Managing Aquatic Species of Conservation Concern in the Face of Climate Change and Invasive Species

FRANK J. RAHEL,* BRITTA BIERWAGEN,† AND YOSHINORI TANIGUCHI‡

*Department of Zoology and Physiology, Department 3166, 1000 East University Avenue, University of Wyoming, Laramie, WY 82071, U.S.A., email frahel@uwyo.edu

†Global Change Research Program, National Center for Environmental Assessment, U.S. EPA–ORD (MC 8601P), 1200 Pennsylvania Avenue NW, Washington, D.C. 20460, U.S.A.

‡Department of Environmental Science and Technology, Meijo University, Tenpaku, Nagoya, Aichi 468-8502, Japan

Abstract: *The difficult task of managing species of conservation concern is likely to become even more challenging due to the interaction of climate change and invasive species. In addition to direct effects on habitat quality, climate change will foster the expansion of invasive species into new areas and magnify the effects of invasive species already present by altering competitive dominance, increasing predation rates, and enhancing the virulence of diseases. In some cases parapatric species may expand into new habitats and have detrimental effects that are similar to those of invading non-native species. The traditional strategy of isolating imperiled species in reserves may not be adequate if habitat conditions change beyond historic ranges or in ways that favor invasive species. The consequences of climate change will require a more active management paradigm that includes implementing habitat improvements that reduce the effects of climate change and creating migration barriers that prevent an influx of invasive species. Other management actions that should be considered include providing dispersal corridors that allow species to track environmental changes, translocating species to newly suitable habitats where migration is not possible, and developing action plans for the early detection and eradication of new invasive species.*

Keywords: aquatic invasive species, climate change, dispersal corridors, habitat improvement, imperiled species, invasive species effects, range shifts, species of conservation concern, species translocation

Manejo de Especies Acuáticas de Interés para la Conservación ante el Cambio Climático y las Especies Invasoras

Resumen: *Es probable que la difícil tarea de manejar especies de interés para la conservación se vuelva más retadora debido a la interacción del cambio climático y las especies invasoras. Adicionalmente a los efectos directos de la calidad del hábitat, el cambio climático propiciará la expansión de especies invasoras hacia nuevas áreas y magnificará los efectos de especies invasoras ya presentes mediante la alteración de la dominancia competitiva, el incremento de las tasas de depredación y el incremento en la virulencia de enfermedades. En algunos casos, especies parapátricas pueden expanderse hacia hábitats nuevos y producir efectos perjudiciales que son similares a los especies invasoras no nativas. La estrategia tradicional de aislar especies en peligro en las reservas puede ser inadecuada si las condiciones del hábitat cambian más allá de los rangos históricos o de manera en que favorezcan a las especies invasoras. Las consecuencias del cambio climático requerirán de un paradigma de manejo más activo que incluya la implementación de mejoramiento del hábitat que reduzca los efectos del cambio climático y la creación de barreras de migración que eviten el influjo de especies invasoras. Otras acciones de manejo que deberían ser consideradas incluyen corredores de dispersión provisionales que permitan que las especies rastreen los cambios ambientales, la translocación de especies a hábitats recién adecuados donde la migración no es posible, y el desarrollo de planes de acción para la detección y erradicación temprana de especies invasoras nuevas.*

Paper submitted October 23, 2007; revised manuscript accepted January 14, 2008.

Conservation Biology, Volume 22, No. 3, 551–561

DOI: 10.1111/j.1523-1739.2008.00953.x

Palabras Clave: cambio climático, cambios en la distribución, corredores de dispersión, efectos de especies invasoras, especies acuáticas invasoras, especies de interés para la conservación, especies en peligro, mejoramiento del hábitat, translocación de especies

Introduction

Habitat alteration and introduction of non-native species are 2 of the most important factors endangering native biodiversity in aquatic ecosystems (Wilcove et al. 1998; Helfman 2007). Climate change will further alter aquatic habitats by modifying thermal and flow regimes, increasing salinization, and promoting the development of reservoir and canal systems to meet the growing human demand for freshwater (Rahel & Olden 2008 [this issue]). These habitat alterations will pose challenges for managing species of conservation concern.

One important issue is the degree to which climate change will make environmental conditions unsuitable for species restricted to protected areas. Protected areas, such as nature reserves and wildlife refuges, are the mainstay of current conservation efforts, yet these areas are geographically fixed and thus vulnerable to habitat changes due to climate warming (Saunders et al. 2002; Hannah et al. 2007). Although mobile species may be able to migrate in concert with climate changes, species with limited mobility will face regional or even global extirpation (Pearson 2006). For example, native fishes in the Great Plains of North America are vulnerable to climate warming because the east–west orientation of river systems and the lack of elevational relief prevents species from retreating to cooler waters by migrating northward or moving up in elevation (Matthews & Zimmerman 1990). In the Rocky Mountains taxa associated with cold water, such as trout (Salmonidae) will be restricted to increasingly higher elevations with climate warming, but eventually such species will run out of habitat and be extirpated (Rahel et al. 1996; Krajick 2004). In the Appalachian Mountains the lower-elevation limit for native brook trout (*Salvelinus fontinalis*) is determined by the interaction of temperature and the presence of non-native trout. Climate change is predicted to increase the lower-elevation limit of brook trout occurrence by 700 m, but because there is little area at higher elevations, the loss of brook trout populations would be substantial (Flebbe 1993). In arid regions climate change will likely increase salinity and decrease stream connectivity, thus leading to the loss of many native fish species (Higgins & Wilde 2005).

Climate change will also have indirect effects on species of conservation concern, such as the facilitation of invasive species. Invasive species are non-native taxa that increase in abundance to the point where they have negative impacts on native species and ecosystem function and may cause economic damage. The mechanisms by which invasive species affect species of conservation concern include predation, competition, and diseases (Fig. 1). Climate change and invasive species may act synergistically if native species that are stressed by changes in temperature or flow regimes must also face challenges from invasive species. For example, bull trout (*S. confluentus*), a declining species in North America, has an optimal temperature range lower than that of other salmonids (Rieman et al. 2007). Cold temperatures give bull trout a competitive advantage over non-native trout present in warmer parts of the drainage. Climate change will produce a direct threat to bull trout through thermally stressful temperatures and an indirect threat by boosting the competitive ability of other trout species present. Holzapfel and Vinebrooke (2005) propose a similar interaction for alpine lakes, where warmer temperatures will lower the invasion resistance of zooplankton communities by stressing native predatory species and accelerating the growth of non-native herbivorous species.

