

Interspecific competition and juvenile Atlantic salmon (*Salmo salar*): on testing effects and evaluating the evidence across scales

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Abstract: A review of 17 controlled experiments of interspecific competition between juveniles of Atlantic salmon (*Salmo salar*) and other fishes revealed relatively little evidence to judge competitive effects at any scale. More than half were unreplicated and so inadequate to test either the existence or relative strength of interspecific competition. Most replicated experiments used one of two designs appropriate to address questions of interest, such as whether nonnative species affect Atlantic salmon via competition or whether interspecific competition from coevolved salmonids is greater than intraspecific competition. Replicated experiments spanned a broad range of spatial and temporal scales, and one well-designed field experiment yielded the strongest inference at useful scales. Nonnative salmonids being introduced worldwide into Atlantic salmon waters have the potential to invade, so experiments testing their effects are most urgently needed. Overall, juvenile coho salmon (*Oncorhynchus kisutch*) are suspected to have the greatest effect, partly due to their inherent size advantage. The potential for complex interactions or indirect effects to modify effects of nonnative species is completely unknown but may be important and needs investigation.

Résumé : L'analyse de 17 expériences contrôlées de compétition interspécifique entre des saumons de l'Atlantique (*Salmo salar*) juvéniles et d'autres poissons n'a produit que peu de données permettant de juger des effets compétitifs à une échelle quelconque. Plus de la moitié des expériences n'étaient pas répétées, et ne permettaient donc pas de vérifier l'existence d'une compétition interspécifique ou sa force relative. Presque toutes les expériences répétées utilisaient l'une des deux approches d'adresser aux questions pertinentes, comme l'influence éventuelle des espèces non indigènes sur le saumon atlantique par la compétition, ou l'importance relative de la compétition interspécifique entre des salmonidés qui ont évolué ensemble et de la compétition intraspécifique. Les expériences répétées couvraient une vaste plage d'échelles spatio-temporelles, et une expérience de terrain bien conçue a permis d'obtenir la plus forte inférence à des échelles utiles. Comme les salmonidés non indigènes sont introduits partout dans le monde dans les eaux à saumon atlantique, qu'ils peuvent les envahir, il est impératif d'élaborer des expériences visant à déterminer leurs effets. En général, les cohos (*Oncorhynchus kisutch*) juvéniles auraient la plus grande influence, en partie à cause de l'avantage inhérent à leur taille. La possibilité que des interactions complexes ou des effets indirects modifient l'impact des espèces non indigènes est encore inconnue, mais elle peut être importante et doit être étudiée.

[Traduit par la Rédaction]

Introduction

Interspecific competition may be an important factor affecting growth and survival of Atlantic salmon (*Salmo salar*) during their juvenile life history in streams. During this freshwater phase Atlantic salmon throughout much of their range are typically part of simple assemblages consisting of only a few fish species. A subset of these, often only one other salmonid, make up a guild that feed on a common resource of drifting invertebrates. Members of such small guilds that exploit single resources are potentially strong interactors (Connell 1975; Paine 1992; Power et al. 1996), and therefore good candidates for showing ecologically significant effects from biotic interactions such as interspecific competition (Wiens 1989). Moreover, salmonids are known to respond quickly when resources or other species are

added or removed (Chapman and Bjornn 1969; Fausch and White 1986), increasing the chances that niche shifts from such changes will occur, have important effects on fitness, and be detectable by experiments or observations.

In addition to the potential salmonid competitors with which Atlantic salmon coevolved, intentional and unanticipated introductions are increasing the chances that nonnative competitors, salmonids or otherwise, will become established in Atlantic salmon waters (Fausch 1988; Harache 1992). Increasingly, researchers and managers are being asked to predict effects of both native and nonnative competitors on Atlantic salmon stocks at a variety of scales and will need a sophisticated understanding to do so.

The purpose of this paper is to evaluate the evidence that native and nonnative interspecific competitors have strong direct effects on Atlantic salmon. Because in my view such data are largely inadequate at present, I begin by considering relevant scales of investigation and describing appropriate study designs for measuring such effects, in order to provide a template against which to measure the available evidence. After reviewing the relevant research to date, I briefly address more complex interactions such as condition-specific

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competition and the potential for indirect effects through food webs and conclude by presenting my views about the most important effects to understand first. I deal here exclusively with interspecific interactions during the freshwater life stage from alevin to smolt, as others in this volume will treat potential competition during spawning (Fleming 1998), interactions between wild and stocked Atlantic salmon (Youngson and Verspoor 1998), and the population dynamics of intraspecific competition (Grant et al. 1998; Kocik and Ferreri 1998).

On scale

At what scale do we understand interspecific competition involving Atlantic salmon, and can knowledge at this scale address important ecological and management questions? This issue is challenging because although interspecific competition occurs moment-to-moment between individual fish by behavioral interactions, it is suspected to have wide-ranging and long-lasting effects on survival and fitness (Connor and Bowers 1987). How can we understand a phenomenon that affects organisms over such a wide range of scales? Here I address this problem by posing four questions.

First, what axes of scale are relevant to the study of biotic interactions like interspecific competition? I consider four — space, time, biological response, and biological organization. All are hierarchical, and should ideally be considered in the context of the life history of the organism studied (Wiens 1989). Thus, relevant spatial scales include individual home ranges, nested within local habitat patches occupied by many individuals, nested within a region that may contain many local patches that support a population linked by dispersal, all within the biogeographic scale that encompasses the entire species range. Stream ecologists also view stream habitat in a similar nested spatial hierarchy, from microhabitats nested within individual habitat units (riffles, pools, etc.), to stream reaches, sub-basins, and finally entire drainage basins (Frissell et al. 1986; Poff 1997). How individual and population processes scale to these physical habitat units will determine the physical dimensions of study designs needed to answer specific questions (Wiens 1989; Wiens et al. 1986). Similarly, the temporal scale relevant for understanding ecological processes can be viewed within a hierarchy ranging from daily and seasonal cycles to annual breeding cycles and mean generation times.

Also important for studying interspecific competition are hierarchical scales of biological response and biological organization. Thus, biological responses to competitors can be measured as changes in behavior, physiology, growth, survival, and fitness (Fausch 1988), each of which may answer a different question about the effects of competition on individuals or populations. Finally, interspecific competition can be measured at different levels of biological organization, those of interest for Atlantic salmon usually being individuals, populations, and perhaps metapopulations.

