FLOOD DISTURBANCE REGIMES INFLUENCE RAINBOW TROUT INVASION SUCCESS AMONG FIVE HOLARCTIC REGIONS

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Abstract. There is growing awareness that predicting biological invasions will require the development of conceptual models for specific taxa at appropriate scales. Salmonids are ideal taxa for testing factors that influence invasions, because large numbers have been introduced worldwide for long periods and their ecology is well known. We evaluated the hypothesis that, among regions with suitable water temperatures, environmental resistance from flood disturbances that wash away trout fry strongly influence invasion success of rainbow trout (Oncorhynchus mykiss), the most widely introduced fish species. We predicted that flow regimes in regions where rainbow trout invasions are successful would match those in their native range and would differ from those in regions where invasions are moderately successful or failed. We tested six specific predictions about how timing, predictability, frequency, duration, and annual variability of floods, as well as timing of low flows, will differ relative to timing of rainbow trout fry emergence among five Holarctic regions. Analysis of hydrologic regimes for eight rivers each in the native range (Pacific Coast) and four regions where rainbow trout invasions varied from highly successful (Southern Appalachians) to moderate (Colorado, USA, and Hokkaido Island, Japan) or failed (Honshu Island) showed that winter flooding and summer low flows in Pacific Coast rivers that favor spring emergence of rainbow trout were closely matched by Southern Appalachian flow regimes. In contrast, the other three regions had spring or summer flooding that hampered rainbow trout recruitment to different degrees, and winter low flows. Rainbow trout invasion success was best explained by a match between timing of fry emergence and months of low flood probability. Alternatively, cold water temperatures, which hamper reproduction, and biotic interactions with brown trout (Salmo trutta) and whirling disease parasites may account for low invasion success in European regions. However, differences in genetic makeup of donor stocks and propagule pressure are unlikely mechanisms to explain invasions. Understanding how abiotic disturbances interact with timing of critical life history events to limit nonnative species will help ecologists develop more robust theories to predict invasion success.

Key words: abiotic habitat filters; fish recruitment; floods and flood disturbance; habitat templet; Holarctic region; hydrologic regime; Indicators of Hydrologic Alteration; invasion biology; Oncorhynchus mykiss; rainbow trout; regional analysis; salmonids.

INTRODUCTION

Biological invasions are a global crisis (e.g., Cohen and Carlton 1998), second only to habitat loss in causing species declines and endangerment worldwide (Vitousek 1994, Schmitz and Simberloff 1997). Replacement of native species by nonnative invaders alters community composition (Rahel 2000) and ecosystem processes (Flecker and Townsend 1994), often with irreversible consequences that degrade human health and economic welfare (Office of Technology Assessment 1993, Vitousek et al. 1996). Given the importance of this environmental problem, ecologists have long sought to predict the locations and conditions under which nonnative organisms will invade (Elton 1958, Carey et al. 1996). First principles of invasion biology hold that invasion success will be influenced by interplay between characteristics of donor populations (e.g., genetic makeup, number of propagules; Simberloff 1989, Mack 1996), and "ecological resistance" (Elton 1958) made up of environmental resistance from physical stresses and biotic resistance from interactions with the receiving biota (Moyle and Light 1996). However, few predictions based on these variables have proven true for communities in general (Lodge 1993), leading ecologists to propose that models for specific taxa and habitats will need to be developed and tested at appropriate scales for predicting invasion success.
scales to improve the theory (Simberloff 1986, Vermeij 1996, Lodge et al. 1998).

