



# **A review and annotated bibliography of the impacts of invasive brown trout (*Salmo trutta*) on native salmonids, with an emphasis on Newfoundland waters**

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**A REVIEW AND ANNOTATED BIBLIOGRAPHY OF THE IMPACTS OF  
INVASIVE BROWN TROUT (*SALMO TRUTTA*) ON NATIVE SALMONIDS,  
WITH AN EMPHASIS ON NEWFOUNDLAND WATERS**

by

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## ABSTRACT

Westley, P.A.H., Ings, D.W., and Fleming, I.A. 2011. A review and annotated bibliography of the impacts of invasive brown trout (*Salmo trutta*) on native salmonids, with an emphasis on Newfoundland waters. Can. Tech. Rep. Fish. Aquat. Sci. 2924: v + 81 p.

Non-native salmonids can detrimentally affect native fishes and alter ecosystem functioning when introduced outside their native range. For example, brown trout (*Salmo trutta*) were introduced to insular Newfoundland in the late 19<sup>th</sup> century and have subsequently spread beyond areas of initial stocking, though the ecological impacts of this range expansion are unclear. Here we review the literature of interspecific competition between brown trout, Atlantic salmon, and brook trout to assess the potential effects of introduced brown trout on native Newfoundland salmonids. To do so, we review the published literature to document current brown trout distribution and habitat utilization in Newfoundland and conduct a literature review of brown trout interactions with Atlantic salmon (*Salmo salar*) and brook trout (*Salvelinus fontinalis*) throughout their ranges. By assimilating a variety of information sources, we show that the distribution of brown trout throughout Newfoundland has continued to expand over the 125 years since introduction. It now extends beyond the Avalon Peninsula, which as little as 20 years ago was the known limit of brown trout distribution on the island. The spatial patterns of colonization appear non-random; however, the mechanisms determining invasion success and failure largely remain unknown. Perhaps most importantly, review of the literature indicates that the outcome of interspecific competitive interactions are highly context specific, varying among habitats, continents, and scales of investigation. This finding indicates that caution must be used when interpreting results among studies that vary across scales. Interspecific competition appears to be strongest during the spawning stage and during the first year of life; however, a paucity of work has investigated interactions in other stages. The introduced Newfoundland brown trout may represent an important model to investigate emergent eco-evolutionary hypotheses of salmonid invasion potential.

## RÉSUMÉ

Westley, P.A.H., Ings, D.W., and Fleming, I.A. 2011. A review and annotated bibliography of the impacts of invasive brown trout (*Salmo trutta*) on native salmonids, with an emphasis on Newfoundland waters. Can. Tech. Rep. Fish. Aquat. Sci. 2924: v + 81 p.

Les salmonidés non indigènes peuvent affecter négativement les poissons indigènes et altérer le fonctionnement des écosystèmes lorsqu'ils sont introduits à l'extérieur de leurs aires de répartition naturelles. Par exemple, la truite brune (*Salmo trutta*) a été introduite à Terre-Neuve à la fin du 19<sup>e</sup> siècle et s'est depuis dispersée au-delà des aires d'introduction initiales avec des impacts écologiques méconnus. Nous faisons ici une revue de littérature de la compétition interspécifique entre la truite brune, le saumon atlantique et l'omble de fontaine afin d'évaluer les effets potentiels de l'introduction de la truite brune sur les salmonidés indigènes de Terre-Neuve. Pour ce faire, nous passons en revue la littérature publiée pour documenter la distribution actuelle de la truite brune ainsi que son utilisation de l'habitat à Terre-Neuve, et nous menons une revue de littérature des interactions entre la truite brune et le saumon atlantique (*Salmo salar*) et l'omble de fontaine (*Salvelinus fontinalis*) à travers leurs aires de répartition. En incorporant une variété de sources d'information, nous démontrons que la distribution de la truite brune à travers Terre-Neuve a continué d'augmenter au cours des 125 années écoulées depuis son introduction. Elle s'étend désormais au-delà de la péninsule d'Avalon, qui était la limite de distribution connue de la truite brune sur l'île il y a aussi peu que 20 ans. La répartition spatiale de colonisation semble non aléatoire, toutefois les mécanismes déterminant le succès et l'échec de l'invasion restent largement inconnus. Un fait possiblement encore plus important, la revue de littérature indique que le résultat des interactions interspécifiques compétitives dépend largement du contexte, variant entre habitats, continents, et échelles d'étude. Cette constatation indique que l'on doit interpréter avec prudence les résultats d'études dont l'échelle varie. La compétition interspécifique semble être la plus forte lors de la période de fraie et durant la première année de vie. Cependant, très peu de recherches ont étudié les interactions à d'autres stades de vie. La truite brune introduite à Terre-Neuve peut représenter un modèle important pour étudier les hypothèses émergentes d'éco-évolution du potentiel d'invasion des salmonidés.



## INTRODUCTION

Humans have a global influence on the biosphere and currently represent a major evolutionary force on earth (Palumbi 2001). Range expansion is an integral component of the evolutionary ecology of organisms, and humans have facilitated the spread of species, via intentional or unintentional introductions, across the globe (Lockwood et al. 2007). Human mediated species introductions often have unforeseen economic, ecological, and evolutionary consequences (Sax et al. 2005). For example, salmonid fishes, particularly species of the genera *Oncorhynchus*, *Salmo*, and *Salvelinus*, have been widely introduced outside of their native ranges and are currently found on all continents except Antarctica (Helfman et al. 1997; Crawford and Muir 2008). A growing body of research indicates that introduced salmonids often compete with native fishes and can alter the ecosystems into which they are released (Waters 1983; Dewald and Wilzbach 1992; Schindler et al. 2001; McDowall 2003, 2006). In addition to being of ecological concern, the spread of salmonids presents an evolutionary challenge. Salmonids have the capacity to evolve rapidly when introduced to new habitats (Hendry et al. 2000; Quinn et al. 2001; Hendry and Stearns 2004), which likely increases their ability to affect native fauna and facilitates their colonizing of other environments (Huey et al. 2005; Kinnison et al. 2008).

Wide-spread introductions, the proclivity to compete with native species, rapid adaptation to various habitats, and the ability to colonize new environments combine to make salmonids a fascinating group of species for the study of invasion biology, yet a challenging group to manage. Multiple introduction and colonization events act as independent “natural experiments” from which ecological and evolutionary questions can be investigated (Cox 2004; Hendry and Stearns 2004). Among these questions are: What is the rate and form of natural selection in nature? What factors (e.g., evolutionary legacy of the invaders, physical habitat conditions of the new environment, and the structure of the biological community of the new environment) determine invasion successes and failures? Are adaptations of exotic species and affected native species predictable or chaotic? The impetus to answer these and other questions extend beyond academic inquiry and have an applied practicality, that is, to prevent societal or ecological problems by predicting the spread and invasiveness of non-native species.

Brown trout (*S. trutta*) is a ‘poster child’ of salmonid introductions world-wide. In a remarkably short period (1852-1938) the distribution of brown trout changed from largely European and Eurasian to cosmopolitan (Elliot 1994; Klemetsen et al. 2003). Brown trout were most often introduced to provide sport and protein for home-sick expatriates and little early consideration was given to the impacts introduced trout may have on native species, including other salmonids. Introduced brown trout, and the resulting competition with native fauna, represent current conservation concerns in many regions including New Zealand (McDowall 2006), the Falkland Islands (McDowall et al. 2001), the Patagonian region of South America (Pascual 2007), and North America (Waters 1983; van Zyll de Jong et al. 2004). A recent extensive review by McDowall (2006) describes and quantifies the impacts of brown trout in New Zealand on native Galaxiids; however, to our knowledge no review has assimilated the wealth of



studies investigating the effect of introduced brown trout on native salmonids (though see Dunham et al. 2002 for review of brook trout invasions).

Brown trout were first introduced to Newfoundland in the late 19<sup>th</sup> century and subsequently established self-sustaining populations (Fig. 1; Scott and Crossman 1964; Andrews 1965; van Zyll de Jong et al. 2004; Hustins 2007). The pattern of brown trout introduction and spread in Newfoundland follows the typical pattern of an invasive species. Brown trout in Newfoundland, like other successfully introduced species, have passed through several identifiable stages in the invasion process (Lockwood et al. 2007), including transport, survival upon introduction, establishment of populations, spread to new areas, and ecological impact. Although we focus our attention on the final invasion stage (i.e., impact on native salmonids), we argue that additional work should focus on other stages to understand the dynamics leading to establishment and spread of brown trout in Newfoundland waters (see Westley and Fleming, *in press*).

Little is known about the current extent of distribution of brown trout on the island and their impact on native salmonids. Moreover, little is known about their evolutionary response to the new environments they experienced in Newfoundland. For example, brown trout populations may have evolved resistance to local parasites (Sandeman and Pippy 1967). Similar introductions of brown trout elsewhere have shown the capacity to evolve rapidly (Ayllon 2006) and early investigations suggest rapid differentiation among Newfoundland trout populations in life history parameters, such as age and size at maturity (Liew 1969). However, whether observed differences in life history characteristics are the result of adaptive genetic change or phenotypic plasticity remains unclear. Furthermore, apparent declines in Atlantic salmon (*S. salar*) and brook trout (*S. fontinalis*) stocks (DFO 2006) in Newfoundland have raised the question of whether interspecific competition with brown trout may be playing a significant role in the declines.

Here we review the literature on interspecific interactions of brown trout with Atlantic salmon and brook trout to assess the potential effects of introduced brown trout on native Newfoundland salmonids. Specifically, our objectives were to *i*) review the literature to document current brown trout distribution and habitat utilization in Newfoundland, and *ii*) conduct a global literature review of brown trout interactions with Atlantic salmon and brook trout.

## **DISTRIBUTION AND HABITAT UTILIZATION OF INTRODUCED NEWFOUNDLAND BROWN TROUT**

### **HISTORY OF BROWN TROUT INTRODUCTIONS TO NEWFOUNDLAND**

We apply the term “invasive” to species that are non-native (i.e., introduced to a novel environment through human actions) that spread without human mediation, and that cause ecological damage (Lockwood et al. 2007). Brown trout in Newfoundland are non-native, introduced, and in all likelihood, invasive (they are spreading without human

intervention and likely detrimentally affecting brook trout and maybe Atlantic salmon). Therefore, in this report we inter-change freely the use of 'introduced' and 'invasive' with respect to brown trout.

The first definitive evidence of brown trout introductions indicates that fertilized ova were imported from the Howietoun hatchery, Scotland, in 1883 (Maitland 1887; Hustins 2007). Accounts exist of introductions occurring as early as 1876; however, these dates should be viewed with caution. The Howietoun hatchery did not begin operation until 1877, and no other plausible source of brown trout is known. The dates reported here and in Hustins (2007) precede the 1886 date provided by Andrews (1965), which until recently has been assumed and cited to be the first date of introductions. Hustins (2007), in a thorough review of brown trout introduction history to Newfoundland, reports that brown trout of the Loch Leven, Scotland, strain were planted in Windsor Lake, near St. John's, and subsequently escaped to the Rennie's River watershed in 1884. Two other strains of brown trout, German and English, were introduced to Newfoundland in 1892 and 1905-06, respectively. Less is known about the locations and numbers of German and English brown trout strains stocked. However, it is clear that these strains were less widely distributed and that the preponderance of brown trout introduced to Newfoundland waters were of the Scottish Loch Leven strain (Hustins 2007). For a detailed list of systems that were initially stocked with brown trout see Table 1.

## **CURRENT BROWN TROUT DISTRIBUTION IN NEWFOUNDLAND**

Our review of current brown trout distribution relies heavily on the recent publication by Hustins (2007) and the DFO Angler's Guide (2008) of scheduled and non-scheduled rivers. Additionally, we incorporated (with caution) testimonials of local sport anglers of the Salmon Association of Eastern Newfoundland (SAEN). Locations of documented brown trout occurrence are presented in Table 1 and shown graphically in Fig. 2. It is important to note that this is a highly conservative estimate of current brown trout distribution in Newfoundland and likely represents the minimum number of colonized systems. Uncertainty in the current known distribution of brown trout arises from a host of complicating factors such as angler effort in certain areas or habitats (e.g., estuaries or salt ponds), misidentification of brown trout as Atlantic salmon, and lack of reporting.

Examination of our estimate of brown trout distribution yields several observations. Self-sustaining brown trout populations currently exist throughout the Avalon Peninsula, Burin Peninsula, Trinity Bay and Bonavista Bay (Scott and Crossman 1964; O'Connell 1982; Gibson and Cunjak 1986; Hustins 2007). Only 20 years ago, brown trout had yet to be reported beyond the Avalon Peninsula (e.g., Gibson and Cunjak 1986; Verspoor 1988), but are now confirmed in locations such as the Robin Hood Pond system near Port Rexton, North Trinity Bay (DFO 2008; Westley and Fleming, *in press*). Furthermore, some systems on the Avalon Peninsula have apparently been colonized by brown trout during this 20 year period. For example, the N.E. Placentia River has been a well-known producer of brown trout; however, the adjacent S.E. Placentia River was apparently void of brown trout until at least the late 1980s. Extensive sampling for

brown trout and brown trout x Atlantic salmon hybrids by Verspoor (1988) failed to produce a single sample leading him to conclude that the S.E. Placentia River, "has been extensively sampled over a number of years and is a popular angling stream, yet no brown trout have been reported taken from it." These lines of evidence suggest that colonization of brown trout on the Avalon Peninsula and beyond is on-going process.

