Alien invasions in aquatic ecosystems: Toward an understanding of brook trout invasions and potential impacts on inland cutthroat trout in western North America

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Abstract

Experience from case studies of biological invasions in aquatic ecosystems has motivated a set of proposed empirical "rules" for understanding patterns of invasion and impacts on native species. Further evidence is needed to better understand these patterns, and perhaps contribute to a useful predictive theory of invasions. We reviewed the case of brook trout (*Salvelinus fontinalis*) invasions in the western United States and their impacts on native cutthroat trout (*Oncorhynchus clarki*). Unlike many biological invasions, a considerable body of empirical research on brook trout and cutthroat trout is available. We reviewed life histories of each species, brook trout invasions, their impacts on cutthroat trout, and patterns and causes of segregation between brook trout and cutthroat trout. We considered four stages of the invasion process: transport, establishment, spread, and impacts to native species. Most of the research we found focused on impacts. Interspecific interactions, especially competition, were commonly investigated and cited as impacts of brook trout. In many cases it is not clear if brook trout invasions have a measurable impact. Studies of species distributions in the field and a variety of experiments suggest invasion success of brook trout is associated with environmental factors, including temperature, landscape structure, habitat size, stream flow, and human influences. Research on earlier stages of brook trout invasions (transport, establishment, and spread) is relatively limited, but has provided promising insights. Management alternatives for controlling

brook trout invasions are limited, and actions to control brook trout focus on direct removal, which is variably successful and can have adverse effects on native species. The management applicability of research has been confounded by the complexity of the problem and by a focus on understanding processes at smaller scales, but not on predicting patterns at larger scales. In the short-term, an improved predictive understanding of brook trout invasions could prove to be most useful, even if processes are incompletely understood. A stronger connection between research and management is needed to identify more effective alternatives for controlling brook trout invasions and for identifying management priorities.

Introduction

Invasions by nonnative species are a serious threat to the integrity of freshwater ecosystems (Claudi and Leach, 1999; Fuller et al., 1999; Kolar and Lodge, 2000, 2001; Rahel, 2002). The rising "tide" of nonnative species invading aquatic ecosystems has overwhelmed available management resources, necessitating prioritization of actions to mitigate negative impacts (Parker et al., 1999). Much of the focus on nonnative invasions has been on potential impacts, but understanding factors that initiate or facilitate invasions is also important (Byers and Goldwasser, 2001; Kolar and Lodge, 2001; Sakai et al., 2001, Figure 1). Understanding both the causes *and* effects of biological invasions is essential for developing effective management strategies. A general theory of biological invasions has yet to emerge (Parker et al., 1999), but lessons from case histories can provide important insights. Moyle and Light (1996) proposed a series of empirical rules for aquatic invasions based on their reviews of several case histories in a variety of estuarine and freshwater habitats. They concluded that invasion success in aquatic ecosystems is difficult to predict from existing theory and suggested that the best practical guidance may come from past experiences and detailed understanding of both the invading species and the receiving systems.

Of the nonnative species invading aquatic ecosystems, fishes of the subfamily salmoninae (salmon, trout, and charr of the genera *Oncorhynchus*, *Salmo*, and *Salvelinus*) are among the most globally widespread (Welcomme, 1988). Nonnative salmonines have been introduced for over a century in North America (Claudi and Leach, 1999; Fuller et al., 1999). In most cases, salmonines were introduced intentionally to provide recreational or commercial fishing. Whether introduced among an existing fish community or in formerly fishless habitats, salmonines have been widely implicated in declines of native aquatic biota (e.g., Minckley and Deacon,

1991; Crowl et al., 1992; Polhemus, 1993; Knapp et al., 2001). In many cases, nonnative salmonines were introduced into habitats that already supported one or more native salmonines. The potential impacts of nonnative salmonines on native species are widely cited (e.g., Moore et al., 1983; Allendorf and Leary, 1988; Gresswell, 1988; Behnke, 1992; Young, 1995), but the mechanisms through which they occur are poorly understood (Fausch, 1988). Because nonnative salmonines are biologically very similar to native salmonines, there is a strong potential for common resource requirements (i.e., high niche overlap) and for interspecific interactions. Interspecific competition is the most frequently cited ecological interaction between native and nonnative salmonines (Fausch, 1988), but the direct and indirect effects of predation, parasite and disease transmission, and hybridization are potentially important as well (Taylor et al., 1984).

In western North America, rainbow trout (*Oncorhynchus mykiss*), brook trout (*Salvelinus fontinalis*), and brown trout (*Salmo trutta*) are the most widespread nonnative salmonine species (Fuller et al., 1999). Many systems in the region also support native rainbow trout, whereas brown trout originated from Europe and brook trout from eastern North America (Fuller et al., 1999). Within the region, the number of native salmonines varies widely among basins. Basins with open access to marine habitats may support several native species, whereas more isolated basins may support only one. In the latter case, invasions by nonnative salmonines could be more successful and have a larger impact on native species because the single native species may not share a recent coevolutionary history with other salmonines (Griffith, 1988).

In this paper, we focus on invasions of brook trout and their potential impacts on native inland cutthroat trout (*Oncorhynchus clarki*). The cutthroat trout is a widespread and polytypic species in western North America (Allendorf and Leary, 1988; Behnke, 1992; Young, 1995; Figure 2). The presence of brook trout is viewed as a major threat to cutthroat trout (Griffith,
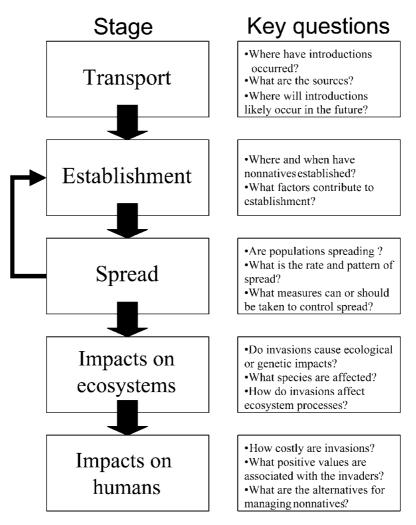
Stage

Key questions

| Transport | •Where have introductions occurred?
•What are the sources?
•Where will introductions likely occur in the future? |

| Establishment | •Where and when have nonnatives established?
•What factors contribute to establishment? |

| Spread | •Are populations spreading ?
•What is the rate and pattern of spread?
•What measures can or should be taken to control spread? |

| Impacts on ecosystems | •Do invasions cause ecological or genetic impacts?
•What species are affected?
•How do invasions affect ecosystem processes? |

| Impacts on humans | •How costly are invasions?
•What positive values are associated with the invaders?
•What are the alternatives for managing nonnatives? |

Figure 1. Generalized steps in the invasion process (modified from Kolar and Lodge, 2001; Sakai et al., 2001). For each step, key questions relevant to understanding and managing invasions are highlighted. Arrows indicate the general direction of events in the invasion process, but interactions among all stages are possible.

1988; Young, 1995), and the issue of brook trout invasions has motivated considerable research and management interest. We begin by reviewing: (1) natural histories of cutthroat trout and brook trout; (2) patterns and causes of brook trout invasions; (3) potential impacts of brook trout on cutthroat trout; and (4) patterns of habitat use and segregation of brook trout and cutthroat trout. In some cases, we illustrate key issues from studies of other fishes, because they have not received attention in the context of brook trout and cutthroat trout. Following this review, we identify directions for future research and offer suggestions for managing brook trout invasions and their impacts. The complexities that emerge from this case study of a single invading species (brook trout) and potential impacts on a similar native species (cutthroat trout) provide important lessons that we believe are broadly relevant to understanding and managing invasions of nonnative species in aquatic ecosystems (Moyle and Light, 1996).

Natural histories of inland cutthroat trout and brook trout

The taxonomy, natural history, and status of inland cutthroat trout is reviewed in depth elsewhere (e.g., Gresswell, 1988; Behnke, 1992; Young, 1995), so we provide only a brief overview. Inland cutthroat trout comprise a complex of seven major subspecies
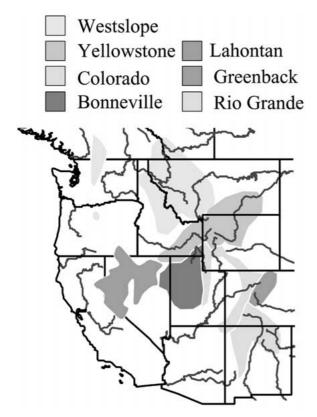
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Figure 2. Geographic distribution of the seven major inland cutthroat trout subspecies, including westslope (*O. clarki lewisi*), Yellowstone (*O. c. bouvieri*), Colorado (*O. c. pleuriticus*), Bonneville (*O. c. utah*), Lahontan (*O. c. henshawi*), Greenback (*O. c. stomias*), and Rio Grande (*O. c. virginalis*) cutthroat trout.

that occupy a large portion of western North America (Figure 2), with several additional subspecies occupying smaller areas (Behnke, 1992). Regardless of taxonomic classification, the species encompasses a large amount of evolutionary diversification (Allendorf and Leary, 1988), which reflects the complex and diverse geological, hydrological, and ecological conditions in the region over evolutionary time (Behnke, 1992). Inland cutthroat trout presently occur from the southern Rocky Mountains and Sierra Blanca in New Mexico (∼33° N latitude) to the northern Cascade and Rocky Mountains in Alberta and British Columbia, Canada (∼52° N latitude; Figure 2). Of the inland subspecies, only the westslope cutthroat trout naturally co-occurs with other native salmonines, including several species of Pacific salmon, rainbow trout (*Oncorhynchus* spp.), and bull trout (*Salvelinus confluentus*).

Historical accounts indicate abundant cutthroat trout populations in the region prior to modern human land development (Trotter, 1987; Gresswell, 1988; Behnke, 1992). Declines in all subspecies were apparent by the late 19th century (Behnke, 1992) and continue into the present. Habitat loss and degradation, harvest, and influences of artificial propagation and nonnative fishes are commonly cited factors in the declines (Young, 1995). There are currently three subspecies formally listed as endangered or threatened under the U.S. Endangered species act (*O. c. seleniris*, *O. c. stomias*, *O. c. henshawi*), but the status of cutthroat trout is a management concern throughout the species' range (Gresswell, 1988; Young, 1995; Duff, 1996).