Another indirect effect of climate change will be the alteration of biotic interactions between species of conservation concern and other native species (Fig. 1). Changes in thermal regimes, flow regimes, or salinity could alter the competitive interactions or predator–prey relations among aquatic species in ways that are detrimental to species of conservation concern. Climate change could allow species considered native to a region to spread to

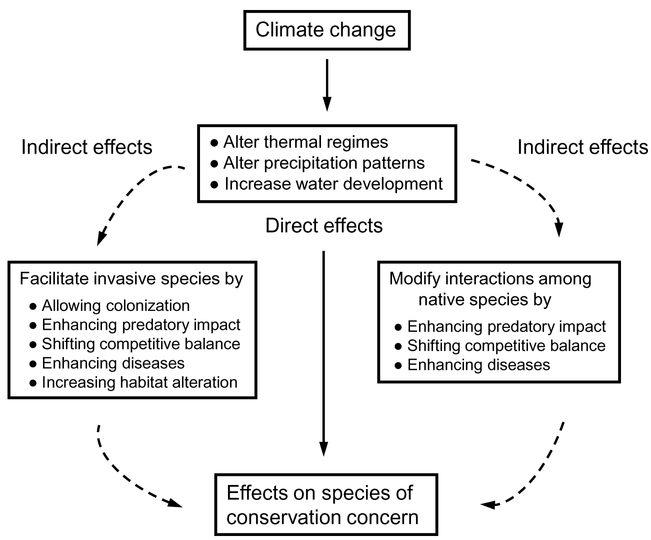
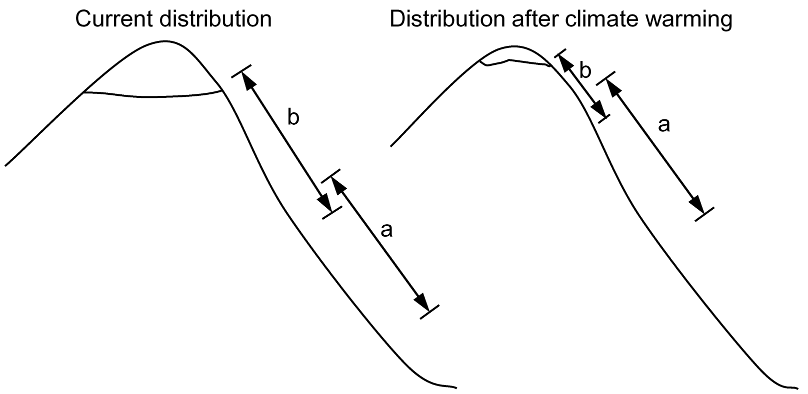


Figure 1. The mechanisms by which climate change and invasive species are expected to affect species of conservation concern.



Species a	Species b	Location (reference)
Brown trout	White-spotted charr	Japan (Hasegawa & Maekawa 2007)
White-spotted charr	Dolly Varden charr	Japan (Taniguchi & Nakano 2000)
Rainbow trout	brook trout	U.S.A. (Larsen & Moore 1985)
Brook trout	bull trout	U.S.A. (Rieman et al. 2007)
Brook trout & rainbow trout	cutthroat trout	U.S.A. (Paul & Post 2001)
Northern pike	Arctic charr	Sweden (Bystrom et al. 2007)
Creek chub	brook trout	U.S.A. (Taniguchi et al. 1998)
Sacramento pikeminnow	rainbow trout	U.S.A. (Reese & Harvey 2002)

Figure 2. Segregation of species groups along elevational and temperature gradients in mountainous regions currently and under climate warming. Elevational ranges of species in group b would be reduced due to displacement by the expanding ranges of species in group a.

new habitats, increase in abundance, and harm other native species—in essence mimicking the negative effects we associate with invasive species.

We examined how interactions between climate change and invasive species will affect the management of species of conservation concern. We use *species of conservation concern* and *imperiled species* to mean any taxa in need of management actions to ensure its continued existence, regardless of the legal status of the taxa under the U.S. Endangered Species Act (ESA) or similar statutory categories in other countries. We discuss the interactions between climate change and invasive species in terms of 2 broad categories. The first involves situations in which climate change facilitates the spread of invasive species or exacerbates their effects on species of conservation concern. The second involves situations in which climate change provides an advantage to some native species that then have negative effects on other native species. We do not discuss the direct effects of climate change on habitat for species of conservation concern, but these topics are discussed elsewhere (Malcolm et al. 2006; IPCC 2007). Our focus is on aquatic environments, but the concepts we discuss also apply to terrestrial environments. Much of the literature involves fish species, but the interactions among climate change and invasive species we highlight will affect a variety of imperiled aquatic taxa.

Expansion of Invasive Species into New Areas

Water temperature plays a dominant role in determining the distribution of aquatic organisms because most are ectothermic (Rahel 2002). Climate-change models project increases in thermal regimes for aquatic habitats (IPCC 2007); thus, species whose distribution are limited by cold temperature will be able to expand poleward and into higher elevations. This means climate change will facilitate the range expansion of invasive aquatic species, potentially into areas being managed for species of conservation concern (Fig. 2).

An example of an invasive species predicted to expand its distribution with climate change is the common carp (*Cyprinus carpio*). Across the United States, the number of stream sites with suitable thermal conditions for common carp is predicted to increase by 33% (Mohseni et al. 2003). This increase reflects both the northward expansion of streams with suitable thermal conditions and expansion of the species into higher elevation sites in the Rocky Mountains.

Numerous other species are also expected to expand their ranges. In the Laurentian Great Lakes basin warmer temperatures, especially in winter, are expected to favor expansion of invasive species, including alewife (*Alosa pseudoharengus*), round goby (*Neogobius melanostomus*), Eurasian ruffe (*Gymnocephalus cernuus*), and sea lamprey (*Petromyzon marinus*) (Holmes 1990; Bronte et al. 2003). These invasions would be detrimental to native species such as yellow perch (*Perca flavescens*) and lake trout (*S. namaycush*). Invasion success of rainbow trout (*Oncorhynchus mykiss*) in mountain streams is greatest in areas that closely match flow regimes within the species' native range, where winter flooding and summer low flows favor spring emergence (Fausch et al. 2001). Climate-change scenarios project greater winter floods and reduced summer flows in some mountainous areas;

changes that would increase the likelihood that rainbow trout could establish populations there.

Some regions of the world will experience reduced precipitation and increased evaporation due to climate change (IPCC 2007). This will mean less surface runoff and, consequently, increased salinity and intermittency of streams. These conditions often will be exacerbated by human water uses in increasingly arid climates. The result will be stresses on native stream biota as has occurred in a northern Mexico drainage, where an endemic freshwater fish fauna has declined owing to salinization following reductions in stream flow (Contreras-Balderas et al. 2002). In estuaries taxa such as the imperiled delta smelt (*Hypomesus transpacifucusi*) will be further threatened by reductions in freshwater inflows that cause salinity to increase and promote invasions by saltwater species (Pringle et al. 2000).

There is evidence that climate change has already facilitated range expansions by invasive species. A period of warm years in the late 1940s may have provided a climatic window for the invasion of white perch (*Morone americana*) into the Great Lakes. This species was native to the Hudson River but failed to move through canals connected with the Great Lakes until a series of warm years allowed overwinter survival of young fish (Johnson & Evans 1990). More recently non-native sea squirts (ascidians) have become established in warming waters along the coast of southern New England (Stachowicz et al. 2002). The transformation of benthic communities in the Gulf of Maine in North America from dominance by native species to dominance by non-native species has been attributed to the interaction of climate change and overfishing (Harris & Tyrrell 2001).