A second question, which gets at the importance of considering scale, is whether answers about interspecific competition change across scales. For example, might intense behavioral interactions at the individual level nevertheless have little effect on survival and fitness at the population

level over the long run? Welden and Slauson (1986) distinguish between the *intensity* of competition, referring to its proximate behavioral or physiological effects on individuals, versus its *importance*, the ecological and evolutionary consequences of those effects relative to all other biotic and abiotic factors. To use a specific example, if limited stream habitat produces strong density-dependent juvenile mortality over winter (e.g., Mason 1976), then above some threshold reduced survival during the previous summer due to strong interspecific competition with another salmonid might have little effect on smolt output and long-term population viability. Thus, one might predict intense interspecific competition between juveniles during summer to be more important where winter conditions are benign and habitat abundant, than where they are harsh and limiting.

These considerations lead to a third question. What are relevant scales along the four axes for studying interspecific competition involving Atlantic salmon? The answer requires striking a balance between asking meaningful questions versus designing experiments that can detect a response. For example, for managers charged with maintaining viable populations of Atlantic salmon, it would be most appropriate to measure survival at the local habitat patch scale over annual time increments (relevant periods for survival of emerging fry would be less), to understand effects of interspecific competitors on local populations (cf. Wiens 1989). I hasten to add however, that the intensity of competition is likely to vary annually and by location, making it necessary to consider other evidence at a variety of scales, from individual behavior and growth to zoogeographic distributions, to place the results of such experiments in an appropriate context (Bender et al. 1984; Wiens 1989).

Because much study of interspecific competition among salmonids has been done at the scale of individuals in laboratory streams (e.g., Griffith 1972), a final question is what evidence we have about its effects at the population level in local habitats over annual increments. I address this in the analysis below.

On testing competition

Before analyzing specific tests with Atlantic salmon, it is appropriate to first define interspecific competition and place it in context among other factors that influence guilds of drift-feeding salmonids. Here I follow Wiens (1989) who defines interspecific competition as an interaction between members of two or more species that, as a consequence of either exploitation of a shared resource or interference related to that resource, has a negative effect on fitness-related characteristics (e.g., growth, fecundity, survival) of at least one species. The interspecific interference displayed by stream salmonids for favorable feeding locations from which to capture drifting invertebrates satisfies many of the criteria needed to clearly demonstrate at least the existence of interspecific competition (Reynoldson and Bellamy 1971; Wiens 1989), such as that species overlap in resource use, intraspecific competition occurs, and resources are limiting. The high natality of fishes, coupled with a seasonal environment where space and invertebrate drift resources decline drastically each year in many systems, ensures that resources will be limited resulting in high intraspecific (e.g., Grant and

Kramer 1990) and interspecific competition. This, in turn, leads to a "critical period" or bottleneck for juvenile survival (Elliott 1994), a feature common to many fishes (LeCren 1965). Moreover, such bottlenecks are generally predictable year to year, because even a relatively low density of adults can saturate the available habitat with progeny (see Ricker 1954; Elliott 1994 for examples).

Despite the primacy of interspecific competition in past explanations of community patterns (see Ross 1986 for a review), it is important to place it in an appropriate context among other factors that affect distribution and abundance of salmon. Although biotic interactions like competition and predation may have strong effects at individual to population scales, species-specific responses to environmental factors set the template upon which those biotic interactions work (Poff 1997). Simply put, these concepts are identical to the fundamental niche (species-specific response to the environment) and realized niche (considered broadly, the niche after including effects of all biotic interactions) of Hutchinson (1957). Similarly, legacies due to history and chance, coupled with lag times after disturbances, often form an even broader template of habitat heterogeneity across landscapes upon which species array themselves according to their fundamental and realized niches. It is wise therefore, to consider that the potential for interspecific competition will be determined by autecology that controls whether species will co-occur at all, as well as the spatial and temporal heterogeneity of habitat and other physical conditions which may modify its outcome (Dunson and Travis 1991).

Experimental design

Assuming that appropriate scales of space, time, and biological response and organization have been selected that are suited to the question of interest, the next issue is how to design an experiment to rigorously test interspecific competition. Appropriate designs will subsequently be used here to assess whether studies to date have yielded strong inferences about competition between Atlantic salmon and other fishes. Before turning to designs, however, I first address the basic theory of population dynamics under interspecific competition.

The Lotka–Volterra competition equations provide a formal mathematical theory long used by ecologists to predict population growth rate of one species from its own abundance and that of one or more competitors (reviewed by Law and Watkinson 1989). Considering a simple community with only two competing species, experiments that manipulate the abundance of each using either single short-term (i.e., "pulse") or sustained ("press") manipulations (Bender et al. 1984), can be employed to estimate the two competition coefficients, basic parameters needed for these equations. The competition coefficients measure the effect on population growth rate of one interspecific competitor relative to the effect of one intraspecific competitor. However, although these coefficients have been successfully measured in the laboratory for organisms like *Drosophila* with simple life cycles, the required field manipulations are logistically impossible for large mobile organisms with complex life histories. Moreover, the theory has proved too simple (Law and Watkinson 1989). Vertebrate populations may not follow Lotka–Volterra dynamics, because competition coefficients

may depend on density or environmental conditions and do not account for age or size structure of populations. After an extensive review, Law and Watkinson (1989) concluded that despite the formal theory, the basic underpinning of empirical field data on interaction strengths needed to adequately test it is lacking. For that reason, I focus here on experimental designs to empirically test such interaction strengths for a mobile vertebrate with a complex life cycle, such as Atlantic salmon.

Two other issues known to most fish ecologists are also important to review before discussing designs. First, it is fundamental that experiments at any scale must be properly controlled, replicated (not pseudoreplicated *sensu* Hurlbert 1984; Underwood 1986, 1997), and randomized. Controls allow separating effects of the added competitor from other disturbances caused by experimental manipulations (e.g., electrofishing and handling), replicates allow separating effects of the competitor from differences among sites used for controls and treatments, and randomization of replicates to treatments and controls avoids bias that might affect results. Second, experiments must be designed with care to closely mimic the natural environment that provides the arena for competition, to minimize disturbances other than adding the competitor, and to control for any other disturbances. Otherwise, the hypothesis being tested by the experiment may be fundamentally changed (Underwood 1986). To use an extreme example, if one tests the effects of heat-branded rainbow trout (*Oncorhynchus mykiss*) on Atlantic salmon in small lentic aquaria with no substrate or cover under abnormal photoperiod, and when feeding pelleted food, then the hypothesis being tested will have little relevance to natural conditions in streams, even when properly controlled and replicated.