Most attempts at prediction in invasion biology have focused on characteristics of successful invaders (e.g., Rejmánek and Richardson 1996), models of spatial spread (Shigesada and Kawasaki 1997), and biotic resistance by receiving biota (Simberloff and Von Holle 1999). In contrast, Elton (1958) and those who followed have paid less attention to the role of environmental resistance from abiotic factors in limiting invasions, especially at the regional scale (but see Carey 1996, Daehler and Strong 1996, Moyle and Light 1996). A general theory in community ecology holds that abiotic conditions act as filters that remove potential colonists, leaving taxa with life history traits adapted for a given habitat template (Keddy 1992, Townsend and Hildrew 1994). The theory is especially well developed for stream ecosystems where abiotic factors play a strong role (Poff 1997, Toner and Keddy 1997, Townsend et al. 1997, Hall and Harcombe 1998). For example, Poff (1997) presented a multiscale model of habitat filters for stream biota in which he proposed that reproductive life history is one of several important traits that respond to the coarse filter of climate and hydrologic regime at the watershed scale, the largest he considered. Both Poff (1997) and Townsend et al. (1997) advocated linking broad-scale comparative studies of such functional attributes across strong physiological gradients to clear biological mechanisms. They proposed that such relationships would help develop better models to predict patterns in stream biota, including establishment of nonnative invaders. A second theory advanced by Poff (Poff and Ward 1989, Poff 1996) is that geographic patterns in flow regimes cause regional-scale differences in stream ecosystem structure and function. Because hydrologic extremes are important constraints for lotic biota, streams with similar flow regimes should share certain ecological features, including the invasion success of given life history types (Poff et al. 1997).

Based on these two complementary theories, we can make specific predictions about how characteristics of flow regimes differ among regions where invaders with certain reproductive life history traits are favored or excluded. If the observed variation in flow regimes among regions matches these predictions, then this supports the hypothesis that these abiotic factors influence invasion success. Moreover, if differences in invasion success among streams within a region, or differences among years within streams, can be explained by the same mechanism, then this provides stronger support, because the explanation is independent of other possible confounding factors that vary by region. Moyle and Light (1996) proposed that predictions about invasions would be most robust at the regional scale (cf. Bennett 1990, Brown 1995), because local-scale patterns of freshwater invasions in California were often idiosyncratic and best explained by a chance concatenation of events (e.g., Strange and Foin 1999). If distributions of invading species are driven by regional-scale variation in flow regimes and biotic resistance, then patterns in invasion success should be detectable primarily at this large scale.

Salmon and trout (subfamily Salmoninae) are among the most widely introduced fishes, an ideal group for studying factors influencing invasion success. Introductions of these salmonids outside their native ranges began in the 1860s (e.g., Welcomme 1988, McDowall 1994, Dill and Cordone 1997), primarily to establish populations for recreational angling. By the early 1990s, three salmonids were among the 12 fish species introduced to >30 countries (Welcomme 1992). In many regions, salmonids have been introduced annually for 50–100 yr (e.g., von dem Borne 1890, Wiltzius 1885), so propagule pressure is high (Ruesink et al. 1995). Dates of first introductions and identity of donor populations are often known (e.g., Scott et al. 1978, Kinnison et al. 1998). Unlike cryptic organisms that go undetected after invasions (Williamson and Fitter 1996), established populations of salmonids are usually detected by interested anglers and managers. Finally, because of their economic importance, effects of many abiotic and biotic factors are well understood (Groot and Margolis 1991, Meehan 1991).

Among the salmonids, rainbow trout (Oncorhyncus mykiss) have been introduced to all U.S. states outside their native range (Fuller et al. 1999) and to 87 countries worldwide, more than any other fish species (Welcomme 1992). They are particularly germane for study, because their invasion success varies strongly among regions that appear suitable otherwise, even though some are in close geographical proximity (Table 1). Rainbow trout have been highly successful at establishing reproducing populations in the Southern Appalachian Mountains, but have failed at all but a few locations in Scandinavia, Central Europe, the United Kingdom, and Honshu, the main island of Japan. In other regions, they have had moderate success, establishing reproducing populations in certain locations but not others, such as in the central Rocky Mountains, the Andes Mountains, and New Zealand and Australia. Their invasion is apparently ongoing in Hokkaido, the northern island of Japan. No mechanisms have been proposed to explain this variation among regions. Invasion of watersheds by rainbow trout is an important problem for fisheries managers, because they readily hybridize with imperiled native cutthroat trout (O. clarki) in the western United States (Behnke 1992) and have replaced native brook trout (Salvelinus fontinalis) throughout long reaches of Southern Appalachian streams (Larson and Moore 1985).