How will colonization by invasive species affect species of conservation concern? In some cases, invasive species suppress or extirpate populations of native species. The zebra mussel (*Dreissena polymorpha*) is associated with declines in native clams (Strayer 1999). The American bullfrog (*Rana catebeiana*) has been introduced widely and has had negative effects on native amphibian populations (Kiesecker & Blaustein 1998; Blaustein & Kiesecker 2002). The parasitic sea lamprey was an important factor in the decline of lake trout in the Great Lakes (Holmes 1990). Rainbow smelt (*Osmerus mordax*) and alewife are thought to have contributed heavily to the extinction of several species of cisco (Salmonidae: coregoninae) in the Great Lakes through competition for zooplankton prey (Crowder 1986). The signal crayfish (*Pacifastacus leniusculus*), native to the northwestern United States, has caused extinction of one crayfish species in the United States and extirpation of many local populations of native crayfishes in England and Europe (Lodge et al. 2000). Rainbow trout have reduced or eliminated populations of native trout, such as brook and cutthroat (*O. clarkii*) trout (Fausch et al. 2001).

With climate change, some areas may become too warm to support invasive species that are currently a problem. For example, as common carp shift their distribution northward in North America (Mohseni et al. 2003), they may retreat from the southern parts of their range. But such retreats will provide little relief for imperiled native species because temperatures are likely to also become too warm for them and because non-native species with even higher thermal tolerances are likely to invade. For example, in the southern United States, tropical fishes in the family Cichlidae appear poised to become invasive if winter temperatures increase (Peterson et al. 2005).

Effects of Invasive Species on Native Species of Conservation Concern

In addition to facilitating colonization of invasive species into new areas, climate change could exacerbate the effects of invasive species that may already be present. Possible mechanisms involve selective mortality of native versus invasive species, reversals in competitive dominance, increased consumption by predators, or increased virulence of disease organisms due to increased water temperatures.

Aquatic ectotherms differ in the maximum temperatures they can tolerate and in optimal temperatures for growth. Consequently, shifts in temperature regimes will likely favor some species at the expense of others. For example, several highly invasive species in the Colorado River basin, such as western mosquitofish (*Gambusia affinis*), yellow bullhead (*Ameiurus natalis*), largemouth bass (*Micropterus salmoides*), red shiner (*Cyprinella lutrensis*), and green sunfish (*Lepomis cyanellus*), have upper thermal tolerances greater than many native species, suggesting they would have an advantage under warmer climatic conditions (Fig. 3). In Japan warmer temperatures will favor the invasive western mosquitofish at the expense of the imperiled Japanese medaka (*Oryzias latipes*) in rice paddy habitats. In the Rocky Mountains bull trout often are restricted to cold, high-elevation streams, and lower-elevation reaches are dominated by non-native brook trout (Rieman et al. 2007). These elevation differences reflect differences in thermal optima; brook trout grow better at warmer temperatures than bull trout. Climate warming is expected to increase stream temperatures in the Rocky Mountains, favoring the growth of brook trout over native bull trout, a species of conservation concern.

Temperature can also influence the outcome of competitive interactions among species. Cutthroat trout are species of conservation concern in the Rocky Mountain region. In many drainages cutthroat trout have been relegated to cold, headwater reaches by invading brook

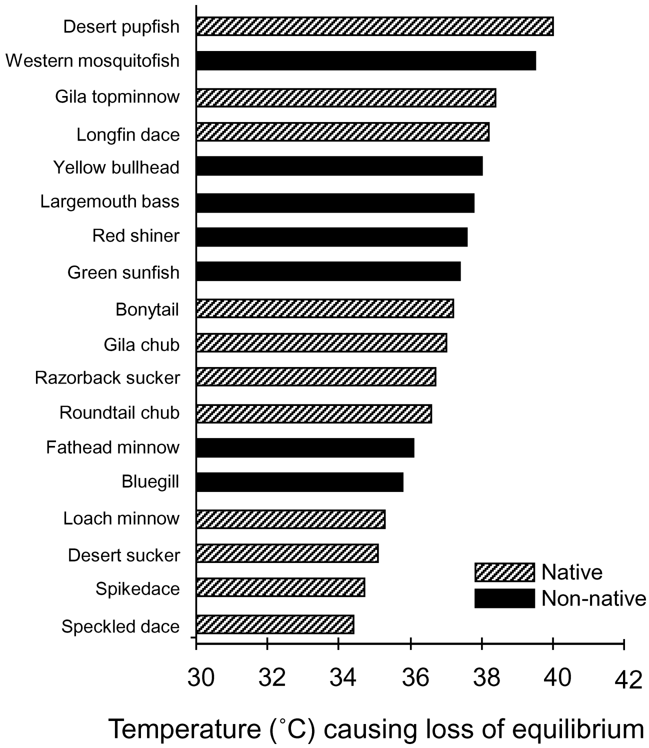


Figure 3. Thermal tolerances of fish from the Colorado River basin (calculated with data in Carveth et al. [2006]).

trout, which dominate warmer, downstream reaches. The species aggressively vie for feeding locations, suggesting that interference competition mediated by temperature could influence the distribution of these species. In the laboratory, the 2 species are nearly equal competitors at 10 °C, but brook trout show a clear competitive dominance over cutthroat trout at 20 °C (De Staso & Rahel 1994). At the warmer temperature, brook trout are more aggressive, consume more food, and occupy the lead position in a dominance hierarchy more often than cutthroat trout. In addition, brook trout maintained equilibrium longer during a thermal challenge test, suggesting they are more tolerant of heat stress than Colorado River cutthroat trout. Climate changes might also favor some life-history traits over others. For example, shifts in temperatures and flow regimes are likely to favor invasive spring-spawning rainbow trout over native fall-spawning chars in Japanese streams. Rainbow trout construct their nests on top of the nests of char, thus reducing reproduction by the native species (Taniguchi et al. 2000). Climate change is expected to cause char to spawn later in winter and trout to spawn earlier in the spring, thus increasing the extent of nest superimposition.

Temperature can influence predator–prey relations among aquatic organisms. In general the amount of food consumed by fish and other aquatic ectotherms increases with temperature until it declines sharply just before lethal temperatures are reached. At high latitudes or elevations, cold water temperatures limit food consumption by these species for much of the year. Climate warming will allow food consumption to increase and thus could exacerbate the effects of invasive, predatory species on native prey species.

In the Columbia River of North America smallmouth bass (*M. dolomieu*) and walleye (*Sander vitreum*) are non-native piscivores that prey on native salmon. An approximate 1 °C increase in annual river temperatures near the Bonneville Dam could result in a 4–6% increase in per capita consumption of salmonids by smallmouth bass and walleye (Petersen & Kitchell 2001). In Lake Michigan consumption of prey fishes by lake trout could increase by 30% under future warming scenarios (Hill & Magnuson 1990). In Yellowstone Lake the predatory impact of invasive lake trout on native Yellowstone cutthroat trout (*O. clarkii bouvieri*) should also increase with climate warming (Ruzycki et al. 2003). If prey consumption of lake trout increases by 30% as projected in Lake Michigan, the effects could be devastating because the average lake trout is estimated to consume about 41 Yellowstone cutthroat trout per year (Ruzycki et al. 2003). Trout introductions into the fishless Sierra Nevada ecosystem have been implicated in the decline of the mountain yellow-legged frog (*R. muscosa*) (Vredenburg 2004), and warmer temperatures could increase predation rates on this species of conservation concern. Warmer temperatures also will enhance predation by non-native brown trout (*Salmo trutta*) on the endangered crayfish (*Cambaroides japonicus*) in Japanese lakes (Nakata et al. 2006).