The life cycle of cutthroat trout is typical of salmonines (Bjornn and Reiser, 1991). Adults deposit eggs in stream gravels in the spring or early summer, where eggs hatch into alevins. Alevins typically remain in or near spawning substrates until the yolk sac is absorbed. Following absorption of the yolk sac, the young (fry) begin active feeding and development into fully formed juveniles. In the "resident" life history form, juveniles remain in their natal stream through maturity. Known migratory life histories include short and long-distance (>100 km) migrations to lakes and rivers (Behnke, 1992).

Similar to cutthroat trout, brook trout evolved under diverse conditions and have developed substantial within-species variability (Power, 1980; Angers et al., 1995). Hatchery and naturalized populations of brook trout also tend to maintain high levels of genetic diversity (McCracken et al., 1993; Ovenden et al., 1993). Compared to cutthroat trout, brook trout evolved with much more diverse fish assemblages, although not with diverse salmonine assemblages. Historically, brook trout commonly co-occurred with lake trout (*Salvelinus namaycush*), arctic charr (*S. alpinus*), and Atlantic salmon (*Salmo salar*). Cutthroat trout and brook trout life histories are similar in many ways, but there are potentially important differences between the two species, including spawning and fry emergence timing, age- and size-at-maturity, and migration patterns (discussed below). Each trait, however, is highly variable within each species. A major distinction is that brook trout are fall spawning. Multiple migratory patterns are evident within the native range of brook trout (Power, 1980), but these are less developed among brook trout populations in western North America. Nonetheless, some individual brook trout can be highly mobile (Gowan and Fausch, 1996; Adams, 1999; Peterson, 2002).

Brook trout invasions

Much of the attention regarding brook trout invasions has focused on impacts to native species and ecosystems. It is becoming increasingly obvious, however, that an understanding of the process of invasion is equally important. Successful biological invasions consist of two early stages: arrival or transport (including human introductions), and establishment (Figure 1). Establishment may be followed by dispersal or spread, thereby initiating a new invasion cycle (Carlton, 1996). The stages may cycle continuously or irregularly, and each can limit a species' invasive ability in a given habitat (D'Antonio, 1993; Kolar and Lodge, 2001). Abiotic and biotic characteristics of the new location will determine success at each stage (Moyle and Light, 1996). Different factors may influence each stage of an invasion, and the time scales over which different factors influence each stage may vary as well (Kolar and Lodge, 2001; Sakai et al., 2001).

Like other intentional introductions (Welcomme, 1988), many brook trout introductions differ from accidental or "natural" introductions in that initial propagules were typically large, and introductions were often made repeatedly. Such intensive introductions, timed appropriately, can radically increase the probability of establishment (Moyle and Light, 1996; Williamson and Fritter, 1996). Beginning in the late 1800s, brook trout were introduced to 35 states in the USA and throughout much of western Canada (Fuller et al., 1999). In the United States, state-supported brook trout stocking continues in at least 7 of the 11 western states, although most restrict stocking to areas where brook trout are not expected to contact native salmonids (see Acknowledgments).

The result of intensive transport (Figure 1) has been widespread establishment of brook trout populations. Extreme plasticity of age at first maturity, ranging from age-1 (McFadden, 1961) to age-16 (Reimers, 1979), may facilitate establishment. The propensity of brook trout to mature rapidly facilitates both establishment and expansion of populations. Under the proper conditions, this may confer a demographic advantage to brook trout, relative to native salmonines (Paul, 2000). This may be particularly true of streams where natural or human influences have reduced densities of native salmonines (Leary et al., 1993; Paul, 2000).

Persistence of established brook trout in individual streams could be limited by physical factors such as hydrologic cycles and temperatures. Pre-emergence (e.g., winter) floods have been shown to reduce brook trout year class strength (Seegrist and Gard, 1972; Strange et al., 1992; Latterell et al., 1998). Forest fires and associated debris flows eliminated brook trout from isolated stream habitats in Arizona (Rinne, 1996), but local extinctions in response to such events have been observed for other species as well (Dunham et al., 2003). Severe drought eliminated brook trout from stream segments in California, but fish rapidly recolonized after normal flows resumed (Erman et al., 1988). In general, established populations of brook trout appear to persist well in stream networks (Adams et al., 2002). Spatial structure of both habitat and brook trout populations appears to maintain distributions in part by maintaining refuges during disturbances (e.g., Rieman and Dunham, 2000; Dunham et al., 2003), or through source-sink dynamics (Adams, 1999).

Although brook trout were initially introduced to western North America via human effort, they have spread and established in secondary (unstocked) locations. In many instances, brook trout populations were established at the site of introduction, but in others, stocking locations are not clearly linked to the locations of established populations (Paul and Post, 2001). The rates and patterns of dispersal by brook trout likely depend on two factors: positive population growth in source populations, and the ability to disperse through hydrologic networks to locate and colonize new habitats. The tendency of brook trout to mature rapidly under favorable growth conditions often allows for positive population growth, even with substantial fishing mortality (Adams, 1999; Paul, 2000).

The ability of brook trout to disperse through hydrologic networks depends on both the topography of the stream network and the location of source population (Adams et al., 2000, 2001). For example, fish introduced to headwater lakes effectively have access to more stream area than those introduced downstream in drainage networks (Adams et al., 2001). In other words, it is easier for fish to colonize in a downstream direction, rather than to disperse upstream against the flow and potential barriers such as steep cascades and waterfalls. However, individual brook trout are capable of moving moderate distances (e.g. >15 km, Shetter, 1968; Gowan and Fausch, 1996; Adams et al., 2001) and up steep stream slopes (e.g. 13% or more, Adams et al., 2000), suggesting that in many stream networks, factors other

than dispersal ability limit invasion (Adams et al., 2002).

Extreme or lethal conditions may limit the spread of invasions, but subtle declines in demographic rates can be sufficient to create a distribution limit (Adams, 1999). A gradual upstream decline in brook trout growth rate associated with declining water temperatures probably created the upstream distribution limit in one Montana stream (Adams, 1999). Also, source-sink population dynamics may have been important in maintaining the brook trout distribution in the stream (Adams, 1999). Thus, all factors that cause declines in fish growth, reduce recruitment of age-0 fish, and inhibit dispersal from source areas can contribute to limiting invasion (Taniguchi and Nakano, 2000; Byers and Goldwasser, 2001).

The very slow or perhaps intermittent spread of invasions by brook trout in some streams suggests that invasion may occur in pulses rather than as a steady process (Adams et al., 2002). In the South Fork Salmon River drainage, Idaho, USA, brook trout distributions in most of the 19 tributary streams studied were relatively unchanged after 24 years, even though only four streams had obvious physical barriers to upstream dispersal. Extensive invasion was evident in only one stream, in spite of frequent observations of wandering or dispersing brook trout (Adams et al., 2001, 2002). Some evidence suggests pulses of invasion by brook trout may be facilitated by habitat degradation. Griffith (1988) assessed brook trout distributions over 10 years in two streams where brook trout and cutthroat trout were sympatric. He observed brook trout invasion in one stream where the habitat was degraded (the riparian forest was logged) over the course of the study, but not in the other where no degradation occurred (see also Leary et al., 1993). As Moyle and Light (1996) hypothesized for nonnative species in general, brook trout invasions may occur largely within limited windows of ecological opportunity associated with short-term changes in the environment, the local fish community, or both.

Effects of brook trout invasions on cutthroat trout

As brook trout have invaded aquatic ecosystems in western North America, native cutthroat trout have declined (Gresswell, 1988; Young, 1995). Two explanations are possible. First, it is possible that brook trout *replace* cutthroat trout as the latter decline

in response to unrelated factors. Second, brook trout may actively *displace* cutthroat trout. A majority of the literature suggests that displacement is the primary mechanism, but the alternative of replacement has not been empirically tested in the field. Three potential mechanisms of displacement are commonly cited: competition, predation, and parasite or disease transmission. These impacts may occur as a result of interactions within single life stages (e.g., adults, juveniles) or across life stages (e.g., predation by adults on juveniles).

Interspecific competition is the most widely cited mechanism of displacement of cutthroat trout by brook trout (Griffith, 1988). Competition can occur through two mechanisms. Individuals may pre-empt others from obtaining limited resources by depleting the resources first ("scramble" or "exploitative" competition), or by actively preventing access to resources ("contest" or "interference" competition). For salmonine fishes, either is a strong possibility (Keeley, 2001). Interspecific competition is relatively straightforward to study under controlled conditions (in a laboratory or field enclosure), but the influence of competition on whole populations under field conditions is less well known. Nakano et al. (1998) provided one of the few descriptions of species interactions under natural conditions. Despite frequent aggressive interactions, consistent differences in dominance between cutthroat trout and brook trout were not discernable. Griffith (1972) also observed aggressive interactions between cutthroat trout and brook trout in natural populations but did not report the frequencies or outcomes of the interactions. Thus, there seems to be little question that interference-type interactions can occur between individual cutthroat trout and brook trout under natural conditions in streams. Field experiments with stream enclosures suggest that brook trout can reduce the feeding efficiency and growth of cutthroat trout and increase mortality (Thomas, 1996; Novinger, 2000). Many studies in the field and laboratory (reviewed below) have addressed conditions that may affect the outcome of interspecific competition.

