

## 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 template; 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

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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 concat-

enation 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 1985), 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 (*Oncorhynchus 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

TABLE 1. Invasion success of rainbow trout in nine selected regions, made up of one or more countries or U.S. states, distributed worldwide.

Region (countries or U.S. states)	Dates first introduced	Invasion success	Primary salmonid competitors or predators†	References
Scandinavia (Norway, Sweden, Denmark)	1892–1902	failed	AS, BN	Svårdson (1968), Hindar et al. (1996), I. Näslund, H. Kristiansen ( <i>personal communication</i> )
Central Europe (Germany, Switzerland)	1882, 1888	failed	BN	von dem Borne (1890); A. Peter ( <i>personal communication</i> )
United Kingdom	1884	failed	AS, BN	Worthington (1940), Lever (1977)
Southern Appalachian Mountains (Tennessee, North Carolina, Virginia)	1880–1884	high	BK (BN)	Jenkins and Burkhead (1994), Clark and Rose (1997), Epifanio (2000)
Central Rocky Mountains (Colorado)	1882	moderate	CT (BK, BN)	Wiltzius (1985), Nehring and Anderson (1993), Epifanio (2000)
Andes Mountains (Venezuela to Chile)	1904–1943	moderate	(BN)	Ruiz and Berra (1994), Pefaur and Sierra (1998)
Honshu Island, Japan	1877	failed	MS, WC	Kawanabe (1980), Yuma et al. (1998)
Hokkaido Island, Japan	1920	moderate	CH, DV, H, MS, P, WC	Kishida (1937), Yuma et al. (1998), Aoyama et al. (1999), Takami and Aoyama (1999)
New Zealand and Australia	1883, 1894	moderate	(BN), galaxiids‡	Scott et al. (1978), McDowall (1989, 1994, 1996), Jowett (1990), Crowl et al. (1992)

*Notes:* Invasion success was based on abundance and distribution of reproducing populations and was categorized as failed if reproducing populations were found at only a few unique locations after many introductions, moderate if they established at various locations throughout the region, and high if they were found in most drainages. Also included are the range of dates of first introduction, the primary native salmonids and naturalized nonnative salmonids (in parentheses) in streams that potentially offer biotic resistance, and references for information from each region. Donor stocks for all regions were of mixed lineage (i.e., hybrids of resident and anadromous races, or of hatchery and wild stocks). In all regions, large numbers of fry, juveniles, or adults ( $10^5$ – $10^7$ ) were introduced each year for decades, or escaped from fish culture facilities, so propagule pressure was high. MacCrimmon (1971, 1972) and Lever (1996) give information for all regions, and Dill (1990, 1993) provide data for Scandinavia, Central Europe, and the United Kingdom.

† Species abbreviations are: AS, Atlantic salmon (*Salmo salar*); BK, brook trout (*Salvelinus fontinalis*); BN, brown trout (*Salmo trutta*); CH, chum salmon (*Oncorhynchus keta*); CT, cutthroat trout (*O. clarki*); DV, Dolly Varden (*Salvelinus malma*); H, huchen (*Hucho perryi*); MS, masu salmon (*O. masou*); P, pink salmon (*O. gorbuscha*); WC, whitespotted charr (*Salvelinus leucomaenis*).

‡ Galaxiids have ecology similar to salmonids and so are included as potential competitors, although most species are excluded by brown trout (Townsend and Crowl 1991).

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,

TABLE 2. Predictions about characteristics of the flow regime relative to timing of rainbow trout fry emergence in regions where invasion success of rainbow trout is high. Characteristics are predicted to be opposite these in regions where rainbow trout invasions have failed.

Hydrologic characteristic	Prediction
1) Flood timing	Flooding season will be during fall or winter, before spring or early summer emergence of rainbow trout fry.
2) Season of low flow	Low flow season will be during summer after rainbow trout fry emergence, to provide rearing habitat.
3) Flood predictability	Floods will be relatively predictable, so few occur during the season of low flow to scour away rainbow trout fry.
4) Flood frequency and duration	Floods that do occur will be relatively infrequent and of longer duration.
5) Floods during fry emergence	In few years will there be floods during the period of peak rainbow trout fry emergence.
6) Annual flow variability	Annual variability will be high in annual mean flows, 3-day maximum flows, and flows during fry emergence, thereby allowing chance invasions during favorable years.