Additive and substitutive designs

There are two basic questions that can be asked about interspecific competition, leading to two different experimental designs. First, does adding species B have any effect on species A, all other things equal? Second, if so, does adding species B have any more (or less) effect than adding the same number of species A (Connell 1975, 1983). The first question leads to an additive design that tests the *existence* of interspecific competition, the second to a substitutive design that measures its *strength* relative to intraspecific competition. Both have advantages and disadvantages (Begon et al. 1996) and situations to which each applies best. A design that combines both is ideal, but may be logistically impossible. Each design is treated *seriatim*.

Additive designs are most useful to address the effects of nonnative species, and competitors that differ markedly in size or ecology. Treatments are typically constructed by adding an equal density of the competitor, compared to controls with ambient density of the target species (Table 1). The advantage of this design is that it holds "all other things equal" (e.g., intraspecific competition; Werner and Hall 1977) except for adding the competitor, a hallmark of logical experimentation (Underwood 1986, 1997; Snaydon 1991). However, it also confounds the effect of interspecific competition with that of doubling total density (Maiorana 1977; Law and Watkinson 1987, 1989). Thus, if performance of species A declines when species B is added, one cannot de-

Table 1. Two different designs for testing relative strengths of interspecific versus intraspecific competition. The additive design is favored by Underwood (1986) and Dunson and Travis (1991).

Characteristic	Experimental treatment		
	1	2	3
<i>Additive design</i>			
Number of species A	5	5	
Number of species B		5	5
<i>Substitutive design</i>			
Number of species A	10	5	
Number of species B		5	10

termine whether species B has any greater effect than adding an equal number of species A, without further experiments (Table 2). Despite this, because it models the process of species invasion it is the most logical design to answer whether nonnative species affect native ones, or whether removing a nonnative competitor will allow a reduced population of a native species to rebound. If not, then some factor other than interspecific competition is affecting the native species. This design is also the most useful when competitors are of different sizes or have different ecology so that total density has little meaning (Snaydon 1991). For example, Beall et al. (1989) tested the effect of yearling coho salmon (*Oncorhynchus kisutch*) on emerging Atlantic salmon using an additive design, which was appropriate because the two are very different sizes. In such experiments it would be logical to use either natural densities or equal biomasses of each species.

Substitutive designs, in contrast, are most useful for assessing the relative effect of one native species on another, where both are similar in ecology and already known to compete. Because animals are expected to be ecologically more similar to their own species than another, one would expect conspecifics to be stronger competitors than heterospecifics. This led Connell (1975, 1983) to propose that the strength of interspecific competition can only be understood in comparison to intraspecific competition. By holding total density constant (Table 1) the substitutive design can be used to determine relative strengths of interspecific versus intraspecific competition, whereas the additive design confounds the effect of the added competitor with increased density and is unable to distinguish two of the three possibilities (Table 2; Dunson and Travis 1991). Substitutive designs work equally well, and additive designs suffer the same deficiency, in cases where a species responds to a superior competitor that dominates a preferred habitat like pools by shifting to use a less favorable habitat such as riffles (i.e., via a niche shift or interactive segregation). However, others argue that the substitutive design is invalid because it changes the two factors simultaneously (Underwood 1986; Snaydon 1991).

In practice, for coevolved species such as Atlantic salmon and brown trout (*Salmo trutta*) which are similar in ecology and already known to compete behaviorally for food and space (e.g., Kalleberg 1958) using the additive design to test the null hypothesis that brown trout have no effect on Atlantic salmon (not even an effect equal to other salmon) may be

of little interest (see Dunson and Travis 1991; Gilliam et al. 1993 for similar examples). Instead, managers may want to use the substitutive design to measure the effects of stocking age-0 brown trout on age-0 Atlantic salmon (interspecific competition) relative to stocking the same number of Atlantic salmon (intraspecific competition). Similarly, this design could be used to ask whether resident brown trout survival would be higher if rainbow trout were stocked versus more brown trout, in waters where one or both are not native. In both cases, the question of interest is best addressed with the substitutive design that contrasts interspecific competition versus added intraspecific competition.

An ideal approach would combine both additive and substitutive designs to test both the existence and relative strength of interspecific competition. This requires a minimum of five treatments to allow separating reciprocal intraspecific versus interspecific effects for two species (see Underwood 1986, 1997; Fausch 1988; Dunson and Travis 1991). Logistical constraints inherent in working with large mobile organisms like stream fish often require minimizing treatments to permit adequate replication (Fausch 1988), so many investigators have reduced designs to the three treatments shown in Table 1, or the minimum of two needed to measure the effect of a competitor on one target species (e.g., 10 species A versus 5 A plus 5 B). In what follows I refer to designs with the three treatments as "full additive" or "full substitutive," and those with two treatments as "minimal additive" or "minimal substitutive" designs.

The two designs described above have long been used by plant population biologists (deWit 1960; Harper 1977; Firbank and Watkinson 1985). Because plant densities and mixtures are more easily manipulated under controlled conditions, a preferred design involves measuring performance under a wide range of frequencies and densities of both species and fitting a response surface (Law and Watkinson 1989; Firbank and Watkinson 1990). However, such large experiments would be impossible for most vertebrates and are not considered further.

Two other experimental design issues are also important. First, the relative intensity and magnitude of intraspecific and interspecific competition depend on the starting densities used. Ideally, experiments would be conducted at carrying capacity for both species. Alternatively, experiments can be designed based on the range or mean of natural densities measured in the field at sites to which the inferences will be applied, or run at a series of densities to assess the density dependence of competition. For an experimental channel, carrying capacity can be operationally defined by stocking fish at high density and removing individuals that emigrate through traps more than twice (cf. Fausch 1984; Fausch and White 1986). Second, body size often determines the outcome of competition among stream salmonids, which compete for territories in relatively homogeneous habitat such as riffles or glides (e.g., Kalleberg 1958) or set up size-structured dominance hierarchies in pools (e.g., Fausch 1984). Therefore, experiments using the designs described above should be run with fish of equal sizes, or the natural range of sizes, depending on the hypothesis being tested (cf. Fausch and White 1981, 1986; MacCrimmon et al. 1983). Finally, testing interspecific competition within size-structured hierarchies requires an individual-based theory in-

Table 2. Per capita performance of species A (e.g., growth) in treatment 2 (interspecific competition; see Table 1) when compared to treatment 1 (intraspecific competition for species A), for two experimental designs and three scenarios of relative strengths of interspecific versus intraspecific competition.