Distribution patterns appear non-random in space, which is attributable at least in part to watershed-scale habitat characteristics associated with population establishment (Westley and Fleming, *in press*). For example, certain areas (e.g., Trinity Bay) seem to have high densities of brown trout systems; while other areas are nearly devoid of brown trout (e.g., southern Avalon Peninsula). Rivers without brown trout often occur adjacent to systems with trout (and vice versa), which highlights the need to further our understanding of the factors controlling brown trout distribution and colonization success. In a recent analysis, Westley and Fleming (*in press*) show that watersheds that are relatively large in area and relatively productive (as measured by conductivity as a surrogate) were more likely to be established with a brown trout populations compared to small and unproductive watersheds. Finally, the majority of systems containing brown trout include estuary habitats that are likely important areas for rearing and transitioning sea-trout (see next section for discussion of habitat use by brown trout). Additionally, unconfirmed reports (not shown in Fig. 2) suggest that the range may now extend to Notre Dame Bay, including the Exploits River along the north shore and to Fortune Bay along the south shore of the island (Hustins 2007).

It is important to note that the vast majority of populations in Fig. 2 were likely colonized by anadromous individuals originating from initial stocked populations; however, the dynamics of colonization are unclear and worthy of future investigation. For example, are populations located in spatial proximity more closely related than populations further apart? Or, are the majority of colonized systems founded by a few successful populations or specific strains of brown trout?

## **NEWFOUNDLAND BROWN TROUT HABITAT USE**

Compared to other parts of the brown trout range, little is known about habitat use, preferences, and suitability in insular Newfoundland. Like previous researchers, we rely heavily on the few studies specific to Newfoundland that have investigated brown trout ecology and supplement our knowledge with literature resulting from work elsewhere. In general, brown trout are capable of utilizing a remarkable range of habitats, including headwater streams, large rivers, ponds, lakes, and estuaries; however, the actual habitat utilized varies as a function of many abiotic and biotic factors (Elliot 1994; Baglinière and Maisse 1999; Crisp 2000). Habitat use varies both within and among populations (Klemetsen et al. 2003) and appears to have both environmental (Baglinière and Maisse 1999) and genetic components (Charles 2006; Thomsen et al. 2007). Like in other parts of the brown trout range, introduced trout in Newfoundland occupy a diversity of habitats. However, the extent of variation in habitat use is undoubtedly large and there is a paucity of detailed studies investigating life history variation and habitat

use of Newfoundland brown trout populations (but see Liew 1969; O'Connell 1982; Gibson and Cunjak 1986).

Bradbury et al. (1999) review lacustrine habitat use by brown trout in Newfoundland and report similar use of lakes as brook trout for rearing and in some cases spawning. Brown trout are also reported in lake systems that are apparently too turbid or warm for brook trout (Scott and Crossman 1998). Evidence from Europe indicates that brown trout may gain a growth advantage from rearing in lakes rather than rivers (Elliot 1994). This is similar to the growth advantage reported for lacustrine rearing Atlantic salmon in Newfoundland (reviewed in Klemetsen et al. 2003). In many Newfoundland systems, brown trout appear to exhibit an adfluvial life history pattern: spawning in small tributaries, limited rearing as fry in spawning streams, followed by an ontogenetic shift to lakes for growth and maturation (Liew 1969; Mackinnon 1998; Bradbury et al. 1999). High densities of spawning trout have been observed in some small spawning tributaries in Newfoundland (Mackinnon 1998), which may have altered the dynamics of those systems formerly devoid of trout (Moore 2006). When salmonids occur sympatrically in Newfoundland lake environments segregation can develop (O'Connell and Dempson 1996; O'Connell et al. 2005), presumably as a mechanism to limit competition. That being said, the extent to which resource partitioning and habitat segregation occurs in Newfoundland lakes and ponds is poorly understood.

Flowing waters are important habitats for brown trout in Newfoundland (Scruton et al. 2000; Grant and Lee 2004) and throughout their current range (Elliot 1994; Baglinière and Maisse 1999; Klemetsen et al. 2003; McDowall 2003). In Newfoundland, brown trout are typically observed in relatively slow and deep habitats (i.e. pools and river margins) and highly associated with riparian cover (Scruton et al. 2000). Thus, brown trout tend to segregate spatially with Atlantic salmon, which tend to prefer relatively fast and shallow habitats (Bietz et al. 1981; Gibson and Cunjak 1986; reviewed by Gibson 1993). These findings corroborate the general pattern of habitat segregation observed in Europe (Baglinière and Champigneulle 1982; Elliot 1994). The degree of spatial segregation among the species, however, differs across systems. In small, relatively simple fluvial systems, Atlantic salmon and brown trout tend to occupy more similar habitat (Bietz et al. 1981). In contrast, segregation between trout and salmon apparently occurs within and across habitats in large complex systems (Gibson and Cunjak 1986). The dynamics underlying this outcome are not known, but presumably relate to population specific preference and local adaptation to certain habitats and disparity in availability of habitats. Though tempting, it is dubious to assume habitat preferences without knowing habitat availability. This issue of preference and availability arises frequently in studies of competition and complicates interpretation.

In contrast to segregation noted previously, brown trout and brook trout tend to use similar fluvial habitats (Dewald and Wilzbach 1992; Grant and Lee 2004), thereby increasing the potential for competition between these species. This similarity in habitat preference may be partly a result of evolutionary convergence in response to competition from Atlantic salmon, which occurs naturally within the native ranges of brook trout (North America) and brown trout (Europe). Indeed, many studies have

reported direct competition for space, and thus feeding opportunities, in streams containing brown trout and brook trout (e.g., Waters 1983). A fascinating dynamic is observed between these species and is the subject of work by Korsu et al. (2007). In their native North American range, brook trout are often out-competed by introduced European brown trout and displaced to headwater streams. However, when brook trout are introduced to Europe they tend to out-compete native brown trout. Ultimately, the spatial distribution of species in systems on both sides of the Atlantic may converge, with brook trout in headwater regions and brown trout in the lower gradient areas (Korsu et al. 2007). The evolutionary history of the introduced species or population likely has direct bearing on the outcome of observed competitive interactions (Fausch 2008; Kinnison et al. 2008). Korsu et al. (2007) did not discuss the origin of the source population of introduced brook trout, which raises the question of whether the source population was locally adapted to headwater systems resulting from competition with introduced brown trout. Regardless, the major conclusion is worthy of emphasis: biotic interactions among stream dwelling salmonids can be *highly context-dependent* and that a species inferior in its native range can be competitively dominant over a presumably superior species, but only if the habitat conditions favour the invader.

A paucity of information exists and only a few studies have focused on the ecology of Newfoundland brown trout in estuaries (O'Connell 1982; O'Connell et al. 1984). While it is clear that many anadromous brown trout populations utilize estuaries during their life history, the relative importance and variation in estuary use is unknown. Anglers encounter brown trout in estuaries during the entire open angling season (Hustins 2007), but it is not clear whether the fish are simply moving through these habitats or relying on them directly for rearing. Tagging studies in the eastern Atlantic typically show limited (<50 km) oceanic migrations by anadromous brown trout populations (Elliot 1994; Klemetsen et al. 2003); however, no studies that we are aware of have focused on Newfoundland populations. Estuaries are important transitional areas where salmonids adjust (metabolically, morphologically, behaviourally) from freshwater to saltwater habitats and vice versa (Quinn 2005), and are critical habitat for some species of salmonids (reviewed in Groot and Margolis 1991). Atlantic salmon and brown trout often hold in estuaries during spring or summer awaiting freshets to raise the level of spawning rivers, which apparently facilitates entry and migration (Crisp 2000). Anadromous brown trout appear, in some systems, to use estuaries as thermal refugia during winter when ocean temperatures exceed the minimum tolerance of the species (Thomsen et al. 2007). In conclusion, comparatively little is known about the importance of estuary habitats, especially by Newfoundland brown trout, and deserves future attention.

## LITERATURE REVIEW OF INTERSPECIFIC COMPETITION

We conducted a literature review of competitive interactions between brown trout and both Atlantic salmon and brook trout within Newfoundland and elsewhere. Discussion of known competitive interactions and gaps in current knowledge was structured around the life cycle of the three salmonid species investigated (Fig. 3). An extensive literature

search was performed for articles with data on brown trout in sympatry with Atlantic salmon or brook trout. Searches for primary literature were conducted on the Aquatic Sciences and Fisheries Abstracts (ASFA) database and an electronic data base for brown trout ([www.qub.ac.uk/bb/prodohl/TroutConcert/references/fr\\_ref\\_H.htm](http://www.qub.ac.uk/bb/prodohl/TroutConcert/references/fr_ref_H.htm)). Published texts and 'grey' literature were discovered through searches of Memorial University Libraries. Additionally, some material was provided by personnel of the Department of Fisheries and Oceans. Individual studies are summarized in an annotated bibliography (Appendix A). A major component of this review and interest in Newfoundland brown trout stems from the objective of determining *competition* among introduced and native salmonids. Though the term competition seems intuitively obvious, it becomes less obvious to observe and quantify without having a strict definition. Here we apply the term competition to situations when individuals exploit the same limited resources (Krebs and Davies 1981). Competition can thus come in two forms, exploitation and interference. Exploitation competition arises when individuals compete for the same resource, but do so without direct contact with one another. In contrast, interference competition arises when individuals displace others through direct aggression or competitive dominance.

A preliminary analysis of the literature identified that data on competition between brown trout and Atlantic salmon or brook trout may be confounded by at least seven variables. First, salmonids often exhibit ontogenic habitat shifts (Fausch and White 1981; Kennedy and Strange 1986; Heggenes and Traaen 1988; Matthews et al. 1997) and the competitive ability of individuals is often linked to size (Harwood et al. 2002a; Orpwood et al. 2003). Second, source populations (wild or hatchery) are important as domestication is known to influence individual fish behaviours, including aggression (Dewald and Wilzbach 1992; see also review by Einum and Fleming 2001) and spawning time (Lura and Sægrov 1993; see also review by Fleming and Petersson 2001). Third, findings from laboratory (aquaria) studies may not be directly transferrable to nature. Fourth, habitat use, growth and survival rates by all three species vary seasonally (e.g., Egglishaw and Shackley 1977; Baglinière and Champigneulle 1982; Cunjak and Power 1986; Harwood et al. 2002b; Carlson and Letcher 2003; Carlson et al. 2008). Fifth, biases introduced by various sampling methods are well documented for salmonids (Heggenes et al. 1990). Sixth, patterns that are observed at one spatial or temporal scale do not necessarily hold across other scales (Heggenes and Saltveit 1996; Bult et al. 1998). Seventh, extremes in water temperature may reduce aggression in salmonids because feeding decreases sharply past critical limits (Taniguchi et al. 1998); also, habitat use varies with water temperature (Heggenes and Traaen 1988a, 1988b; Quist et al. 2004). Furthermore, habitat alteration through anthropogenic disturbance and population-level plasticity in habitat use may represent additional confounds. The seven primary confounding variables identified above were tabulated for each reference to aid with interpretation of findings that appeared inconsistent and in an attempt to control for their effect. Also, the influences of spatial and temporal scale on findings were investigated through plots of the spatial resolution of sampling and whether competition was observed in the study.



## MATURE FISH

### *Interactions on the Spawning Grounds*

Brown trout are known to interact with both Atlantic salmon (Scott et al. 2005) and brook trout (Grant et al. 2002) on the spawning grounds. Much of what has been observed comes from studies where one or other of the species is introduced. In a Lake Ontario tributary with naturalized brown trout and reintroduced Atlantic salmon, Scott et al. (2005) observed one instance (of 43 spawnings) where a brown trout (male) courted an Atlantic salmon. Interspecific courtships also occur between introduced brook trout and native brown trout. For example, Sorensen et al. (1995) observed male brook trout and brown trout to court females of the opposite species approximately 10% of the time in a small Minnesota stream, with male brook trout doing so at a higher frequency (ca. 20%) than male brown trout. Higher incidences of interspecific courtship were observed in southwest France where brook trout were introduced (Cucherousset et al. 2008); they observed that four of five mixed spawning pairs contained male brook trout and 22 percent of sexually active female brown trout were courted by male brook trout. We did not find studies that report hybridization rates that result from observed interspecific courtships.

### *Hybridization*

Factors influencing hybridization between Atlantic salmon and brown trout are not well known. Hybrids between Atlantic salmon and brown trout are viable (Day 1884) and may be fertile and produce both  $F_2$  and backcross progeny (Nygren et al. 1975; Hindar et al. 1997; Castillo et al. 2007). Hybrids show an intermediate phenotype with morphological characteristics of both Atlantic salmon and brown trout, which serve to complicate identification of hybrids in the field (Fig. 4). In Europe, where brown trout and Atlantic salmon occur naturally, the rates of hybridization between the two species appears to be higher in disturbed than undisturbed systems (e.g., Vurorinen and Pirronen 1984; Youngson et al. 1993; Hindar and Balstad 1994; Hindar et al. 1997; Jansson and Öst 1997; Castillo et al. 2008). In less disturbed systems, behavioural differences at spawning time, including a tendency for brown trout to spawn 2-3 weeks earlier than salmon, and in smaller tributaries containing finer gravel appears to serve to minimize the likelihood of hybridization (Heggberget et al. 1998). In European rivers, natural hybridization rates between Atlantic salmon and brown trout have been reported in the range of 0.0 and 18.2 % among rivers, with a median value of <1% (Payne et al. 1972, Crozier 1984; Heggberget et al. 1988; Garcia de Leaniz and Verspoor 1989; Jansson et al. 1991; Jordan and Verspoor 1993; Hindar and Balstad 1994; Hartley 1996; Hindar et al. 1997). Rates of similar magnitude, but of somewhat higher median values (2.6%), have been found in North American rivers (Beland et al. 1981; Verspoor 1988; McGowan and Davidson 1992; Gephard et al. 2000). These somewhat higher rates accord with the prediction of higher hybridization where one of the species pair is introduced than where both are native (Verspoor and Hammar 1991; Allendorf et al. 2001). Local rates of hybridization between Atlantic salmon and brown trout in

Newfoundland rivers have been found to range from 0 to 18.8% (Verspoor 1988; McGowan and Davidson 1992).