Climate change will likely alter the distribution and virulence of disease-causing organisms and parasites in aquatic environments (Marcogliese 2001). For example, the effect of whirling disease (a non-native disease) on trout is temperature dependent. The disease is caused by a protozoan (*Myxobolus cerebralis*) that destroys cartilage in young fish. The disease is native to Europe and was introduced into western North America, where it has affected salmonid populations. The virulence of *M. cerebralis* increases with temperature (Hiner & Moffitt 2001); thus, stream warming will likely magnify the impact of this parasite on populations of native salmonids. Whirling disease has contributed to declines in Yellowstone cutthroat trout and is one of the reasons, along with habitat loss and predation by invasive lake trout, that this subspecies has been proposed for listing as a threatened or endangered species (Koel et al. 2006).

Modified Interactions among Native Species

Species that shift their ranges on their own following anthropogenic-induced climate change raise an interesting issue: should they be considered native or non-native (Suffling & Scott 2002)? In some cases these recent colonists become abundant and cause ecological or economic damages—traits associated with invasive species. Whatever terminology is used, species that expand their ranges can have detrimental effects on species of conservation concern.

Recent range expansions by species moving poleward or up in elevation have been documented for a variety of aquatic species and have led to a reduction or extirpation of resident species (Hickling et al. 2006; Parmesan 2006). In most cases it is difficult to determine whether declines in resident species are due to direct effects of climate change or to interactions with the newly invading parapatric species. One example in which the decline of a northern species appears to be due to interactions with an expanding southern species rather than thermal stress involves northern pike (*Esox lucius*) and Arctic char (*S. alpinus*). Recent warming has allowed northern pike to migrate upstream in a watershed and colonize a subarctic lake in Sweden (Byström et al. 2007). Through predation, the northern pike extirpated one native species, the Arctic char, and greatly reduced densities of another, ninespine stickleback (*Pungitus pungitus*). Circumstantial evidence suggests that colonization by northern pike is a result of climate change. Northern pike had been present downstream for many years but moved upstream during a recent period of warm summer temperatures. The optimal temperature at which northern pike grow is higher than the optimal temperature for Arctic char; thus, pike are favored by increasing temperatures. Finally, a nearby lake that was not invaded by northern pike showed no change in its population of Arctic char during the same period, suggesting that warming alone is not the cause of the extirpation of Arctic char in the study lake.

Even when major range shifts are not involved, climate change may alter interactions among parapatric native species in ways that are detrimental to species of conservation concern. For example, temperature influences the competitive balance between Dolly Varden char (*S. malma*) and white-spotted char (*S. leucomaenis*), which are native to streams in Japan (Taniguchi & Nakano 2000). At cold temperatures the species are relatively equal competitors, but at warm temperatures white-spotted char are more aggressive, capture more food, and grow faster than Dolly Varden char. This result is consistent with field data that show that Dolly Varden char are largely restricted to higher elevations in drainages where white-spotted char are present. Dolly Varden char would be more severely affected by climate warming because there is little opportunity for them to move up in elevation, whereas white-spotted char would be able to shift its distribution upward into areas now dominated by Dolly Varden char.

A similar temperature-related shift in competitive superiority exists among brook trout, brown trout, and creek chub (*Semotilus atromaculatus*) (Taniguchi et al. 1998). When the 3 species are forced to compete for food in a laboratory stream tank, the 2 trout species are codominant at cold temperatures (3–10 °C), brown trout become dominant at intermediate temperatures (20–24 °C), and creek chubs become dominant at the warmest temperature (26 °C). These results are consistent with field data that show brook trout occupy the highest elevations, brown trout intermediate elevations, and creek chubs the lowest elevations in Rocky Mountain streams.

Crayfish in the Ozark Plateau of Missouri and Arkansas (U.S.A.) provide an example in which climate warming could favor a common species over species of conservation concern. A widespread species, *Orconectes virilis*, occurs at the periphery of the Ozark Plateau, whereas 2 endemic species of conservation concern (*O. eupunctus* and *O. hylas*) are limited to single drainages within the plateau (Whitledge & Rabeni 2003). *O. virilis* has a major growth advantage at warm temperatures, and there is concern that warming will allow this species to expand its range and cause the extinction of the 2 endemic species.

Climate warming also could increase the rate at which native predators consume prey species of conservation concern. In the Columbia River of western North America, Pacific salmonids (*Oncorhynchus* spp.) have declined to the point where several stocks are listed as threatened or endangered under the ESA. Northern pikeminnows (*Ptychocheilus oregonensis*) are a native predator on juvenile salmon in this system, and their consumption of salmon is expected to increase by 26–31% with a 2 °C increase in summer water temperatures (Petersen & Kitchell 2001). Such increased consumption would cause a further decline in salmonid populations.

Native diseases that have only minor effects on host organisms under past climate conditions could emerge to have devastating impacts. Such a situation may explain the massive loss of amphibian species in Central America (Pounds et al. 2006). Regional warming has increased cloud cover in the mountains of Costa Rica and resulted in locally cooler days but warmer nights. This has shifted temperatures toward the growth optimum of a pathogenic chytrid fungus (*Batrachochytrium dendrobatidis*) that is implicated in the mass extinction of harlequin frogs (*Atelopus* spp.). Climate change has also exacerbated the effect of a previously present disease in brown trout in Switzerland (Hari et al. 2006). Warming temperatures caused an elevational shift in thermal habitat of brown trout that was accelerated by an increased incidence of temperature-dependent proliferative kidney disease at the lower boundary of the habitat.

Changes in Management Paradigms for Species of Conservation Concern

A dominant management paradigm for species of conservation concern is to isolate them in a reserve and hope that the species will prosper in the absence of human disturbances. In fresh waters reserve design is typically focused on maintaining intact habitat throughout the catchment, maintaining natural flow regimes, reducing harvest, and preventing colonization by non-native species (Saunders et al. 2002).

Protection in reserves may be effective when the main threats are habitat destruction or direct exploitation. Climate changes, however, may cause environmental conditions to exceed the historic range of variability to which species are adapted in a particular region. Some species may be able to respond to these changes through latitudinal or elevational migration. Nevertheless, species of conservation concern may be less able to respond because of the threats that caused their imperiled status. For example, a species restricted to a small geographic range because of habitat destruction or alteration in other parts of its former range will have difficulty tracking environmental changes if the intervening habitat serves as a barrier or the species has limited dispersal capabilities. Furthermore, other species may respond positively to these environmental changes and thus invade the reserve or make movement across the intervening habitat even more difficult. When species of conservation concern cannot keep pace with the environmental changes, existing reserves may not be adequate to protect the species (Hannah et al. 2007). These situations may require a change from a passive management paradigm to a more active management paradigm that includes manipulation of habitats in ways that ameliorate the effects of climate change and favor native species over invasive species, provision of dispersal corridors, translocation of species, and creation of migration barriers that prevent the influx of invasive species (Fig. 4).

