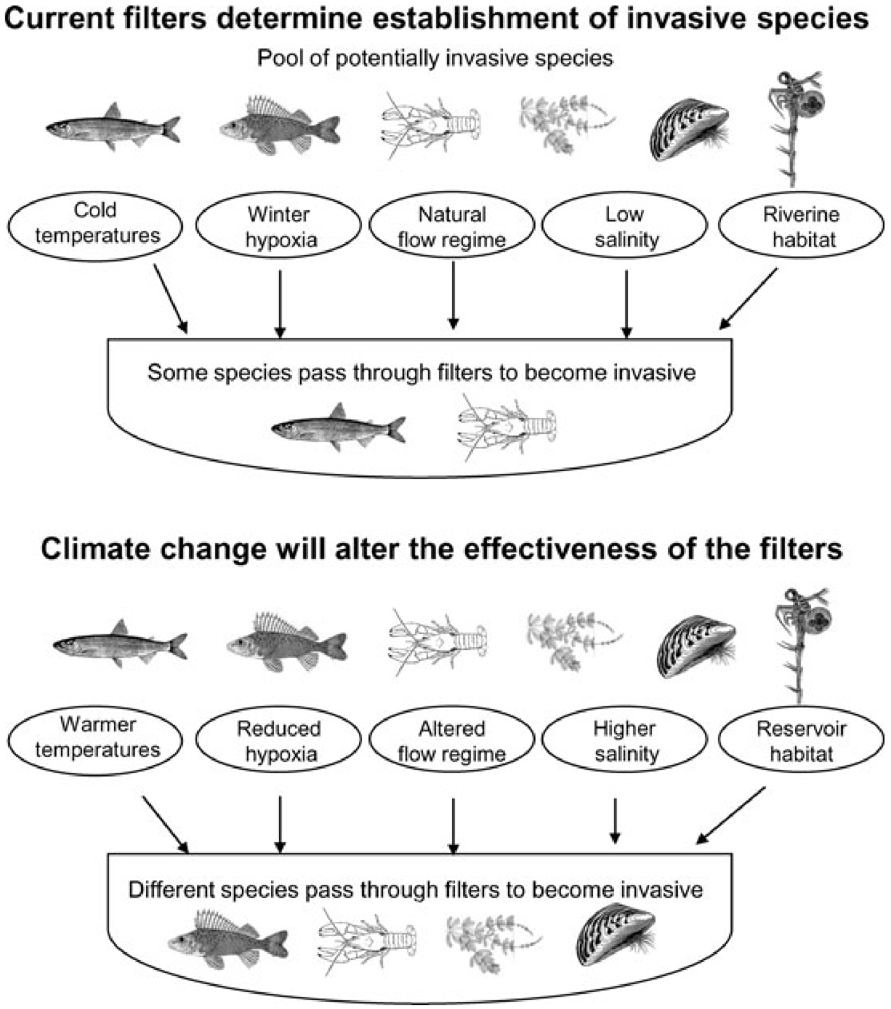

Figure 2. How climate change could alter the effectiveness of abiotic filters that prevent the establishment of invasive species.

et al. 2006). In the Andes, anurans have extended their range to higher elevations in response to deglaciation (Seimon et al. 2007). In general, however, there are relatively few examples of range expansions for freshwater taxa compared with the extensive documentation of this phenomenon for terrestrial taxa.

Mediation of the Impact of Non-Native Species

Altered thermal regimes could mediate the impacts of established non-native species on native species through shifts in competitive dominance between native and non-native species, increased consumption of native prey species by non-native predators, or increased effects of non-native parasites on native species. In some cases competitive superiority among aquatic species can be reversed with changes in water temperature. For example, in laboratory experiments, brook trout and brown trout (*Salmo trutta*) were equal competitors for food at cold temperatures, but brown trout were superior competitors at warm temperatures (Fig. 3) (Taniguchi et al. 1998). Differences in performance relative to temperature are supported by field data that show that brook trout are dominant in streams at higher elevations and brown trout are dominant in streams at lower elevations.