Hybrids between Atlantic salmon and brown trout have been found to be predominately the progeny of female Atlantic salmon, where the two species coevolved, i.e., northwestern Europe (Youngson et al. 1992; Jansson and Öst 1997; Hindar et al. 1997; Castillo et al. 2008, 2010). There are rare exceptions to this pattern, where populations show either an absence of a maternal bias (e.g., River Leven, England; Hartley 1996) or bias towards trout mothers (Rivers Tweed [Scotland; Jordan and Verspoor 1993, Hindar et al. 1997] and Mørkri [Norway; Hindar et al. 1997]). In contrast, in North America, where brown trout and Atlantic salmon did not co-evolve, hybridization predominantly involves brown trout females (McGowan and Davidson 1992; Gephard et al. 2000). For both directions of hybridization, the main route is thought to involve spawning participation by early maturing, heterospecific male parr (Gephard et al. 2000; Garcia-Vazquez et al. 2001). The predominance of Atlantic salmon female hybrids in Europe may result from the aggressive behaviour of brown trout males towards Atlantic salmon parr, which creates a strong interspecific barrier (Hindar et al. 1997, Garcia-Vazquez et al. 2002). This may not have had time to evolve to the same degree in North America (see Verspoor 1988). Where brown trout female hybrids predominate in Europe, spawning adults of both species tend to be similarly sized (Jordan and Verspoor 1988, Hindar et al. 1997), and in at least one case, the River Mørkri, a shortage of salmon spawners may also contribute (Hindar et al. 1997; see also Castillo et al. 2010).

Hybridization also occurs between brook trout and brown trout. Rates of hybridization between brown trout and brook trout may differ between areas where the two species occur naturally and where one is introduced; however, relative to the work of hybridization between species of *Salmo* little is known about hybridization between genera. Hybrids between brown trout and brook trout are referred to as tiger trout (Waters 1983; Witzel and MacCrimmon 1983a); they are sterile and short lived (Cheevassus 1979), which may explain their low numbers in the wild (Allan 1977). In a one year study, Cucherousset et al. (2008) found that only 2% of the fish sampled (n=1033) were hybrids between brown trout and brook trout. Also in a one year study, Witzel and MacCrimmon (1983b) failed to find a significant influence of brown trout on brook trout populations through reproductive interactions. However, based on a longer term study (3 years), Sorensen et al. (1995) concluded that brown trout were impacting brook trout populations negatively because of the relatively high investment by brook trout males in spawning activities with brown trout. The influence of interactions between brown trout males and brook trout females on the spawning grounds has received little attention, and warrants additional study. To our knowledge, no study has investigated brook trout and brown trout hybridization in Newfoundland, though hybridization has been observed in wild populations (Fig. 5).

### ***Redd superimposition***

Superimposition of Atlantic salmon redds (i.e., aggregations of gravel nests) by brown trout or vice versa may occur when spawning is not segregated spatially. There are locations where Atlantic salmon (e.g., Norway, Heggberget et al. 1988) or brook trout (e.g., Ontario, Witzel and MacCrimmon 1983) spawning overlaps spatially with that of brown trout in the presence and absence temporal segregation. We could not determine the general pattern of spawning of salmonids in Newfoundland because there were too few studies. However, our preliminary observations suggest that brook and brown trout spawn prior to Atlantic salmon. Information on egg loss due to physical damage and predation resulting from interspecific reuse of redds for the three species studied in this report is lacking.

Atlantic salmon and brown trout tend to select similar spawning habitats, which contributes to redd superimposition. Both species were found to construct redds in areas with similar water depths, water velocities and distance to stream banks and there was a large overlap in gravel size (Heggberget et al. 1988; Louhi et al. 2008). Fine substrates (Crisp and Carling 1989 [20-30 mm], Louhi et al. 2008 [16-64 mm]) are selected for redd construction by both Atlantic salmon and brown trout.

Spatial overlap in brown trout and brook trout redd sites may depend on the physical characteristics of sites and measurement scale. Existing brook trout redds are sometimes selected preferentially by later spawning brown trout (Essington et al. 1998). However, brook trout redds may be associated with groundwater upwelling seepage at fine spatial scales (Witzel and MacCrimmon 1983a; Sorensen et al. 1995), relative to those of brown trout, which are known to spawn in areas where groundwater mixes with surface waters (Benson 1953; Sorensen et al. 1995), but undiluted groundwater is avoided (Hansen 1975). Larger scale segregation between brook trout and brown trout redds may be influenced by water depth and velocity. For example, Sorensen et al. (1995) found that spawning sites in relatively deep and slow moving water of a small Minnesota stream were used exclusively by brook trout in sympatry with brown trout. Other variables (e.g., gravel size) are suspected to spatially separate redds of brown trout and brook trout, but confounding variables such as water velocity have made results difficult to interpret (Witzel and MacCrimmon 1983b). Whether spatial segregation between brown trout and brook trout sites is determined by interspecific competition or behavioural preferences and physiological tolerances is not known.

### **JUVENILE FISH**

Below we discuss factors that may influence interactions between brown trout and Atlantic salmon or brook trout, with emphasis on the first year of life. Emergence timing in salmonids may influence competitive interactions between post-emergent fish. Einum and Fleming (2000) observed strong selection pressure for early emergence in Atlantic salmon (see also Skoglund et al. 2011). Chemical cues from brown trout “competitors” causing Atlantic salmon to emerge earlier than individuals in control treatments and

predator treatments (Jones et al. 2003) is consistent with interspecific competition at the emergent stage. The timing of emergence of fish depends on spawning time and development rate of eggs. Brown trout eggs develop more quickly than Atlantic salmon eggs at temperatures below 8 °C, but development rates are similar at higher temperatures (Jensen et al. 1989). At cool temperature regimes, brook trout may spawn earlier, develop comparatively faster and therefore, emerge earlier than brown trout (Ottaway and Clarke 1981). However, brown trout may emerge earlier than Atlantic salmon and brook trout in some areas (Egglishaw and Shackley 1977; Bardonnet et al. 1993). Early emergence is thought to provide an advantage in selecting territories, as a prior resident effect is well known in salmonids (O'Conner 2000). However, early emergent fry may experience poor environmental conditions and high predation risk (Brannas 1995).

Early emergent salmonids are postulated to attain a larger size at the end of the first growing season, but the evidence for this is equivocal. Egglishaw and Shackley (1977) found that brown trout emerged earlier than salmon and over ten years, grew consistently to more than 20 % larger than young-of-the-year Atlantic salmon by mid-September. However, Baglinière et al. (1994) observed that the size differential between brown trout and salmon was not significant after the first growing season. By contrast, Gibson and Cunjak (1986) found that brown trout in the Salmonier River, Newfoundland, were slightly smaller than Atlantic salmon after the first growing season, but were the same size as one year olds. How emergence timing influences critical processes during the first growing season, particularly as affected by interspecific interactions, requires further study.

There are interspecific differences in the displacement of alevins (yolk-sac still remaining) and fry from redds that are influenced by water velocity (Ottaway and Clarke 1981; Heggenes and Traaen 1988b; Crisp and Hurley 1991). Atlantic salmon actively move away from redd sites at low water velocities and movement does not increase at relatively strong water velocities. By contrast, brown trout do not move from redds at low velocities and passive displacement is observed at relatively high velocities (Ottaway and Clarke 1981; Saltveit et al. 1995). Active movement of salmon is suggested by displacement at night (Saltveit et al. 1995) and only the relatively large individuals tend to move at low water velocities (Ottaway and Clarke 1981). Sensitivity to water flow decreases with time since emergence for salmon (Heggenes and Traaen 1988b). The same pattern does not appear to hold for brown trout, which at eight weeks post emergence tend to be more sensitive to water flow than at earlier stages (Ottaway and Clarke 1981). A confounding variable in interpreting the relationship between fish displacement and critical water velocity is water temperature; critical water velocities increase with water temperature for brook trout, brown trout and Atlantic salmon (Heggenes and Traaen 1988b).

Impacts of interactions between brown trout and Atlantic salmon or brook trout are thought to be highest during the first year of life when density-dependent processes are most intense (Milner et al. 2003). Growth of Atlantic salmon and trout during their first summer has been found to be inversely related to 0+ salmon densities (Egglishaw and

Shackley 1977). Moreover, survival rates of both species were more closely related to the total population (brown trout plus salmon) size than to the density of an individual species. Stocking Atlantic salmon did not impact on the density of brown trout in one river in Norway (Saltveit 1993), but prey availability was not measured concurrently in this system. Brown trout and Atlantic salmon may influence critical rates such as growth and mortality of juveniles of the other species in systems where resources are limiting.

Physical variables may influence interactions between brown trout and brook trout that are observed at the population level. Based on an analysis of 1000 sites in Sweden, Ohlund et al. (2008) concluded that brown trout reduced brook trout densities except in headwater streams where brook trout exhibit higher growth rates and fecundity than sympatric brown trout or allopatric brook trout. Water temperature may influence interspecific interactions in headwater streams, but this has not been tested.

## **Rivers**

*Stream size and headwaters:* Stream size may influence spatial segregation between brown trout and Atlantic salmon. In small streams, brown trout may exclude young (1+) salmon (Lindroth 1955; Karlstrom 1977). However, small headwater streams may have relatively high densities of age 0+ salmon if older brown trout do not occur there because of blockages (Haury et al. 1995) or cooler water temperatures (Quist et al. 2004).

Stream size may also influence interactions between brown trout and brook trout. Brown trout may outcompete brook trout in the main stem of rivers but brook trout may have an advantage over brown trout in headwater streams (Ohlund et al. 2008).

*River banks:* Explaining lateral segregation of salmonids in rivers is difficult because of confounding variables such as substrate, cover, water velocity, and water depth, but there is evidence to suggest that competition from brown trout restricts Atlantic salmon from areas near river banks in larger streams (Heggenes et al. 1990). Lindroth (1955) found that 0+ brown trout occurred mostly near river banks and Atlantic salmon (1+) were present over a wide range of depths but concentrated near the centre of the river. Accordingly, Hvidsten (1985) observed high stranding rates of young brown trout relative to Atlantic salmon in a regulated river, presumably because brown trout were using areas near river banks while salmon were concentrated in mid-stream areas. How competition between brown trout and Atlantic salmon for habitats near river banks is influenced by stream size warrants further study.

We found little evidence that brook trout use river banks extensively. Stoneman and Jones (2000) observed that the biomass of brook trout decreased slightly following modification (filling) of undercut banks while the biomass increased by approximately the same amount at control sites, suggesting limited movement between sites.

*Water velocity:* Changes in habitat use under sympatric versus allopatric conditions may indicate competition between species as growth and survival rates may be influenced by access to high quality habitats. Many studies (see Heggenes et al. 1990) have found shifts in the water velocities and depths used by Atlantic salmon and brook trout in sympatry with brown trout as compared to allopatry. For example, Kennedy and Strange (1986) observed that 0+ salmon used shallow and high velocity waters when age 1 and older brown trout were present, but preferred deeper and low velocity waters when they were absent. High densities of salmon (0+ and 1+) are often found in the rapids throughout the summer, even though 0+ brown trout use these areas as well (Baglinière and Champigneulle (1982). During late summer, 1+ Atlantic salmon appear to move from riffles to deeper water habitats such as pools (L'Abée-Lund and Heggberget 1995). Thus, by late August, the highest density and biomass of both 1+ salmon and brown trout can be found in pools rather than riffles (Bremset and Berg 1997). Brown trout become increasingly nocturnal during this time and this shift occurs prior to that observed in Atlantic salmon (L'Abée-Lund and Heggberget 1995). When other species, such as Arctic charr, are present and utilizing pools in late summer (i.e. in addition to brown trout), Atlantic salmon remain in waters that are fast and shallow (Heggenes and Saltveit 2007). Whether the relatively early onset of nocturnal behaviour by brown trout influences a seasonal shift in the use of pools by salmon has not been tested.

Brown trout and brook trout may compete for some pool habitats. Dewald and Wilzbach (1992) observed that wild brook trout, in sympatric trials (seminatural stream, 71-142 mm fish) with hatchery brown trout, used pools with cover more frequently, remained closer to the bottom, captured fewer prey, lost weight, and were infested with a fungus (*Saprolegnia* sp.) as compared to those in allopatric trials and to brown trout. In nature, brown trout have also been observed to exclude same size brook trout (15-30 cm) from preferred resting positions in streams characterized by relatively low focal point, water velocity and reduced light levels (Fausch and White 1981). Interspecific interactions in the wild may also occur over larger spatial scales as brook trout and brown trout can become segregated within streams along an altitudinal gradient. For example, Quist et al. (2004) found brook trout within a Rocky Mountain stream to be found predominantly at higher elevations and in areas with a high proportion of pools, whereas brown trout formed part of a diverse assemblage of many species located at lower elevations with low gradients and many deep pools. Evidence suggests that over time, competition from brown trout may restrict brook trout to the headwater pools of some systems (Korsu et al. 2007).

Physiological characteristics of Atlantic salmon and brook trout have been theorized to give them a competitive advantage over brown trout in certain habitats. Peake et al. (1997) found that Atlantic salmon and brook trout (same river) had similar swimming abilities to brown trout of comparable size (48-260 mm), while Atlantic salmon smolts were stronger swimmers than brown trout. Age 0+ and 1+ Atlantic salmon are less buoyant than brown trout in relatively high velocity water, but salmon can adjust their buoyancy to equal that of trout in still water (Sosiak 1982). Presumably, reduced buoyancy aids in holding position near the bottom in current. Tolerance of relatively cold



waters (Quist et al. 2004) or undiluted groundwater (Hansen 1975) by brook trout may segregate them from brown trout in some areas. Thus, subtle interspecific differences in physiological tolerances may give Atlantic salmon a competitive advantage over brown trout in fast flowing waters and brook trout an advantage in some areas with extreme water parameters.