Design	Interspecific >> intraspecific	Interspecific = intraspecific	Intraspecific >> interspecific
Additive	Decreased growth (confounded ^a)	Decreased growth (confounded ^a)	No growth difference
Substitutive	Decreased growth (unconfounded)	No growth difference	Increased growth (unconfounded)

^aEffect is confounded because it could be due either to adding the competitor, or increasing the total density, or both.

corporating behavioral interactions, which is beyond the scope of this paper. Readers are referred to Fausch (1984), Parker and Sutherland (1986), and Milinski and Parker (1991) for possible approaches.

Practical constraints

What of the "real world" of testing interspecific competition, where logistic, economic, and ethical considerations all play strong roles in determining which research is actually conducted? Many researchers and managers must settle for conducting research that may not conform to the ideal standards above. One such line of evidence is comparative analysis of many field sites where a competitor is present versus absent. Although very useful for generating testable hypotheses, the effect of the competitor is confounded with differences in environmental factors among locations, a problem that may be addressed only with a large sample of sites and analysis of covariates (e.g., temperature). Even so, at these large scales it is difficult to rule out alternative hypotheses for the patterns (Connor and Bowers 1987; Wiens 1989), such as differences in abiotic (e.g., altitude, gradient) or other biotic factors (e.g., predation, disease), or interactions among them. Fausch (1989) and Fausch et al. (1994) present these kinds of analyses.

Because setting up enclosures and manipulating densities may itself introduce unwanted effects on fish, one of the simplest ways to conduct a competition experiment is by removing the competitor and comparing the response of the target species before versus after (e.g., Fausch and White 1981) or to that in an unmanipulated control reach. This is, in effect, a minimal additive design (Table 1) and is particularly useful for determining whether a nonnative invader has effects at least as strong as conspecifics (Table 2).

Finally, it is important to realize that one experiment does not a complete understanding make. The ideal circumstances are to conduct multiple experiments in both laboratory and field, and combine these with observational field data at various scales. Thus, whereas tightly controlled and replicated experiments can be used to test focused hypotheses about the mechanisms of competition, broad field surveys will be important for placing the results into an appropriate context for resource managers.

Coevolved competitors

Atlantic salmon coevolved with brook trout (*Salvelinus fontinalis*) in North America and brown trout in Europe, and occur in sympatry with both as juveniles in streams. They also coevolved with other salmonids (e.g., Arctic charr, *Salvelinus alpinus*) and nonsalmonids (e.g., *Rhinichthys*

atratulus, *Cottus gobio*), but only one experiment has been conducted on interactions with any of these (Symons 1976). Here I use the framework of scale and experimental designs laid out above to review the experiments that have been done and, ultimately, to address three questions. First, which studies have used controlled and replicated experiments with designs appropriate for the question of interest to yield valid inferences at any scale? Second, what information do we have at larger scales along the four axes, such as for populations in local patches over annual increments? Third, how might the answers change across scales?

Brook trout

Brook trout alevins emerge from gravel redds before Atlantic salmon in spring and are therefore larger (Randall 1982) and presumably dominant in their preferred habitat. Observational evidence indicates that age-0 brook trout use positions in pools whereas age-0 Atlantic salmon occupy riffles (Gibson 1993; Rodríguez 1995). However, when allopatric each species may use the opposite habitat (MacCrimmon et al. 1983) suggesting that in sympatry niche shifts due to interspecific competition, also known as interactive segregation (Nilsson 1967), may be occurring. If so, interspecific competition by either species may have negative effects on growth or survival (and hence biomass or density) of the other that are stronger than intraspecific competition.

Few controlled experiments have been done that can adequately answer these questions for brook trout and Atlantic salmon, primarily because most were unreplicated and in several additive designs were used that prevent determining the relative strength of interspecific competition (Table 3). For example, Gibson et al. (1993) reported on a long-term, large-scale manipulative experiment in three southeast Newfoundland streams. Microhabitat selection and salmonid biomass in individual habitat units (i.e., riffles, flats, pools) were measured 2 years before and 5 years during which spawning Atlantic salmon were placed above a migration barrier into a stream with only brook trout. Another stream with brook trout alone was used as a control, and a third stream had brook trout and wild salmon. After stocking, total salmonid biomass in three riffles of the stream where salmon were stocked was about half that in two riffles of the stream with brook trout alone, but because there were no replicate streams this difference could have been due to factors unique to each. Moreover, the design was confounded because pretreatment densities in the specific habitat types being compared varied 2 to 5 times among different streams. Similarly, not all data for all habitat types sampled, nor all streams, were provided, preventing further analysis. The

Table 3. Design and main results of controlled experiments testing competition between Atlantic salmon and coevolved competitors. Spatial scale is of the entire experimental unit manipulated, even though responses may have been measured at a smaller scale. Full and minimal additive (A) and substitutive (S) designs are described in the text and Table 1. For replicated experiments only, the relative strengths of intraspecific (intra) versus interspecific competition (inter) are shown as the outcome.

Reference	Scale				Experimental unit	Replication	Design	Outcome
	Space (m ²)	Time (d)	Biological response	Biological organization				
<i>Brook trout</i>								
Dickson and MacCrimmon (1982)	0.90	14	Behavior, growth	Individual	Tank	7–11	Full S	Intra = inter ^a for both responses
Gibson and Dickson (1984)	1462–4075 ^b	64–79 ^b	Growth, biomass	Individual, “population” ^c	Reach	1–2	Minimal A ^d (add trout)	Unreplicated
Gibson and Power (1975)	7.5	>1 ^b	Behavior	Individual	Tank	1	S ^e	Unreplicated
Gibson et al. (1993)	ca. 38 000 ^b	ca. 2190	Behavior, biomass	Individual, “population”	Stream	1–2	Minimal A ^f (add salmon)	Unreplicated
MacCrimmon et al. (1983)	0.90, 5.25	14, 29	Behavior, growth	Individual	Tank, enclosure	7–11, 2–3	Full S	Asymmetry for behavior, intra = inter for growth ^g
<i>Brown trout</i>								
Kennedy and Strange (1980)	ca. 1980, 8880	ca. 730	Growth, density, survival	Individual, “population”	Stream	2	Minimal A ^h (add salmon)	Inter ≥ intra for both responses
Kennedy and Strange (1986a,b)	ca. 2960 ⁱ	ca. 730	Behavior, growth, survival	Individual, “population”	Reach	1	Minimal S (add trout)	Unreplicated
<i>Non-salmonids</i>								
Symons (1976)	26.6	21	Behavior, growth	Individual	Tank	2–3	Full A ^j	Intra > inter for salmon, inter > intra for others

^aResults suggested intraspecific > interspecific for growth of both salmon and brook trout, but low power may have prevented detecting it.