Interspecific predation is a less commonly cited but potentially important mechanism for displacement. Given the relative size differences between age-0 and older brook trout and age-0 cutthroat trout (due to later spawning and emergence by the latter), predation has been postulated as a mechanism through which brook trout could reduce cutthroat trout populations and consequently enhance displacement of the latter species (Griffith, 1972; Irving, 1987; Griffith, 1988;

Dunham et al., 2000; Novinger, 2000). Novinger (2000) observed several instances of predation by large age-0 brook trout on smaller age-0 cutthroat trout when both species were placed together in field enclosures. Laboratory experiments also revealed predation by brook trout on smaller cutthroat trout. A gape-limited predation model predicted that cutthroat trout aged 0 to 1 month would be vulnerable to predation by 90–100% of the age-0 brook trout in a typical population (Novinger, 2000). However, after an additional 2 months of growth by both species, the percentage of potential brook trout predators decreased to 18%. Gregory and Griffith (2000) attributed overwinter losses of age-0 cutthroat trout in field enclosures to predation by age-0 brook trout, but predation was not directly observed in their study. Dunham et al. (2000) studied diets of free-ranging sympatric brook trout and cutthroat trout, and found no evidence for predation by brook trout on cutthroat trout, or vice-versa. This study was limited in time and space, so the possibility of predation cannot be eliminated. Irving (1987) conducted a series of short-term (≤6 week) experiments to study predation by resident cutthroat and brook trout on cutthroat trout fry stocked in stream pools in northern Idaho. Following stocking, cutthroat trout fry densities declined more quickly in habitats containing brook trout only or both cutthroat and brook trout, compared to those containing only cutthroat trout. Presumably, declines in fry densities were due at least in part to predation by brook trout, but other factors (e.g., emigration, mortality from other predators or starvation) cannot be ruled out. Irving (1987) also directly observed predation on cutthroat trout fry by large and small (age-0) brook trout in streams. However, several aspects of the study (e.g., cutthroat trout fry were raised in captivity, and stocked at high densities ranging from 500–1,000/m²) may not have reflected natural conditions.

Parasite or disease transmission is another possible influence of brook trout on cutthroat trout, but evidence for this mechanism is lacking. Disease transmission is a tremendous concern in hatchery-supplemented fisheries (Stewart, 1991). Because many brook trout populations originated from past or continued stocking, disease transmission to cutthroat trout could be important. The single study specifically addressing this issue did not find evidence of disease transmission (Peterson, 2002). It is also possible that indigenous diseases could inhibit invasions of nonnative trout (Currens et al., 1997). Finally, competition, predation, and disease transmission may act
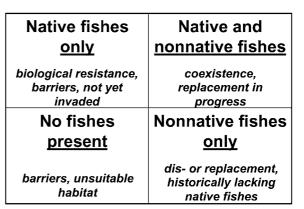
Native fishes only	Native and nonnative fishes
biological resistance, barriers, not yet invaded	*coexistence, replacement in progress*
No fishes present	Nonnative fishes only
barriers, unsuitable habitat	*dis- or replacement, historically lacking native fishes*

Figure 3. Four possible patterns of distribution between native and nonnative fishes (underlined text). Below each possible state is a brief list of potential explanations for each pattern (italic text).

in concert to affect segregation between cutthroat and brook trout. Disease, for example, can strongly modify interspecific interactions in other systems (e.g., Mesa et al., 1998).

Habitat use patterns and potential causes of species segregation

Whereas direct evidence from natural populations for specific mechanisms of displacement of cutthroat trout populations by brook trout is lacking, there is abundant information on patterns of segregation between brook trout and cutthroat trout. Patterns of distribution and segregation among species can provide important preliminary insights into community interactions and organization (Crowder, 1990). Non-overlapping distributions or patterns of spatial or temporal segregation of species may indicate interactions between species, differential use or preference of habitat, or both (Figure 3). The large degree of variability in patterns of segregation reported in the literature and in our own personal observations and communications with numerous biologists throughout the western United States suggests there may be predictable biotic or abiotic factors that affect co-occurrence of cutthroat and brook trout. Alternatively, patterns of segregation may be due to unpredictable chance events that may or may not be evident at different scales of observation (Fausch et al., 1994; Cooper et al., 1998). We reviewed the evidence for temporal and spatial segregation of the species to look for clues about the relative influences of biotic and abiotic factors, chance, and scale.

Spatial segregation

Spatial segregation of cutthroat trout and brook trout in streams has been observed at several scales. Often cutthroat trout dominate upstream reaches, whereas brook trout dominate in lower reaches. This longitudinal pattern of segregation has been attributed to several potential factors, including gradients in stream temperature, channel slope, habitat structure, disturbance, and human influences such as angling and fish stocking.

Temperature. Temperature appears to be an important factor influencing the distributions of brook and cutthroat trout, but one that is expressed via subtle and complex avenues. One line of evidence for interspecific differences in the influence of temperature on competitive ability comes from comparisons of behavioral traits between cutthroat trout and brook trout. DeStaso and Rahel (1994) compared microhabitat selection by and behavioral interactions between similar-sized juvenile Colorado River cutthroat trout and brook trout at 10 °C and 20 °C in a laboratory environment. At 20 °C, brook trout initiated more aggression, consumed more food, and held dominant positions in a hierarchy more often than cutthroat trout. The species were equivalent competitors at 10 °C. Novinger (2000) used similar metrics to compare competitive ability of age-0 fish of each species under diel temperature fluctuations (1–8 °C and 9–17 °C). In these experiments, brook trout maintained a naturally occurring size advantage and were more aggressive, consumed more food, and initiated more inter- vs. intraspecific aggression under all temperature conditions tested. However, the relative magnitude of the difference between species in competitive ability increased at warmer temperatures. Thomas (1996) found that juvenile Colorado River cutthroat trout had reduced feeding efficiency at 13–17 °C when similar-sized brook trout were present. Griffith (1972) compared competitive abilities of juvenile westslope cutthroat trout and brook trout at 15 °C. Brook trout were behaviorally dominant when they maintained a size advantage over cutthroat trout, but there was no difference between equal-sized competitors.

There is also evidence for interspecific differences in the influence of temperature on physiological traits associated with competitive ability. Both DeStaso and Rahel (1994) and Novinger (2000) found that brook trout tolerated warmer temperatures than cutthroat trout. In addition, Novinger (2000) found that brook

trout had higher sprint swimming speeds compared to cutthroat trout at temperatures ranging from 3–22 °C. The greatest difference between species occurred at 22 °C when cutthroat trout sprint speeds declined significantly, apparently due to thermal stress. There was no difference between species in sustained swimming ability (3–22 °C) or in resistance to starvation at cold temperatures (0.4 °C). Thus, differences in thermal tolerance and sprint swimming favored brook trout, especially at warmer temperatures, but there was no indication that cutthroat trout had improved physiological performance relative to brook trout at cooler temperatures.

The means by which cold temperatures may contribute to upper distribution limits of brook trout are less obvious and may operate on population-level processes. Adams (1999) found that brook trout grew slower and matured later in cold than warm stream reaches. Modeling results indicated that, due to later maturity at smaller sizes with lower fecundity relative to fish in warmer reaches, brook trout populations in the coldest reaches may not be self-sustaining and would require immigration from warmer reaches to persist. The cutthroat trout life history strategy (later maturity at a larger size with higher fecundity) may be more successful than the brook trout strategy (early maturity at a smaller size with lower fecundity) in cold temperatures (Adams, 1999). In summary, there is evidence to support a competitive advantage for brook trout at warmer temperatures, but there is no corresponding evidence for a competitive advantage for cutthroat trout at cooler temperatures, where the distribution of brook trout may be limited by growth opportunities. A similar example was documented for segregation between Dolly Varden charr (*Salvelinus malma*) and white-spotted charr (*S. leucomaenis*; Taniguchi and Nakano, 2000).

Channel slope. Stream channel slopes are often steeper in the headwater portions of streams, where cutthroat trout tend to occur when in sympatry with brook trout. Studies of brook trout standing stocks (MacPhee, 1966; Chisholm and Hubert, 1986; Kozel and Hubert, 1989) and distributions (Bozek and Hubert, 1992; Hilderbrand, 1998) indicate stream channel slope may be a limiting factor. Steep stream reaches could limit brook trout distribution or abundance through a variety of mechanisms, including limited swimming ability, survival, or reproductive success (Fausch, 1989). However, recent evidence suggests brook trout are fully capable of moving

through and occupying streams with steep (>10%) slopes (Schroeter, 1998; Adams, 1999; Adams et al., 2000, 2001). Furthermore, the nature of the relationship between velocity and channel slope in streams suggests that swimming ability is unlikely to limit the distribution of brook trout in steep streams. Due to the flow patterns and channel roughness typical of natural headwater streams, water velocity is often negatively correlated with stream channel slope (Dunne and Leopold, 1978).

Hilderbrand (1998) studied interactions between cutthroat trout and brook trout in a system with variable stream channel slopes. Brook trout exhibited highest relative abundances in stream reaches with beaver ponds, where channel slopes were less than 0.5%. Cutthroat trout were most abundant in stream reaches with steeper slopes (3–5%). In stream reaches with intermediate channel slopes (<1.5%), brook trout and cutthroat trout were equally abundant. Experimental trials within enclosed sections of stream indicated no relationship between reach type (stream channel slope) and the outcome of interactions between cutthroat trout and brook trout.

Because many habitat characteristics, such as stream temperature, habitat size, patterns of disturbance, and a host of other potentially important characteristics may be correlated with stream channel slope, it is difficult to attribute patterns of species segregation to stream channel slope per-se. Isaak and Hubert (2001) addressed this problem directly by using a study design to control for these potentially confounded factors. They found that species composition of age-1+ trout (including brook trout and cutthroat trout) in stream reaches (mean length = 183 m) was not related to stream channel slope. Effects of stream channel slope on the abundance of individual species were not examined, due to the numerical dominance of cutthroat trout in the sampled reaches. Similarly, Paul and Post (2001) found that stream channel slope was not associated with distributional patterns of cutthroat trout and brook trout.

Aspects of the environment related to stream channel slope could favor reproduction by cutthroat trout over brook trout in headwater habitats, as suggested by Fausch (1989). Adams et al. (2001) found no age-0 or age-1 brook trout in very steep stream reaches, suggesting that steep slopes inhibit brook trout reproduction, but the factors contributing to limited reproduction are unknown. Thus, the distribution of channel slopes along a stream may influence brook trout invasions by limiting repro-

ductive success or recruitment. In summary, the existing body of evidence suggests that stream channel slope does not directly influence patterns of segregation between cutthroat and brook trout. However, stream channel slope is commonly associated with a host of other factors that may have a direct influence on patterns of segregation (Hubert and Kozel, 1993). We caution that studies to date have been focused on juvenile and older (age-1+) fish, and published evidence for relationships between stream channel slope and other life stages (e.g., spawning success or age-0 fish) is very limited.