To ameliorate the effects of climate change, managers may need to manipulate habitats in ways that favor native species. For example, the effects of warmer air temperatures can be countered by planting riparian vegetation to shade streams and reduce solar inputs. Shading helps maintain cool water temperatures needed by native species that might otherwise be replaced by invasive warmwater species. In Utah streams warm temperatures are thought to favor the invasive mosquitofish over the imperiled native least chub (*Lotichthys phlegethontis*) (Mills et al. 2004). Increasing stream shading by restoring riparian vegetation would reduce water temperatures and improve physical habitat conditions, both of which would favor native over invasive species.

A drier climate coupled with new reservoir construction will alter stream flow regimes by reducing the extent

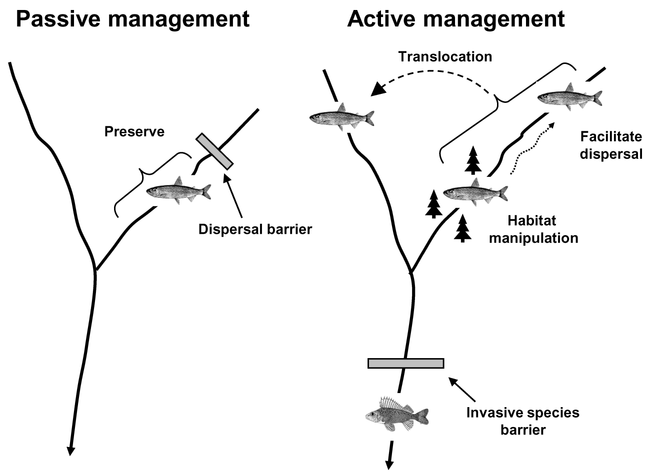


Figure 4. Passive versus active strategies for managing a species of conservation concern in a stream network. Active strategies include habitat manipulation, translocation to unused habitat, and management of barriers to facilitate movement by native species and exclude invasive species.

of high spring runoff (IPCC 2007). Such alterations often favor non-native aquatic species and, therefore, restoration of natural flow regimes can be an important management strategy for restoring native species and reducing invasive species with climate change (Hellmann et al. 2008 [this issue]). In Putah Creek, California, naturally high winter and spring flows flush many non-native fishes from the system and favor reproduction by spring-spawning native species versus summer-spawning non-native species (Marchetti & Moyle 2001). Restoring high-flow events dampened by reservoir storage is likely to be an important tool for controlling non-native fishes as humans respond to water shortages by building more reservoirs. Another situation in which proactive habitat management could help imperiled species under climate change involves pumping groundwater to maintain water levels in ponds used by amphibians for breeding (Seigel et al. 2006).

Creating corridors or stepping stones (hereafter corridors) of habitat for dispersal to keep populations connected and allow for genetic exchange is a fundamental concept in conservation biology. Biologists and managers creating these landscape connections need to consider whether these corridors can be used for species migrations associated with climate change (Hannah et al. 2007). In some cases the habitat that provides connectivity today may not be useful as a corridor in the future because of habitat changes caused by climate change. For example, many fish species of conservation concern migrate between disjunct areas that provide habitat for different life-history stages (Schrank & Rahel 2004; Rieman et al. 2007). These species would be threatened if the migration corridors between such habitats become unsuitable because of warm temperatures, desiccation, or construction of reservoirs. Therefore, it is important to consider how protected-area habitats may change and how habitat in areas used for connectivity may change.

The response of species currently existing in corridor habitats will also need to be considered, including the response of invasive species that may be a competitive or predatory threat to the species of conservation concern. Creating corridors may be challenging for aquatic species with narrow habitat preferences or limited mobility across the landscape matrix such as mollusks. Maintaining or creating corridors may not be an option in arid regions, where reduced precipitation associated with climate change may reduce the limited connectivity that presently exists among aquatic habitats. In these situations, species may be better protected through translocation.

Translocation involves the intentional movement of species to new areas to increase the species' range, supplement small populations, or establish new populations to reduce the risk of extinction due to local catastrophes (Rout et al. 2007). It is a widely used management tool for species of conservation concern, although success rates vary. Recently the term "assisted migration" has been used to describe efforts to establish populations of declining species in areas that are outside their historic range but that have become suitable due to climate change (Hulme 2005; McLachlan et al. 2007). Assisted migration presents a range of issues. There are concerns about transmitting diseases to new areas and disrupting genetic patterns across the landscape. A big concern is ensuring that translocated species do not cause harm to existing species. Translocating imperiled trout species to higher elevations to escape climate warming would cause problems for native amphibians that are themselves species of conservation concern (Vredenburg 2004). We need better understandings of which non-native species are likely to become invasive and which species of conservation concern could cause problems if translocated to environments outside their historical range.

In some situations a species of conservation concern may be able to adapt to climate change, but may face competition or predation from invasive species. Creating migration barriers to keep out invasive species that are expanding their range in response to climate change may be a viable solution (Fig. 4). Barriers are already used to control the spread of certain aquatic invasive species (Novinger & Rahel 2003; Stokstad 2003). If climate change increases the suitability of habitats for invasive species, barriers may be effective in allowing species of conservation concern to respond to climate changes without the competitive or predatory effects of non-native species. For example, cutthroat trout could respond to climate change by migrating to higher elevations that are currently too cold to support populations in Rocky Mountain streams. But such a response would only be successful if barriers are present to prevent incursion by highly competitive brook trout (Cooney et al. 2005). Barriers that prevent passage of invasive species but allow passage of native species would be especially useful. Much effort has been devoted to developing low-head dams that prevent upstream movement of sea lampreys into tributaries of the Great Lakes but do not impede movements of native fish species with better leaping abilities (Lavis et al. 2003). In Europe waterfall barriers >35 cm in height may prevent upstream colonization by the invasive European minnow (*Phoxinus phoxinus*) but allow normal migratory movements by native brown trout. The species selectivity of waterfalls is based on the superior leaping ability of brown trout relative to the minnow (Holthe et al. 2005).

Recommendations for Managing Species of Conservation Concern in the Face of Climate Change and Invasive Species

Resource and conservation managers should consider the interactive effects of climate change and invasive species when formulating management plans to conserve or restore species and populations. For example, the effectiveness of habitat conservation plans (HCPs) and associated recovery plans for federally threatened or endangered species are likely to be compromised if the effects of climate change on range shifts and species interactions are not considered. Although climate change is not always discussed in recovery plans, some recent plans do consider its direct and indirect consequences.