Predation is one of the major ways non-native species affect aquatic communities (Schindler & Parker 2002;

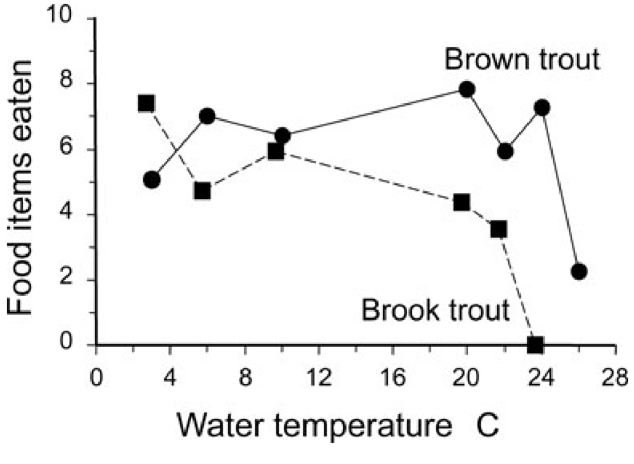

Figure 3. Effects of water temperature on the number of items eaten by brook trout and brown trout in a laboratory competition experiment (from data in Taniguchi et al. [1998]).

Kats and Ferrer 2003). Because most aquatic species are ectothermic, their food consumption rate increases with water temperature until thermally stressful conditions are reached. Thus, climate warming could magnify the impacts of non-native predators on native prey species. In the Columbia River (North America) smallmouth bass and walleye (*Sander vitreum*) are non-native piscivores that prey on native salmon. Bioenergetics models indicate that a 1 °C increase in annual river temperatures near the Bonneville Dam on the Columbia River will result in a 4–6% increase in per capita consumption of salmonids by smallmouth bass and walleye (Petersen & Kitchell 2001). It is estimated that climate-related range expansion by smallmouth bass in Canada may lead to the loss of over 25,000 populations of minnow species (Cyprinidae) in Ontario (Jackson & Mandrak 2002).

Climate warming may increase the virulence of non-native parasites and pathogens to native species. Warmer temperatures allow disease organisms to complete their life cycle more rapidly and thus attain higher population densities (Marcogliese 2001). *Myxobolus cerebralis*, which causes whirling disease in fish, is an example of a non-native pathogen whose impact is likely to increase with climate warming. This pathogen is native to Europe and was introduced to North America, where it may severely affect salmonid populations. The virulence of *M. cerebralis* increases with temperature and thus warmer streams will likely magnify the impact of this parasite on populations of native salmonids.

Changes in Control Strategies and Their Initiation

With warmer temperatures, managers may need to modify control strategies for established non-native species or develop new strategies for species that were not problematic historically (Fig. 1). There are ongoing control programs for many aquatic invasive species that have become established. Mechanical harvesting and herbicides are used to control Eurasian watermilfoil (*Myriophyllum spicatum*) in the littoral zone of lakes, and scrubbing or molluscicides are used to prevent clogging of water intake pipes by zebra mussels (*Dreissena polymorpha*) in the Laurentian Great Lakes (MacIsaac 1996). Warmer water temperatures could allow these and other invasive species to begin growth earlier in the year and maintain growth later into the fall; thus, costly control actions would need to be implemented more frequently.

In other situations non-native species that pose little threat under current thermal regimes may be able to establish populations and become invasive with climate warming, including many tropical fish species or aquatic plants that are released into the wild by aquarists (Maki & Galatowitsch 2004; Padilla & Williams 2004). Establishment of tropical species within the coterminous United States has generally been limited to southern states, but releases of tropical species into open waterways have been recorded throughout North America (Fuller et al. 1999). For example, piranha (*Pygocentrus* or *Serrasalmus*) have been recorded in 22 states, and although no populations have become established, areas where overwinter survival is possible may increase with climate warming (Fig. 4).