Habitat structure and social behavior. One of the most obvious changes in stream habitats is increasing size (discharge) as the contributing area of a watershed increases in a downstream direction. Stream size is commonly associated with changes in stream channel slope, and may be an important factor influencing segregation of cutthroat trout and brook trout. Increasing stream depth, width, and size and frequency of pools generally are found with both decreasing channel slope and decreasing elevation within a stream (e.g., Hubert and Kozel, 1993; Schroeter, 1998). In particular, brook trout are often more abundant in larger slow-water habitats, including pools and beaver ponds (e.g., Griffith, 1972; Chisholm and Hubert, 1986; Kozel and Hubert, 1989; Hilderbrand, 1998).

Behavioral differences between species may explain patterns of segregation in relation to habitat size (Schroeter, 1998; see also Buys, 2002). Stream-living salmonines are known to defend territories, and territorial behavior may limit population density (McFadden, 1961; Grant et al., 1998). Territorial behavior, and hence territory size and characteristic population densities, may be influenced by a number of factors, including body size (Grant and Kramer, 1990) and differences in social behavior among species. Differences in social behavior may explain why brook trout generally occur at much higher densities than cutthroat trout (Griffith, 1972, 1988; Fausch, 1988; Schroeter, 1998; Dunham et al., 2000). If brook trout have lower per-capita spatial requirements, they may be tolerant of higher fish densities than are cutthroat trout.

Schroeter (1998) hypothesized that high densities of brook trout may increase territorial defense costs for cutthroat trout (Marchand and Boisclair, 1998), and that smaller-sized streams may be the only habitats where individual cutthroat trout can

effectively defend territories in the presence of brook trout. Experiments and field observations reported by Schroeter (1998) lend support to this hypothesis. In the field, brook trout densities responded much more strongly than cutthroat trout densities to increases in habitat size. Higher densities of brook trout and apparent schooling behavior contrasted with much lower observed densities of cutthroat trout. Experimental trials examining social behavior in both sympatry and allopatry indicated that cutthroat trout were more strongly affected by increased fish densities than were brook trout. Aggression, feeding rates, and social position of cutthroat trout declined significantly when brook trout densities were high, whereas brook trout showed little behavioral response to changes in fish density regardless of species composition. At high densities of brook trout (two brook trout in a 0.24 m^3 tank), individual cutthroat trout were never behaviorally dominant.

Disturbance. Differential vulnerability to disturbance is often invoked as an explanation for the success or failure of nonnative fish invasions (Moyle and Light, 1996). Natural disturbances are believed to play an essential role in creating habitat for native species in aquatic ecosystems (e.g., Rieman et al., in press). In contrast, human-caused disturbances may be important to the success of nonnative invaders (Moyle and Light, 1996). Many habitats occupied (or formerly occupied) by inland cutthroat trout have been extensively altered by a wide variety of human activities, particularly in the downstream portions of watersheds (Gresswell, 1988; Young, 1995). The coincidence of human-caused disturbances and widespread, intentional fish introductions may help explain the prevalence of brook trout in many downstream habitats, although no published data are available to test this explanation for the patterns of segregation. Investigations of other species have shown that coexistence of natives and nonnatives may be strongly conditioned by flow regime, and that natives are more likely to dominate in streams with more natural flow regimes (Strange et al., 1992; Moyle and Light, 1996; Fausch et al., 2001).

Stocking location. Many brook trout stocking locations have been in the downstream portions of watersheds (see **Brook trout invasions** above). The prevalence of brook trout in downstream habitats may therefore be a result of the fact that stocking of brook trout has often occurred in the same locations.

However, Paul and Post (2001) found that brook trout spread to establish populations far from initial stocking locations. This may be especially true of invasions that originate from stocking of brook trout in headwater lakes (Adams et al., 2001).

Angling. Angling is another factor that could facilitate replacement of cutthroat by brook trout, perhaps causing a spatial pattern of segregation. While probably not an important factor in all cases of brook trout invasion, angling effects may be integral to brook trout success in some instances, even where regulations mandate release of native fishes (Paul, 2000). Angling is expected to disproportionately reduce cutthroat populations because of differences in both catchability and demography between species. Catchability of cutthroat trout is two to three-fold higher than for similar sized brook trout (MacPhee, 1966; Paul, 2000). Moreover, compared to brook trout, cutthroat trout populations usually contain a larger proportion of individuals in size classes vulnerable to angling (MacPhee, 1966; Paul, 2000).

Small cutthroat trout populations may actually be extirpated by fishing (McIntyre and Rieman, 1995), whereas brook trout populations have repeatedly exhibited resilience to intensive harvest (McFadden et al., 1967; Paul, 2000; Stelfox et al., 2001; Peterson, 2002). Because cutthroat trout are slower growing, and mature later at a larger size than brook trout, they are less resilient to increased mortality in late juvenile and adult life stages. Paul (2000) modeled the effects of fishing on cutthroat trout and brook trout in 5 km of a small stream and found that even catch-and-release fishing with a 10% hooking mortality rate could lead to the extirpation of cutthroat trout in 5 years, whereas brook trout could sustain harvest with no bag limit indefinitely. This is due in part to early age-at-maturity and the ability of brook trout to mature at small sizes that are not highly vulnerable to angling. Indeed, after a long presence in downstream reaches, brook trout moved into the upper reaches of Quirk Creek, Alberta, shortly after construction of an access road that may have facilitated increased angling pressure (Paul, 2000). If roads, angling by humans, and related human disturbances are more common in lower elevation habitats, brook trout may be able to invade and replace, or perhaps displace, cutthroat trout in such habitats. Finally, because of vulnerability of large fish, higher mortality rates, and angler preferences for catching large fish and fishing larger rivers, angling tends to reduce maximize sizes in a population

(McIntyre and Rieman, 1995). Angling could therefore eliminate or greatly reduce migratory life history forms that are important to maintaining populations of cutthroat trout (Rieman and Dunham, 2000; Dunham et al., 2003), perhaps especially in the face of invasion pressures from brook trout.

Temporal segregation

Several temporal factors could influence segregation and interactions between brook trout and cutthroat trout. The timing of reproduction is critical, as incubating eggs, emerging fry, young juveniles, and spawned adults (kelts) may face radically different conditions. Spawning by cutthroat trout in spring is followed by a season of relative abundance of resources and favorable conditions, at least until midsummer, when seasonal low flows and drought conditions may be limiting. Fall-spawning brook trout face potentially stressful winter conditions that include colder temperatures, ice, greater vulnerability to warm-blooded predators, and potentially unfavorable discharge regimes (Cunjak et al., 1998).

Many native fishes within the natural range of inland cutthroat trout reproduce in the spring, and this timing is thought to reflect adaptation to prevailing temperature and stream discharge regimes (Moyle and Light, 1996; Latterell et al., 1998; Fausch et al., 2001). Strange et al. (1992) showed that relative abundances of fall and spring-spawning fishes in streams of northern California were affected dramatically by the timing and magnitude of stream discharge. Strange et al. (1992) modeled the effect of variable discharge regimes on recruitment of four fishes, including three nonnative salmonines (native Lahontan cutthroat trout were extirpated from the system). Recruitment by fall-spawning species (brook trout and brown trout) was reduced by winter flooding, whereas post-spawning spring floods reduced recruitment of rainbow trout, a spring-spawning species (see also Seegrist and Gard, 1972; Latterell et al., 1998). Similar dynamics may apply to spring-spawning cutthroat trout, but published data are lacking.

Temporal segregation of spawning times minimizes interspecific interactions associated with reproductive activity. The most important implications for temporal segregation of spawning times on species interactions are probably indirect. Indirect effects include interactions between timing of spawning and effects of environmental variability, and size of juveniles entering their first summer of life. Differential timing of spawning can result in large size differences between brook and cutthroat trout juveniles. Brook trout fry emerge from stream gravels earlier than fry from spring-spawning cutthroat trout, and therefore enter their first summer of life at a larger size. This may serve to minimize size or age-related overlap in resource use, or alternatively lead to competitive asymmetries between species or predation by larger brook trout juveniles on smaller cutthroat trout (Griffith, 1988; Novinger, 2000). While seldom mentioned in the literature, it is also possible that age-1 cutthroat trout have a size advantage over age-0 brook trout emerging during the winter and spring. Most of the focus has been on interactions during summer, as is the case for salmonids in general (Cunjak et al., 1998). Other seasonal differences in species ecology, such as use of over-wintering habitat, feeding migration patterns, and changes in habitat use have not been adequately documented.

Seasonal and annual variation in conditions is clearly important, but diel variation may be important as well. Salmonines are variably active during different parts of the day. A large body of evidence points toward temperature as an important factor influencing diurnal activity in salmonines, with a trend toward increasing nocturnal activity with declining temperatures (Thurow, 1997). Evidence for differences in diurnal activity between sympatric cutthroat trout and brook trout is limited. Cavallo (1997) found that both brook trout and cutthroat trout were more active at night in cold ($<10\,°C$) springbrooks, and suggested that relatively constant, cold temperatures led to reduced diurnal partitioning of activity between the two species. In contrast, Hilderbrand (1998) found little evidence for consistent differences in habitat use by sympatric brook trout and cutthroat trout during day or night, but relationships between temperature and activity were not noted. A second factor influencing diel activity patterns is visual acuity under low-light conditions. For example, studies of Dolly Varden charr and coastal cutthroat trout (*O. c. clarki*) suggest differences in retinal structure and increased visual acuity of charr relative to trout under low light conditions (Northcote, 1995). Therefore, charr may be more active during periods of low light (e.g., at night, or on cloudy days), and in areas of low light (e.g., deep water). A third factor, ontogenetic variation in diel activity (Bourke et al., 1996), could potentially affect segregation of some age or size classes.