^bData to calculate area of sites or duration of experiments were not given for many or all cases.

^cRefers simply to all fish present in each reach studied, not to a defined interbreeding population.

^dDensities not measured for most treatments, so can't separate effects of changes in density from added/removed competitors.

^eMinimal substitutive (shallow tank) and full substitutive (deep tank) experiments, but densities were not equal among treatments.

^fPre-treatment densities varied 2 to 5 times among habitat types between treatments, and post-treatment densities were reported only for some habitats.

^gBrook trout were 13% longer in enclosures, equal size in tanks. Low power for enclosure experiments masked large differences in growth. Experiments in tanks were the same ones described in Dickson and MacCrimmon (1982).

^hTotal density after salmon were stocked was 2.5–3.8 times higher than for brown trout alone in the two streams over 2 years.

ⁱBased on mean width from Kennedy and Strange (1980). Exact dimensions not reported.

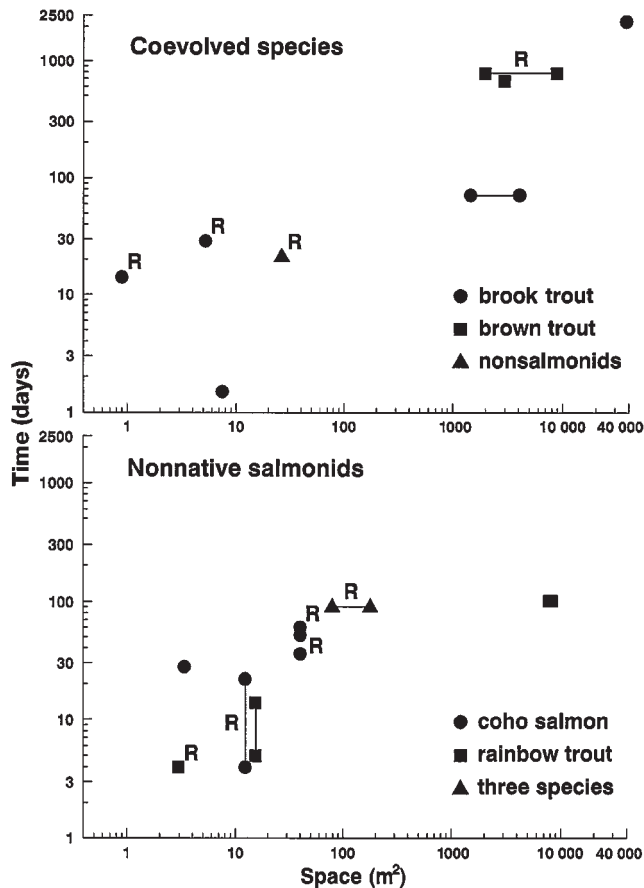
^jOnly ranges of densities of nonsalmonids were reported, but were about twice that of salmon.

lack of replication and incomplete data reporting are unfortunate given that these experiments addressed changes in brook trout biomass in whole streams over 7 years. This is the largest temporal and spatial scale of any experiment reviewed (Fig. 1) and just the scale at which managers need answers.

An interesting set of experiments by Dickson and MacCrimmon (1982) and MacCrimmon et al. (1983) can be used to assess whether answers about interspecific competition change across a small range of scales. They studied microhabitat use, agonistic behavior, and growth of brook trout and both wild and hatchery Atlantic salmon in controlled environments at two different spatial and temporal scales, in

compartments in an outdoor stream tank (<1 m², 14 d) and enclosures in a nearby stream (ca. 5 m², 29 d). They measured changes in agonistic behavior (stream tank only) and microhabitat use and growth for both species in allopatry and sympatry, using the full substitutive design (Table 1). The two experiments differed in that species were of equal size in the stream tank, but brook trout were 13% larger in the stream enclosures, which is the natural size differential due to their earlier emergence. Comparisons of wild salmon and brook trout showed that growth was similar and not significantly different among sympatry and each species in allopatry in the stream tank, indicating that interspecific and intraspecific competition were about equal and symmetric

Fig. 1. Spatial and temporal scales of experiments testing interspecific competition between Atlantic salmon and coevolved fishes (top) and nonnative salmonids (bottom). Lines show ranges of scale for different sites in single experiments, and replicated experiments are marked (R). Some points were offset slightly to enhance clarity. Data are in Tables 3 and 4.



when fish were the same size. In contrast, brook trout greatly suppressed growth of Atlantic salmon in sympatry compared to allopatry in the stream enclosures. Unfortunately, this difference was not significant due to few replicates that caused low statistical power. Brook trout also apparently displaced the smaller Atlantic salmon from beneath cover into open positions in the enclosures, whereas in the stream tank both won similar numbers of interspecific bouts. Overall, although the differences in scales were not large and some inferences were hampered by low statistical power, it is reassuring that results from both experiments supported the hypothesis that brook trout dominance increases as they become larger than salmon.

Brown trout

Like brook trout, brown trout alevins emerge before Atlantic salmon and are larger throughout their first year of life in European streams (Egglishaw and Shackley 1973, 1977, 1985). Observational studies on sympatric populations indicated that age-0 salmon used shallow swift riffles during summer and fall, whereas age-0 brown trout used the shallow margins of runs and pools where velocity was lower (Jones 1975; Egglishaw and Shackley 1982; Kennedy and Strange 1982; Heggenes et al. 1995). Age-1 salmon parr

used a variety of habitats with different depths, whereas age-1 and older brown trout were found primarily in deeper runs and pools. Early reports suggested that trout dominated salmon, even at the same size (Kalleberg 1958), and that age-0 salmon shifted to use different habitats in allopatry than sympatry with trout (Lindroth 1956; Heggenes 1990). Salmon are thought to be better adapted for riffles than trout due to their larger pectoral fins (Jones 1975; Arnold et al. 1991) and lower buoyancy (Sosiak 1982).