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.,  $20 \times 10^6$  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  $12 \times 10^6$  rainbow trout were stocked each year during 1944–1978, reaching  $28 \times 10^6$  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-

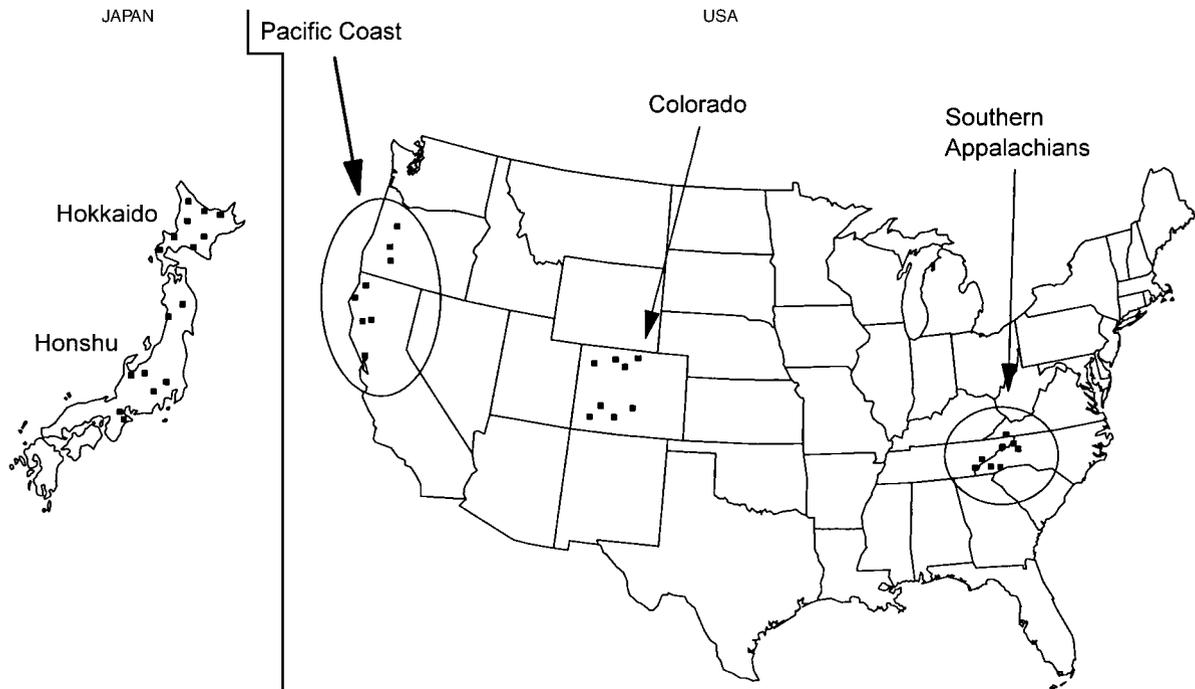


FIG. 1. Locations of five study regions and streams chosen for analysis. Islands in the Japanese archipelago are matched for latitude with the Pacific coast of the conterminous United States.

itude (Fig. 1, Table 3). For each basin, we chose the stream discharge gauge within the range of elevations occupied by salmonids that was least affected by flow regulation from dams or diversions (see the Appendix). In all regions except Hokkaido, rainbow trout introductions succeeded or failed before most river regulation. In the native range on the Pacific Coast, rather than selecting basins randomly, we chose gauges from unregulated reaches of representative streams and rivers from which eggs were first taken and shipped throughout the world for propagation and introduction. Behnke (1990) reported that the first sources of eggs were resident rainbow trout and anadromous steelhead from tributaries of San Francisco Bay (e.g., Sonoma Creek in the 1870s; Scott et al. 1978) and the upper Sacramento River, California (McCloud River, 1877–1888; Needham and Behnke 1962), and steelhead from rivers in northern California and Oregon (~1890–1900; Redwood Creek, and Klamath–Trinity, Rogue, and Willamette rivers). Therefore, we chose gauges from Sonoma Creek, Deer and Elder creeks (surrogates for the McCloud River, inundated by Shasta Dam), Redwood Creek, and the Salmon River (Klamath–Trinity River tributary) in California, and the Rogue River, Steamboat Creek (North Umpqua River tributary), and the South Santiam River (Willamette River tributary) in Oregon for study. We assumed that rainbow trout introduced to our four “test” regions were adapted to flow regimes in rivers like these.

In the Southern Appalachians (defined as 34.5°–36.5°

N latitude) we randomly selected four unregulated basins in each of two 1°-latitude strata, from a total of 24 U.S. Geological Survey (USGS) Hydrologic Units shown in this region by Clark et al. (2001). Where possible, we selected gauges below 760 m elevation, the altitude zone where trout are most abundant (Clark et al. 2001), and above minimum elevations where rainbow trout were reported from the major basins by Flebbe (1994; range, 300–500 m). One gauge was just above this altitude range (Table 3), and one just below. For the latter, however, no other tributaries entered in the intervening reach, so the flow regime should be similar to that upstream. In Colorado, we randomly chose eight of the nine major river basins (cf. Nehring and Anderson 1993) and selected gauges in the least regulated reaches. Nearly all the basins had diversions or small dams that regulated base flow, but none of them prevented annual floods caused by melting snow. For all basins in North America we retrieved data for the entire period of record ( $n = 25\text{--}91$  yr) from the USGS web site (<http://water.usgs.gov>) or CD-ROM (Hydrosphere, Inc., Boulder, Colorado, USA). One exception was Coweeta Creek, North Carolina, for which data were provided by the U.S. Forest Service Coweeta Hydrologic Laboratory ( $n = 13$  yr).