*Substrate:* Both Atlantic salmon and brown trout use coarse substrates, but as discussed above, the lateral position within streams often differs between the species. For example, Hvidsten and Johnsen (1992) observed that densities of Atlantic salmon older than 0+ increased when central regions of a river section were covered with blasted rock and densities of brown trout increased at sites with blasted rock near river banks; numbers of both species decreased in upstream and downstream sections. Densities of 0+ Atlantic salmon have been reported to correlate with coarse substrates and are negatively associated with roots and detritus, while that of 0+ brown trout are correlated with homogeneous areas having detritus shelter and bryophytes (Haury et al. 1995). Thus, there is little evidence that brown trout and Atlantic salmon segregate by substrate alone.

Substrate preferences by brook trout have received comparatively less attention than those of brown trout or Atlantic salmon. Brook trout were observed to use small substrates (mostly <27 mm) while in sympatry with brown trout, except at the colder sites or when few other trout species were present (Stoneman and Jones 2000).

*Cover:* Cover can be important in providing protection from predation, particularly for species or age classes occupying shallow waters, such as young-of-the-year salmonids (Huntingford et al. 1988). Age 0+ Atlantic salmon and brown trout (0+ and older) may be strongly associated with cover, unlike brook trout. Heggenes and Traaen (1988a) observed that Atlantic salmon fry (just after yolk sac absorption) showed a strong preference for cover, brown trout were weakly associated with cover and brook trout showed no consistent pattern with respect to cover. In aquaria, Pickering et al. (1987) observed that Atlantic salmon grew faster and showed fewer signs of chronic stress when cover was present, whereas brown trout responded similarly to the presence and absence of cover. In a river in Finland, Mäki-Petäys et al. (1997) found that 0+ brown trout preferred habitats with abundant aquatic vegetation. In large river sections, brown trout older than 0+ have also been found mostly in areas characterized by abundant riparian vegetation and emergent substratum and age 0+ Atlantic salmon infrequently use these areas (Haury et al. 1995), presumably because water velocities are low. A disturbed water surface, as is often associated with riffle habitats, or water depth may substitute for cover in some instances (Gibson 1978).

*Winter habitat use:* Fish size rather than species appears to be important in determining habitat use by brown trout and Atlantic salmon during winter. Generally, salmonids prefer shelter and low water velocities during winter, and movement out of summer habitats may not occur in autumn if summer habitats provide appropriate overwintering conditions (see Huusko et al. 2007 for review). Size of individual brown trout and Atlantic salmon determines use of over-wintering shelters (Harwood et al.

2002a; Orpwood et al. 2003), which may provide brown trout with a competitive advantage in areas where they reach a larger size than Atlantic salmon at the end of the first summer.

Various forms of cover are used by both brown trout and brook trout (0+ and 1+) during winter. For example, brown trout and brook trout were observed using woody debris frequently during winter (Cunjak 1996). Similar habitats may be used by both species during winter, but brown trout sometimes occupy deeper areas than brook trout (Cunjak and Power 1986).

## ***Lakes***

Interactions between brown trout and Atlantic salmon or brook trout in lakes have received relatively little attention. Atlantic salmon, brown trout and brook trout are known to occur in sympatry in Newfoundland lakes (O'Connell and Dempson 1996), and Atlantic salmon and brown trout occur in sympatry in lakes in Ireland (Matthews et al. 1997). In two western Ireland systems, Matthews et al. (1997) found that most of the brown trout occurring in rivers were 0+ and 1+, while production of older fish depended on lacustrine habitats. They also observed considerable movement of 0+ and 1+ salmon parr that were in good condition into the lakes during summer. Juvenile salmon are also known to use lacustrine habitats extensively in Newfoundland (Gibson 1993; O'Connell and Dempson 1996; Bradbury et al. 1999), but this is far less common elsewhere within the species' natural range.

We found only one study that suggested that brown trout and brook trout interact within lakes. Spens et al. (2007) found that brown trout were more likely to go extinct in lakes with introduced brook trout than in lakes without brook trout, though clearly more work in these habitats is needed.

## ***Parr-smolt transformation***

We found no evidence to suggest that competition occurs between brown trout and Atlantic salmon (or brook trout) during the smolt migration. Smolt age was found to be more variable in brown trout (2-7 years) than Atlantic salmon (2-6 years) and variability increased with latitude (Økland et al. 1993). During the smolt migration, Garnas and Hvidsten (1985) observed that brown trout and Atlantic salmon consumed the same food items and the diets of both species changed similarly throughout the migration. Data on food availability were not available to determine whether there was a prey preference or whether food was limiting.

### **Marine areas**

In marine environments, interactions between brown trout and Atlantic salmon or brook trout are likely limited to nearshore areas. Brown trout may consume a high proportion of Atlantic salmon smolts entering estuaries (Piggins 1958); data from this study were reanalyzed by (Thurrow 1966) to suggest that 50-70 % of smolt mortality occurred in estuaries and the lower sections of rivers. Predation on salmon smolts by other species of fish or birds that occur in estuaries can also be high enough to regulate population numbers in Atlantic salmon (Larsson 1985).

Little is known about salmonids in marine areas outside of estuaries. Interactions between brown trout and Atlantic salmon in open sea areas may be limited in time (i.e. a few weeks) as salmon move quickly out of estuaries and spend one to three years at sea distant from their natal river, while brown trout remain relatively close to their natal rivers (O'Connell 1982, Elliot 1994). We found only one article on interactions between brown trout and Atlantic salmon in the nearshore marine environment. Based on data collected near the coast of Norway, Grønvik and Klemetsen (1987) postulated that Atlantic salmon were relatively specialized mid-water piscivores and that brown trout consume a wider variety of fish species, fish sizes and, occasionally invertebrates. Similar to brown trout, brook trout remain near their natal rivers, spending as little as a few weeks at sea. Thus, there is greater opportunity for brown trout to interact with brook trout during the marine phase than with Atlantic salmon, but to our knowledge this has not been examined.

### **SPATIAL SCALE**

Patterns observed at one spatial scale do not necessarily hold at other scales (Wiens 1989). Changes in patterns across scales may be due to loss of information when spatial data are analyzed at coarse resolutions (Schneider and Piatt 1986) or when processes differ across scales (Farmer and Adams 1991). To disentangle these possibilities, multi-scale studies have been suggested (Schneider et al. 1997). A multi-scale analysis of salmonid distributions with respect to habitat use has shown that results are scale dependent; for example, Bult et al. (1998) showed that Atlantic salmon abundance was positively associated with shallow depth at large, but not smaller spatial scales. Processes such as mortality and movement of fish are known to be more important at some scales than others (Schneider et al. 1999). Interspecific competition between salmonids was considered across scales by Fausch (1998) who concluded that there was insufficient evidence to evaluate the effects of interspecific competition on Atlantic salmon at any scale. His analysis on brown trout and Atlantic salmon was limited to two studies. Thus, a broader analysis of the literature is warranted.

Studies on habitat use by brown trout in sympatry with Atlantic salmon suggest that scale should be considered when evaluating interactions between species. In small

ivers, depth is an important determinant of distributions of Atlantic salmon parr when in sympatry with brown trout, but this is not observed in large rivers (reviewed by Heggenes et al. 1990). Bult et al. (1998) demonstrated that spatial scale influences conclusions about use of shallow waters by Atlantic salmon in sympatry with brown trout in Newfoundland. At small scales, age 0+ Atlantic salmon distributions appeared random, at larger scales, salmon were negatively associated with shallow depths (0-8 cm) and at the largest scales tested, salmon were positively associated with shallow depths. How the distribution of habitat changes with spatial scale should also be considered in investigations of habitat use by fish. Haury et al. (1995) concluded that brown trout and Atlantic salmon did not appear to be competing at the larger scale of river sections (versus the smaller scale of geological features) because of spatial heterogeneity of habitat within river sections. Similarly, Armstrong et al. (2003) reviewed habitat use by brown trout and Atlantic salmon and concluded that habitat heterogeneity determined interactions between the two species.

Combining information from behavioural ecology with habitat association or landscape-level studies may be useful in analyzing interactions between brown trout and Atlantic salmon or brook trout. It is, however, problematic because these disciplines typically operate at different spatial scales (Lima and Zollner 1996). Spread of an introduced species, such as brown trout in Newfoundland, is most apparent at the landscape level (kilometers) as populations become established in some rivers while others are skipped. Most data currently available to determine how brown trout interact with Atlantic salmon and brook trout were collected at smaller spatial scales (Fig. 6). This report is a preliminary attempt to combine literature from the behavioural and habitat use fields to evaluate competitive interactions between salmonids.

The influence of scale on competition between brown trout and Atlantic salmon may be observed by plotting the spatial resolution of studies from both the fields of behavioural ecology and habitat use against their outcomes (consistent or inconsistent with competition). Studies conducted at smaller scales have found that brown trout is a superior competitor to Atlantic salmon and restricts the habitats they use (Fig. 6). However, relatively large scale studies do not find evidence of competition. There is a distinct difference in conclusions about competition between studies conducted at spatial scales below 44 m<sup>2</sup> and above 775 m<sup>2</sup>. Studies within the transition zone are typified by the Gibson and Cunjak (1986) study from Newfoundland, where competition seemed to occur in one river, but not in another sampled at a different spatial scale.

In contrast with Atlantic salmon, brook trout seem to be competing with brown trout over a wide range of spatial scales and the superior competitor is not clear (Fig. 7). At relatively small spatial scales (~1 m<sup>2</sup>), brook trout were observed to be more aggressive than brown trout during the first summer. At larger scales, brown trout out-compete brook trout in some instances but not others.

Competition between brown trout and Atlantic salmon or brook trout is greatest during two periods; the mating season and the early juvenile stage. During the mating season, reproductive females are limiting resources, as are spawning sites. Behavioural

observations conducted at small scales are consistent with interspecific competition for mating opportunities (Garcia-Vazquez et al. 2002) and this is verified by studies (large scale distributional) finding relatively high rates of hybridization in some areas (Verspoor 1988). At the scale of continents, differences in competitive interactions during spawning are postulated to exist. Mature salmon parr are hypothesized to hybridize with brown trout more frequently in North America than in areas where both species coevolved because “sneaky” mating behaviours may disrupt interspecific barriers to hybridization (Gephard et al. 2000). Also, interspecific competition occurs for redds and this has been shown by both small scale distributional studies (Witzel and MacCrimmon 1983b) and larger scale behavioural observations on site selection (Essington et al. 1998).

Studies on interspecific competition during the early juvenile stage in salmonids may benefit from investigations that attempt to scale up from behavioural models to landscape-level patterns (Lima and Zollner 1996) because there is a disconnect between small scale behavioural studies and habitat use studies conducted at larger scales. Consistently, fine resolution studies have found that brown trout are more aggressive than Atlantic salmon of similar or slightly larger sizes (Harwood et al. 2002a, Höjesjö et al. 2005). At relatively small spatial scales, brown trout and Atlantic salmon compete for profitable stream positions. However, at the scale of relatively large river sections, Atlantic salmon do not redistribute quickly (months) to areas where brown trout were removed (Armstrong et al. 1994) and brown trout have been found to segregate from salmon at large spatial scales (e.g., Bremset and Berg 1997). These seemingly contradictory findings may be explained by habitat heterogeneity (Haury et al. 1995; Heggenes et al. 1999). Patterns of habitat use by salmonids vary with spatial scale (Bult et al. 1998), as do the critical processes of movement and mortality (Schneider et al. 1999).

In contrast with studies on Atlantic salmon, juvenile brown trout may not out-compete brook trout at relatively small spatial scales ( $<15 \text{ m}^2$ ). Non-anadromous brook trout of hatchery origin were observed by Hutchinson and Iwata (1997) to display agonistic behaviour more frequently than ten other species or forms of salmonids, including brown trout (Atlantic salmon were not tested). Similarly, Fausch and White (1986) observed that brook trout dominated brown trout in small artificial streams, though the conditions of this experiment were far from natural (i.e. no cover, high fish densities). In contrast, at a slightly larger spatial scale and under more natural conditions (e.g., cover added and a different flow regime) Dewald and Wilzbach (1992) found that brown trout were the superior competitor. Ultimately these disparate results suggest that subtle differences in habitat characteristics may influence competitive interactions between brown trout and brook trout.

In conclusion, competition between brown trout and Atlantic salmon or brook trout was found to be most intense during the mating season and the early juvenile stage. A combination of studies involving behavioural ecology, habitat associations and fish distributions showed that interspecific interactions must be viewed in the context of scale. At fine spatial scales, brown trout may out-compete Atlantic salmon for many

habitats, except those with relatively high water velocity. At large spatial and temporal scales, segregation of Atlantic salmon and brown trout among habitats may be apparent. Brown trout and brook trout may use similar habitats (pools) and competition may occur across many scales, because only subtle differences in physiological tolerances may influence habitat use by the two species. Hence, the competitive ability of brook trout compared to brown trout is difficult to determine in many systems. Taking a scaling approach to consider interactions between salmonids was useful in explaining inconsistencies among previous studies and identifying research gaps.

## SUMMARY

- Humans through intentional or non-intentional introductions have facilitated species dispersal, often to the detriment of native species.
- The first documented brown trout introduction to the island of Newfoundland came from the Howietoun hatchery near Loch Leven, Scotland, in 1883. This date is earlier than frequently cited information from Andrews (1965). Subsequent strains from England and Germany were introduced later, though the majority of stockings were comprised of the Loch Leven strain.
- Current brown trout distribution on insular Newfoundland includes many areas of the Avalon Peninsula and increasingly, areas beyond. This is in stark contrast to published reports as recently as twenty years ago (Gibson and Cunjak 1986) that indicate that the distribution of brown trout was limited to the Avalon. Anecdotal evidence suggests fish are colonizing Notre Dame Bay to the north and Bay d'Espoir to the south.
- Brown trout habitat use in Newfoundland is highly variable both within and among populations, and likely is determined by a host of environmental and genetic factors. In general, habitat preferences overlap more with brook trout than Atlantic salmon, indicating a greater potential for competition among trout species.
- The amount of competition (and outcome of interactions) between species tends to be context specific and vary with the spatial scale of the system examined. In small streams, species tend to overlap more in time and space, while in larger systems a higher degree of segregation tends to occur. Thus, the potential for competition is heightened in smaller, less complex systems, and is likely minimized in large systems.
- Interspecific competition appears to be most intense during the adult spawning and the months following fry emergence. However, the preponderance of studies have focused on these stages, and largely ignored other, presumably important, periods of the life history.
- The role of contemporary evolution in the success and failure of biological invasions has long been overlooked and increasing evidence suggests that rapid adaptation following introduction can increase a species' ability to colonize and spread to new areas. Thus, an understanding of the interplay between ecology and evolution are likely necessary in predicting the spread of Newfoundland brown trout.