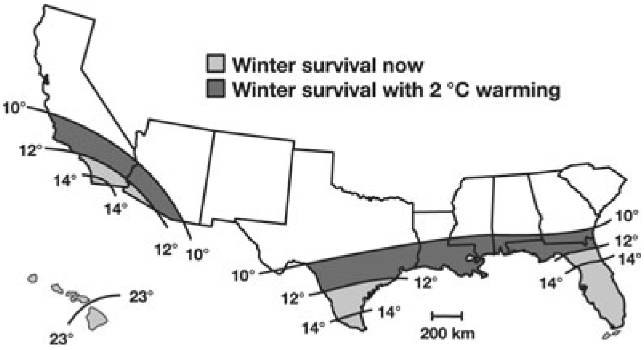

*Figure 4. Winter survival of red-bellied piranha (*Pygocentrus nattereri*) currently and with a future 2 °C increase in temperature (from information in Bennett et al. [1997]).*

To preserve some populations of native trout, it may be necessary to construct migration barriers that prevent non-native trout from expanding their range to higher elevations as stream temperatures warm (Cooney et al. 2005). Efforts to reduce water temperature, such as reducing solar input into streams by increasing shading from riparian vegetation, may also help reduce the impact of invasive species. This strategy has been suggested as a way to reduce the impact of invasive western mosquitofish (*Gambusia affinis*) on native least chub (*Lotichthys phlegethontis*) in Utah (Mills et al. 2004).

Effects of Reduced Ice Cover

Climate change will reduce the extent of ice cover on lakes in the northern hemisphere (Magnuson et al. 2000), which may influence the invasion process by increasing light levels for aquatic plants, reducing the occurrence of low oxygen conditions in winter, and exposing aquatic organisms to longer periods of predation from terrestrial predators.

Altered Pathways of Species Introductions

Lakes that experience low oxygen concentrations under ice cover are generally not managed for sport fisheries and thus often retain assemblages of native fishes, amphibians, or invertebrates (Rahel 1984; Schindler & Parker 2002). If global warming reduces ice cover and thus the extent of winter hypoxia, there will be increased pressure to manage these lakes for sports fisheries. This will increase the pool of non-native fish species likely to be introduced into these lakes, either by agency biologists or by the public (Rahel 2004).

Changes in Likelihood That Non-Native Species Will Establish

Low light conditions under the ice can limit the occurrence of aquatic plants, and therefore a reduction in ice cover could allow colonization by new species. The recent invasion by threadleaf water-crowfoot (*Ranunculus trichophyllus*) into several high-elevation lakes in the Himalayas has been attributed to a decrease in the length of ice cover due to climate warming (Lacoul & Freedman 2006). Ice cover also promotes hypoxia that acts as a filter to prevent the establishment of large piscivorous fishes (Fig. 2). As a result, lakes with winter hypoxia often contain distinctive assemblages of small-bodied fishes or amphibians that cannot coexist with predators (Rahel 1984). Climate warming will reduce the extent of ice cover and thus lessen the occurrence of winter hypoxia (Stefan et al. 2001). This could allow colonization of these lakes by piscivorous fish, such as bass (*Micropterus* spp.), that would, in turn, cause local extirpation of populations of small-bodied fishes (Jackson & Mandrak 2002) and amphibians (Kats & Ferrer 2003).

Mediation of the Impact of Non-Native Species

Ice provides protection for fish from terrestrial predators. The swimming ability of fish is greatly reduced at low temperatures, making them more vulnerable to bird and mammalian predators (Greenwood & Metcalfe 1998). Loss of ice cover in streams in North America could increase predation rates on native minnows and suckers and possibly favor non-native species (e.g., green sunfish [*Lepomis cyanellus*]) that have better antipredator adaptations. Zebra mussels in shallow, eutrophic lakes may be limited by winter hypoxia (Strayer 1999). If this is the case, then elimination of winter hypoxia would foster expansion of zebra mussel populations in such lakes.

Changes in Control Strategies and Their Initiation

Invasion by piscivorous fishes into lakes where they were formerly excluded by winterkill could necessitate management actions to protect native species from local extirpation. For example, removal of non-native predatory fish has allowed populations of amphibians and aquatic invertebrates to recover in mountain lakes that were historically fishless (Schindler & Parker 2002; Knapp et al. 2007).