These data, as well as correlative evidence on changes in density resulting from different combinations of sympatry and allopatry (Mills 1969; Gee et al. 1978), led investigators to suspect that, as for brook trout, interspecific competition by brown trout might be important in affecting Atlantic salmon habitat use and, ultimately, growth and survival. For example, Egglishaw and Shackley (1973) stocked advanced salmon ova in a Scottish trout stream so that the fry produced were 12 mm (fork length) longer than the native brown trout by the end of the growing season. They reported high survival rates of salmon compared to nearby streams. Similarly, competition from Atlantic salmon might affect brown trout. These are important problems because managers are interested in maximizing Atlantic salmon production when fry are stocked in streams with brown trout (Mills 1969) and in other cases are interested in maximizing brown trout fry survival in streams stocked with salmon (Saltveit 1993). To resolve both issues would require experiments that incorporate substitutive designs.

Unfortunately, as for brook trout, few experiments provide sufficient evidence to address relative strengths of interspecific and intraspecific competition between brown trout and Atlantic salmon (Table 3). Kennedy and Strange (1980) stocked salmon ova during March each of 2 years in two streams tributary to a reservoir in northern Ireland. Growth and density of trout and salmon were measured and compared to the year before stocking when only trout were present. They reported significant reductions in mean length of age-0 trout and salmon after the second year of stocking in one stream. They also found marked declines in density of age-0 trout, and survival of age-0 salmon, but only during the second year of salmon stocking in both streams. Because age-1 salmon parr were not present until the second year, they attributed the declines in density and survival to competition from the salmon parr rather than fry. However, while the study was minimally replicated ($n = 2$ streams) and controlled in time (via pretreatment data), it cannot be used to assess whether interspecific competition from salmon was any greater than intraspecific competition from trout. This is because total salmonid density was increased 2.5–3.8 times, among the replicates and years, by stocking the salmon, thereby creating an additive design (see Tables 1 and 2). Thus, similar effects on growth and survival of trout fry might have resulted from heightened intraspecific competition, if trout density alone had been increased this much.

Kennedy and Strange (1986a, b) conducted an unreplicated experiment to measure the effect of brown trout on Atlantic salmon behavior, growth, and survival. They constructed a weir dividing one of the streams described above in half and removed brown trout from the upstream half using rotenone. Salmon ova were again stocked for 2 years and the resulting assemblages sampled the fall and

spring after each stocking. Fortunately, total salmonid densities were similar between sections over the four samples, their means varying by only 4%, resulting in a minimal substitutive design (Table 1).

The experiment demonstrated that interspecific interactions by all ages of brown trout on Atlantic salmon were stronger than intraspecific interactions among salmon, although without replication one cannot determine how much was due to differences between the sections. Growth and density of age-0 salmon were lower in the reach with brown trout than without in both years, even though the second year age-1 salmon parr were also present and had an additional effect (Kennedy and Strange 1986b). During the second year of the experiment, density of the age-1 salmon parr remaining was also higher in allopatry than sympatry, suggesting that brown trout also reduced parr density. Moreover, this effect may have been underestimated due to apparent downstream dispersal of salmon from the allopatric to sympatric section over winter, and possible increased growth in allopatry that may have increased the number of parr smolting as age-1+. Changes in habitat use were also evident, with age-0 salmon selecting deeper habitat when alone or with age-1 salmon parr than in sympatry with all age classes of brown trout (Kennedy and Strange 1986a). In contrast, age-1 salmon used deep habitat with or without trout, as did all age classes of trout including age-0.

Although the experiment suggested that interspecific competition from brown trout changed behavior of juvenile Atlantic salmon and reduced their growth and density beyond that due to intraspecific competition, an alternative hypothesis is that salmon fry were restricted to shallow habitats by predation risk from older brown trout in deeper habitats (Kennedy and Strange 1986a; Bardonnet and Heland 1994). Stomach sampling indicated that some predation occurs (Kennedy and Strange 1986a), especially just after fry emergence (Kennedy and Strange 1980), but density-dependent interspecific and intraspecific competition probably play a larger role. Further research would be needed to assess the relative strengths of predation and competition. Although the experiment by Kennedy and Strange (1986a,b) did not fully test cause and effect because it was unreplicated and could not rule out alternative hypotheses such as predation, the results were biologically significant and can be used to plan further replicated experiments.

LeCren (1965, 1973) described experiments where different proportions of Atlantic salmon and brown trout eggs were stocked in enclosed sections of a small Scottish stream. Although no details of methods or results were given, he reported that mortality of the resulting trout fry was proportional to trout density alone, whereas mortality of salmon fry depended on density of both species. He inferred from this that trout dominated salmon under these conditions. Further analysis of these data, if extant, might prove fruitful.

Nonsalmonids

Symons (1976) conducted an experiment in a laboratory stream using the full additive design to assess interspecific competition between Atlantic salmon and four nonsalmonids frequently found sympatric with them in eastern North American streams (Table 3), blacknose dace (*Rhinichthys atratulus*), common shiner (*Luxilus cornutus*), creek chub

(*Semotilus atromaculatus*), and white sucker (*Catostomus commersoni*). He found that salmon preferred boulder and open stream habitats and easily displaced nonsalmonids from them at fast and slow velocities, whereas without salmon the nonsalmonids shifted to use these habitats. Growth of dace and suckers was depressed when sympatric with salmon in fast velocity trials relative to allopatry. Overall, there was a clear pattern of stronger intraspecific than interspecific competition for salmon, using the additive design appropriate for competitors of different size and ecology (see above). In contrast, for the three nonsalmonids interspecific competition was at least as strong as intraspecific and may have been stronger, given the strong exodus from habitats used by salmon when all species were sympatric.

Nonnative species

Nonnative species of salmonids, particularly coho salmon (Harache 1992) and rainbow trout (Hearn and Kynard 1986), have often been introduced into the native range of Atlantic salmon in both North America and Europe. Concern has been raised repeatedly about the potential for negative effects should these introduced species become established (Gibson 1981; Fausch 1988; Mills 1989). What experimental evidence can be brought to bear on this issue?

Coho salmon

Beall et al. (1989) conducted four experiments in indoor and outdoor artificial streams to test the effects of three life stages of coho salmon (emerging fry, older fry, and yearlings), and Atlantic salmon yearlings, on newly emerged Atlantic salmon fry behavior, growth, and survival (Table 4). Two experiments in the outdoor channels were generally well designed and yielded clear results. In one, older coho fry had strong interspecific effects on survival and growth of emerging Atlantic salmon, probably because coho had a large size advantage (ca. 14 mm). Based on their data, a 7–11-mm size advantage might be expected if coho emerged naturally (Beall et al. 1989). In the other experiment, yearlings of both species increased emigration and decreased growth of Atlantic salmon fry, with stronger effects from yearling Atlantic salmon than coho, but neither species preyed on fry. Both experiments used additive designs appropriate for questions about competition from invading species, and different age classes that vary in size, but the total biomasses of the two species were probably not equal in either.