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

TABLE 3. Characteristics of the eight drainage basins (median, range in parentheses; ranges only for latitude and longitude) in each of the five study regions.

Region	Rainbow trout invasion success	Basin locations <sup>†</sup>		Gauge Elevation (m)	Basin area at gauge (km <sup>2</sup> )
		Latitude	Longitude		
Pacific Coast	native range	38°19'–44°24'	121°57'–123°49'	228 (32–799)	495 (151–1945)
Southern Appalachians	high	35°04'–36°57'	81°34'–84°17'	460 (258–795)	257 (15–2085)
Colorado	moderate	37°42'–40°40'	105°13'–108°02'	2069 (1591–2569)	2079 (272–10 269)
Hokkaido	moderate	42°53'–44°44'	140°02'–144°06'	30 (10–140)	938 (361–3558)
Honshu	failed	34°19'–39°48'	136°27'–140°53'	46 (7–499)	859 (304–2335)

Notes: Basins encompassed the area upslope from the gauge where stream discharge was measured and were bounded by the topographic divide. The dates encompassing the central 80% of the 4-wk periods of estimated peak emergence for rainbow trout fry in rivers of the region are shown, with the entire range of dates in parentheses. See the Appendix for characteristics of flow regimes for each river.

<sup>†</sup> Rivers used are listed by region from south to north, with U.S. Geological Survey or Japan Ministry of Construction gauge numbers. U.S. Pacific Coast: Sonoma Creek (11458500), Deer Creek (11383500), Elder Creek (11379500), Redwood Creek (11481500), Salmon River (11522500), Rogue River (14328000), Steamboat Creek (14316700), South Santiam River (14185000). Southern Appalachians: Davidson River (03441000), Coweeta Creek (U.S. Forest Service Coweeta Hydrologic Laboratory), Tellico River (03518500), Little River (03497300), Yadkin River (02111000), Nolichucky River (03465500), Watauga River (03479000), Clinch River (03524000). Colorado: Dolores River (09165000), Rio Grande River (08217500), Arkansas River (07093700), Gunnison River (09128000), White River (09304500), Colorado River (09034500), Yampa River (09239500), Cache la Poudre River (06752000). Hokkaido: Saru River (10902), Goshiribetsu River (10704), Tokachi River (11002), Toyohira River (10543), Abashiri River (11203), Ishikari River (10401), Shokotsu River (11502), Teshio River (10110). Honshu: Miya River (51602), Kumozu River (51401), Kamanashi River (31209), Iruma River (30717), Sai River (40218), Jintzu River (40802), Koyoshi River (20402), Kitakami River (20915).

<sup>‡</sup> From *personal communication* with eight research and management biologists who study steelhead or rainbow trout in the eight rivers: R. Leidy, P. Moyle, B. Harvey, M. Evenson, R. Stauff, P. Reimers, V. Shaw, and G. Harkleroad.

<sup>§</sup> From Couch (1985), Clark and Rose (1997), Clark et al. (2001), and G. D. Grossman and R. Ratajczak (*unpublished data*).

<sup>||</sup> From rainbow trout emergence dates reported in Nehring and Anderson (1993) for the eight rivers or those nearby.

<sup>¶</sup> From Aoyama et al. (1999) for northwestern Hokkaido, and Y. Taniguchi and S. Nakano (*unpublished data*) for southern Hokkaido.

<sup>#</sup> From Onodera and Ueno (1961) for central Honshu, and S. Nakano (*unpublished data*) and S. Yamamoto (*unpublished data*) for northern Honshu.

were significantly different. The alternative hypothesis was that values for all regions were different. All statistical analyses were calculated using SYSTAT Version 8.0 (SPSS 1998).

We then evaluated the six specific predictions (Table 2) about how the 12 individual characteristics of flow regimes differed among regions by testing each using a univariate one-way analysis of variance (ANOVA), followed by the same two a priori contrasts among regions. Finally, we interpreted the biological significance of these results for each variable in light of the means and standard error (SE) for each region. We conducted further analysis to test whether there were few floods during peak rainbow trout emergence in regions where invasions were successful (Prediction 5). For each stream we calculated the percentage of floods in each month for the period of record and averaged these for all streams in each region to estimate the overall probability of flooding by month. We then overlaid the estimated period of peak fry emergence for each region (see Table 3) on these flood distributions to assess their overlap.

## RESULTS

We found little evidence that the length of flow record influenced the characteristics of flow regimes used

in our analysis. Regression slopes of three flow characteristics on periods of record during 11–72 yr were not significant for any of the three streams ( $P = 0.11$ – $1.00$ ), except for the percentage of years with floods during fry emergence in the Southern Appalachian stream ( $P = 0.01$ ). However, the gradual linear decline of this variable by only 10% (from 55% to 45%) with the 61 additional years of data was not deemed to be biologically significant. We therefore concluded that the 11-yr record used for Japan streams was sufficient to characterize the differences in flow regimes we sought to analyze.