Effects of Altered Streamflow Regimes

The magnitude, frequency, duration, and timing of floods, droughts, and intermittent flows (i.e., the flow regime) are primary drivers of ecological structure and function in aquatic ecosystems (Poff et al. 1997). There is a general consensus that climate change will modify patterns of precipitation, evapotranspiration, and runoff (Frederick & Gleick 1999). Although the geography of these changes is uncertain, altered patterns of runoff will fundamentally modify many aquatic ecosystems (Poff et al. 2002).

Increases in air temperature will cause concomitant increases in river temperatures and rates of evapotranspiration. Coupled with drier climates, this will result in periods of prolonged low flows and stream drying in many regions. In mountainous watersheds of the United States, higher temperatures will increase the ratio of rain to snow and accelerate the rate of spring snowmelt. In addition, a shift from snow to rain in high elevation or northern latitudes will lead to a reduction in streamflow in late summer. Although increasing drought conditions are likely for many regions, climate models also predict increases in the variability and intensity of rainfall events; a pattern already observed over the last century (Frederick & Gleick 1999). This will modify disturbance regimes by changing the magnitude and frequency of floods.

Altered Pathways of Species Introductions

Altered flow regimes resulting from climate change may influence the pathways by which non-native species are introduced into new environments. There could be an increase in the frequency of escapes from aquaculture and tropical fish farm facilities when rearing ponds overflow during flood events (Padilla & Williams 2004). Climate-driven changes to the timing and quantity of stream flow may influence rates of secondary spread of non-native species through river networks. An increase in floods may increase the dispersal of non-native species, such as zebra mussels, whose planktonic larvae are transported through streams (Havel et al. 2005). River ecosystems are subject to invasion by non-native riparian plants because rivers act as conduits for the efficient dispersal of propagules (Richardson et al. 2007).

Changes in Likelihood That Non-Native Species Will Become Established

Altered flow regimes could remove a filter that limits the occurrence of non-native species. For example, dams in the western United States have severely reduced flood flows that previously flushed non-native fishes from streams, while native species were able either to resist displacement or to repopulate rapidly after such events (Minckley & Meffe 1987). Long-term flow alteration by dams and diversions in the lower Colorado River basin is, in part, responsible for the continued spread of invasive fish species (Olden et al. 2006). Increased drought conditions and prolonged low flows associated with climate change may enhance establishment success of non-native species. The density of non-native fishes in the San Juan River is greatest in years with the lowest spring and summer discharge (Propst & Gido 2004). During extended low summer flows, nuisance species, such as the red shiner (*Cyprinella lutrensis*), common carp, and western mosquitofish, dominate the fish communities. In the Guadiana River in Portugal non-native species, such as pumpkinseeds (*L. gibbosus*) and largemouth bass, dominate the fish fauna in drought years, whereas native species dominate in years with normal flows (Bernardo et al. 2003).

Climate change is projected to cause a shift in peak stream flows from spring to late winter in snowmelt-dominated regions, which could affect the reproductive cycles of riverine fishes. Fausch et al. (2001) compared the hydrologic regimes for rivers across the world where rainbow trout (*Oncorhynchus mykiss*) invasions ranged from unsuccessful to highly successful. Invasion success was greatest in areas that closely matched flow regimes within the species' native range (i.e., flooding in winter and low flows in summer). Climate-change scenarios project more winter floods and reduced summer flows in mountain rivers; therefore, the invasion success of rainbow trout may increase in areas where only moderate success has been observed previously (e.g., Colorado, U.S.A.). Shifts in flood timing and recession rates associated with river regulation are strongly associated with the invasion dynamics of riparian ecosystems, including salt cedar (*Tamarix* spp.) in the arid southwestern United States (Stromberg et al. 2007).

Patterns of non-native species establishment will be influenced by episodic desiccation of streams and rivers associated with more frequent and prolonged droughts. For example, the New Zealand mud snail (*Potamopyrgus antipodarum*)—which has invaded Europe, Asia, Australia, and North America—is tolerant of desiccation. Consequently, this species may have an advantage in streams that become intermittent during droughts. Similarly, the globally invasive red swamp crayfish (*Procambarus clarkii*) can survive desiccation by burrowing into substrates (Correia & Ferreira 1995), which facilitates its invasion into harsh environments. For freshwater fishes changes in the frequency and magnitude of ephemeral conditions may favor species with opportunistic life-history strategies (Olden et al. 2006). In the lower Colorado River, for example, opportunist non-native species, such as the western mosquitofish, guppies, mollies (*Poecilia* spp.), and red shiners, are likely to increase in distribution and abundance.