Here, we use rainbow trout as an example of a well-known taxon for which the hypothesis that flow regime influences invasion success can be tested among regions at the global scale. We test specific predictions about how flow regimes differ among five Holarctic
regions where invasion success contrasts strongly, and link these with species life history to propose a biological mechanism. Finally, we consider alternative hypotheses to explain invasion success, including other abiotic factors like temperature, characteristics of donor populations, and biotic resistance.

**Predictions**

Abiotic factors, such as flow fluctuations, offer environmental resistance that limits survival of salmonids, especially of delicate eggs and early life stages when natural mortality is highest (Elliott 1987a, 1994). Rainbow trout, like most salmonids, require running water to spawn, but high flows from natural floods or artificial flow fluctuations can scour eggs and larvae from gravel redds (nests dug by females; Elwood and Waters 1969, Strange and Foin 1999). There is strong experimental and observational evidence that salmonid fry are most susceptible to being washed away by high flows during the first 30-70 d after absorbing their yolk sac and emerging from the gravel (Elliott 1987b, Heggenes and Traaen 1988, Nehring and Anderson 1993, Latterell et al. 1998). Characteristics of flow regimes, such as seasonality of flooding and low flow periods, vary markedly among regions (Haines et al. 1988, Poff 1996) and may account for invasion success. Therefore, our working hypothesis is that rainbow trout invasion success is high where flow regimes match those in its native range, but low where flows diverge strongly from this habitat template, primarily because recently emerged fry are displaced by untimely floods. Rainbow trout typically spawn in late winter and early spring, and fry emerge during late spring and early summer.

Given this hypothesis, we make six predictions about how specific characteristics of flow regimes will differ among regions that vary in rainbow trout invasion success (Table 2). Our metrics for these hydrologic characteristics were modified from Poff and Ward (1989, Poff 1996) and Richter et al. (1996, 1997), as described in Methods. We predict that in regions where invasion success is high, and in the native range of rainbow trout, flooding will occur during fall or winter before spring or early summer emergence of fry, followed by low flows during summer after emergence. Overall,
floods also will be relatively predictable, infrequent, and of longer duration. In few years will there be floods during the period of peak rainbow trout emergence. Annual variation in mean flows, maximum flows, and flows during fry emergence may provide the chance concatenation of events that allow invasions (Moyle and Light 1996), so we predict this variation to be relatively high in regions with high invasion success. In contrast, regions where rainbow trout invasions failed are predicted to have spring and summer flooding, fall and winter low flows, frequent unpredictable floods of shorter duration, many floods during the period of peak fry emergence, and low annual flow variabilities. Regions where invasion success is moderate are predicted to have flow regimes between these extremes.

**METHODS**

**Study regions**

In addition to the native range of rainbow trout along the Pacific Coast of North America (Fig. 1, Table 3), we chose four Holarctic regions that (1) were potentially suitable for rainbow trout reproduction, as indicated by presence of native salmonids; (2) had received widespread introductions of rainbow trout for at least five decades; (3) had known rainbow trout invasion success that varied markedly among regions; and (4) had a network of stream discharge gauges for which at least a decade of data were available. We restricted our analysis to regions where brown trout (*Salmo trutta*) are not native, because biotic interactions with this species are thought to limit rainbow trout invasion (see Discussion: Alternative hypotheses). Among the regions we chose, invasion success varies from highly successful in the Southern Appalachians, where most suitable stream reaches were colonized from early introductions (Larson and Moore 1985; Table 1), to nearly complete failure in Honshu Island, Japan. Rainbow trout were first introduced to Honshu in 1877 (Kawanabe 1980), and large numbers have been stocked in many locations by commercial fishermen’s unions during the last 50 years (e.g., 20 x 10^6 juveniles in 1988; Yuma et al. 1998). Invasion success of rainbow trout was moderate in Colorado before 1991. Populations were established in some rivers but not others (Nehring 1992), despite >100 yr of widespread stocking of both hatchery and wild fish. For example, an average of 12 x 10^4 rainbow trout were stocked each year during 1944–1978, reaching 28 x 10^6 fish in 1969 (Wiltzius 1985). However, since 1991, whirling disease, caused by the parasite *Myxobolus cerebralis*, has decimated most of the wild populations that became established (Nehring and Walker 1996). We also consider the ongoing rainbow trout invasion in Hokkaido Island as moderately successful. Releases of rainbow trout by private individuals since the 1950s have caused a gradual increase in records of rainbow trout occurrences since 1970, ultimately at 72 sites distributed in every major river basin by 1996 (Takami and Aoyama 1999). Many of these populations are self-sustaining (Aoyama et al. 1999, Taniguchi et al. 2000). Given this variation in invasion success among regions, we make the additional specific prediction that flow regime characteristics of biological relevance to rainbow trout fry after emergence (Table 2) will be similar to the native range (Pacific Coast) in the region where rainbow trout are highly successful invaders (Southern Appalachians) and will be similar in the two regions with moderate invasion success (Colorado and Hokkaido), whereas these groups will differ from each other and from the region where invasion failed (Honshu).