### *Tests of predictions about flow regimes among regions*

Principal Components Analysis of 12 biologically relevant characteristics of flow regimes showed that study streams formed distinct clusters by region, based on two factors that describe flood predictability, frequency, and duration, and seasonality of flooding and low flows (Fig. 2). Principal Component 1 contrasts sites with more short unpredictable floods (e.g., sites in the Southern Appalachians and Honshu) with those having fewer long predictable floods (Colorado). Principal Component 2 contrasts sites with maximum dis-

TABLE 3. Extended.

Years of discharge records	Period of peak rainbow trout emergence (range)
52 (25–72)	1 Apr–30 Jun‡ (7 Mar–31 Jul)
56 (13–75)	25 Apr–24 May§ (21 Apr–31 May)
84.5 (34–91)	15 Jun–14 Jul   (1 Jun–31 Jul)
11 (11–11)	15 Jun–31 Jul¶ (1 Jun–7 Aug)
11 (11–11)	15 May–30 Jun# (7 May–7 July)

charge in winter and minimum discharge in summer (Pacific Coast and Southern Appalachians) with those having summer maxima and winter minima (Colorado, Hokkaido, and Honshu). Together the first two factors accounted for 55% of the variation in sites in multivariate space (Table 5). The MANOVA and a priori contrasts revealed that the flow regime in each region differed significantly from all other regions (e.g., Wilks' lambda = 0.02,  $F_{24,48} = 13.0$ ,  $P < 0.001$  for contrasts), indicating that each was unique based on the 12 flow variables.

Analyses of individual flow regime characteristics using one-way ANOVA and a priori contrasts among regions (Table 6) upheld the first two of our six specific predictions and partially supported the third (Table 2), whereas results were equivocal for the other three predictions. First, the a priori contrasts for median date of maximum flow and month of highest mean flow indicate that Southern Appalachian (high invasion success)

TABLE 4. Twelve hydrologic characteristics used to test the six predictions about how flow regimes vary among five regions that differed in rainbow trout invasion success (see Table 2).

Predictions and flow variables	Biological significance to rainbow trout	Defined in Poff and Ward (1989)	Derived from IHA
1) Flood timing			
a) Median date of maximum daily flow	index of flood timing	FLODTIME	NP
b) Month of highest mean flow	index of seasonality of flooding	...	P
2) Season of low flow			
a) Median month of three months of lowest mean flow	index of seasonality of base-flow	...	P
3) Flood predictability			
a) Maximum percentage of floods in any 60-d period over all years	index of flood predictability	FLOD60D	P and NP
b) Maximum number of consecutive dates in all years during which no floods occurred	flood-free season	FLODFREE	P and NP
c) Coefficient of variation of median dates of maximum daily flow	measure of annual variation in flood timing	...	NP
4) Flood frequency and duration			
a) Median number per year of floods $\geq 1$ day duration	measure of the frequency of flood disturbances	FLODFREQ†	A
b) Median duration of floods (d)	measure of duration of flood disturbances that displace fry	FLODDUR†	A
5) Floods during peak fry emergence			
a) Percentage of years in which $\geq 1$ flood occurred during peak fry emergence	measure of flood occurrence during fry emergence	...	A‡
6) Annual flow variability			
a) Coefficient of variation of mean annual discharge	measure of annual variability in flows	ANNCV§	A
b) Coefficient of variation of mean of the three consecutive days of highest discharge	measure of annual variability of flood magnitude	...	A
c) Coefficient of variation of mean annual discharge during peak fry emergence	measure of annual variability of discharge during fry emergence	...	A‡

Notes: Variables defined by Poff and Ward (1989) are shown. Variables were calculated using the Indicators of Hydrologic Alteration algorithm (IHA) of Richter et al. (1996; The Nature Conservancy 1997), and were derived from either the Parametric (P) or Nonparametric (NP) Scorecard, or calculated from the Summary of Annual Statistics (A). Floods were defined as discharge events exceeding the 95th percentile mean daily flow for one or more days (see text).

† Poff and Ward (1989) used the mean flood duration and mean frequency per year of floods  $> 1$  d.

‡ Calculated from the Parametric Scorecard or Summary of Annual Statistics after restricting the analysis to the critical period defined for each stream (see Table 1).

§ Poff and Ward (1989) calculated the cv for daily flows each year, then averaged them (see their Table 1).