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Table 1. Locations of confirmed brown trout populations, the general area, geographical coordinates, year of introduction and number introduced (if known), strain (natural colonization, Loch Leven, German, English), and source of information.

Location	Latitude	Longitude	Source strain	Reference
Aquaforte River	47 00 17.86	52 59 10.07	Natural colonization (source unknown)	DFO (2008)
Avondale River	47 26 07.09	53 12 23.99	Natural colonization (source unknown)	DFO (2008)
Biscay Bay River	46 47 01.46	53 16 43.93	Natural colonization (source unknown)	DFO (2008)
Cape Broyle River	47 05 35.41	52 58 38.33	Natural colonization (source unknown)	DFO (2008)
Chance Cove Brook	47 38 38.07	53 48 39.73	Natural colonization (source unknown)	DFO (2008)
Chapel Arm River	47 31 07.57	53 42 09.20	Natural colonization (source unknown)	DFO (2008)
Clement's Pond	47 30 58.28	52 55 31.50	English	Hustins (2007)
Colinet river	47 13 15.60	53 32 56.26	German	Hustins (2007)
Colliers Bay River	47 35 16.04	53 42 37.94	Natural colonization (source unknown)	DFO (2008)
Colliers River	47 27 17.76	53 14 07.10	Natural colonization (source unknown)	DFO (2008)
Come by Chance River	47 50 48.23	53 58 54.65	Natural colonization (source unknown)	DFO (2008)
Cove Road Ponds	47 25 02.28	53 09 00.70	Loch Leven	Hustins (2007)
Gallows Cove	47 27 14.39	53 05 26.14	Natural colonization (source unknown)	Ian Gall (personal communication)
Green's Harbour River	47 37 37.20	53.29 36.14	Natural colonization (source unknown)	DFO (2008)
Harry's Pond	47 46 53.25	53 11 00.34	Natural colonization (source unknown)	DFO (2008)
Heart's Content Brook	47 52 39.88	53 20 28.96	Natural colonization (source unknown)	DFO (2008)
Heart's Delight River	47 46 10.72	53 27 01.85	Natural colonization (source unknown)	DFO (2008)
Hodgewater Pond	47 30 27.73	53 16 17.24	German	Hustins (2007)
Hodge Water Cat Hills	47 24 46.72	53 31 59.86	German	Hustins (2007)
Holyrood Pond	46 49 35.72	53 36 27.08	Natural colonization (source unknown)	Ian Gall (personal communication)
Hopeall River	47 36 06.82	53 30 35.12	Natural colonization (source unknown)	DFO (2008)
Indian Pond	47 27 15.21	53 05 25.17	Natural colonization (source unknown)	DFO (2008)
Island Pond Brook	47 43 59.14	53 13 50.18	Natural colonization (source unknown)	DFO (2008)
Kelligrews River	47 29 40.21	53 00 32.78	Natural colonization (source unknown)	DFO (2008)
Lee's Pond	47 24 30.92	53 11 35.91	German	Hustins (2007)
Lee's Pond	47 24 30.92	53 11 35.91	English	Hustins (2007)
Little Salmonier River	47 02 43.23	53 44 10.37	Natural colonization (source unknown)	Ian Gall (personal communication)
Long Pond	47 34 40.99	52 44 00.74	Loch Leven	Hustins (2007)
Lower Gullies River	47 28 27.36	53 01 48.30	Natural colonization (source unknown)	DFO (2008)
Lower Island Ponds	48 00 13.02	52 59 46.28	Loch Leven	Hustins (2007)
Manuels River	47 30 59.72	52 46 30.97	Natural colonization (source unknown)	DFO (2008)
Mobile River	47 15 12.06	52 53 06.83	Natural colonization (source unknown)	DFO (2008)
Mundy's Pond	47 33 06.30	52 44 22.10	Loch Leven	Hustins (2007)
Mozzen Pond	47 52 26.15	53 22 05.66	Natural colonization (source unknown)	DFO (2008)
Murray's Pond	47 36 51.69	52 49 13.01	English	Hustins (2007)

Table 1 (Cont'd.)

Location	Latitude	Longitude	Source strain	Reference
Musquash Pond	47 52 26.15	53 22 05.66	Loch Leven	Hustins (2007)
NE Placentia River	47 13 37.19	53 52 30.66	Natural colonization (source unknown)	DFO (2008)
NE River	46 45 15.81	53 16 47.27	Natural colonization (source unknown)	Verspoor (1988)
North Arm River	47 23 34.44	53 09 27.80	Natural colonization (source unknown)	Gibson and Cunjak (1986)
New Harbour River	47 34 38.55	53 32 32.52	Natural colonization (source unknown)	DFO (2008)
North Harbour River	47 10 55.10	53 37 47.84	German	Hustins (2007)
Northwest River	46 45 52.76	53 21 05.91	Natural colonization (source unknown)	DFO (2008)
North River	47 32 27.60	53 18 39.74	Natural colonization (source unknown)	DFO (2008)
Ocean Pond	47 27 23.13	53 37 45.18	German	Hustins (2007)
O'Donnells	46 45 05.12	53 36 10.66	Natural colonization (source unknown)	Ian Gall (personal communication)
Old Shop	47 32 00.40	53 35 47.40	Natural colonization (source unknown)	Ian Gall (personal communication)
Point Verde	47 13 31.39	54 00 48.75	Natural colonization (source unknown)	Ian Gall (personal communication)
Petty Harbour Ponds	47 27 07.41	52 42 35.68	Loch Leven	Hustins (2007)
Pierre's Brook	47 15 08.18	52 51 40.21	Natural colonization (source unknown)	DFO (2008)
Pipers Hole River	47 55 24.89	54 16 26.16	Natural colonization (source unknown)	DFO (2008)
Princeton Brook	48 39 33.36	53 06 56.66	Natural colonization (source unknown)	DFO (2008)
Quidi Vidi	47 34 52.53	52 41 23.77	Loch Leven	Hustins (2007)
Quidi Vidi River	47 34 52.53	52 41 23.77	Natural colonization (source unknown)	DFO (2008)
Renews River	46 56 33.03	52 58 32.11	Natural colonization (source unknown)	DFO (2008)
Rennie's River	47 34 40.45	52 42 57.34	Loch Leven	Hustins (2007)
Robin Hood Pond	48 23 42.28	53 19 32.12	Natural colonization (source unknown)	DFO (2008)
Robin's Ponds	47 39 25.87	52 45 42.90	German	Hustins (2007)
Rocky River	47 13 57.03	53 33 22.01	German	Hustins (2007)
Salmon Cove River	47 46 55.43	53 10 30.50	Natural colonization (source unknown)	DFO (2008)
Salmonier	47 10 25.84	53 39 47.84	German	Hustins (2007)
SE Placentia River	47 13 10.96	53 55 13.49	Natural colonization (source unknown)	DFO (2008)
Seal Cove River	47 27 59.53	53 04 11.72	Natural colonization (source unknown)	DFO (2008)
Shearstown River	47 35 26.05	53 18 15.23	Natural colonization (source unknown)	DFO (2008)
Shoal Harbour River	48 11 36.66	54 00 58.52	Natural colonization (source unknown)	DFO (2008)
South Dildo Pond	47 29 46.97	53 32 46.90	Loch Leven	Hustins (2007)
South Dildo River	47 32 50.77	53 31 38.99	Natural colonization (source unknown)	DFO (2008)
South River	47 32 13.73	53 16 27.39	Natural colonization (source unknown)	DFO (2008)
Spread Eagle River	47 31 50.73	53 36 56.52	Natural colonization (source unknown)	DFO (2008)
Stone Ducky Brook	47 19 46.39	52 49 14.84	Natural colonization (source unknown)	DFO (2008)
Stony Brook	46 47 01.46	53 16 43.93	Natural colonization (source unknown)	Enders et al. 2007
Topsail River	47 31 35.38	52 54 19.92	Natural colonization (source unknown)	DFO (2008)
Topsail Road Ponds	47 32 03.92	52 56 39.64	Loch Leven	Hustins (2007)
Trinity Bay Ponds	48 22 20.32	53 23 22.84	Loch Leven	Hustins (2007)
Upper Long Pond	47 34 16.08	52 45 46.64	Loch Leven	Hustins (2007)
Virginia Lake	47 36 24.39	52 42 07.18	Loch Leven	Hustins (2007)
Waterford River	47 32 24.86	52 43 39.12	Natural colonization (source unknown)	DFO (2008)
Whiteway's	47 39 52.23	52 45 55.74	German	Hustins (2007)
Whiteway's River	47 41 05.59	53 28 13.50	Natural colonization (source unknown)	DFO (2008)
Windsor Lake	47 35 55.07	52 47 34.00	Loch Leven	Hustins (2007)

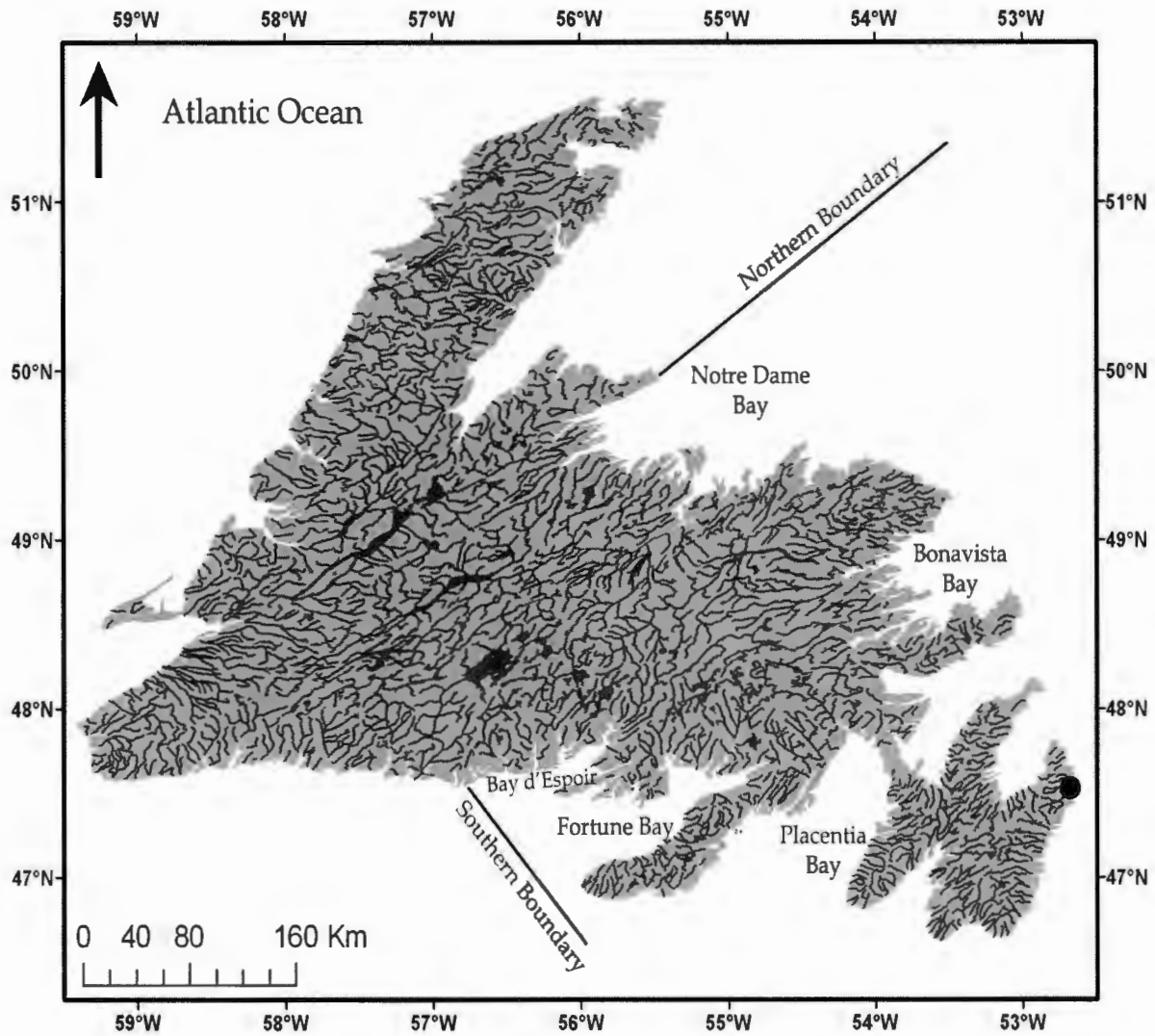


Figure 1. Island of Newfoundland showing plausible northern and southern boundaries of brown trout distribution. The provincial capital of St. John's is denoted by the filled circle.