Mediation of the Impact of Non-Native Species

More frequent and severe drought conditions and decreasing base flow may intensify the negative effects of invasive species by forcing native fish species into environments where they become prey to non-native piscivores (Matthews & Marsh-Matthews 2003). The concentration of species during low-flow conditions may also increase the rate of hybridization between non-native and native species, especially in small habitats, such as desert springs, which are particularly prone to drought.

Climate-induced changes in stream flow regimes may, in certain situations, reduce the negative effects of invasive species by minimizing spatial overlap among native and non-native species. For example, disjunct distributions of non-native brown trout and native galaxiids in New Zealand are mediated, in part, by water removal for irrigation (Leprieur et al. 2006). Brown trout are more susceptible than native fishes to stresses associated with low flows and cannot displace galaxiid populations in low-gradient streams where there is a high level of water removal.

Changes in Control Strategies and Their Initiation

In some cases current management strategies may need to change to accommodate altered flow regimes. The sea lamprey (*Petromyzon marinus*) entered the Laurentian Great Lakes in the 1920s and has contributed greatly to the decline of native salmonid populations. The U.S. and Canadian governments have implemented an aggressive sea lamprey control program, including the construction of low-head dams to block the upstream spawning migrations of sea lampreys. Nevertheless, with increasing magnitude of flood events, the effectiveness of these barriers may be compromised. Restoring natural flow regimes, including periods of high and low flows, may help reduce populations of invasive aquatic species. In the western United States, the success of non-native fish species can be reversed, in part, by restoration of natural flow regimes (Marchetti & Moyle 2001; Scoppettone et al. 2005).

Effects of Increased Salinity

A warmer climate and the resulting effects on precipitation and the amount of snow are projected to increase rates of desiccation and alter the salinity of freshwater and estuary ecosystems. Naturally saline aquatic systems in arid regions such as the southwestern United States will experience increased desiccation and salinization (Seager et al. 2007), and saltwater intrusions will occur in some coastal areas (Frederick & Gleick 1999).

Altered Pathways of Species Introductions

Increasing salinization in coastal ecosystems will likely have a strong influence on pathways of species introductions. Many of the recent invasions of the Laurentian Great Lakes and of the Caspian, Azov, Black, and Baltic seas have resulted from shipping activities, particularly through the release of contaminated ballast water (Carlton & Geller 1993). The primary method used to reduce the spread of non-native species via ballast-water discharge is open-ocean ballast-water exchange.

Nevertheless, not all shipping companies practice open-ocean exchange, and even if they did, ballast waters would still contain viable propagules that would be released at the port of entry. Increasing salinity in coastal waters may therefore increase the probability of survival of propagules in ballast water, particularly for brackish water species such as the Chinese mitten crab (*Eriocheir sinensis*).

Changes in Likelihood That Non-Native Species Will Become Established

Increases in salinity from water diversions and withdrawals provide insight into how climate-induced changes in salinity may influence the likelihood of future invasions by non-native species into lakes. The Aral Sea, one of several large, closed-basin lakes in the desert of central Asia, is a good example. In the 1960s inflows to the Aral Sea were diverted for irrigation, which decreased the lake's volume and increased its salinity (Létolle & Chesterikoff 1999). In the 1960s salinity reached 12–14%, and native fish species started to disappear. At the same time, introduced fishes increased in dominance, causing a complete shift in the lake's fish communities (Kolar & Lodge 2000). Species invasions into other large saline lakes, such as Lake Issyk-Kul (Kyrgyzstan) and Lake Nakuru (Kenya), may provide additional insight into how increases in salinity may promote the establishment of invasive species in the future.