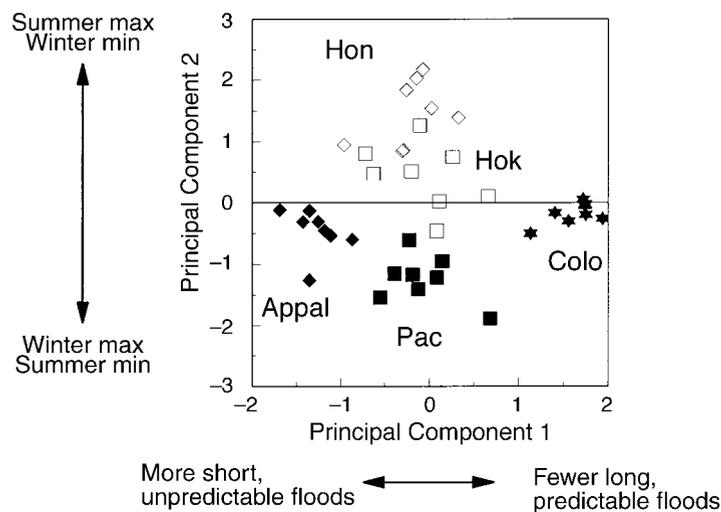


FIG. 2. Results of Principal Components Analysis of 12 characteristics of flow regimes. The eight streams in each of the five study regions are plotted in the plane defined by the first two principal components. Descriptions of axes are based on the variables with loadings greater than 0.6 for each factor (see Table 5). Regions are: U.S. Pacific Coast (Pac; solid squares), Southern Appalachians (Appal; solid diamonds), Colorado (Colo; stars), Hokkaido (Hok; open squares), and Honshu (Hon; open diamonds). Points for two streams each in Colorado and Honshu overlap and cannot be distinguished.

and Pacific Coast streams (native range) had similar flooding regimes in winter and early spring before peak emergence (mean dates for both variables are during January and February), whereas Colorado and Hokkaido (moderate invasion success) had flooding regimes in early summer (April–June;  $P = 0.16$  and  $P = 0.21$  for contrasts, respectively). In contrast, in Honshu, where invasions failed, high flows were during summer after emergence (July and August). Standard errors of means were generally low, except for Hokkaido due to a bimodal flooding regime (Fig. 3), indicating that statistical power was sufficient to detect differences. Overall, these results provide strong support for Prediction 1. Second, in the Southern Appalachians and Pacific Coast, streams reached lowest discharge during summer and early fall (August, on average; Table 6), whereas the other three regions had

low flows during winter (January and February). The a priori contrasts showed that the regions differed as predicted ( $P = 0.90$ ), upholding Prediction 2. Third, floods were relatively predictable in the native range and two of three regions where rainbow trout invasions were moderately or highly successful (all except Southern Appalachians), and unpredictable in Honshu where rainbow trout invasions failed. Means were high for the maximum percentage of floods in 60 d and the maximum number of dates with no floods for the three former regions, and low for Honshu. This general pattern supported Prediction 3, even though the contrasts indicated significant differences among all regions. In the Southern Appalachian region the largest floods were during winter, but many small floods occurred throughout summer from rains and in early fall due to hurricanes (Fig. 3). Therefore, the few dates without

TABLE 5. Loadings for the first two principal components accounting for variation in flow regime characteristics among five regions that vary in rainbow trout invasion success.

Flow regime characteristic	Principal Component	
	1	2
Median date of maximum flow	0.326	<b>0.887</b>
Month of highest mean flow	0.450	<b>0.799</b>
Low-flow season	-0.497	<b>-0.697</b>
Maximum percentage of floods in 60 d	<b>0.831</b>	-0.346
Maximum consecutive dates with no floods†	<b>0.898</b>	-0.158
cv of median date of maximum flow	<b>-0.712</b>	0.121
Median number of floods	<b>-0.838</b>	0.324
Median duration of floods†	<b>0.793</b>	-0.184
Percentage of years with floods during peak emergence	0.024	0.349
cv of mean annual discharge	0.359	-0.211
cv of mean 3-day maximum discharge†	0.022	0.340
cv of discharge during peak emergence	0.345	-0.006
Percentage of variation explained (cumulative percentage)	34.5%	20.8% (55.3%)

Note: Variables with loadings  $>0.6$  (in bold) are used in Fig. 2 to interpret the two principal components, and their ecological significance is discussed in *Methods: Statistical analysis of flow regime characteristics*.

† Variables transformed using square root to stabilize variance and reduce skewness.

floods during the periods of record made this region appear an outlier. The cv of median date of maximum flow showed no relationship with invasion success.

In contrast, our remaining three predictions were not supported by these data. The median number and duration of floods varied significantly among regions (Table 6) and did not match Prediction 4 that floods would be relatively infrequent and of longer duration in regions where invasions were successful. Colorado, a region with moderate invasion success, had the fewest longest floods, whereas the other regions were similar to one another. The Pacific Coast and Hokkaido had the fewest years with floods during the period of peak fry emergence, whereas the other regions had similar frequencies, which did not match our Prediction 5. However, this may mean that the ongoing invasion in Hokkaido streams will proceed more rapidly than expected. Moreover, the large number of small floods in Southern Appalachian streams may be less devastating to fry than suspected. Finally, our Prediction 6 that annual variability in three flow variables would be high in regions where invasion was successful was not upheld, either because these variables did not vary significantly among regions or the pattern did not match that predicted.