Discussion

The evidence we reviewed provided interesting insights into selected aspects of brook trout invasions and their effects on cutthroat trout, but we found little evidence to suggest a common set of patterns or empirical rules (Moyle and Light, 1996). We conclude this despite the many investigations (including our own) that have addressed this topic over the past three decades. Instead, it appears that research has added more new questions than answers, especially in terms of guidance for management of brook trout invasions. Based on the available evidence, we conclude the value of research could be improved by addressing the following issues: (1) improved study designs; (2) considering multiple stages of the invasion process; (3) understanding the roles of displacement versus replacement; and (4) developing a predictive understanding of nonnative fish invasions, in spite of the underlying complexities.

Approaches to studying ecological phenomena range from using theoretical models (e.g., verbal, analytical, simulation) to field observations and experiments. Experimental approaches provide important evidence for understanding the potential effects of brook trout invasions. Because experimental studies employ tightly controlled conditions, they should have a high degree of "internal" validity (Manly, 1992). In other words, the outcome of specific treatments (e.g., brook trout) should be repeatable under the range of conditions examined with an experimental study. This, of course, assumes that experiments are properly designed, which has not always been true (Fausch, 1988). Regardless of how they are designed, experiments suffer from a lack of external validity (Manly, 1992), because they cannot fully represent natural conditions or population-level responses (Cooper et al., 1998). Observational studies conducted under natural conditions provide a measure of external validity because they can cover a wider range of factors operating at spatial or temporal scales that are relevant to the systems of interest (e.g., populations or ecosystems). Of course, these characteristics also make it difficult to isolate individual causal factors that could explain observed patterns (limited internal validity). Clearly, a range of approaches and evidence is required. Only a few of the studies we reviewed followed an integrated chain of inference involving series of experimental and observational study approaches (e.g., Bernardo, 1998).

An important part of any investigation is clearly linking the study design to different stages of the invasion process (Figure 1). Most of the research and management concerns in the past have focused on impacts of brook trout invasions, and potential mechanisms that may account for displacement of cutthroat trout by brook trout. Considerably less effort has been expended on understanding the invasions themselves. Thus, the emphasis has been on the impacts of brook trout invasions, rather than on factors affecting invasion processes (Figure 1). Clearly, understanding both the causes and effects of a biological invasion is important, but in the present case, emphasis on the mechanisms behind potential impacts has not provided conclusive results. In contrast, emerging patterns from research on the causes of brook trout invasions has provided some promising insights (Adams, 1999; Adams et al., 2000, 2001, 2002; Paul, 2000; see also Fausch et al., 2001). We suggest future efforts give equal weight to addressing both causes and effects of brook trout invasions.

Well-intentioned concerns over the impacts of brook trout invasions have likely contributed to a widespread perception that brook trout pose an unconditional risk to cutthroat trout. There are many reasons to reject this notion. First, the published literature and our experience and communications with many biologists revealed direct evidence for variable success in brook trout invasions and their impacts. Second, there is tremendous variability in the environmental conditions throughout the range of inland cutthroat trout. Thus, there is a possibility that conditions in some places may confer an advantage to cutthroat trout, in terms of invasion resistance relative to brook trout. For example, there is evidence for variably successful invasions of brook trout in cutthroat trout habitats in the Great Basin, but the causes are unknown (Dunham et al., 1999, 2000). We found evidence to suggest specific environmental conditions that could favor cutthroat trout (e.g., temperature, habitat size, lack of angling mortality). Alternatively, invasion resistance by cutthroat trout could be related to the coevolutionary history of a given subspecies or population with other closely related salmonines. The evidence we reviewed suggests brook trout have invaded successfully within the ranges of all subspecies, regardless of coevolutionary history, however. In other words, brook trout appear to have successfully invaded without regard to composition of the native salmonine community.

A more fundamental issue is the role of displacement versus replacement for explaining patterns of segregation between brook trout and cutthroat trout. We found that many investigators assumed or concluded that brook trout invasions affect cutthroat trout through displacement. However, the evidence for displacement versus replacement in natural populations is weak, and we are not aware of any empirical study that has explicitly tested these alternatives. In the case of displacement, brook trout would play a direct and active role in declines of cutthroat trout. Displacement can be caused by a variety of interspecific interactions described above. Replacement is the process whereby nonnative brook trout colonize areas where cutthroat trout have been temporarily or permanently extirpated by other factors (e.g., habitat loss or angling; Paul, 2000). In other words, replacement is not driven by interspecific interactions with the invader (brook trout). If brook trout invasions of former cutthroat trout habitat succeed primarily by replacement, then research into biological interactions would not be expected to yield useful insights. In reality, both dis- and replacement likely play important roles at some times and places for the outcome of brook trout invasions. Lack of useful insights from research on interspecific interactions between brook and cutthroat trout could stem in part from the variable roles of displacement and replacement.

Many complexities belie the superficial simplicity of the "two-species" system of nonnative brook trout and native inland cutthroat trout. Our review provides lessons similar to a four-decade case history of research on interactions between coastal cutthroat trout and Dolly Varden charr described by Northcote (1995), and the general failure of ecological theory in predicting invasion success in aquatic ecosystems (Moyle and Light, 1996). Given the challenges posed by these case histories, is it worthwhile or even possible to develop a useful understanding of brook trout invasions? We believe there are many opportunities to do so, in spite of the challenges and complexities. A tremendous volume of existing data could be brought to bear on understanding the causes of brook trout invasions and their effects on cutthroat trout. Unfortunately, in many cases, utility of the data is limited by inconsistent sampling approaches, and lack of a connection between data and specific hypotheses related to nonnative brook trout invasions (Rieman et al., 1999). In particular, improved documentation and synthesis of results from various management treatments to control brook trout (see below) and associated responses of cutthroat trout would be very useful.

The evidence suggests a variety of factors potentially influence brook trout invasions and their impacts. It is unlikely that research will be able to uncover all of the details behind these influences in the near future, but we anticipate encouraging progress. In the short-term, we believe there are substantial opportunities for understanding patterns of co-occurrence (Figure 3) between brook and cutthroat trout, particularly with studies that address patterns at multiple scales (e.g., Fausch et al., 1994; Dunham et al., 1999). Models to predict where, and possibly when brook trout invasions will occur, and where and when they will pose potential threats to cutthroat trout and other native species could be used by managers to prioritize management actions (Figure 4). Studies of patterns cannot reveal conclusive insights into causal mechanisms, but they can provide immediately useful information for prioritizing management activities (Parker et al., 1999; McIntosh, 2000; Kolar and Lodge, 2001) and generate testable hypotheses regarding mechanisms. Some examples from salmonid invasions in other systems highlight the potential value of this approach. Fausch et al. (2001) studied patterns of invasions by rainbow trout across five holoarctic regions, and found that aspects of the stream discharge regime, including flood timing, season of low flow, and flood predictability were associated with invasion success. Managing these aspects of the flow regime could provide effective controls for nonnative rainbow trout. McIntosh (2000) studied conditions associated with coexistence of native galaxiid fishes and nonnative trout in streams in New Zealand. Galaxiids dominated in sites with unstable streambeds, and coexisted most often with trout in sites with intermediate levels of stability, whereas trout dominated in larger sites with stable streambeds. In this case, protection or restoration of conditions facilitating coexistence or dominance by native galaxiids could become an important management strategy.

Managing brook trout invasions: Identifying alternatives and assessing priorities

Nonnative species such as brook trout pose serious problems for protection and restoration of aquatic ecosystems. In western North America, threats to native salmonids are commonly framed in terms of the "4-H" factors: hatcheries, harvest, hydropower, and habitat (National Research Council, 1996). However,
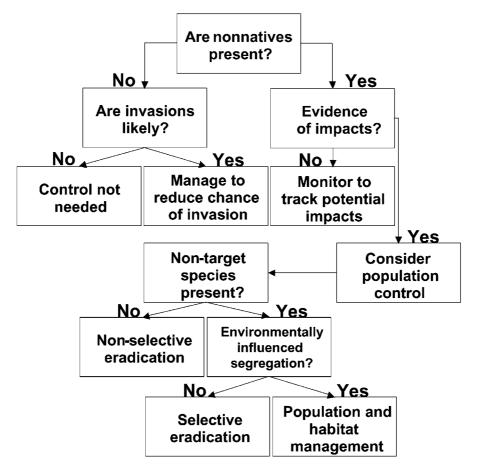
Figure 4. One possible scheme for prioritizing management actions to control nonnative fish invasions. This scheme is focused on nonnative invasions only and does not consider social, political, or economic factors, or other potentially important biological criteria for prioritizing conservation actions (see Allendorf et al., 1997).

nonnative species constitute a fifth factor that is often disregarded, particularly in restoration planning. For example, many wilderness areas are scarcely affected by the "4-H" factors, but commonly support a number of nonnative species, including brook trout. Nonnative invasions may be the most difficult to address and may limit benefits to native species accruing from management of other factors. Management approaches to controlling brook trout invasions and their impacts span a range of alternatives, including no action, direct and indirect control, construction of barriers, or a mixture of the latter three strategies (Montana Bull Trout Scientific Group, 1996). The choice to adopt any approach can be informed by an assessment of threats posed by nonnatives and of potential benefits and impacts of management on affected native species (Figure 4). The primary objective is to remove the effects of nonnative brook trout on cutthroat trout

populations, thereby enhancing the latter. However, management to control brook trout may also have unintended adverse impacts on cutthroat trout and associated native species. Here, we discuss management alternatives and provide perspectives on how to choose among the variety of available alternatives for managing brook trout invasions.

No action. The choice of not taking action to control brook trout invasions may be reasonable if there is no imminent threat to cutthroat trout or if the situation is impossible to manage. In some situations, cutthroat trout populations appear to be viable and productive, in spite of the fact that brook trout have been present for many years, or even decades. When there is no evidence to suggest negative impacts, management efforts to control brook trout may produce few, if any, benefits. Continued coexistence may be likely in some

systems, although changes in habitat conditions could potentially benefit brook trout, or vice-versa. Regular monitoring of such populations can allow detection of important changes in conditions. Many biological invasions in fresh water have little or no detectable effect (Moyle and Light, 1996), and thus may not be of immediate concern to managers.