Several recovery plans in the Pacific Northwest specifically mention that climate change is an additional threat to Chinook salmon (*O. tshawytscha*), Chum salmon (*O. keta*), and bull trout because it may cause detrimental summer low flows and interact with the primary threats of habitat alteration, harvesting, and hatcheries (NMFS 2007*a*, 2007*b*). Specific recovery actions only deal with the primary threats, but the Puget Sound salmon recovery plan also calls for watershed and regional adaptive management plans to address climate-change impacts (NMFS 2007*a*). These steps are important because models show that attaining salmon recovery targets in the Pacific Northwest will become more difficult with climate warming. Habitat restoration may offset some effects of climate change, with greater population gains likely in lower-elevation rivers (Battin et al. 2007). Nevertheless, in addition to the direct threats of climate change, warmer waters may also increase the consumption of juvenile salmonids by invasive predators (Petersen & Kitchell 2001).

The recovery plan for the federally threatened Chiricahua leopard frog (*R. chiricahuensis*) considers the direct and indirect effects of climate change, including its interaction with predation by invasive species, disease, and habitat loss and degradation (USFWS 2007). If precipitation in the desert Southwest increases, it could benefit leopard frog populations, but allow populations of native and invasive predators to increase. If drought conditions increase, habitat for invasive predators may decrease, but Chiricahua leopard frog populations may also decline if frogs cannot disperse from drying habitats and reach drought refugia (USFWS 2007).

Increasing precipitation and temperatures also may affect disease dynamics. The fungus causing chytridiomycosis is expected to increase in warmer and wetter climates (Kriger & Hero 2007). Although reproductive rates may increase in warmer waters, the fungus is most pathogenic to frogs when air temperatures are cooler (Kriger & Hero 2007). The outcome for the Southwest is uncertain because warmer temperatures may reduce the impacts of chytridiomycosis, whereas increased precipitation may be favorable for the fungus. The recovery units for Chiricahua leopard frog populations contain elevation and microsite variability, which may buffer against some temperature and precipitation changes. Furthermore, actions are proposed to eliminate invasive predators and prevent further introductions (USFWS 2007).

Another important component of management plans for species of conservation concern is monitoring of status and trends. Monitoring programs should include efforts to detect new threats associated with climate change, such as invasive species that may be parasites, predators, competitors, or ecosystem engineers. In the case of the Chiricahua leopard frog, several recovery actions are aimed at detecting and eliminating invasive predators such as bullfrogs and non-native tiger salamanders (*Ambystoma tigrinum*) that can also carry the chytrid fungus (USFWS 2007). The interaction of climate change and invasive species may have an ironic twist in that the regulations designed to protect species of conservation concern may create bureaucratic impediments to the quick removal of invasive species. The need to detect and quickly act against invasive species responding to climate change should be considered in recovery and HCPs.

Most management plans such as HCPs and recovery plans incorporate static concepts of reserves, such as designating critical habitat for preservation. These protected areas could be designed with climate resiliency in mind by identifying areas that remain suitable for species of conservation concern over time, despite a changing climate (Williams et al. 2005). New reserves should consider the inclusion of areas that may be more resilient to climate-change effects (Hansen & Biringer 2003). Reserves that contain a variety of microclimates may provide areas that remain suitable for the species even with climate change. For example, in habitats where the duration of ice cover may be an important factor limiting the presence of invasive species, restoration of riparian vegetation can alter the local microclimate and increase the duration of ice cover (Wynn & Mostaghimi 2006). Promoting resilience by controlling other threats such as habitat destruction, pollution, or exploitation should also decrease interactive effects between invasive species and climate change (Harris & Tyrrell 2001).

Another idea to consider is dynamic reserves in which management intensity for species of conservation concern changes depending on effects of climate change, invasive species, or other threats. In a dynamic reserve network, managers would ideally respond to environmental changes by acquiring or protecting new areas to accommodate range shifts. For instance, The Nature Conservancy has been preparing for climate change in the Albemarle River estuary in North Carolina and Virginia by purchasing uplands along major waterways that could serve as escape zones for wetland species displaced inland by rising sea levels (Pearsall 2006). In many cases, however, existing reserves are constrained by surrounding land uses, land costs, and other processes that make dynamic solutions challenging.

The difficult task of managing species of conservation concern is likely to become even more challenging due to the interaction of climate change and invasive species. Species whose continued existence relies on protected areas will be particularly vulnerable because they will face increasingly unsuitable habitat conditions and growing threats from invasive species better adapted to the new climate regime. The problem will be especially acute for the many aquatic species of conservation concern that have limited ability to migrate to new habitats. A proactive management philosophy that incorporates habitat manipulation, migration corridors, assisted migration, and active management of invading species will be needed to prevent the loss of these species.

Acknowledgments

This manuscript was the result of a workshop hosted by the U.S. Environmental Protection Agency and the Environmental Law Institute. Helpful comments were provided by P. Moyle and 2 anonymous reviewers. The findings and conclusions in this report are those of the authors and do not necessarily represent the views of the U.S. Environmental Protection Agency.

Literature Cited

Battin, J., M. W. Wiley, M. H. Ruckelshaus, R. N. Palmer, E. Korb, K. K. Bartz, and H. Imaki. 2007. Projected impacts of climate change on salmon habitat restoration. Proceedings of the National Academy of Sciences of the United States of America **104:**6720–6725.

Blaustein, A. R., and J. M. Kiesecker. 2002. Complexity in conservation: lessons from the global decline of amphibian populations. Ecology Letters **5:**597–608.

Bronte, C. R., M. P. Ebener, D. R. Schreiner, D. S. DeVault, M. M. Petzold, D. A. Jensen, C. Richards, and S. J. Lozano. 2003. Fish community change in Lake Superior, 1970–2000. Canadian Journal of Fisheries and Aquatic Sciences **60:**1552–1574.

Byström, P., J. Karlsson, P. Nilsson, T. Van Kooten, J. Ask, and F. Olofsson. 2007. Substitution of top predators: effects of pike invasion in a subarctic lake. Freshwater Biology **52:**1271–1280.

Carveth, C. J., A. M. Widmer, and S. A. Bonar. 2006. Comparison of upper thermal tolerances of native and nonnative fish species in Arizona. Transactions of the American Fisheries Society **135:**1433–1440.

Contreras-Balderas, S., P. Almada-Villela, M. de Lourdes Lozano-Vilano, and M. García-Ramírez. 2002. Freshwater fish at risk or extinct in Mexico: a checklist and review. Reviews in Fish Biology and Fisheries **12:**241–251.

Cooney, S. J., A. P. Covich, P. M. Lukacs, A. L. Harig, and K. D. Fausch. 2005. Modeling global warming scenarios in greenback cutthroat trout (*Oncorhynchus clarkii stomias*) streams: implications for species recovery. Western North American Naturalist **65:**371–381.

Crowder, L. B. 1986. Ecological and morphological shifts in Lake Michigan fishes: glimpse of the ghost of competition past. Environmental Biology of Fishes **16:**147–157.

De Staso, J., III, and F. J. Rahel. 1994. Influence of water temperature on interactions between young Colorado River cutthroat trout and brook trout in a laboratory stream. Transactions of the American Fisheries Society **123:**289–297.