*Flood disturbance regime vs. timing of rainbow trout emergence*

Independent estimates of rainbow trout fry emergence overlapped relatively little with months having high probability of floods in regions where rainbow trout had high invasion success or are native, but overlapped strongly where invasions failed (Fig. 3). Fry emergence occurs during the period of declining flood probability in Southern Appalachian and Pacific Coast streams, whereas in Honshu it occurs just before the months with most floods. In Colorado, emergence begins in June, the month when floods from snowmelt runoff are most probable, but extends into July when rivers decline toward base flow. The flooding regime in Hokkaido streams is bimodal, with highest probabilities in April and May from melting snow in mountain headwaters, and in August and September from typhoons (hurricanes) that move north in the Pacific Ocean during late summer. Rainbow trout emergence in Hokkaido occurs during a two-month period with few floods during June and July, as indicated by the low percentage of years with floods during the period of peak fry emergence (mean, 8%; Table 6). The concordance between rainbow trout emergence and low or declining flood probability in regions where rainbow trout are successful or moderately successful invaders, and the opposite pattern where they have failed, provides strong support for Prediction 5.

#### DISCUSSION

Our analysis supported our most specific prediction, that differences in rainbow trout invasion success

among five Holarctic regions could be accounted for by the match between the timing of rainbow trout fry emergence and months with low probability of flood disturbance. This prediction was upheld despite flooding regimes and trout emergence timing that varied markedly among regions. For example, floods in Pacific Coast and Southern Appalachian streams are produced by winter rains, after which flows decline to baseflow in early summer. Rainbow trout and steelhead in these regions have peak emergence during this declining flow in April through June, reducing the chance that their fry will be displaced by flooding. By contrast, Hokkaido streams flood both from melting snow in late spring and typhoons in early fall, but rainbow trout emerge during a two-month "window" in June and July when few floods occur, substantially later than in the Pacific Coast or Southern Appalachian regions. By early fall, fish may have grown large enough to withstand higher flows (cf. Heggenes and Traaen 1988). Moreover, the occurrence and strength of typhoons vary among years, so rainbow trout invasions may be driven by high recruitment during years with weak storms. Floods in Colorado streams are highly predictable, resulting from melting snow in June, but emergence spans the period from June through late July (Nehring and Anderson 1993) when flood probability is declining rapidly, suggesting that recruitment success also depends on annual variation in flooding. In Honshu streams, where rainbow trout have failed to invade, floods are produced by summer monsoon rains followed by fall typhoons, resulting in a relatively high probability of flooding during all months from April through October. Rainbow trout fry emerge in May and June, just prior to the months of highest flood probability. These data suggest that the relative timing of flood disturbances and fry emergence is more important to invasion success than the absolute timing of either.

Our results support the hypothesis that differences in timing of the flooding regime among regions has a strong influence on rainbow trout recruitment and therefore invasion success. However, because ours is a mensurative study (*sensu* Underwood 1997), another unmeasured factor that varies among regions in the same pattern might explain invasion success as well (see *Discussion: Alternative hypotheses*). Nevertheless, our hypothesis is strengthened by three cases where this same factor, the timing and magnitude of flooding, explains variation in invasion success *within* regions, or among years within streams. In the Southern Appalachian region, rainbow trout established reproducing populations in most streams except "tailwaters" below reservoirs (Bettoli et al. 1999). Even where temperature and water quality are suitable, highly fluctuating flows from hydropower operations scour away nearly all spawning gravel, and therefore also trout eggs and fry. In the South Fork Holston River, Tennessee, below South Holston Dam, flows fluctuate less than in other tailwaters and spawning gravel is suffi-

TABLE 6. Twelve characteristics of flow regimes for five study regions that differ in rainbow trout invasion success (see Table 4 and the Appendix).

Region	Median date of maximum flow	Month of highest mean flow <sup>†</sup>	Median month of low-flow season <sup>†</sup>	Maximum percentage of floods in 60 d	Maximum consecutive dates with no floods	cv of median date of maximum flow
Pacific Coast	21 Jan (3.2 d)	2.2 (0.65)	8.3 (0.16)	47 (2.6)	127 (9.1)	0.14 (0.013)
Southern Appalachians	15 Feb (16.8 d)	2.6 (0.38)	8.4 (0.53)	37 (1.4)	12 (3.1)	0.28 (0.03)
Colorado	5 Jun (1.5 d)	6.0 (0.00)	2.1 (0.99)	65 (1.8)	195 (10.9)	0.05 (0.004)
Hokkaido	1 Jul (19.5 d)	4.7 (0.19)	2.5 (0.66)	50 (2.9)	84 (2.8)	0.30 (0.035)
Honshu	9 Aug (12.7 d)	6.9 (0.90)	1.1 (0.23)	35 (1.6)	63 (8.3)	0.17 (0.026)
<i>P</i>	<0.001	<0.001	<0.001	<0.001	<0.001 <sup>‡</sup>	<0.001
<i>P</i> for contrasts	0.16	0.21	0.90	<0.001	<0.001 <sup>‡</sup>	<0.001