Direct control and barriers. When there is evidence for adverse impacts of established populations of brook trout, or an opportunity to interfere with the early stages of an undesirable invasion (Figure 2), direct control may be warranted. Direct control includes activities that directly impact brook trout, such as removal by electrofishing (Thompson and Rahel, 1996), selective angling (Paul, 2000), selective trapping (Young et al., 2003), or toxicants (Rinne and Turner, 1991; Bettoli and Maceina, 1996; Finlayson et al., 2000). Brook trout removal by electrofishing and selective angling have limited potential for success (Thompson and Rahel, 1996; Paul, 2000; but see Shepard et al., in press). Typically brook trout are not completely eradicated by these methods and will reinvade habitats (Thompson and Rahel, 1998) with populations that rapidly rebound unless treatments are sustained (Paul, 2000; Peterson, 2002). Toxicants can be effective in completely eradicating brook trout and are commonly used to control invasions (e.g., Gresswell, 1991; Buktenica, 1997). Typically, eradication of brook trout involves multi-year, intensive treatments with non-selective fish toxicants such as rotenone or antimycin (Rinne and Turner, 1991; Bettoli and Maceina, 1996; Finlayson et al., 2000). Once brook trout are eradicated, cutthroat trout are introduced or allowed to recolonize from untreated sources. Dispersal barriers are installed at the downstream end of the treated section of stream to prevent re-invasion by brook trout or other nonnative species.

Eradication of brook trout with toxicants may have unintended short and long-term consequences for cutthroat trout. In the short-term, the immediate effects of toxicants on cutthroat trout, if they are present, may outweigh the benefits of treatment. For example, temporary reductions in cutthroat trout populations associated with application of toxicants may lead to losses of genetic variation, as documented for other native species impacted by well-intentioned eradication projects (e.g., DeMarais et al., 1995). The long-term potential negative consequences of eradication efforts result from isolation of cutthroat trout populations upstream of barriers. Isolation of populations can increase the risk of local extinction through a variety of genetic, demographic, behavioral, and environmental influences (Dunham et al., 1997; Harig et al., 2000; Rieman and Dunham, 2000; Kruse et al., 2001; Novinger and Rahel, 2003). To consider the full range of impacts associated with direct control, managers can evaluate the short-term threats posed by nonnative brook trout and longer-term considerations for persistence of isolated cutthroat trout populations.

Indirect control. Existing research provides only limited guidance for managers considering indirect methods to control brook trout invasions. There are two basic approaches to indirect control of nonnative species. The first is to manage environmental conditions to favor native species. A second, and related approach, is to maintain conditions that are unfavorable to nonnative species. In theory, environmental conditions could be managed to maintain healthy populations of cutthroat trout that may be more resistant to invasions by brook trout. For example, watersheds that support strong headwater populations of cutthroat trout and allow development of migratory life histories should be more resistant to brook trout invasions. Development of migratory life histories can be important for both population productivity and persistence (Rieman and Dunham, 2000; Dunham et al., 2003). Limited evidence reviewed here suggests other factors (e.g., natural and human disturbance, discharge, and temperature) could be managed to promote healthy cutthroat trout populations that may be resistant to brook trout invasions.

Prioritization of management actions. Management plans that include strategic prioritization of actions to control the effects of nonnative brook trout to benefit cutthroat trout populations will be more effective. Prioritization is necessary because opportunities for management are constrained by funding and logistical considerations, and because the relative effectiveness of different management approaches likely varies among populations and habitats. Biological criteria for prioritizing management actions could include considerations of the relative threats posed by nonnative species and relative costs and benefits of feasible management actions (Figure 4). In the case of brook trout impacts on cutthroat trout, the relative threats could clearly vary substantially among populations and perhaps among subspecies or regions as well.

Threats may result from different mechanisms acting in different areas (Figure 4), but information at this level of resolution is generally unavailable. Simpler measures of the apparent impacts of nonnative species may still be useful (e.g., distribution patterns; Dunham et al., 1999; McIntosh, 2000).

The relative costs and benefits of different management actions can be weighed in light of the feasibility of management alternatives. Eradication of brook trout via non-selective toxicants may not be possible due to concerns over impacts to non-target taxa, including other fishes, amphibians, and invertebrates. Regardless of the action taken, if the costs (e.g., impacts to desirable native taxa) and net benefits are explicitly considered and documented, management will be more effective (Finlayson et al., 2000). Often the focus is on immediate eradication of nonnative taxa, without full consideration of the overall risks involved. Furthermore, management activities driven primarily by short-term opportunities may fail to consider the larger context in which they are conducted. For example, removal of nonnative brook trout may be conducted in a system with easy access and strong stakeholder support, but where brook trout pose less of a threat than in other systems where work may be more difficult. If the overall management goal is to benefit the species (or subspecies) as a whole, then individual management actions to control nonnative fish will be most effective when evaluated in the context of the overall goal, not just of local costs and benefits.

Acknowledgments

References

Adams, S.B. (1999) Mechanisms limiting a vertebrate invasion: brook trout in mountain streams of the northwestern USA. Ph.D. Dissertation, The University of Montana, Missoula, MT, 188 pp.

Adams, S.B., Frissell, C.A. and Rieman, B.E. (2000) Movements of nonnative brook trout in relation to stream channel slope. *Trans. Am. Fish. Soc.* **129**, 623–638.

Adams, S.B., Frissell, C.A. and Rieman, B.E. (2001) Geography of invasion in mountain streams: consequences of headwater lake fish introductions. *Ecos.* **4**, 296–307.

Adams, S.B., Frissell, C.A. and Rieman, B.E. (2002) Changes in distribution of nonnative brook trout in an Idaho drainage over two decades. *Trans. Am. Fish. Soc.* **131**, 561–568.

Allendorf, F.W. and Leary, R.F. (1988) Conservation and distribution of genetic variation in a polytypic species: the cutthroat trout. *Conserv. Biol.* **2**, 170–184.

Allendorf, F.W., Bayles, D., Bottom, D.L., Currens, K.P., Frissell, C.A., Hankin, D., Lichatowich, J.A., Nehlsen, W., Trotter, P.C. and Williams, T.H. (1997) Prioritizing Pacific salmon stocks for conservation. *Conserv. Biol.* **11**, 140–152.

Angers, B., Bernatchez, L., Angers, A. and Desgroseillers, L. (1995) Specific microsatellite loci for brook charr (*Salvelinus fontinalis* Mitchill) reveal strong population subdivision on a microgeographic scale. *J. Fish. Biol.* **47**(suppl. A) 177–185.

Behnke, R.J. (1992) *Native Trout of Western North America*. American Fisheries Society, Bethesda, Maryland.

Bernardo, J.M. (1998) The logic, value, and necessity for grounding experiments in reality: an essential link in the inferential chain back to nature. *In*: Resetarits, W.J. Jr. and Bernardo, J.M. (eds.), *Experimental Ecology: Issues and Perspectives*. Oxford University Press, New York, NY, pp. 370–393.

Bettoli, P.W. and Maceina, M.J. (1996) Sampling with toxicants. *In*: Murphy, B.R. and Willis, D.W. (eds.), *Fisheries Techniques, Second Edition*. American Fisheries Society, Bethesda, MD, pp. 303–333.

Bjornn, T.C. and Reiser, D.W. (1991) Habitat requirements for salmonids in streams. *In*: Meehan, W.R. (ed.), *Influences of Forest and Rangeland Management on Salmonid Fishes and their Habitats*. American Fisheries Society, Bethesda, MD, pp. 83–138.

Bourke, P., Magnan, P. and Rodriguez, M.A. (1996) Diel locomotor activity of brook charr, as determined by radiotelemetry. *J. Fish. Biol.* **49**, 1174–1185.

Bozek, M.A. and Hubert, W.A. (1992) Segregation of resident trout in streams as predicted by three habitat dimensions. *Can. J. Zool.* **70**, 886–890.

Buktenica, M.W. (1997) Bull trout restoration and brook trout eradication at Crater Lake National Park, Oregon. *In*: Mackay, W.C., Brewin, M.K. and Monita, M. (eds.), *Friends of the Bull Trout Conference Proceedings*. The Bull Trout Task Force (Alberta), Calgary, Alberta, pp. 127–135.

Buys, D. (2002) Competition between Bonneville cutthroat trout and brook trout in laboratory and field experiments. M.S. Thesis, Utah State University, Logan, UT, 108 pp.

Byers, J.E. and Goldwasser, L. (2001) Exposing the mechanism and timing of impact of nonindigenous species on native species. *Ecology* **82**, 1330–1343.

Carlton, J.T. (1996) Pattern, process, and prediction in marine invasion ecology. *Biol. Conserv.* **78**, 97–106.

Cavallo, B.J. (1997) Floodplain habitat heterogeneity and the distribution, abundance and behavior of fishes and amphibians in the Middle Fork Flathead River Basin, Montana. M.S. Thesis, The University of Montana, Missoula, MT, 128 pp.

Chisholm, I.M. and Hubert, W.A. (1986) Influence of stream gradient on standing stock of brook trout in the Snowy Range, Wyoming. *Northwest Sci.* **60**, 137–139.

Claudi, R. and Leach, J. (eds.) (1999) *Non-indigenous Freshwater Organisms: Vectors, Biology and Impacts.* Lewis Publishers, Boca Raton, Florida.

Cooper, S.D., Diehl, S., Kratz, K. and Sarnelle, O. (1998) Implications of scale for patterns and processes in stream ecology. *Aust. J. Ecol.* **23**, 27–40.

Crowder, L.B. (1990) Community ecology. *In*: Schreck, C. and Moyle, P.B. (eds.), *Methods in Fish Biology.* American Fisheries Society, Bethesda, MD, pp. 607–629.

Crowl, T.A., Townsend, C.R. and McIntosh, A.R. (1992) The impact of introduced brown and rainbow trout on native fish: the case of Australasia. *Rev. Fish Biol. Fish.* **2**, 217–241.