**Discharge data for basins within regions**

Within each region, eight drainage basins were chosen for study, using random sampling stratified by lat-
FIG. 1. Locations of five study regions and streams chosen for analysis. Islands in the Japanese archipelago are matched for latitude with the Pacific coast of the conterminous United States.

In Hokkaido, of the 12 major basins with gauges, we randomly chose two or three basins from each of three strata defined by longitude and latitude. In Honshu, we randomly chose two basins from each of four such strata, of the 28 major basins with gauges above
the southern limit of native salmonid distribution in central Japan (see Fausch et al. 1994: Fig. 1). In each basin, we selected a gauge in the least regulated reach, but in two Honshu basins base flows at all gauges appeared highly regulated, so we chose a gauge in the closest adjacent basin. Although base flows in most Japanese rivers were regulated to some extent, floods from monsoon rains, typhoons, and snowmelt runoff were damped relatively little by reservoirs, as in Colorado. Discharge data for rivers in Japan were available only from annual reports of the Ministry of Construction River Bureau (Tokyo, Japan), and the 1986–1996 (n = 11 yr) period was chosen because the most gauges were operating.

Analysis of flow regimes

We selected 12 characteristics of flow regimes that we judged to be biologically significant for rainbow trout early life history after emergence (Table 4, Appendix) to test our six predictions about rainbow trout invasion success (Table 2). Variables were modeled after those defined by Poff and Ward (1989, Poff 1996) and used in the Indicators of Hydrologic Alterations (IHA) algorithm of Richter et al. (1996, 1997). We used the IHA algorithm (version 4; The Nature Conservancy 1997) to calculate the variables, or intermediate quantities. For example, coefficients of variation (cv) of annual mean flow, mean 3-day maximum flow, and flow during peak fry emergence were calculated from values in the IHA Annual Statistics Summary.

An important criterion for our analysis was the definition of a flood, which was used to define 5 of 12 flow regime characteristics (Table 4). Fluvial geomorphologists define floods as channel-forming bankfull discharge events that recur every two years, on average (Dunne and Leopold 1978). This standard benchmark was also used by Poff and Ward (1989) to characterize flow regimes for streams throughout the United States. However, recently emerged salmonid fry are likely washed away by flows much lower than bankfull, so we defined a biologically significant flood as events that exceeded the 95th percentile mean daily discharge (i.e., the discharge exceeded 18 d/yr, on average) for one or more days. This threshold was calculated over the entire period of record using the IHA algorithm.

We used two variables to indicate the frequency of floods and the annual variability of flows during the period of peak rainbow trout fry emergence. We determined approximate dates of the four-week period of peak fry emergence for individual rivers or subregions from literature or personal communication with fish biologists in each region (Table 3). Although dates of spawning are often known, fry emergence is more difficult to detect and usually has not been reported. Dates of peak emergence vary most for the Pacific Coast region, due to the wide range in latitude among basins and presence of sympatric locally adapted winter-spawning and summer-spawning races of steelhead in the Oregon rivers. Estimates of fry emergence dates were available for most rivers on the Pacific Coast and in Colorado. Because of this, we tallied the peak emergence periods in two-week intervals and report the central 80% of their distribution and total range. In contrast, emergence dates were available for few locations in the Southern Appalachians and both regions in Japan. Thus, we combined these with biologists’ reports for larger subregions to make similar estimates. Rainbow trout reproduce successfully few places in Honshu, so estimates are based on a small sample.