Notes: Results are reported as means with 1 SE in parentheses. Coefficients of variation (cv) are based on annual data and are expressed as percentages. For each variable, overall significance of differences among regions by one-way ANOVA, and significance of two simultaneous a priori contrasts among regions, are shown at the bottom (see *Methods: Statistical analysis of flow regime characteristics*).

<sup>†</sup> Converted to integers (January = 1; see *Methods: Statistical analysis of flow regime characteristics*).

<sup>‡</sup> ANOVA and a priori contrasts were calculated after square-root transformation to stabilize variance and reduce skewness.

cient for trout reproduction, but rainbow trout recruitment was much lower than brown trout (Bettoli et al. 1999). Flows fluctuated much less during peak brown trout emergence (maximum mean daily discharge, 35 m<sup>3</sup>/s), estimated to be during late February from spawning dates and time to emergence based on temperature (Crisp 1988), than during peak rainbow trout emergence in late April and May (Table 3) when the maximum discharge for the year occurred (85 m<sup>3</sup>/s). Overall, these data indicate that periodic high flows during emergence reduce rainbow trout recruitment below reservoirs in this region. Similarly, in Hokkaido streams, rainbow trout have established reproducing populations more readily in stable spring streams fed by aquifers of lava tuff at the bases of old volcanoes (Kitano et al. 1993, Taniguchi et al. 2000) than in mountain streams fed by snowmelt runoff that produces high peak flows. Lastly, annual recruitment of age-1 rainbow trout and brown trout in 10 of 11 Colorado rivers studied by Nehring and Anderson (1993) was strongly negatively correlated with snowmelt discharge during the month of peak emergence the previous year when fish were age-0. This indicates that annual variation in trout recruitment in Colorado streams can also be explained by floods (cf. Schlosser 1985, Latterell et al. 1998, Mion et al. 1998).

Our hypothesis is also supported by a substantial body of experimental and observational evidence showing that high water velocities displace salmonid fry and reduce their survival. For example, Heggnes and Traaen (1988) reported that newly emerged fry of four salmonid species (mean, 24–28 mm total length [TL]) were washed out of a laboratory channel at velocities of only 10–25 cm/s, depending on temperature. During floods in natural streams, velocities would rap-

idly 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 dead fry, indicating that they would be highly susceptible to displacement when scoured from velocity refuges by floods. 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 base-flow 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<sup>6</sup> by 1922; McDowall 1989), reproducing populations have established only in certain regions. Jowett (1990) found that rainbow trout distribution among 157

TABLE 6. Extended.

Median number of floods	Median duration of floods (d)	Percentage of years with floods during emergence	CV of mean annual discharge	CV of mean 3-day maximum discharge	CV of discharge during emergence
4.8	2.8	19	36	58	52
(0.37)	(0.14)	(6.4)	(5.6)	(3.6)	(9.7)
7.4	2.2	41	25	43	47
(0.26)	(0.06)	(3.5)	(1.1)	(3.1)	(3.5)
1.7	5.2	42	35	43	65
(0.19)	(0.65)	(6.0)	(4.2)	(5.6)	(6.8)
5.2	3.2	8	15	84	50
(0.53)	(0.33)	(4.4)	(1.7)	(17.2)	(8.2)
7.5	2.1	47	31	71	59
(0.60)	(0.11)	(4.0)	(4.0)	(10.6)	(7.6)
<0.001	<0.001‡	<0.001	0.002	0.03‡	0.45
<0.001	0.001‡	<0.001	<0.001	0.02‡	0.33

sites throughout New Zealand was most closely related to low variability of flows and presence of volcanic ash aquifers. Rivers with reproducing rainbow trout had stable flows fed by springs or headwater lakes, whereas only brown trout occurred in other rivers with more variable flows. Jowett (1990) concluded that rainbow trout distribution was related mainly to climatic and geologic factors that controlled flow variability, supporting our claim that the regional scale is appropriate for analyzing their invasion success. Smith (2000) reported that abundance of adult spawning steelhead in their native range of British Columbia was negatively correlated with discharge during their juvenile rearing phase in northern rivers that are driven by summer snowmelt, but not in southern rivers that flood during winter rains. As in Colorado, discharge peaked in British Columbia snowmelt rivers during June, and Smith proposed that these high flows flushed juvenile steelhead from suitable habitats (cf. Shirvell 1990).