Fausch, K. D., Y. Taniguchi, S. Nakano, G. D. Grossman, and C. R. Townsend. 2001. Flood disturbance regimes influence rainbow trout invasion success among five Holarctic regions. Ecological Applications **11:**1438–1455.

Flebbe, P. A. 1993. Comment on Meisner (1990): effect of climate warming on the southern margins of the native range of brook trout *Salvelinus fontinalis*. Canadian Journal of Fisheries and Aquatic Sciences **50:**883–884.

Hannah, L., G. Midgley, S. Andelman, M. Araujo, G. Hughes, E. Martinez-Meyer, R. Pearson, and P. Williams. 2007. Protected area needs in a changing climate. Frontiers in Ecology and the Environment **5:**131–138.

Hansen, L. J., and J. L. Biringer. 2003. Building resistance and resilience to climate change. Pages 7–12 in L. J. Hansen, J. L. Biringer, and J. R. Hoffman, editors. Buying time: a user's manual for building resistance and resilience to climate change in natural systems. World Wildlife Fund, Berlin, Germany.

Hari, R. E., D. M. Livingstone, R. Siber, P. Burkhardt-Holm, and H. Güttinger. 2006. Consequences of climate change for water temperature and brown trout populations in Alpine rivers and streams. Global Change Biology **12:**10–26.

Harris, L. G., and M. C. Tyrrell. 2001. Changing community states in the Gulf of Maine: synergism between invaders, overfishing and climate change. Biological Invasions **3:**9–21.

Hasegawa, K., and K. Maekawa. 2008. Different longitudinal distribution patterns of native white-spotted charr and non-native brown trout in Monbetsu stream, Hokkaido, northern Japan. Ecology of Freshwater Fish: **17:**189–192.

Helfman, G. S. 2007. Fish conservation: a guide to understanding and restoring global aquatic biodiversity and fishery resources. Island Press, Washington, D.C.

Hellmann, J. J., J. E. Byers, B. B. Bierwagen, and J. S. Dukes. 2008. Five potential consequences of climate change for invasive species. Conservation Biology **22:** in press.

Hickling, R., D. B. Roy, J. K. Hill, R. Fox, and C. D. Thomas. 2006. The distributions of a wide range of taxonomic groups are expanding polewards. Global Change Biology **12:**450–455.

Higgins, C. L., and G. R. Wilde. 2005. The role of salinity in structuring fish assemblages in a prairie stream system. Hydrobiologia **549:**197–203.

Hill, D. K., and J. J. Magnuson. 1990. Potential effects of global climate warming on the growth and prey consumption of Great Lakes fish. Transactions of the American Fisheries Society **119:**265–275.

Hiner, M., and C. M. Moffitt. 2001. Variation in infections of *Myxobolus cerebralis* in field-exposed cutthroat and rainbow trout in Idaho. Journal of Aquatic Animal Health **13:**124–132.

Holmes, J. A. 1990. Sea lamprey as an early responder to climate change in the Great Lakes basin. Transactions of the American Fisheries Society **119:**292–300.

Holzapfel, A., and R. D. Vinebrooke. 2005. Environmental warming increases invasion potential of alpine lake communities by imported species. Global Change Biology **11:**2009–2015.

Holthe, E., E. Lund, B. Finstad, E. B. Thorstad, and R. S. McKinley. 2005. A fish selective obstacle to prevent dispersion of an unwanted fish species, based on leaping abilities. Fisheries Management and Ecology **12:**143–147.

Hulme, P. E. 2005. Adapting to climate change: is there scope for ecological management in the face of a global threat? Journal of Applied Ecology **42:**784–794.

IPCC. 2007. Climate change 2007: Impacts, adaptation and vulnerability. Contribution of Working Group II to the Fourth assessment report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom.

Johnson, T. B., and D. O. Evans. 1990. Size-dependent winter mortality of young-of-the-year white perch: climate warming and invasion of the Laurentian Great Lakes. Transactions of the American Fisheries Society **119:**301–313.

Kiesecker, J. M., and A. R. Blaustein. 1998. Effects of introduced bullfrogs and smallmouth bass on microhabitat use, growth, and survival of native red-legged frogs (*Rana aurora*). Conservation Biology **12:**776–787.

Koel, T. M., D. L. Mahony, K. L. Kinnan, C. Rasmussen, C. J. Hudson, S. Murcia, and B. L. Kerans. 2006. *Myxobolus cerebralis* in native cutthroat trout of the Yellowstone Lake ecosystem. Journal of Aquatic Animal Health **18:**157–175.

Krajick, K. 2004. All downhill from here? Science **303:**1600–1602.

Kriger, K. M., and J. M. Hero. 2007. Large-scale seasonal variation in the prevalence and severity of chytridiomycosis. Journal of Zoology **271:**352–359.

Larsen, G. L., and S. E. Moore. 1985. Encroachment of exotic rainbow trout into stream populations of native brook in the southern Appalachian Mountains. Transactions of the American Fisheries Society **114:**195–203.

Lavis, D. S., A. Hallett, E. M. Koon, and T. C. McAuley. 2003. History of and advances in barriers as an alternative method to suppress sea lampreys in the Great Lakes. Journal of Great Lakes Research **29**(supplement 1):362–372.

Lodge, D. M., C. A. Taylor, D. M. Holdich, and J. Skurdal. 2000. Nonindigenous crayfishes threaten North American freshwater biodiversity: lessons from Europe. Fisheries **28:**7–20.

Lovejoy, T. E., and L. Hannah, editors. 2005. Climate change and biodiversity. Yale University Press, New Haven, Connecticut.

Malcolm, J. R., C. Lui, R. P. Neilson, L. Hansen, and L. Hannah. 2006. Global warming and extinctions of endemic species from biodiversity hotspots. Conservation Biology **20:**538–548.

Marchetti, M. P., and P. B. Moyle. 2001. Effects of flow regime on fish assemblages in a regulated California stream. Ecological Applications **11:**530–539.

Marcogliese, D. J. 2001. Implications of climate change for parasitism of animals in the aquatic environment. Canadian Journal of Zoology **79:**1331–1352.

Matthews, W. J., and E. G. Zimmerman. 1990. Potential effects of global warming on native fishes of the southern Great Plains and the Southwest. Fisheries **15:**26–32.

McLachlan, J. S., J. J. Hellmann, and M. W. Schwartz. 2007. A framework for debate of assisted migration in an era of climate change. Conservation Biology **21:**297–302.

Mills, M. D., R. B. Rader, and M. C. Belk. 2004. Complex interactions between native and invasive fish: the simultaneous effects of multiple negative interactions. Oecologia **141:**713–721.

Mohseni, O., H. G. Stefan, and J. G. Eaton. 2003. Global warming and potential changes in fish habitat in U.S. streams. Climate Change **59:**389–409.

NMFS (National Marine Fisheries Service). 2007*a*. Puget Sound salmon recovery plan. Volume 1. NMFS, Seattle.

NMFS (National Marine Fisheries Service). 2007*b*. Recovery plan for the Hood Canal and eastern Strait of Juan de Fuca summer chum salmon (*Oncorhynchus keta*). NNFS, Northwest Region, Portland, Oregon.