Statistical analysis of flow regime characteristics

We first tested whether the length of flow records strongly influenced three key flow regime characteristics of the 12 used: median date of maximum flow, month of highest mean flow, and the percentage of years with floods during peak fry emergence. To address whether the 11-yr records available for Honshu and Hokkaido streams were sufficient to accurately characterize their flow regimes, we calculated these three flow variables for the stream with the longest record in each of the other three regions (n = 72–91 yr) using data from the most recent 11, 20, 40, 60, and 72 yr. We then used linear regression to test for a significant time trend (i.e., slope) in each variable, which would indicate changes in climate, land use, or other factors.

For the main analysis, we tested the prediction that differences in flow regimes among regions match rainbow trout invasion success using multivariate statistical analysis. We first conducted a Principal Components Analysis (PCA) on all 12 characteristics of flow regimes (Table 4) as a heuristic tool to assess hydrologic variables important in separating regions with different invasion success. We plotted all variables to assess normality and used square-root transformations to stabilize variance and reduce skewness of the maximum number of dates with no floods, median flood duration, and the cv of mean 3-day maximum discharge. Median date of maximum flow was converted to water year date (1 October to 30 September) in order to group floods in the same season (Dunne and Leopold 1978). For ease of interpretation, the month of highest flow and median month of the low-flow season were converted to integers (January = 1), but December was coded as zero to ensure that winter high- or low-flow periods were grouped in the same season.

After PCA, we then tested whether regions differed as predicted using multivariate analysis of variance (MANOVA) on the same transformed set of 12 flow variables, followed by two specific a priori contrasts. The contrasts tested the null hypothesis that two equalities were simultaneously true; that values for the Pacific Coast and Southern Appalachians (native range and high invasion success) were equal, and values for Colorado and Hokkaido (moderate success) were equal, but that all other pairwise comparisons among regions...
During floods in natural streams, velocities would rapidly exceed these thresholds as rising flows reach channel walls and eliminate low velocity microhabitats. Elliott (1987b) released brown trout fry of different ages and conditions in a natural stream and found that distances they traveled downstream before regaining positions increased linearly with velocity (range, 10–52 cm/s). Newly emerged fry drifted similar distances as many fry downstream, based on large reductions (50–62%) in their abundance after each flood, compared to little change between floods. Only 2–10% of fry displaced were estimated to have survived downstream. Water velocities reached 1.5 m/s and displaced the few wild fry present, in a small Honshu mountain stream. Rains from monsoons and typhoons produced snowmelt runoff that produces high peak flows. Onodera and Ueno (1961) measured survival of stocked rainbow trout fry (63 mm TL), and the few wild fry present, in a small Honshu mountain stream. Rains from monsoons and typhoons produced three main floods measuring from 49 to 60 times baseflow during May through September of the year studied. Water velocities reached 1.5 m/s and displaced many fry downstream, based on large reductions (50–62%) in their abundance after each flood, compared to little change between floods. Only 2–10% of fry displaced were estimated to have survived downstream. These results indicate that displacement of rainbow trout fry by poorly timed floods in regions like Honshu is a likely mechanism explaining failures in recruitment, and therefore invasion.