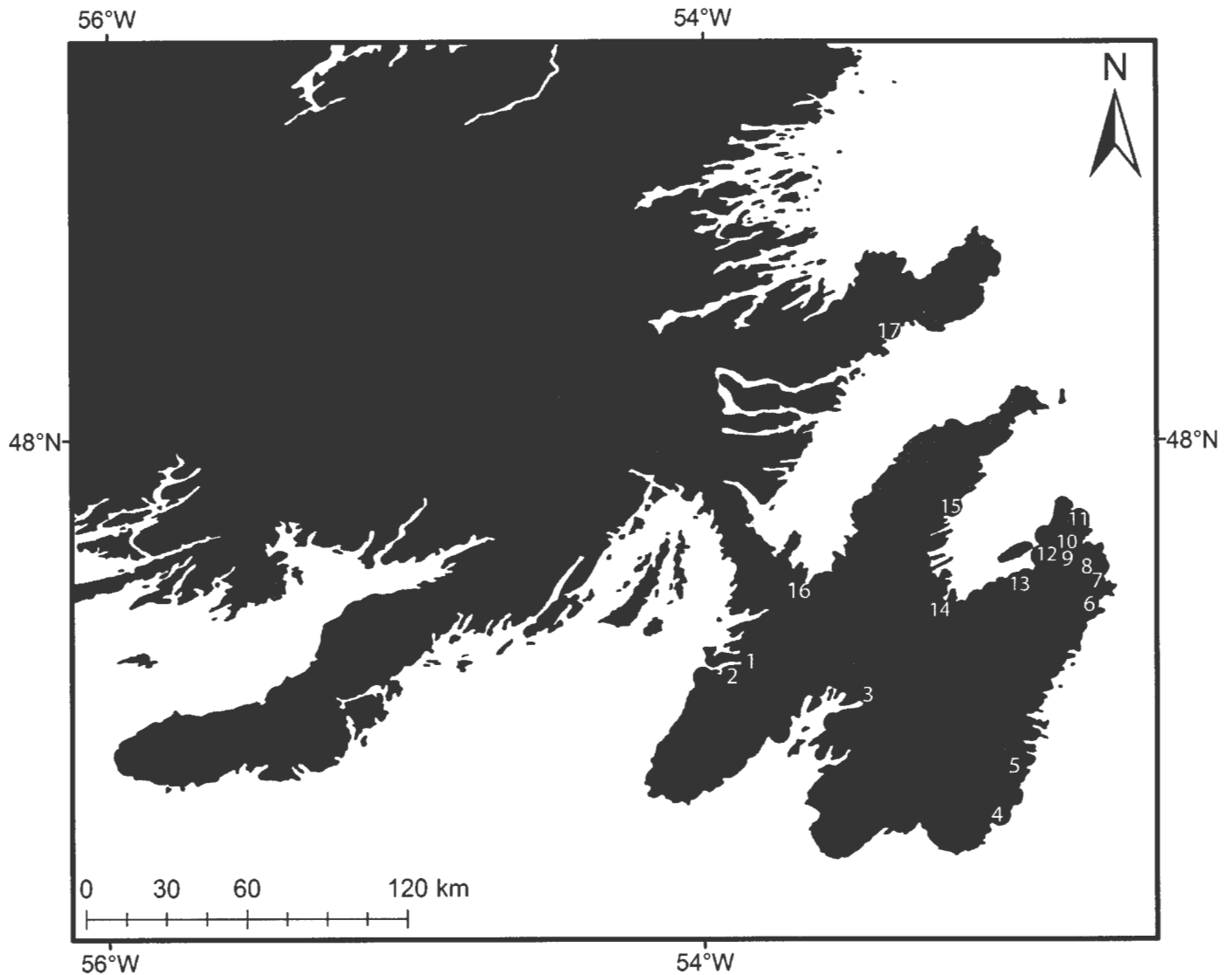


Figure 2. Current distribution of brown trout populations in insular Newfoundland based on literature reports and personal communications. Numbers indicate systems where we verified populations based on electrofishing surveys. Counter-clock wise from west to east: 1) Northeast Placentia River, 2) Southeast Placentia River, 3) Salmonier River, 4) Chance Cove Brook, 5) Renews River, 6) Pierre's Brook, Witless Bay, 7) Raymond's Brook, Petty Harbour, 8) Waterford River, 9) Rennie's Mill River, 10) Virginia River, 11) Savage Creek, 12) Windsor Lake, 13) Topsail River, 14) Avondale River, 15) Salmon Cove River, 16) Chapel Arm River, 17) Robin Hood Pond, Port Rexton.



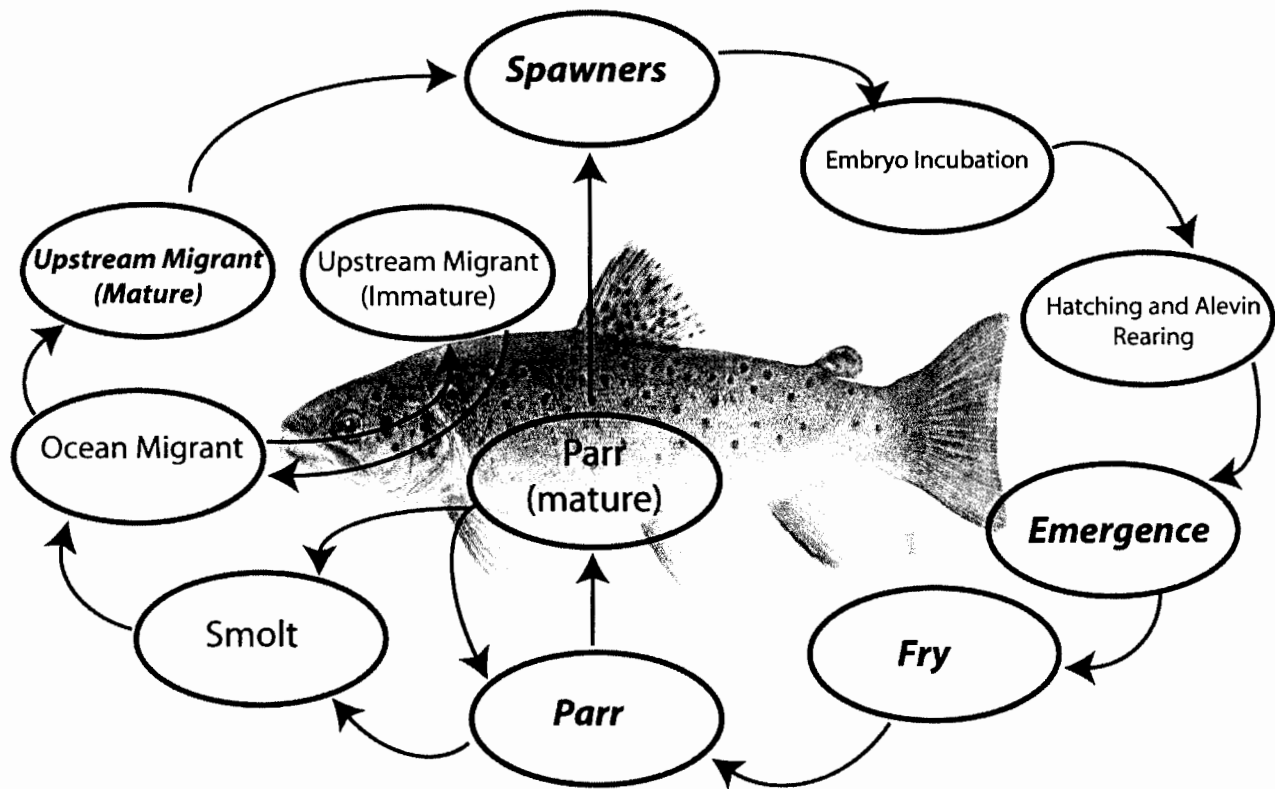
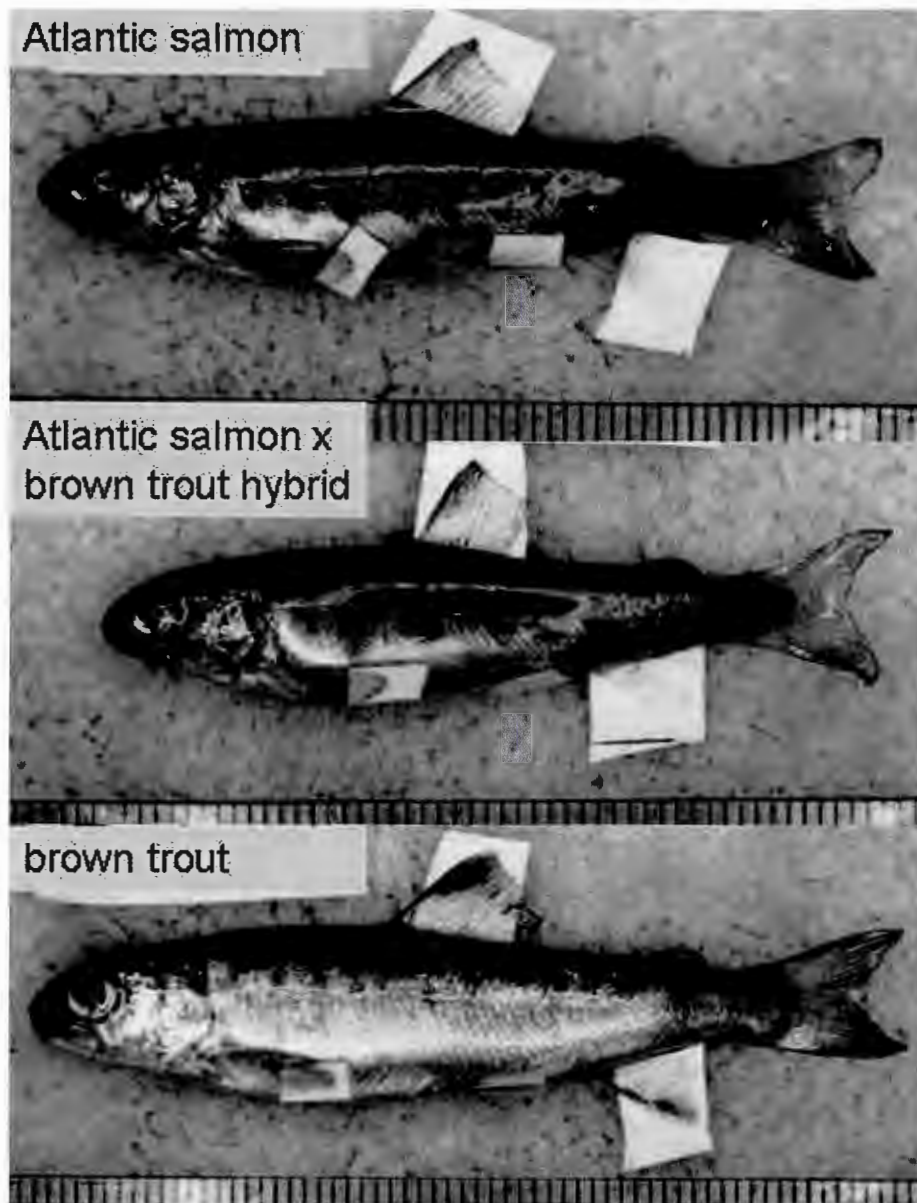


Figure 3. Simplified brown trout life cycle. Stages that have received extensive attention in terms of inter-specific competitive interactions are emphasized by bold font.



**FIGURE 4**

Figure 4. Atlantic salmon, Atlantic salmon x brown trout hybrids, and brown trout photographs. Note shortening of the pectoral fins, deepening of the caudal peduncle, lengthening of the maxilla in the hybrids. Note also that pigmentation and parr marks are intermediate between full strain Atlantic salmon and brown trout. Fish were produced as part of a study to investigate hybridization in several rivers of Norway and is discussed in Hindar et al. 1997.



**FIGURE 5**

Figure 5. A 150 mm tiger trout (brook x brown hybrid) captured in October 2008 by P. Westley in Savage Creek, Outer Cove, Newfoundland.

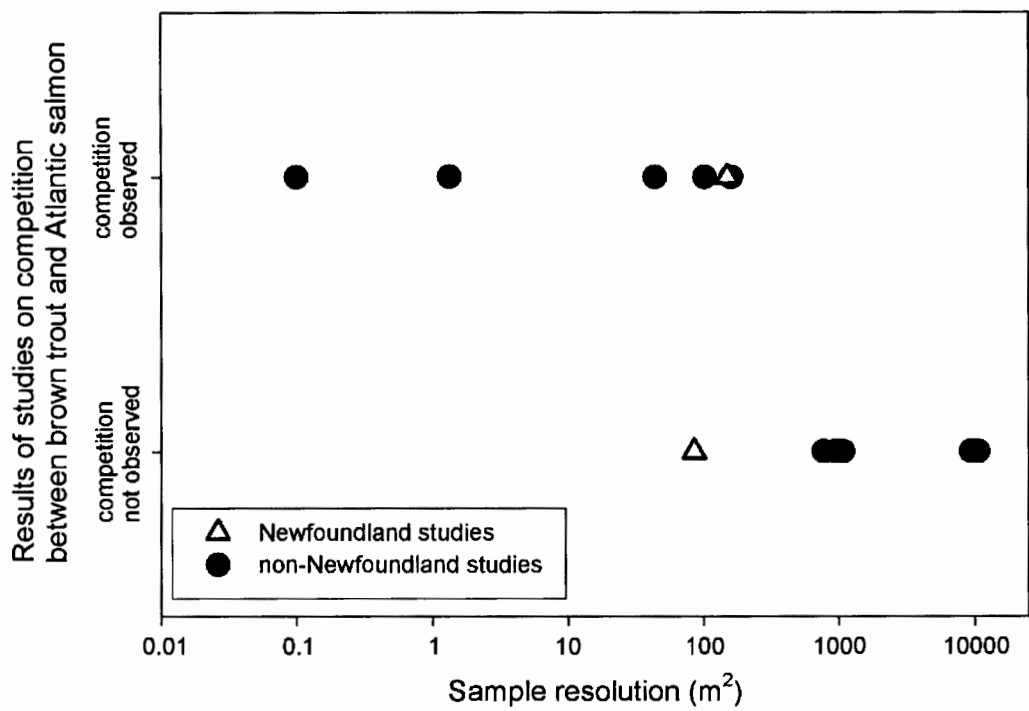


Figure 6. Results of studies on competition between brown trout and Atlantic salmon plotted against the resolution of sampling