Shifts in the quantity, timing, and quality of freshwater inflow are implicated in the decline of native fish species and the proliferation of invasive species in some estuaries. In the Suisan Marsh of the San Francisco Estuary, long-term increases in salinity are responsible, in part, for invasion by the shimofuri goby (*Tridentiger bifasciatus*) (Moyle & Marchetti 2006). The Chinese mitten crab, which is native to eastern Asia, has become established throughout Europe and parts of North America. The species has free-swimming planktonic larvae that develop predominantly in saline water, but adults spend much of their life in fresh water. Mitten crabs must reproduce in water with $>15‰$ salinity, which limits their dispersal ability in coastal regions of North America (Herborg et al. 2007). But, salinity changes in coastal regions associated with climate change may open the landscape to greater invasion risk.

Aquatic systems in arid regions that are naturally saline are likely to become even more saline due to climate change. Whether this will allow marine species to invade inland waters is unknown, although the Salton Sea in California provides insight into this issue. When the Salton Sea became a permanent water body in 1905, it had a freshwater fish fauna derived from the Colorado River (Moyle 2002). High evaporation and the high salinity of inflow water from irrigated fields caused the salinity of the Salton Sea to increase to levels comparable to the ocean. As native fishes were eliminated, fisheries managers introduced 3 saltwater fish species to provide a sport fishery. Thus, extremely high salinities might provide opportunities for saltwater organisms to become established, most likely due to introductions by humans.

Mediation of the Impact of Non-Native Species

Even though it may not reach lethal concentrations, salinity can influence the outcome of competition among aquatic species. For example, competitive superiority among species of cattails (*Typha* spp.) and killifishes (*Lucania* spp.) changes with salinity (Dunson & Travis 1991). Salinity-intolerant species incur an increased physiological cost to maintain osmotic balance as salinity increases, and they grow more slowly than salinity-tolerant species. Thus, climate-induced increases in salinity may favor invasive aquatic species if they are more salinity tolerant than native species. This may be especially important in the Colorado River system, where expected increases in salinity may favor invasive species capable of living in saline waters such as the red shiner, western mosquitofish, and plains killifish (Olden et al. 2006). In riparian areas, saline conditions favor halophytic invasive species such as salt cedar and reduce the germination, productivity, and survivorship of native riparian species such as cottonwoods (*Populus* spp.) and willows (*Salix* spp.) (Stromberg et al. 2007).

Changes in Control Strategies and Their Initiation

How increased salinization will influence control strategies for invasive species is difficult to predict. Elevated salinity in floodplains may favor the ongoing invasion and impact of salt cedar, and current efforts to eliminate it and reestablish native riparian species by flooding areas below dams may need to account for salt deposits in riparian soils.

Effects of Increased Water Development Activities

Decreases in annual runoff will mean less surface water for human use, which will prompt the construction of new reservoirs to increase water supplies (Vörösmarty et al. 2004). In areas with adequate supplies of surface water, reservoirs may be built for flood control. In addition, there will be increased pressure to transport water from areas where it is abundant to areas where it is scarce. This will necessitate building canals and aqueducts that will move not only water but also aquatic organisms over long distances and across watershed divides. As a result, water development will influence the pathways of species introductions, enhance the likelihood of establishment of non-native species, modify impacts of existing non-native species, and require initiation or alteration of control strategies for species that may not currently be a problem (Fig. 1).

Altered Pathways of Species Introductions

Reservoirs and canals may alter pathways by which non-native species enter the regional species pool. Reservoirs provide recreational opportunities that attract humans from far away; thus, they represent potential hot spots for species invasions (Havel et al. 2005). Humans can transport new species into a water body on their boats, boat trailers, and fishing gear (e.g., the zebra mussel; Bossenbroek et al. 2007). Canals transport water and organisms across what historically were biogeographic barriers to species movement (Rahel 2007). This creates a new pool of potentially invasive species and opens up the landscape to continued spread of non-native species (Galil et al. 2007). For example, sea lamprey and alewife (*Alosa pseudoharengus*) colonized the upper Laurentian Great Lakes through the Welland Canal.