Although our hypothesis strictly applies only to the regions we chose for study, the variability and timing of high flows may also account for differences in rainbow trout recruitment and invasion success in other regions. For example, rivers in New Zealand have high flow variability relative to those in the U.S. (Biggs et al. 1990). Although large numbers of rainbow trout have been introduced widely since 1883 (e.g., >10 × 10^6 by 1922; McDowall 1989), reproducing populations have established only in certain regions. Jowett (1990) found that rainbow trout distribution among 157...
Trout populations are adapted to spawn during spring, and eggs incubate in rising temperatures. Embryo survival. However, low water temperature may also limit invasion success in some regions. Most rainbow analyses to watersheds where native whitespotted charr (Salvelinus leucomaenis) and masu salmon (O. masou) reproduce. However, low water temperature may also limit invasion success in some regions. Most rainbow trout populations are adapted to spawn during spring, and eggs incubate in rising temperatures. Embryo survival is reduced if water is too cold during this period for normal egg development and hatching (Stonecypher et al. 1994). Nehring (1992) reported that translocations of wild fingerling rainbow trout failed to establish populations in four high-altitude Colorado rivers where temperatures did not reach 6–7°C by June, despite successful recruitment in four other rivers with warmer temperatures. Cold summer water temperatures may also help explain the general lack of invasions in Scandinavia (Svardson 1968, Hindar et al. 1996) and northern England and Scotland (Worthington 1940; J. M. Elliott, personal communication), but cannot explain why rainbow trout are invading the coldest northern regions of the Japanese archipelago. Nevertheless, this hypothesis deserves more attention.

Characteristics of donor populations like genetic makeup, number of propagules introduced, and frequency of introductions (i.e., propagule pressure; Ruesink et al. 1995) may also influence invasion success (Simberloff 1989). If genetic makeup is important, then invasion success should depend on the source of fish introduced. In many rivers of their native range, rainbow trout evolved unique life history characteristics to form locally adapted populations of both resident fish and anadromous steelhead (Behnke 1992). Although the earliest shipments of fertilized eggs to a few locations like New Zealand were from single genotypes (e.g., steelhead from Sonoma Creek; Scott et al. 1978), most were hybrids of anadromous steelhead and resident “redband” rainbow trout, like those from the McCloud River which were distributed widely (Behnke 1990, 1992). By 1900, many such mixed stocks were being propagated throughout the world (e.g., von dem Borne 1890, McDowall 1996), and subsequent artificial selection and interbreeding with stocks imported later changed life history characteristics of progeny (Worthington 1940; R. Behnke, personal communication). In all the regions we list (Table 1), and many others, large numbers of these cultured rainbow trout were introduced at many locations, or escaped from fish cul-

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<th>Table 6. Extended.</th>
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<th>Median duration of floods (d)</th>
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FIG. 3. Representative flow regimes, and probability of floods relative to timing of rainbow trout fry emergence, for the five study regions. Panels at left show representative annual hydrographs for one stream in each region. Panels at right show mean percentage of floods by month for the eight streams in each region, and the estimated timing of peak rainbow trout fry emergence (see Table 3). The horizontal bars show the central 80% of the 4-wk periods of estimated peak fry emergence for all streams within each region, and the horizontal lines show the entire range of dates for these periods.
turing operations, totaling on the order of $10^5$–$10^7$ fish released annually for decades in each state or country (e.g., MacCrimmon 1971, Dill 1990, 1993, Yuma et al. 1998, Epifanio 2000). For example, in Colorado, rainbow trout fry, fingerlings, or adults have been introduced every year since the 1880s, reaching 11–28 $\times$ $10^6$ fish annually during 1955–1978 (Wiltzius 1985). These fish were propagated from at least four different hatchery strains. Therefore, because nearly all regions received many large introductions of fish of mixed lineage, it is unlikely that differences in invasion success among regions are primarily due to genetic differences in donor stocks, or to lack of sustained releases of large numbers of propagules.