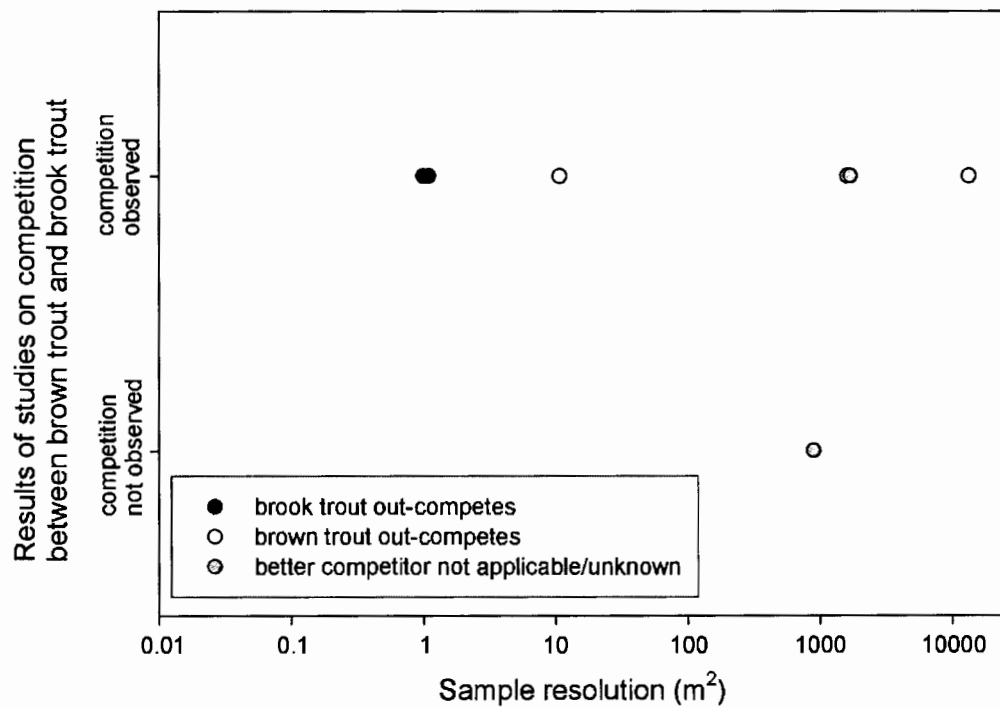


Figure 7. Results of studies on competition between brown trout and brook trout plotted against the resolution of sampling.

**Reference:** Armstrong, J.D, Shackley, P.E., and Gardiner, R. 1994. Redistribution of juvenile salmonid fishes after localized catastrophic depletion. J. Fish Biol. 45: 1027-1039.

Species comparisons	Brown trout, Atlantic salmon
Fish age/size	0+, 1+
Source population	Wild
Type of study	Field
Location	Central highlands of Scotland
Time of year	Summer
Sample method	Mark/recapture, electroshocking
Spatial scale	3 sites, 5 m x 60 m x 6.3 m, 3 m x 20 m x 5.4 m, 3 m x 20 m x 6 m
Temporal scale	2 years, 1991-92
Water temperature	Not provided

**Purpose:** 1) To distinguish between localized redistribution and colonization by long distance migrants. 2) To identify movement artifacts associated with handling and marking procedures.

**Findings:** There was little movement of salmon parr to nearly depleted areas of the streams, inconsistent with the concept of the ideal free distribution. Density dependent movement (upstream, from high to low density) and growth rate of 0+ brown trout was observed though. The authors noted resident and migratory components in the 1+ salmon population, which settled in cleared and non-cleared areas.

**Conclusion:** Resident salmon parr are strongly site attached and have a different behavioural response to resource limitation than brown trout.

**Reference:** Baglinière, J.L., and Champigneulle, A. 1982. Population-density of brown trout (*Salmo trutta* L) and Atlantic salmon (*Salmo salar* L) juveniles on the river Scorff (Brittany) - Habitat selection and annual variations (1976-1980). Acta Oecol. Applicata 3: 241-256.

Species comparisons	Brown trout, Atlantic salmon
Fish age/size	0+, 1+
Source population	Wild
Type of study	Field
Location	Scorff River, Brittany, France
Time of year	Sept. – Oct.
Sample method	Electroshocking
Spatial scale	12302, 12302, 12384, 8498, 7733.7 m <sup>2</sup>
Temporal scale	1976-1980
Water temperature	Not provided

**Purpose:** Determine variation in density of brown trout and Atlantic salmon with respect to habitat characteristics in the River Scorff.

**Findings:** 0+ Atlantic salmon and brown trout were found in the same habitats, riffles and rapids; these areas were characterized by high water velocities ( $\geq 40 \text{ cm s}^{-1}$ ), depths of 10-40 cm and substrates of stones or rocks. 1+ salmon were found principally in the rapids. 1+ and older brown trout did not exhibit a habitat preference, but they were found mostly in the rapids.

**Conclusions:** The highest densities of age 0+ and 1+ salmon and brown trout occur in the rapids. Brown trout 1+ and older can be found in various habitats if shelter in the form of cover or depth is present.

**Reference:** Bardonnnet, A., Gaudin, P., and Thorpe, J.E. 1993. Diel rhythm of emergence and of first displacement downstream in trout (*Salmo trutta*), Atlantic salmon (*Salmo salar*) and grayling (*Thymallus thymallus*). J. Fish Biol. **43**: 755-762.

Species comparisons	Brown trout, Atlantic salmon (plus grayling)
Fish age/size	Emergent fry
Source population	Wild parents
Type of study	Aquaria
Location	Scotland
Time of year	April –May
Sample method	Traps (two types)
Spatial scale	12 m x 1.2 m x 0.5 m
Temporal scale	15 days (trout), 12 days (salmon); 3 hour resolution
Water temperature	5.4-8 °C (trout), 8.6-13.4 °C (salmon)

**Purpose:** To test the hypothesis that emergence and displacement behaviour was the same in the three species, by observing them in semi-natural conditions.

**Findings:** Trout emerged earlier than salmon, but both species had similar activity rhythms; emergence began to increase at dusk into the night with displacement mostly at night.

**Conclusions:** There is a similar pattern of emergence and downstream displacement of salmon and trout alevins.

**Reference:** Bietz, B.F., Gibson, R.J., and Cunjak, R.A. 1981. Resource competition between brown trout (*Salmo trutta* L.) and juvenile Atlantic salmon (*Salmo salar* L.) in Newfoundland. Report submitted by MacLaren Plansearch Limited to Department of Fisheries and Oceans (Newfoundland Region). 74 p.

Species comparisons	Brown trout, Atlantic salmon
Fish age/size	Juvenile
Source population	Wild
Type of study	Field
Location	Broad Cove Brook, North Arm River, Salmonier, Northwest River, Newfoundland
Time of year	Spring, Summer, Fall
Sample method	Snorkeling
Spatial scale	150,70, 51,110,143,53,32,2914,17,126,75 m
Temporal scale	5 months
Water temperature	15.8-12.1 °C

**Purpose:** To examine interspecific interactions between brown trout and Atlantic salmon

**Findings:** Density of Atlantic salmon does not appear to affect brown trout growth rate. In general brown trout were found to be growing very slowly, at the extreme low end of that observed world wide. Habitat utilization differed among species but was more dramatic in larger streams where salmon preferred 'riffles' and trout preferred 'pools'. This relationship broke down in smaller streams but it was not clear if this was a habitat availability effect or differences in fish density and preference

**Conclusions:** Brown trout are not likely important competitors of Atlantic salmon in Newfoundland and their low growth rate likely explains why they have not spread far off the Avalon Peninsula. Concluded that their study design limited their ability to show direct evidence of competition, but in-direct evidence suggests that the competition between these species is fairly weak.



**Reference:** Bremset, G., and Berg, O.K. 1997. Density, size-at-age, and distribution of young Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) in deep river pools. Can. J. Fish. Aquat. Sci. **54**: 2827-2836.

Species comparisons	Brown trout, Atlantic salmon
Fish age/size	1+ parr
Source population	Wild
Type of study	Field
Location	Central Norway
Time of year	Late August
Sample method	Beach seine, diver with hoop net, electroshocker (mark recapture)
Spatial scale	4 pools (570-980 m <sup>2</sup> ), 12 riffles (~ 200 m <sup>2</sup> )
Temporal scale	1987 and 1994
Water temperature	Not provided

**Purpose:** Determine use of deep river pools by Atlantic salmon and brown trout.

**Findings:** There was a higher density and biomass of parr in pools than in riffles. Aggregations of parr were observed in pools, usually in deeper areas and often in backwaters near fast current. For both species, parr in pools were larger at age (salmon were 6 % longer, brown trout were 10 % longer) than those in riffles. Densities of both species combined were 95.3/100 m<sup>2</sup> (65.7-159.3) in pools and 37.5/100 m<sup>2</sup> in riffle habitats. Note that the author's definition of a pool precluded most pool sites to those below waterfalls and restriction of movement upstream may have influenced their findings.

**Conclusions:** Deep pools in rivers are the most attractive habitats for both brown trout and salmon. This is inconsistent with many studies on the habitat preferences of salmon and with studies that suggest habitat segregation between brown trout and salmon.

**Reference:** Bult, T.P., Haedrich, R.L., and Schneider, D.C. 1998. New technique describing spatial scaling and habitat selection in riverine habitats. Regul. Rivers Res. Manag. **14**: 107-118.

Species comparisons	Brown trout, brook trout, Atlantic salmon
Fish age/size	0+, 1+, 2+, >2+
Source population	Wild
Type of study	Field/Modeling
Location	North Harbour River, Newfoundland
Time of year	Summer
Sample method	Snorkeling
Spatial scale	1080m <sup>2</sup>
Temporal scale	1 season (2 sampling events)
Water temperature	16-21

**Purpose:** Develop a new technique to quantify fish distribution at multiple spatial scales, for analyzing patchiness of fish distributions and associations of fish with habitats over a range of spatial scales, from far smaller than the river width to several times the river width.

**Findings:** Show that age 0+ fish appeared to distribute randomly when viewed at fine spatial scales, but were clumped at larger spatial scales. Habitat selection was most different from random at fine scales (0.7 m) and less so at larger scales. Young fish negatively associated with shallow depths at fine scales (<0.2 m), but positively associated at large scales (>4-6 m).

**Conclusions:** The overarching conclusion is that spatial scale is a necessary consideration when observing fish behaviour and apparent behavioural 'preferences'. Fine scale observations of fish behaviour may not reflect larger scale patterns.

**Reference:** Crisp, D.T., and Hurley, M.A. 1991. Stream channel experiments on downstream movement of recently emerged trout, *Salmo trutta* L. and salmon *Salmo salar* L. – 1 effect of four different water velocity treatments upon dispersal rate. J. Fish Biol. **39**: 347-361.

Species comparisons	Brown trout, Atlantic salmon
Fish age/size	Emergent fry
Source population	Wild parents
Type of study	Aquaria – artificial stream
Location	Great Britain
Time of year	18 April – 25 June
Sample method	Collection nets and electroshocking
Spatial scale	4 channels, 10.7 m x 0.99 m x 0.45 m depth
Temporal scale	One year, 1983 (3, 24 or 72 hour trials)
Water temperature	4.7 – 11.8 °C

**Purpose:** 1) Is the instantaneous rate of downstream dispersal of young trout and salmon modified by water velocity. 2) Does the nature of response differ between trout and salmon.

**Findings:** The downstream dispersal rate for young salmon was high when water velocities were low (7.5 cm s<sup>-1</sup>) and dispersal rate was low at high velocities (25-70 cm s<sup>-1</sup>). Dispersal rates for trout were lowest at 25 cm s<sup>-1</sup>, slightly higher at 7.5 cm s<sup>-1</sup> and increased with water velocity in the range of 25 – 70 cm s<sup>-1</sup>. These findings are consistent with other studies that suggest that juvenile salmon can use habitats with stronger water velocities than brown trout.

**Conclusions:** Emerging brown trout and salmon actively avoid certain water velocities or their behaviour varies with water velocity and these changes in behaviour modify the likelihood of downstream displacement, or some combination of the two.

**Reference:** Cunjak, R.A., and Power, G. 1986. Winter habitat utilization by stream resident brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*). Can. J. Fish. Aquat. Sci. **43**: 1970-1981.

Species comparisons	Brown trout, brook trout
Fish age/size	0+ and > 1 year old
Source population	Wild
Type of study	Field
Location	Southern Ontario, Canada
Time of year	Winter and summer
Sample method	Underwater observations
Spatial scale	88 x 12.3 m, 56 x 5.2 m, 60 x 9.4 m
Temporal scale	2 winter seasons, 8 December to 29 March; 55 dives/ 45 hours of observations (20-60 minutes each)
Water temperature	1.5-16.5 °C

**Purpose:** To describe the winter habitat and behaviour of brook trout and brown trout. They tested whether winter habitat utilization differed between species and between age groups (within species).

**Findings:** In sympatry, brown trout occupied greater focal point water depths than brook trout during winter. Both species and both age classes preferred cover during winter and the preference for shelter was less during summer. Fish >1 year of age of both species occupied deeper water than 0+ fish during winter. Most fish were observed in aggregations during winter, and fish were often observed near groundwater seepage. However, brown trout were not observed at one site, a small tributary with suspected undiluted groundwater seepage.

**Conclusions:** Brown trout and brook trout in the study system show the behavioural plasticity needed to survive the rigors of winter. The strategies used by both species depend on local hydrology, stream morphology and life stage.

**Reference:** Dewald, L., and Wilzbach, M.A. 1992. Interactions between native brook trout and hatchery brown trout: effects on habitat use, feeding, and growth. *Trans. Am. Fish. Soc.* **121**: 287-296.

Species comparisons	Brown trout, brook trout
Fish age/size	107 mm (range: 71-142 mm)
Source population	Wild brook trout, hatchery brown trout
Type of study	Artificial stream
Location	Maryland, USA
Time of year	Year round
Sample method	Observation
Spatial scale	2 oval channels, each 3.6 x 4.8 m with 0.78 m cross section
Temporal scale	March 1988-June 1989
Water temperature	14 °C

**Purpose:** To document foraging behaviour, habitat use, and growth of wild, stream dwelling brook trout and hatchery brown trout in the presence and absence of each other.