In contrast to older juvenile and yearling coho salmon, experiments with emerging fry, conducted both in homogeneous laboratory troughs (3.4 m²) and outdoor riffle-pool channels (ca. 40 m²), gave conflicting results. While residency of emerging Atlantic salmon was strongly reduced by emerging coho in the laboratory stream, intraspecific competitors had the stronger effect on both species in the outdoor channel, probably because the heterogeneous habitat in the latter allowed normal habitat segregation of Atlantic salmon into riffles and coho into pools. The difference could not be explained by initial density, which was high but similar in the two experiments. Neither experiment on emerging

Table 4. Design and main results of controlled experiments testing competition between Atlantic salmon (AS) and nonnative competitors (coho salmon [CO], rainbow trout [RT], and both with brown trout [BT]). Full and minimal additive (A) and substitutive (S) designs are described in the text and Table 1. For replicated experiments only, relative strengths of intraspecific (intra) versus interspecific competition (inter) are shown as the outcome.

Reference	Life stage	Scale				Experimental unit	Replication	Design	Outcome
		Space (m ²)	Time (d)	Biological response	Biological organization				
<i>Coho salmon</i>									
Beall et al. (1989)	1. Emerging fry	40.4 ^a	52 ^b	Behavior, growth, survival	Individual, “population” ^c	Reach	1	Full S	Unreplicated
	2. Emerging fry	3.4	28	Behavior	Individual	Tank	1	Full S	Unreplicated
	3. Emerging AS with older CO fry	40.4 ^a	61	Behavior, growth, survival	Individual, “population”	Reach	3	Minimal A (add CO)	Inter >> intra for AS for all responses
	4. Emerging AS with CO or AS yearlings	40.4 ^a	36	Behavior, growth, survival	Individual, “population”	Reach	2	Full A	Inter > intra for fry with either spp.
Gibson (1981)	Older juveniles	14.3	4–22	Behavior, growth	Individual	Tank	2–3	Full A	— ^d
<i>Rainbow trout</i>									
Gibson (1981)	Older juveniles	14.3	5–14	Behavior, growth	Individual	Tank	1–2	Full A ^e	— ^d
Hearn and Kynard (1986)	1. Age-0 and age-1 (lab stream)	3.0	4	Behavior	Individual	Tank	3–9	Full A ^f	Intra > inter for age-0 AS, inter ≥ intra for age-1 AS
	2. Age-0 (natural stream)	ca. 7945, 8338	101	Behavior	Individual	Reach	1	Minimal A (add AS)	Unreplicated
<i>Combination of nonnative salmonids</i>									
Jones and Stanfield (1993)	Age-0 CO, ages-0 and -1 BT, age-1 RT	80–180	ca. 90	Growth, survival	Individual, “population”	Reach	4	Minimal A (add nonnative spp.)	Inter ≥ intra for AS

^aAn estimate from the information given, because lengths of outdoor channel reaches were not reported.

^bCalculated from beginning of fry emergence to end of experiment.

^cRefers simply to all fish present in each reach studied, not to a defined interbreeding population.

^dThe same fish were used repeatedly in various replicates of the three different treatments (see Table 1), so results were not independent.

^eDensities for one species were not equal in sympatry and allopatry.

^fFor age-0 Atlantic salmon, density was unequal in allopatry, and results of a full substitutive design were not reported.

fry was replicated, however, so no strong inferences can be made.

Rainbow trout

Hearn and Kynard (1986) studied interactions between juvenile Atlantic salmon and rainbow trout in a laboratory stream and two reaches of a natural Vermont stream bounded by weirs (Table 4). In the laboratory stream age-0 Atlantic salmon used riffles, runs, and pools equally when alone and when age-0 rainbow trout were added (in an additive design), suggesting that intraspecific competition among salmon was greater than interspecific competition with trout (Table 2). In contrast, age-1 salmon showed a significant shift toward riffle habitat when age-1 trout were added, indicating that the trout had a competitive effect. Both age-0 and age-1 trout preferred pools with or without salmon, indicating that for them intraspecific competition was stronger than interspecific. For both ages and species, agonistic behavior was more frequent between conspecifics than heterospecifics (except for age-0 salmon). However, rainbow trout initiated 3 to 4 times more aggressive behavior than Atlantic salmon at each age and attacked age-1 salmon twice as much as vice versa. This greater aggression by trout yearlings may help explain their apparent dominance over salmon in pools.

In the field experiment, more than twice as many age-0 rainbow trout emigrated from an allopatric control section than one stocked with Atlantic salmon (Hearn and Kynard 1986), even though total salmonid density was 20% less in the control. Although the experiment was unreplicated, it suggests that intraspecific competition among wild rainbow trout is stronger than interspecific competition with stocked salmon.

Combinations of nonnative species

Reestablishment of Atlantic salmon to Lake Ontario, to which they were native, will require stocking them in tributaries that support nonnative salmonids, including coho salmon, brown trout, and rainbow trout. Jones and Stanfield (1993) conducted a controlled and replicated field experiment in short reaches of one such tributary (Table 4) to test the effects of competition from this suite of species on growth and survival of stocked large Atlantic salmon fry (mean total length 72 mm). Growth was 39% higher and survival 136% higher (both significant; $P < 0.001$), on average, at sites where nonnative salmonids had been removed by electrofishing before the experiment than paired sites with similar habitat where their abundance had been estimated but the fish returned. This additive design was appropriate to address whether competition from nonnative salmonids (or perhaps predation by the older fish) could negatively affect Atlantic salmon stocked for restoration, and also stands as the best example of a controlled and replicated field experiment conducted at appropriate scales along the four axes outlined above. Jones and Stanfield (1993) also concluded that the effect could not be explained by competition from mottled sculpin (*Cottus bairdi*) or age-0 rainbow trout, because these were not effectively removed by electrofishing and so were at similar density in both sympatry and allopatry.

Gibson (1981) also studied interactions between Atlantic salmon and either coho or steelhead in a laboratory stream.

However, in many cases the same fish were used repeatedly in different replicates and treatments of the same experiments so results were not independent.