Changes in the Likelihood That Non-Native Species Will Become Established

Reservoirs replace flowing water with standing water and thus eliminate a filter that prevents establishment of invasive species whose trophic or reproductive needs cannot be met in flowing water (Fig. 2). This is especially true for the many fish species that are introduced into reservoirs for recreational fishing (Moyle & Marchetti 2006). For example, the bluegill (*L. macrochirus*) is adapted to standing water. When this species was accidentally introduced into a river system in South Carolina, it failed to become established in flowing water portions of the drainage, but did colonize a reservoir (Meffe 1991). Once established, invasive non-native species can occur for considerable distances upstream and downstream of a reservoir source population.

Mediation of the Impact of Non-Native Species

Reservoirs may also influence biotic interactions between native and non-native species. Non-native species may be minor components of the biota in streams but can become competitively dominant species in reservoirs (e.g., common carp and zebra mussels; Havel et al. 2005). Reservoirs can provide a source of predators that can eliminate native small-bodied prey species. For example, largemouth bass originating from impoundments were thought to be a primary reason for the extirpation of endangered Topeka shiners (*Notropis topeka*) from stream sites in Kansas (Schrank et al. 2001). Reservoirs also can increase the incidence of disease organisms. The parasite that causes whirling disease, *M. cerebralis*, thrives in warm, silt-laden reservoirs because such conditions favor its intermediate host, *Tubifex tubifex* (Nehring et al. 2003). In tropical areas reservoirs have facilitated the spread of *Schistosoma* by creating new habitat for the parasite's snail host (Havel et al. 2005).

Changes in Control Strategies and Their Initiation

The creation of reservoirs within a watershed could result in the need to control invasive aquatic species that are currently absent or present in low abundance. For example, a 75% increase in impounded water in the Powder River basin of Wyoming has raised concerns that West Nile virus, a mosquito-born disease, will increase and have negative impacts on humans and Sage Grouse (*Centrocercus urophasianus*) (Zou et al. 2006). Increased movement of water through canals will necessitate more action to prevent the transport of unwanted aquatic organisms among basins. The Central Arizona Project canal delivers water from the Colorado River basin into the Gila River basin. To prevent transport of non-native fishes into the Gila River basin, electrified fish barriers have been placed on the canal (Clarkson 2004). An electrified fish barrier also has been constructed on the Chicago Sanitary and Shipping Canal (Stokstad 2003) to prevent the movement of non-native fish such as bighead carp from the Mississippi River basin into the Laurentian Great Lakes basin, where they could have severe impacts on recreational and commercial fisheries.

Conclusions

Climate change may force a redefinition of *invasive species*. Current definitions focus on species that are not indigenous, such as species transferred among continents (e.g., European brown trout introduced into North America) or across major drainage basins (e.g., largemouth bass from the Mississippi River basin introduced to the Colorado River basin). But species that are native to a region may expand their distribution or increase their abundance and harm other native species as a result of climate change (Rahel et al. 2008). For example, warmwater stream fishes may expand their ranges northward (Sharma et al. 2007) or to higher elevations (Taniguchi et al. 1998), where warming temperatures would allow them to displace native populations. Loss of winter ice cover could allow piscivorous fish species naturally present in a drainage basin to colonize lakes that formerly experienced winter anoxia, thereby causing a loss of amphibians or small-bodied fish species. A final example involves parapatric species whose distributions are determined by temperature-mediated shifts in competitive dominance. In Japan native white-spotted charr (*S. leucomaenis*) are predicted to displace native Dolly Varden (*S. malma*) following climate change because white-spotted charr are the superior competitor at warmer temperatures (Nakano et al. 1996). These examples suggest that even species considered indigenous to a region may spread, increase in abundance, and harm other native species with climate change; these are all the characteristics ascribed to invasive species.

Climate change will alter abiotic filters that determine the success of invasive species in aquatic environments (Fig. 2). Most researchers have focused on how climate change will increase the number and severity of invasions, but there may be circumstances in which invasions will be reduced. For example, warmer temperatures and reduced winter hypoxia would expand the pool of invasive species to include warmwater or hypoxia-intolerant species but would reduce the success of coldwater invasive species (Rahel 2002). Such a situation could benefit native species in Patagonian streams, where non-native salmonids have restricted native fishes to warm headwater reaches (Pascual et al. 2007). Increasing salinity in estuaries or arid land streams could reduce invasions by non-native species intolerant of saline conditions (Higgins & Wilde 2005). Because native species have evolved adaptations to historic flow regimes, alteration of flow regimes is most likely to benefit non-native species adapted to the changed conditions (Marchetti & Moyle 2001; Olden et al. 2006). Similarly, conversion of riverine habitat to reservoir habitat will allow a new pool of lentic species to invade, the effects of which could extend for a considerable distance up- and downstream of the reservoir (Havel et al. 2005).