A third alternative hypothesis is that biotic interactions from competitors, predators, or parasites account for differences in rainbow trout invasion success among regions (Table 1). If the first two are important, we predict that rainbow trout would be unable to invade faunas with high fish species richness, especially of native and introduced salmonids having similar ecology. However, other salmonids were unable to prevent rainbow trout invasion in the Southern Appalachian Mountains and Rocky Mountains (Table 1). This hypothesis also cannot explain why rainbow trout failed to invade Honshu Island but are actively invading Hokkaido Island which has more native salmonids, including the same species as Honshu. Many investigators believe that rainbow trout invasion in Europe and the United Kingdom is limited by native brown trout or the whirling disease parasite *M. cerebralis* (Hindar et al. 1996, Lever 1996). Persistent stocking established rainbow trout populations in only a few locations in many European countries (MacCrimmon 1971, 1972, Lever 1996; A. Peter, personal communication), although naturalized populations of rainbow trout and brown trout coexist at various locations throughout North and South America and Australasia. Thus, biotic interactions from brown trout or parasites like *M. cerebralis* in their native ranges in Europe may be an important factor resisting rainbow trout invasions, but this alternative hypothesis is unlikely to explain differences in invasion success among other regions that lacked them. Finally, the hypothesis that release of rainbow trout from parasites that infect them in their native range makes establishment more likely farther away (cf. Kennedy and Bush 1994) also cannot explain the pattern of invasions among other regions. For example, this would predict invasions to be more likely in regions like Honshu or Europe, farther from the Pacific Coast, than in Colorado or the Southern Appalachians. Therefore, in light of our results and the evidence for alternative hypotheses, the most plausible mechanisms accounting for differences in rainbow trout invasions among regions where other salmonids reproduce are the effects of cold temperatures on reproduction, of flooding on recruitment, and of biotic interactions from brown trout and certain parasites on various life stages.

### Interactions among factors

Single factors are unlikely to fully explain most invasions (e.g., Case 1996), and interactions among several factors combined with chance events may play a strong role in invasion success, especially at the local scale (Moyle and Light 1996). Interactions between flow regime and biotic interactions with brown trout were reported to play a role in invasion success or recruitment of rainbow trout in at least two cases. Strange et al. (1992, Strange and Foin 1999) reported that low winter flows in a Sierra Nevada stream followed by an extreme spring flood in one year favored recruitment of fall-spawning nonnative brown trout while decimating recruitment of nonnative rainbow trout and native spring-spawning minnows (cyprinids). Predation by adult brown trout from this strong cohort apparently prevented the spring spawners from recruiting well in subsequent years until a severe winter flood scoured brown trout eggs and alevins from gravel redds, decimating brown trout recruitment and reducing their competition with juvenile rainbow trout. In this case, invasion success of both brown and rainbow trout depended on the interaction between annual flooding disturbance and predation and competition among the resultant assemblage.

In a second case, Peter et al. (1998) found that nonnative rainbow trout invaded the Alpine Rhine River and artificial channels tributary to it in Switzerland and Liechtenstein that were once occupied solely by native brown trout. They reported that the stable flow and temperature regimes produced by flow regulation allowed rainbow trout to begin spawning earlier than before, in late fall. Moreover, their eggs incubate faster than brown trout, so rainbow trout fry began emerging at about the same time as brown trout and were of similar size, instead of smaller as is usual. Laboratory experiments showed that rainbow trout fry dominated brown trout of equal size, which likely explains the invasion success relative to other sites with flow regimes that are more natural.

If further direct evidence on rainbow trout invasion success from these and other regions under different flood disturbance regimes bears out these hypotheses, the resulting theory will be highly useful for those conducting ecological restoration and fisheries management. For example, biologists could use data on flood disturbance timing and fry emergence to analyze the risks of continued stocking of rainbow trout outside their native range on native salmonids (e.g., Hindar et al. 1996) and other stream fishes (Townsend 1996). Conversely, ecologists interested in restoration of native species may use information on their life history to plan manipulations of flow regimes that favor recruitment of native species more than rainbow trout. Fisheries managers interested in managing to full ad-
vantage established populations of nonnative rainbow trout may find the results useful for planning flow regimes of regulated rivers, a goal currently being pursued for many rivers in the western United States and other regions (cf. Nehring and Anderson 1993).

Finally, our results are useful as contributions to the nascent theory of invasion biology (e.g., Vermeij 1996, Parker et al. 1999). The role of natural disturbances in providing environmental resistance that prevents establishment of nonnative species has long been a part of the lore of biological invasions (Lodge 1993, Moyle and Light 1996), but there are relatively few empirical examples demonstrating clear patterns and providing plausible mechanisms, especially at the regional scale (cf. Bennett 1990). We hope that results like these will help ecologists develop more robust models that link critical life history events with the timing of disturbances to explain the complex interactions in communities that will inevitably drive invasion success.

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