Cunjak, R.A., Prowse T.D. and Parrish, D.L. (1998) Atlantic salmon (*Salmo salar*) in winter: the season of parr discontent? *Can. J. Fish. Aquat. Sci.* **55**(Suppl. 1), 161–180.

Currens, K.P., Hemmingson, A.R., French, R.A., Buchanan, D.V. Schreck, C.B. and Li, H.W. (1997) Introgression and susceptibility to disease in a wild population of rainbow trout. *N. Am. J. Fish. Manage.* **17**, 1065–1078.

D'Antonio, C.M. (1993) Mechanisms controlling invasion of coastal plant communities by the alien succulent *Carpobrotus edulis. Ecology* **74**, 83–95.

DeMarais, B.D., Dowling, T.E. and Minckley, W.L. (1993) Post-perturbation genetic changes in populations of endangered Virgin River chubs. *Conserv. Biol.* **7**, 334–341.

DeStaso, J. III and Rahel, F.J. (1994) Influence of water temperature on interactions between juvenile Colorado River cutthroat trout and brook trout in a laboratory stream. *Trans. Am. Fish. Soc.* **123**, 289–297.

Duff, D.A. (ed.) (1996) *Conservation Assessment for Inland Cutthroat Trout Status and Distribution.* USDA Forest Service, Intermountain Region, Ogden, UT, 120 pp.

Dunne, T. and Leopold, L.B. (1978) *Water in Environmental Planning.* W.H. Freeman, New York.

Dunham, J.B., Vinyard, G.L. and Rieman, B.E. (1997) Habitat fragmentation and extinction risk of Lahontan cutthroat trout (*Oncorhynchus clarki henshawi*). *N. Am. J. Fish. Manage.* **17**, 910–917.

Dunham, J.B., Peacock, M.M., Rieman, B.E., Schroeter, R.E. and Vinyard, G.L. (1999) Local and geographic variability in the distribution of stream-living Lahontan cutthroat trout. *Trans. Am. Fish. Soc.* **128**, 875–889.

Dunham, J., Rahn, M., Schroeter, R. and Breck, S. (2000) Diet selection by sympatric Lahontan cutthroat trout and brook trout: implications for species interactions. *West. N. Am. Nat.* **60**, 304–310.

Dunham, J.B., Young, M.K., Gresswell, R. and Rieman, B.E. (2003). Effects of fire on fish populations: landscape perspectives on persistence of native fishes and non-native fish invasions. *For. Ecol. Manage.* **178**, 183–196. Available from the internet URL http://www.fs.fed.us/rm/boise

Erman, D.C., Andrews, E.D. and Yoder-Willams, M. (1988) Effects of winter floods on fishes in the Sierra Nevada. *Can. J. Fish. Aquat. Sci.* **45**, 2195–2200.

Fausch, K.D. (1988) Tests of competition between native and introduced salmonids in streams: what have we learned? *Can. J. Fish. Aquat. Sci.* **45**, 2238–2246.

Fausch, K.D. (1989) Do gradient and temperature affect distribution of, and interactions between juvenile brook char and other salmonids in streams? *Physiol. Ecol. Jap. Spec. Vol.* **1**, 303–322.

Fausch, K.D., Nakano, S. and Ishigaki, K. (1994) Distribution of two congeneric charrs in streams of Hokkaido Island, Japan: considering multiple factors across scales. *Oecologia* **100**, 1–12.

Fausch, K.D., Taniguchi Y., Nakano, S., Grossman G.D. and Townsend, C.R. (2001) Flood disturbance regimes influence rainbow trout invasion success among five holoarctic regions. *Ecol. Appl.* **11**, 1438–1455.

Finlayson, B.J., Schnick, R.A., Cailteux, R.L., DeMong, L., Horton, W.D., McClay, W., Thompson, C.W. and Tichacek, G.J. (2000) *Rotenone Use in Fisheries Management: Administrative and Technical Guidelines Manual.* American Fisheries Society, Bethesda, Maryland.

Fuller, P.L., Nico, L.G. and Williams, J.D. (1999) *Nonindigenous Fishes Introduced into Inland Waters of the United States.* American Fisheries Society Special Publication Number 27.

Gowan, C. and Fausch, K.D. (1996) Mobile brook trout in two high-elevation Colorado streams: re-evaluating the concept of restricted movement. *Can. J. Fish. Aquat. Sci.* **53**, 1370–1381.

Grant, J.W.A. and Kramer, D.L. (1990) Territory size as a predictor of the upper limit to population density of juvenile salmonids in streams. *Can. J. Fish. Aquat. Sci.* **47**, 1724–1737.

Grant, J.W.A., Steingrímmson, S.Ó., Keeley, E.R. and Cunjak, R.A. (1998) Implications of territory size for the measurement and prediction of salmonid abundance in streams. *Can. J. Fish. Aquat. Sci.* **55**(Suppl. 1), 181–190.

Gregory, J.S. and Griffith, J.S. (2000) First-winter survival of caged wild and hatchery cutthroat trout in allopatry and sympatry with brook trout. *Intermountain J. Sci.* **6**, 217–222.

Gresswell, R.E. (ed.) (1988) *Status and Management of Cutthroat Trout.* American Fisheries Society Symposium 4, Bethesda, Maryland.

Gresswell, R.E. (1991) Use of antimycin for removal of brook trout from a tributary of Yellowstone Lake. *N. Am. J. Fish. Manage.* **11**, 83–90.

Gresswell, R.E., Liss, W.J. and Larson, G.L. (1994) Life-history organization of Yellowstone cutthroat trout (*Oncorhynchus clarki bouvieri*) in Yellowstone Lake. *Can. J. Fish. Aquat. Sci.* **51**(Suppl. 1), 298–309.

Griffith, J.S. (1972) Comparative behavior and habitat utilization of brook trout (*Salvelinus fontinalis*) and cutthroat trout (*Salmo clarki*) in small streams in northern Idaho. *J. Fish. Res. Board Can.* **29**, 265–273.

Griffith, J.S. (1988) Review of competition between cutthroat trout and other salmonids. *In*: Gresswell, R.E. (ed.), *Status and Management of Cutthroat Trout.* American Fisheries Society Symposium 4, Bethesda, MD, pp. 134–140.

Harig, A.L., Fausch, K.D. and Young, M.K. (2000) Factors influencing success of greenback cutthroat trout translocations. *N. Am. J. Fish. Manage.* **20**, 994–1004.

Hilderbrand, R.H. (1998) Movements and conservation of cutthroat trout. Ph.D. Dissertation, Utah State University, Logan, UT, 135 pp.

Hubert, W.A. and Kozel, S.J. (1993) Quantitative relations of physical habitat features to channel slope and discharge in unaltered mountain streams. *J. Freshwat. Ecol.* **8**, 177–183.

Irving, D.B. (1987) Cutthroat trout abundance, potential yield, and interaction with brook trout in Priest Lake tributaries. M.S. Thesis, University of Idaho, Moscow, ID, 225 pp.

Isaak, D.J. and Hubert, W.A. (2001) Are trout populations affected by reach-scale stream slope? *Can. J. Fish. Aquat. Sci.* **57**, 468–477.

Keeley, E.R. (2001) Demographic responses to food and space competition by juvenile steelhead trout. *Ecology* **82**, 1247–1259.

Knapp, R.A., Corn, P.S. and Schindler, D.E. (2001) Fish stocking impacts to mountain lake ecosystems. *Ecos.* **4**, 275–278.

Kolar, C.S. and Lodge, D.M. (2000) Freshwater nonindigenous species: interactions with other global changes. *In*: Mooney, H.A. and Hobbs, R.J. (eds.), *Invasive Species in a Changing World*. Island Press, Washington, D.C., pp. 3–30.

Kolar, C. and Lodge, D.M. (2001) Progress in invasion biology: predicting invaders. *Trends Ecol. Evol.* **16**, 199–204.

Kozel, S.J. and Hubert, W.A. (1989) Factors influencing the abundance of brook trout (*Salvelinus fontinalis*) in forested mountain streams. *J. Freshwat. Ecol.* **5**, 113–122.

Kruse, C.G., Hubert, W.A. and Rahel, F.J. (2001) An assessment of headwater isolation as a conservation strategy for cutthroat trout in the Absaroka Mountains of Wyoming. *Northwest Sci.* **75**, 1–11.

Latterell, J.J., Fausch, K.D., Gowan, C. and Riley, S.C. (1998) Relationship of trout recruitment to snowmelt runoff flows and adult trout abundance in six Colorado mountain streams. *Rivers* **6**, 240–250.

Leary, R.F., Allendorf, F.W. and Forbes, S.H. (1993) Conservation genetics of bull trout in the Columbia and Klamath River drainages. *Conserv. Biol.* **7**, 856–865.

MacPhee, C. (1966) Influence of differential angling mortality and stream gradient on fish abundance in a trout-sculpin biotope. *Trans. Am. Fish. Soc.* **95**, 381–387.

Manly, B.F.J. (1992) *The Design and Analysis of Research Studies*. Cambridge University Press, New York.

Marchand, F. and Boisclair, D. (1998) Influence of fish density on the energy allocation pattern of juvenile brook trout (*Salvelinus fontinalis*). *Can. J. Fish. Aquat. Sci.* **55**, 796–805.

McCracken, G.F., Parker, C.R. and Guffey, S.Z. (1993) Genetic differentiation and hybridization between stocked hatchery and native brook trout in Great Smoky Mountains National Park. *Trans. Am. Fish. Soc.* **122**, 533–542.

McFadden, J.T. (1961) A population study of the brook trout. *Wildl. Monog.* **7**, 1–73.

McFadden, J.T., Alexander, G.R. and Shetter, D.S. (1967) Numerical changes and population regulation in brook trout *Salvelinus fontinalis*. *J. Fish. Res. Board Can.* **24**, 1425–1459.

McIntosh, A.R. (2000) Habitat- and size-related variations in exotic trout impacts on native galaxiid fishes in New Zealand streams. *Can. J. Fish. Aquat. Sci.* **57**, 2140–2151.