#### Alternative hypotheses

Our results support the hypothesis that flood disturbance can limit rainbow trout invasion success at the regional scale, but other abiotic factors like temperature, and biotic factors like characteristics of donor populations and biotic interactions, may also play a role. Although water temperature too high for rainbow trout egg survival or proper incubation is an important physical constraint, it is an unlikely mechanism in regions where other salmonids reproduce. Optimum temperature for incubation of rainbow trout eggs is among the highest for salmonids (e.g., Kwain 1975), so they should be able to reproduce where other salmonids can. For example, in central Honshu we restricted our analysis 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 sur-

vival 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 (Svårdson 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-

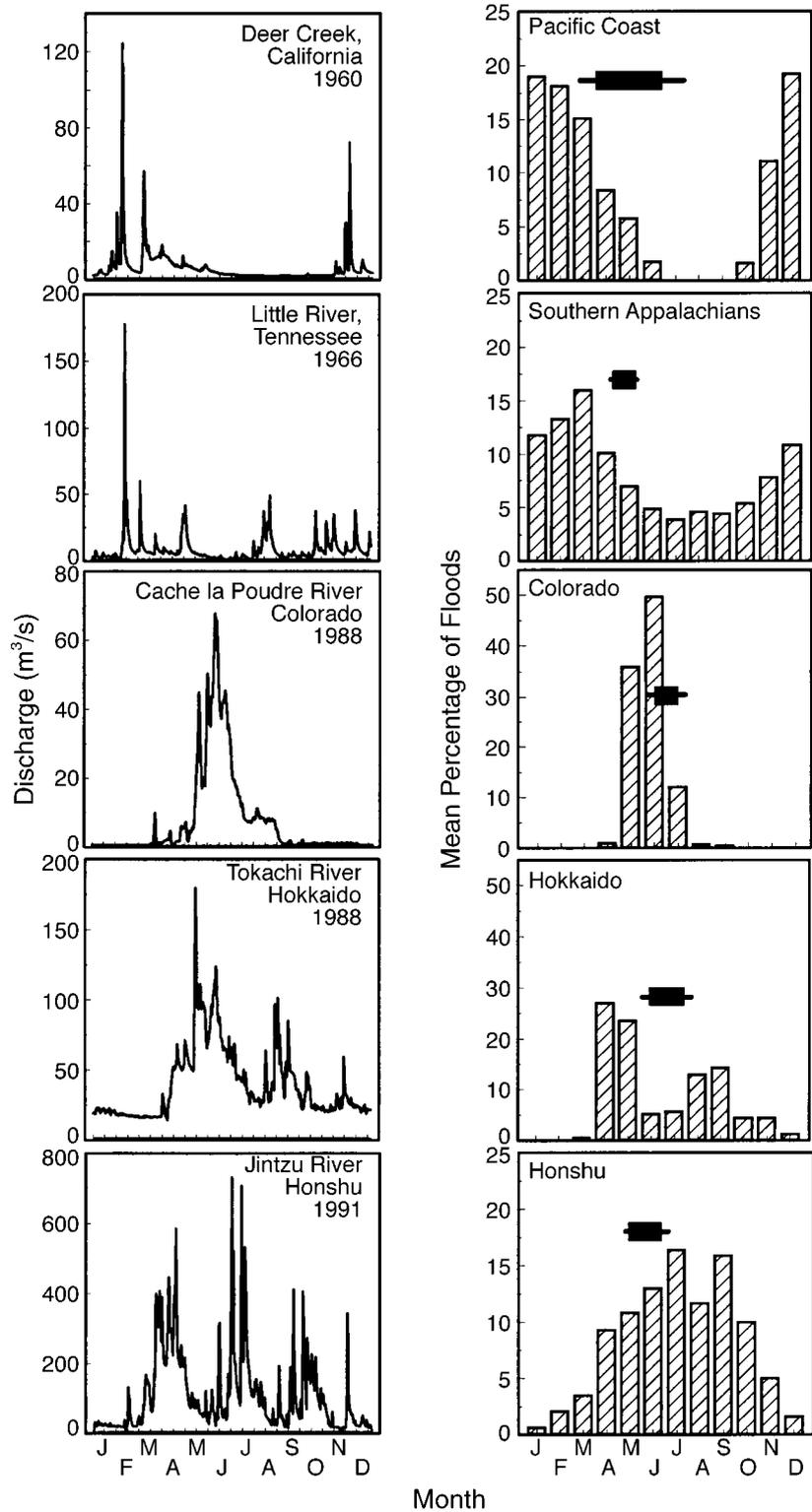


FIG. 3. Representative flow regimes, and probability of floods relative to timing of rainbow trout fry emergence, for the five study regions. Panels at left show representative annual hydrographs for one stream in each region. Panels at right show mean percentage of floods by month for the eight streams 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.

ture 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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#### APPENDIX

A table presenting characteristics of the flow regimes for the eight rivers in each of the five study regions is available in ESA's Electronic Data Archive: *Ecological Archives* A011-017.