Complex interactions

Despite the difficulty of carrying out experiments to adequately test competition between two species under one set of conditions, more detailed studies will ultimately be needed to fully address the complex set of interacting factors that are likely important in nature. For example, for co-evolved competitors the relative strengths of interspecific and intraspecific competition often vary with temperature, habitat, or other factors, so that each species dominates in different parts of the environment (Dunson and Travis 1991), thereby promoting coexistence (McPeck 1990). Dunson and Travis (1991) termed such interactions condition-specific competition (see also Power et al. 1996; Poff 1997 on context-dependent interactions) and described a protocol for testing for them.

Condition-specific competition may also explain why results for the same species change across spatial scales. If larger stream enclosures or reaches incorporate the full range of habitat complexity in which two species evolved, such as riffles and pools, then it is likely that each species will be successful in the portion that includes its realized niche. In contrast, restricting the species to only one habitat or confining them to habitat that is too simple in an artificial channel may allow one species to dominate. This may explain why results differed markedly for emerging Atlantic salmon and coho fry tested at two different spatial scales by Beall et al. (1989). It also suggests that if research is to address managers' questions about competition in natural habitat it will need to be conducted at the largest scale at which adequate control and replication are possible.

Information on condition-specific competition will be most important for predicting how Atlantic salmon populations will respond to altered conditions. These include effects of nonnative species introductions and potential reversals in dominance of coevolved or introduced species when environmental factors such as temperature (e.g., Reeves et al. 1987; DeStaso and Rahel 1994) and flow regime are changed by human agents. For example, nonnative rainbow trout have been unsuccessful at establishing reproducing populations throughout much of Europe where brown trout are native, except in places like eastern Switzerland and Liechtenstein. Here, dikes were built along the upper Rhine River and new channels parallel to the river were created on the former floodplain to drain water from its tributaries. These channels have very stable flow and temperature regimes and are rarely disturbed by flooding. This modification has apparently favored rainbow trout, which now reproduce and reach high densities in a region where streams were once inhabited solely by brown trout (A. Peter, Swiss Federal Institute for Environmental Research, Kastanienbaum, personal communication).

A second class of complex interactions that may ultimately be important are indirect effects through food webs, caused either by nonnative species or the effects of humans. Recent work in New Zealand indicates that introduction of nonnative salmonid predators may affect invertebrate prey

behavior and ultimately alter the structure and productivity of entire food webs (Flecker and Townsend 1994; McIntosh and Townsend 1994). Nonnative salmonids like rainbow trout or coho salmon might also cause such indirect effects, thereby affecting sympatric Atlantic salmon. Similarly, Wootton et al. (1996) recently proposed that regulating river flow has strong indirect effects on salmonids by releasing a predator-resistant grazing caddisfly (Trichoptera) from scouring floods that kept population numbers down. In regulated rivers these grazing caddisflies depressed algae that reduced production of other grazers on which fish fed. Overall, it is clear that fish ecologists will need even more sophisticated experimental approaches incorporating entire river food webs on which salmonids depend to assess the relative strengths of complex interactions like these.

Conclusions

Overall, there is relatively little evidence from which to judge the effects of interspecific competition on juvenile Atlantic salmon at any scale. More than half the experiments reviewed were unreplicated (9 of 17) and therefore inadequate to test either the existence or relative strength of interspecific competition between juveniles of Atlantic salmon and other fishes (Tables 3 and 4). In contrast, for all but one of the eight replicated experiments, experimental designs were appropriate to address the questions of interest. Thus, for nonnative species, and nonsalmonid competitors of different size or ecology, additive designs were used to test the existence of interspecific competition in all five cases. For coevolved salmonids with similar ecology, substitutive designs were used to test the strength of interspecific competition relative to intraspecific in two of three experiments. A plot of spatial and temporal scales of replicated experiments revealed that at least minimal replication was possible over a broad range of scales (Fig. 1), including a study that spanned 2 years and ca. 9000 m² of habitat. However, even some of the smallest scale experiments were unreplicated. The best study incorporated adequate replication and an appropriate design in a field experiment conducted at useful scales to address questions about effects of nonnative salmonids (Jones and Stanfield 1993).

The most urgently needed experiments are indeed those testing effects of nonnative salmonids on growth and survival of juvenile Atlantic salmon at appropriate spatial and temporal scales, using fish of the sizes and age classes found in nature. Of the nonnative salmonids considered to date, juvenile coho salmon may have the strongest effect on age-0 Atlantic salmon due to their innate aggressiveness and inherent size advantage caused by earlier emergence and larger size at emergence (cf. Fausch and White 1986; Beall et al. 1989), although habitat segregation by Atlantic salmon into riffles (Gibson 1993; Heggenes et al. 1995) and coho into pools (Hartman 1965; Bisson et al. 1988) may ameliorate this interaction somewhat. In addition to the experiment of Jones and Stanfield (1993), the work of Beall et al. (1989) is a useful model (provided appropriate experimental designs and replication are used), because they conducted experiments on emerging Atlantic salmon at a relevant scale for this life stage, considered several sizes and ages of coho salmon competitors and predators, and explicitly considered

the role of emigration. Movement of stream fishes is an important feature to consider in any experimental design, because it can complicate studies of their population biology (Gowan et al. 1994; Gowan and Fausch 1996a, b), most often by transferring effects from one experimental reach to another (e.g., Kennedy and Strange 1986b).

Finally, it is clear that managers will need this knowledge soon for it to be helpful. Introductions of sport fish, and the large amounts of cage culture now underway throughout the world, will continue to release nonnative fish outside their native ranges and further the chances for new invasions (Townsend 1991; Moyle and Light 1996). For example, Atlantic salmon are now reared in sea cages along the Pacific coasts of North and South America (e.g., McKinnell et al. 1997), while Pacific salmonids have been both introduced and cage-reared in the Atlantic Ocean (Harache 1992). Cage culture of Atlantic salmon in British Columbia has apparently produced substantial numbers of spawning adults migrating up rivers (B. Ward, British Columbia Ministry of Environment, personal communication), while native steelhead populations continue to decline for other reasons, leading to the question of whether the combination of these factors may eventually allow Atlantic salmon to successfully invade. In addition, recent efforts to restore Atlantic salmon to their former range in the face of stocked or naturally reproducing nonnative salmonids (e.g., rivers in Belgium stocked with rainbow trout; streams tributary to Lake Ontario, Jones and Stanfield 1993), pose similar problems for managers attempting to predict the potential for Atlantic salmon to be successfully reintroduced.

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