McIntyre, J.D. and Rieman, B.E. (1995) Westslope cutthroat trout. *In*: Young, M.K. (ed.), *Conservation Assessment for Inland Cutthroat Trout*. U.S. Forest Service General Technical Report RM-GTR-256, Fort Collins, CO, pp. 1–15.

Mesa, M.G., Poe, T.P., Maule, A.G. and Schreck, C.B. (1998) Vulnerability to predation and physiological stress responses in juvenile chinook salmon (*Oncorhynchus tshawytscha*) experimentally infected with *Renibacterium salmoninarum*. *Can. J. Fish. Aquat. Sci.* **55**, 1599–1606

Minckley, W.L. and Deacon, J.E. (1991) *Battle Against Extinction: Native Fish Management in the American West*. University of Arizona Press, Tucson.

Montana Bull Trout Scientific Group (1996) *Assessment of Methods for Removal and Suppression of Introduced Fish to Aid in Bull Trout Recovery*. Montana Fish, Wildlife, and Parks, Helena, Montana.

Moore, S.E., Ridley, B. and Larson, G.L. (1983) Standing crops of brook trout concurrent with removal of rainbow trout from selected streams in Great Smoky Mountains National Park. *N. Am. J. Fish. Manage.* **3**, 72–80.

Moyle, P.B. and Light, T. (1996) Biological invasions of fresh water: empirical rules and assembly theory. *Biol. Conserv.* **78**, 149–161.

Nakano, S., Kitano, S., Nakai, K. and Fausch, K.D. (1998) Competitive interactions for foraging microhabitat among introduced brook charr, *Salvelinus fontinalis*, and native bull charr, *S. confluentus*, and westslope cutthroat trout, *Oncorhynchus clarki lewisi*, in a Montana stream. *Environ. Biol. Fishes* **52**, 345–355.

National Research Council (U.S.) Committee on Protection and Management of Pacific Northwest Anadromous Salmonids (1996) *Upstream: Salmon and Society in the Pacific Northwest*. National Academy Press, Washington D.C.

Northcote, T.G. (1995) Confessions from a four decade affair with Dolly Varden: a synthesis and critique of experimental tests for interactive segregation between Dolly Varden char (*Salvelinus malma*) and cutthroat trout (*Oncorhynchus clarki*) in British Columbia. *Nordic J. Freshwat. Res.* **71**, 49–67.

Novinger, D.C. (2000) Reversals in competitive ability: do cutthroat trout have a thermal refuge from competition with brook trout? Ph.D. Dissertation, University of Wyoming, Laramie, WY, 124 pp.

Novinger, D.C. and Rahel, F.J. (2003) Isolation management with artificial barriers as a conservation strategy for cutthroat trout in headwater streams. *Conserv. Biol.* **17**, 772–781.

Ovenden, J.R., Bywater, R. and White, R.W.G. (1993) Mitochondrial DNA nucleotide sequence variation in Atlantic salmon (*Salmo salar*), brown trout (*S. trutta*), rainbow trout (*Oncorhynchus mykiss*) and brook trout (*Salvelinus fontinalis*) from Tasmania, Australia. *Aquaculture* **114**, 217–227.

Parker, I.M., Simberloff, D., Lonsdale, W.M., Goodell, K. Wonham, M., Kareiva, P.M., Williamson, M.H., Von Holle, B., Moyle, P.B., Byers, J.E. and Goldwasser, L. (1999) Impact: toward a framework for understanding the ecological effects of invaders. *Biolog. Invasions* **1**, 3–19.

Paul, A.J. (2000) Recruitment dynamics in bull trout (*Salvelinus confluentus*): linking theory and data to species management. Ph.D. Dissertation, University of Calgary, Calgary, Alberta, Canada, 259 pp.

Paul, A.J. and Post, J.R. (2001) Spatial distribution of native and nonnative salmonids in streams of the eastern slopes of the Canadian Rocky Mountains. *Trans. Am. Fish. Soc.* **130**, 417–430.

Peterson, D. (2002) Population ecology of an invasion: demography, dispersal and the effects of nonnative brook trout on native cutthroat trout. Ph.D. Dissertation, Colorado State University, Fort Collins, CO, 213 pp.

Polhemus, D.A. (1993) Conservation of aquatic insects: worldwide crisis or localized threats? *Am. Zool.* **33**, 588–598.

Power, G. (1980) The brook charr, *Salvelinus fontinalis*. *In*: Balon, E.K. (ed.), *Charrs, Salmonid Fishes of the Genus* Salvelinus. Dr. W. Junk Publishers, The Hague, Netherlands, pp. 141–203.

Rahel, F.J. (2002) Homogenization of freshwater faunas. *Ann. Rev. Ecol. Syst.* **33**, 291–315.

Reimers, N. (1979) A history of a stunted brook trout population in an alpine lake: a lifespan of 24 years. *Calif. Fish Game* **65**, 196–215.

Rieman, B.E., Dunham, J.B. and Peterson, J.T. (1999) Development of a database to support a multi-scale analysis of the distribution of westslope cutthroat trout. U.S. Geological Survey, Reston, Virginia 20192 Available at http://www.fs.fed.us/rm/boise

Rieman, B.E. and Dunham, J.B. (2000) Metapopulations and salmonid fishes: a synthesis of life history patterns and empirical observations. *Ecol. Freshwat. Fish* **9**, 51–64.

Rieman, B.E., Dunham, J.B. and Clayton, J.L. (2003) Emerging concepts for management of river ecosystems and challenges to applied integration of physical and biological sciences in the Pacific Northwest, USA. Proceedings of a NATO Advanced Research Workshop on New Paradigms in River and Estuary Management (in press). Available at http://www.fs.fed.us/rm/boise

Rinne, J.N. and Turner, P.R. (1991) Reclamation and alteration as management techniques, and a review of methodology in stream renovation. *In*: Minckley, W.L. and Deacon, J.E. (eds.), *Battle Against Extinction: Native Fish Management in the American West*. University of Arizona Press, Tucson, AZ, pp. 219–243.

Rinne, J.N. (1996) Short-term effects of wildfire on fishes and aquatic macroinvertebrates in the southwestern United States. *N. Am. J. Fish. Manage.* **16**, 653–658.

Sakai, A.K., Allendorf, F.W., Holt, J.S., Lodge, D.M., Molofsky, J., With, K.A., Baughman, S., Cabin, R.J., Cohen, J.E., Ellstrand, N.C., McCauley, D.E., O'Neil, P., Parker, I.M., Thompson, J.N. and Weller, S.G. (2001) The population biology of invasive species. *Ann. Rev. Ecol. Syst.* **32**, 305–332.

Schroeter, R.E. (1998) Segregation of stream dwelling Lahontan cutthroat trout and brook trout: patterns of occurrence and mechanisms for displacement. M.S. Thesis, University of Nevada, Reno, NV, 93 pp.

Seegrist, D.W. and Gard, R. (1972) Effects of floods on trout in Sagehen Creek, California. *Trans. Am. Fish. Soc.* **101**, 478–482.

Shepard, B.B., Spoon, R. and Nelson, L. (2003) A native westslope cutthroat trout population responds positively after brook trout removal and habitat restoration. *Intermountain J. Sci.* (in press).

Shetter, D.S. (1968) Observations on movements of wild trout in two Michigan stream drainages. *Trans. Am. Fish. Soc.* **97**, 472–480.

Stelfox, J.D., Baayens, D.M., Paul, A.J. and Shumaker, G. (2001) Quirk Creek brook trout suppression project. *In*: Brewin, M.K., Paul A.J. and Monita, M. (eds.), *Bull Trout II Conference Proceedings*. Trout Unlimited Canada, Calgary, Alberta, pp. 37–46.

Stewart, J.E. (1991) Introductions as factors in diseases of fish and aquatic invertebrates. *Can. J. Fish. Aquat. Sci.* **48**, 110–117.

Strange, E.L., Moyle, P.B. and Foin, T.D. (1992) Interactions between stochastic and deterministic processes in stream fish community assembly. *Environ. Biol. Fish.* **36**, 1–15.

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

Taylor, J.N., Courtenay, W.R. and McCann, J.A. (1984) Known impacts of exotic fishes in the continental United States. *In*: Courtenay W.R. Jr. and Stauffer, J.R. (eds.), *Distribution, Biology, and Management of Exotic Fishes*. Johns Hopkins University Press, Baltimore, MD, pp. 322–373.

Thomas, H.M. (1996) Competitive interactions between a native and exotic trout species in high mountain streams. M.S. Thesis, Utah State University, Logan, UT, 44 pp.

Thompson, P.D. and Rahel, F.J. (1996) Evaluation of depletion-removal electrofishing of brook trout in small Rocky Mountain streams. *N. Am. J. Fish. Manage.* **16**, 332–339.

Thompson, P.D. and Rahel, F.J. (1998) Evaluation of artificial barriers in small Rocky Mountain streams for preventing the upstream movement of brook trout. *N. Am. J. Fish. Manage.* **18**, 206–210.

Thurow, R.F. (1997) Habitat utilization and diel behavior of juvenile bull trout (*Salvelinus confluentus*) at the onset of winter. *Ecol. Freshwater Fish* **6**, 1–7.

Trotter, P.C. (1987) *Cutthroat: Native Trout of the West*. Colorado Associated University Press, Boulder, CO, 219 pp.

Welcomme, R.L. (1988) *International Introductions of Inland Aquatic Species*. United Nations Food and Agricultural Organization, Rome, Italy, 318 pp.

Williamson, M. and Fritter, A. (1996) The varying success of invaders. *Ecology* **77**, 1661–1666.

Young, M.K. (ed.) (1995) *Conservation Assessment for Inland Cutthroat Trout*. U.S. Forest Service General Technical Report RM-256. Rocky Mountain Research Station, Fort Collins, CO, 61 pp.

Young, M.K., Micek, B.K. and Rathbun, M. (2003) Probable pheromonal attraction of sexually mature brook trout to mature male conspecifics. *N. Am. J. Fish. Manage.* **23**, 276–282.