Nakata, K., T. Nakaoka, and S. Goshima. 2006. Negative effects of the invasive brown trout, *Salmo trutta,* on freshwater crustacean species: predation on the endangered Japanese endemic crayfish species *Cambaroides japonicus* by the trout. Nippon Suisan Gakkaishi **72:**447–449.

Novinger, D. L., and F. J. Rahel. 2003. Is isolating cutthroat trout above artificial barriers in small headwater streams an effective long-term conservation strategy? Conservation Biology **17:**772–781.

Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. Annual Review of Ecology, Evolution, and Systematics **37:**637–669.

Paul, A. J., and J. R. Post. 2001. Spatial distribution of native and nonnative salmonids in streams of the eastern slopes of the Canadian Rocky Mountains. Transactions of the American Fisheries Society **130:**417–430.

Pearsall, S. 2006. Adapting coastal lowlands to rising seas. Pages 366–370 in M. J. Groom, G. K. Meffe, and C. R. Carroll, editors. Principles of conservation biology. 3rd edition. Sinauer Associates, Sunderland, Massachusetts.

Pearson, R. G. 2006. Climate change and the migration capacity of species. Trends in Ecology & Evolution **21:**111–113.

Petersen, J. H., and J. F. Kitchell. 2001. Climate regimes and water temperature changes in the Columbia River: bioenergetic implications for predators of juvenile salmon. Canadian Journal of Fisheries and Aquatic Sciences **58:**1831–1841.

Peterson, M. S., W. T. Slack, and C. M. Woodley. 2005. The occurrence of non-indigenous Nile tilapia *Oreochromis niloticus* (Linnaeus) in coastal Mississippi, USA: ties to aquaculture and thermal effluent. Wetlands **25:**112–121.

Pounds, J. A., et al. 2006. Widespread amphibian extirpations from epidemic disease driven by global warming. Nature **439:**161–167.

Pringle, C. M., M. C. Freeman, and B. J. Freeman. 2000. Regional effects of hydrologic alterations on riverine macrobiota in the New World: tropical-temperate comparisons. BioScience **50:**807–823.

Rahel, F. J. 2002. Using current biogeographic limits to predict fish distributions following climate change. Pages 99–110 in N. A. McGinn, editor. Fisheries in a changing climate. Symposium 32. American Fisheries Society, Bethesda, Maryland.

Rahel, F. J., and J. D. Olden. 2008. Assessing the effects of climate change on aquatic invasive species. Conservation Biology **22:** in press.

Rahel, F. J., C. J. Keleher, and J. L. Anderson. 1996. Potential habitat loss and population fragmentation for cold water fish in the North Platte River drainage of the Rocky Mountains: response to climate warming. Limnology and Oceanography **41:**1116–1123.

Reese, C. D., and B. C. Harvey. 2002. Temperature-dependent interactions between juvenile steelhead and Sacramento pikeminnow in laboratory streams. Transactions of the American Fisheries Society **131:**599–606.

Rieman, B. E., D. Isaak, S. Adams, D. Horan, D. Nagel, C. Luce, and D. Myers. 2007. Spatial variation in anticipated climate change effects on bull trout habitats across the interior Columbia River basin. Transactions of the American Fisheries Society **136:**1552–1565.

Rout, T. M., C. E. Hauser, and H. P. Possingham. 2007. Minimise long-term loss or maximise short-term gain? Optimal translocation strategies for threatened species. Ecological Modelling **201:**67–74.

Ruzycki, J. R., D. A. Beauchamp, and D. L. Yule. 2003. Effects of introduced lake trout on native cutthroat trout in Yellowstone Lake. Ecological Applications **13:**23–37.

Saunders, D. L., J. J. Meeuwig, and A. C. J. Vincent. 2002. Freshwater protected areas: strategies for conservation. Conservation Biology **16:**30–41.

Schrank, A. J., and F. J. Rahel. 2004. Movement patterns in inland cutthroat trout (*Oncorhynchus clarkii utah*): management and conservation implications. Canadian Journal of Fisheries and Aquatic Sciences **61:**1528–1537.

Seigel, R. A., A. Dinsmore, and S. C. Richter. 2006. Using well water to increase hydroperiod as a management option for pond-breeding amphibians. Wildlife Society Bulletin **43:**1022–1027.

Stachowicz, J. J., J. R. Terwin, R. B. Whitlatch, and R. W. Osman. 2002. Linking climate change and biological invasions: ocean warming facilitates nonindigenous species invasions. Proceedings of the National Academy of Sciences of the United States of America **99:**15497–15500.

Stokstad, E. 2003. Can well-timed jolts keep out unwanted exotic fish? Science **301:**157–158.

Strayer, D. L. 1999. Effects of alien species on freshwater mollusks in North America. Journal of the North American Benthological Society **18:**74–98.

Suffling, R., and D. Scott. 2002. Assessment of climate change effects on Canada's national park system. Environmental Monitoring and Assessment **74:**117–139.

Taniguchi, Y., and S. Nakano. 2000. Condition-specific competition: implications for the altitudinal distribution of stream fishes. Ecology **81:**2027–2039.

Taniguchi, Y., Y. Miyake, T. Saito, H. Urabe, and S. Nakano. 2000. Redd superimposition by introduced rainbow trout, *Oncorhynchus mykiss*, on native charrs in a Japanese stream. Ichthyological Research **47:**149–156.

Taniguchi, Y., F. J. Rahel, D. C. Novinger, and K. G. Gerow. 1998. Temperature mediation of competitive interactions among three fish species that replace each other along longitudinal stream gradients. Canadian Journal of Fisheries and Aquatic Sciences **55:**1894–1901.

USFWS (U.S. Fish and Wildlife Service). 2007. Chiricahua leopard frog (*Rana chiricahuensis*) recovery plan. USFWS, Southwest Region, Albuquerque, New Mexico.

Vredenburg, V. T. 2004. Reversing introduced species effects: experimental removal of introduced fish leads to rapid recovery of a declining frog. Proceedings of the National Academy of Sciences of the United States of America **101:**7646–7650.

Whitledge, G. W., and C. F. Rabeni. 2003. Maximum daily consumption and respiration rates at four temperatures for five species of crayfish from Missouri, U.S.A. (Decapoda, *Orconectes* spp.). Crustaceana **75:**1119–1132.

Wilcove, D. S., D. Rothstein, J. Dubow, A. Phillips, and E. Losos. 1998. Quantifying threats to imperiled species in the United States. BioScience **48:**607–615.

Williams, P., L. Hannah, S. Andelman, G. Midgley, M. Araujo, G. Hughes, L. Manne, E. Martinez-Meyer, and R. Pearson. 2005. Planning for climate change: identifying minimum-dispersal corridors for the Cape Proteaceae. Conservation Biology **19:**1063–1074.

Wynn, T., and S. Mostaghimi. 2006. The effects of vegetation and soil type on streambank erosion, southwestern Virginia, USA. Journal of the American Water Resources Association **42:**69–82.