There are many examples of geographic range shifts or phenological shifts consistent with climate-change predictions for terrestrial species and marine species (Perry et al. 2005; Parmesan 2006). By contrast, there are relatively few examples of such shifts for freshwater organisms. It is not clear whether the dearth of examples reflects a lack of response by freshwater organisms to climate change or simply a lack of historic data to detect changes. Many of the published examples involve species that are of great interest to the public (birds and butterflies); are relatively easy to census (plants); or are commercially important (marine fishes). Except for sport fish, most freshwater organisms lack such characteristics; thus, there are less historical data on which to base predictions of their responses to climate change. In addition, it may be more difficult for freshwater organisms to track geographic changes in thermal conditions because they have less ability to circumvent biogeographic barriers than terrestrial or marine species. There are probably more historical survey data available for fishes than for other freshwater organisms; thus, assessment of historical changes in freshwater-fish distributions should consider whether changes are consistent with predictions expected under climate change (e.g., Sharma et al. 2007).

Predictions as to how climate change will influence aquatic invasive species are hampered by uncertainty in climate-change scenarios and by inadequate knowledge of how factors, such as temperature and flow regime, influence the distribution and abundance of aquatic organisms. In addition, many predictions of climate-change effects are derived only from species responses to changes in temperature. Temperature models are likely to be good for broad-scale predictions of species invasions (Jackson & Mandrak 2002; Rahel 2002), but less useful for local-scale predictions in which multiple factors likely interact to determine the success of invasive species (Schrank et al. 2001; Mercado-Silva et al. 2006). Better understanding of what limits the current distribution of invasive species is needed before the influence of climate change on the spread of invasive species can be predicted accurately.

Climate change may cause shifts in water development policies that would be detrimental to native biodiversity. Reservoir and canal construction were viewed as a sign of progress during European settlement of North America. In the last few decades, however, the attention has shifted to the negative aspects of reservoirs, and dam removal is now viewed as a sign of ecologically forward thinking. Nevertheless, the pendulum may shift again as policy makers view increased water storage as a necessary option for dealing with water shortages caused by human population growth and exacerbated by climate change (Limerick 2003). Although large reservoirs are rarely constructed in North America now, the area of the United States covered by impoundments continues to increase by about 1% per year, mainly due to construction of small impoundments (Downing et al. 2006). Reservoirs may be promoted as beneficial because they provide water for domestic use and habitat for aquatic organisms. But reservoirs are typically dominated by non-native species, especially fishes stocked for sport fishing (Havel et al. 2005). Construction of new reservoirs or canals will not bode well for conservation of native biodiversity in stream ecosystems under a changing climate.

The likelihood of imminent climate change should make us reflect on current practices that involve intentional stocking of non-native species. For example, butterfly peacock bass (*Cichla ocellaris*) have been introduced as a sport fish in Florida. The bass are highly piscivorous and there is concern that they could have a negative impact on native fishes (Courtenay 1997). The species was introduced into southern Florida canals based largely on the rationale that cold winter temperatures would prevent it from spreading elsewhere (Shafland 1995). Climate warming may, in fact, eliminate cold winter temperatures as a filter that prevents the butterfly peacock bass from expanding its range in the southern United States.

Climate change represents a new challenge for resource managers charged with preventing, controlling, and eradicating invasive species. Warmer water temperatures, reduced ice cover, altered flow regimes, increased salinization, and the need for more reservoirs and canals will remove filters that currently limit the geographic range or local abundance of many invasive species. As both native and non-native species expand their ranges in response to climate change, we will need to develop integrated monitoring and information systems that support a new set of decision-making tools for managing invasive aquatic species (Lee et al. 2008 [this issue]).

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