**Findings:** The use of habitat by brook trout depended on the presence/absence of brown trout and the presence/absence of food. Habitat use by brown trout did not change between sympatric and allopatric trials. Brook trout occurred less frequently in open pools and more frequently in pools with cover when brown trout were present; use of riffles did not change. Vertical distributions of brook trout, but not brown trout, within the water column changed in sympatric versus allopatric trials. Brook trout occurred most frequently near the bottom and at mid-depths under allopatric conditions but most individuals were observed at depths very close to the bottom in sympatry with brown trout. Brown trout occurred at mid-depths in allopatry and sympatry with brook trout. Prey capture rates for both brook and brown trout were higher in allopatry than in sympatry. Generally, brown trout captured comparatively more food items per unit time than brook trout. In allopatry, both brook and brown trout maintained weight, but under sympatric conditions, brook trout lost weight and brown trout gained weight.

**Conclusions:** Prefaced by the low growth rates observed in the study, the authors conclude that the decline in instantaneous growth rate of brook trout in sympatry with brown trout relative to their growth in allopatry, suggests a depressive effect of brown trout on brook trout. Also, their data suggest that brook trout alter their behaviour in the presence of brown trout. Note that generally, the findings above are contrary to Fausch and White (1986) who found that brook trout dominate wild brown trout of similar size; the present authors suggest that domestication (brown trout) may have influenced their results.

**Reference:** Egglishaw, H.J., and Shackley, P.E. 1977. Growth, survival and production of juvenile salmon and trout in a Scottish stream, 1966-75. *J. Fish Biol.* **11**: 647-672.

Species comparisons	Brown trout, Atlantic salmon
Fish age/size	0+, 1+
Source population	Wild
Type of study	Field
Location	Scotland
Time of year	Throughout year
Sample method	Electroshocking with stop nets
Spatial scale	6 sections: 26x4.2 m, 31x3.9 m, 28x3.2 m, 28x3.8 m, 29x3.0 m, 25x3.2 m
Temporal scale	10 years, 1966-75
Water temperature	~2-17 °C

**Purpose:** To obtain knowledge of the growth, population changes and production of young Atlantic salmon, *Salmo salar* L., and brown and sea trout, *S. trutta* L., in one stream over a period of several years.

**Findings:** 0+ brown trout grew comparatively more (72-117 % heavier) during the first year than salmon; trout grew faster than salmon only during September and October of each year. Brown trout emerged first, and grew later into the fall, hence they had a longer growing season. The length of both salmon and trout at the end of the first growing season depended on the population size of 0+ salmon. Also, at the end of the first growing season, population densities of salmon and trout were more closely related to the total population (both salmon and trout) than to numbers at the beginning of the season. 1+ salmon were observed to grow faster (15 %) than 1+ trout during April, May and June and growth rates were 29 % higher for salmon than trout in July. 0+ trout have a higher survival rate than salmon up to December, then survival rates are similar between the two species until April-May.

**Conclusions:** During the first two years of life, critical rates of growth and mortality differ between periods (1-4 months) for Atlantic salmon and brown trout. Survival rates are more closely related to the total population size of salmonids than to densities of individual species, suggesting competition for resources within and among species.

**Reference:** Essington, T.E., and Sorensen, P.W. 1996. Overlapping sensitivities of brook trout and brown trout to putative hormonal pheromones. J. Fish Biol. 48: 1027-1029.

Species comparisons	Brown trout, brook trout
Fish age/size	1+
Source population	Hatchery
Type of study	Physiological, aquaria
Location	Minnesota, USA
Time of year	Autumn
Sample method	Hormone sampling
Spatial scale	Not applicable
Temporal scale	Several months
Water temperature	Not applicable

**Purpose:** To determine whether the olfactory systems of brook and brown trout were equally sensitive to prostaglandin  $F_{2a}$  and its derivatives.

**Findings:** Both brook and brown trout were sensitive to  $PGF_{2a}$ , 15 k- $PGF_{2a}$ , and  $PGF_{2a}$ , but only brook trout were sensitive to testosterone glucuronide. There were no differences in the olfactory sensitivities of males and females.

**Conclusions:** The olfactory sensitivities of brook and brown trout to hormonal compounds were very similar. Research is needed to determine whether these compounds influence hybridization between brook and brown trout.

**Reference:** Essington, T.E., Sorensen, P.W., and Paron, D.G., 1998. High rate of redd superimposition by brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*) in a Minnesota stream cannot be explained by habitat availability alone. Can. J. Fish. Aquat. Sci. 55: 2310-2316.

Species comparisons	Brown trout, brook trout
Fish age/size	Mature
Source population	Wild
Type of study	Field
Location	Valley Creek, Minnesota, USA
Time of year	September to November
Sample method	Visual observations
Spatial scale	Section 1=920 m <sup>2</sup> , section 2=850 m <sup>2</sup> ; microhabitat survey = all redds plus 50 subsections ranging from 17-57 m <sup>2</sup>
Temporal scale	Observations on spawning; 2 or 3 times daily, 29 September to 23 November 1993 and 1 October to 25 November 1994
Water temperature	Not provided

**Purpose:** To test whether fish spawn on existing redd sites because of a preference to do so, or solely as a result of competition for limited space.

**Findings:** Rates of redd superimposition were relatively high with 19 of 36 brook trout and 37 of 108 brown trout females superimposing redd sites. Rates of redd superimposition were not related to fish density, female abundance or habitat availability. The frequency of superimposition was greater than that expected if redds were located randomly over available habitat.

**Conclusions:** Areas may be used repeatedly for spawning, not because they possess unique habitat characteristics, but because the existence of an existing redd makes the site more attractive.

**Reference:** Fausch, K.D., and White, R.J. 1981. Competition between brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*) for positions in a Michigan Stream. Can. J. Fish. Aquat. Sci. **38**: 1220-1227.

Species comparisons	Brown trout, brook trout
Fish age/size	All ages
Source population	Wild
Type of study	Field
Location	Michigan, USA
Time of year	July 21-August 23
Sample method	Diving observations
Spatial scale	1800 m stretch of River, mean width = 7.5 m
Temporal scale	One year 1977
Water temperature	Not provided

**Purpose:** Determine whether use of resting and feeding positions by brook trout was influenced by brown trout presence.

**Findings:** Following the removal of brown trout from test areas, the distributions of brook trout changed indicating that brown trout exclude brook trout from preferred resting habitats. Brook trout 15-20 and 20-30 cm used better resting positions in allopatry compared to sympatry, switching to sites with lower focal point velocity, and a greater water velocity difference. For fish 15-20 cm, water depth and distance to the stream bed decreased in allopatry compared to sympatry while these parameters increased for the 20-30 cm size class. Water velocity at resting positions increased for 20-30 cm fish in allopatry relative to sympatry. Brook trout 15-30 cm chose positions with lower light more frequently in allopatry than in sympatry with brown trout. Feeding positions did not differ in allopatry and sympatry suggesting that there was no competition for food.



**Conclusions:** At the limits of their distributions within streams, brown trout may not be able to compete successfully with brook trout but, where physical conditions are suitable, brown trout can exclude brook trout from preferred resting positions.

**Reference:** Fausch, K.D., and White, R.J. 1986. Competition among juveniles of coho salmon, brook trout, and brown trout in a laboratory stream, and implications for Great Lakes tributaries. *Trans. Am. Fish. Soc.* **115**: 363-381.

Species comparisons	Brown trout, brook trout (plus coho salmon)
Fish age/size	13 months; Brook trout mean=70.6 mm (68.0-72.5), brown trout mean=69.7 mm (67.0-72.5)
Source population	Hatched from wild parents
Type of study	Aquaria
Location	Michigan, USA
Time of year	February
Sample method	Visual observations
Spatial scale	1.09 m <sup>2</sup>
Temporal scale	Once daily for 22.5 days; one year 1979
Water temperature	15 °C

**Purpose:** To measure competition for profitable stream positions among pairs of the three species, brown trout, brook trout and coho salmon, by comparing positions they occupied in sympatry and allopatry at equal densities.

**Findings:** Brook trout positions were upstream of brown trout, but in the subsequent allopatric trial the same brown trout held positions upstream of where they were in sympatry with brook trout. In allopatry, brook trout were generally distributed downstream of their positions in sympatry with brown trout because a few dominant brook trout held upstream positions and restricted subordinates to downstream areas.

**Conclusions:** Competitive superiority of brook trout over brown trout was shown by the ability to defend energetically profitable upstream positions during sympatry.

**Reference:** Garnas, E., and Hvidsten, N.A. 1985. The food of Atlantic salmon *Salmo salar* and brown trout *Salmo trutta* smolts during migration in the Orkla River Norway. Fauna Norv Ser A 5:1986.

Species comparisons	Brown trout, Atlantic salmon
Fish age/size	Smolts (Atlantic salmon mean age =3.1, 3.0, 3.1; brown trout mean age= 2.6, 2.8, 2.8 during 1982-84)
Source population	Wild
Type of study	Field
Location	Orkla River, Norway
Time of year	20 April -15 June
Sample method	1x1 m trap
Spatial scale	1 m <sup>2</sup>
Temporal scale	3 year study (1982-84)
Water temperature	Not provided

**Purpose:** Determine the major food items for Atlantic salmon and brown trout smolts during migration to the sea.

**Findings:** There was a significant overlap in the diet of Atlantic salmon and brown trout smolts both within and between years. The main items in the stomachs of both species were Trichoptera larvae and nymphs of Plecoptera and Ephemeroptera. The volume of Trichoptera larvae decreased during the migration while Plecoptera and Ephemeroptera nymphs became increasingly important.

**Conclusions:** There is a significant overlap in the diets of brown trout and Atlantic salmon during the smolt runs, but this may simply represent food availability as data on whether food was limiting were not collected in this study.

**Reference:** Gibson, R.J., and Cunjak, R.A. 1986. An investigation of competitive interactions between brown trout (*Salmo trutta* L.) and juvenile Atlantic salmon (*Salmo salar* L.) in rivers of the Avalon Peninsula, Newfoundland. Can. Tech. Rep. Fish. Aquat. Sci. 1472: 82 p.

Species comparisons	Brown trout, Atlantic salmon
Fish age/size	Juvenile
Source population	Wild
Type of study	Field
Location	Salmonier River, North Arm River, Broad Cove Brook
Time of year	Spring, Summer, Fall
Sample method	Snorkeling
Spatial scale	150,70,29,50.7,85,29,17.2 m
Temporal scale	5 months
Water temperature	11.5-18.2 °C

**Purpose:** To test for ecological compatibility between Atlantic salmon and brown trout and assess negative effects of brown trout on salmon

**Findings:** Species compatible in terms of habitat suitability and overlap in diet. However, spatial segregation in large rivers perhaps mediates competitive interactions in some systems

**Conclusions:** Habitat use is system specific and segregation likely mediates competition, especially in larger streams. Authors suggest that the limitation of brown trout range expansion is due to interspecific interactions, habitat, and climate.

**Reference:** Grønvik, S., and Klemetsen, A. 1987. Marine food and diet overlap of co-occurring Arctic charr *Salvelinus alpinus* (L.), brown trout *Salmo trutta* L. and Atlantic salmon *Salmo salar* L. off Senja, N. Norway. *Polar Biol.* **7**: 173-177.

Species comparisons	Brown trout, Atlantic salmon (plus Arctic charr)
Fish age/size	Brown trout (~ 34-51 cm); Atlantic salmon (44-56 cm)
Source population	Wild
Type of study	Field (marine)
Location	Senja, Norway
Time of year	June-July
Sample method	Gillnet
Spatial scale	60 m
Temporal scale	Diet data = 1 to 3 years; catch data = 11 years
Water temperature	Not provided

**Purpose:** To determine the feeding habits and diet overlap of Arctic charr, brown trout and small Atlantic salmon caught at the same locality off Senja, northern Norway.

**Findings:** Stomachs of brown trout contained seven prey categories and those of Atlantic salmon contained only two prey species, herring (*Clupea harengus*) and sand eel (*Ammodytes* sp). However, during the only year when data were available for both species, diet overlap indices were similar among species. Brown trout tended to take larger prey than salmon of the same size. For both brown trout and Atlantic salmon, prey length increased with predator size.

**Conclusions:** Small salmon are relatively specialized midwater fish predators, and the brown trout may take a wider variety of fish species, fish sizes and some invertebrates.

**Reference:** Harwood, A.J., J.D. Armstrong, S.W. Griffiths and N.B. Metcalfe, 2002a  
 Sympatric association influences within-species dominance relations among juvenile Atlantic salmon and brown trout. *Anim. Behav.* 64: 85-95.

Species comparisons	Brown trout, Atlantic salmon
Fish age/size	Mean $\pm$ SE for salmon= 68.4 $\pm$ 0.62 mm; trout= 71.1 $\pm$ 0.69 mm
Source population	Wild
Type of study	Aquaria
Location	Rowardennan, Scotland
Time of year	August-October
Sample method	Visual observation
Spatial scale	2.25 x 0.6 x 3 m
Temporal scale	1 hour observations, 6-10 hours per day for 5 days
Water temperature	10.9-18.1 °C

**Purpose:** To test whether (1) size correlates positively with feeding success in allopatric and sympatric groups of Atlantic salmon and brown trout; (2) food acquisition is positively correlated with aggressiveness in allopatric and sympatric groups; (3) groups of Atlantic salmon and brown trout have the same diel pattern of feeding, with peaks at dawn and dusk; and (4) within this overall trend, dominants and subordinates will have different temporal patterns of feeding, both in allopatry and sympatry, to partition resources

**Findings:** Feeding success tended to be positively related to size for salmon and trout (significantly) in allopatry, but not in sympatry. Aggressiveness and food intake were positively correlated in both allopatric and sympatric trials. In allopatric trials, dominant and subordinate fish fed at different times and rates but subordinate fish adopted a nonaggressive strategy in sympatry and continued to feed at rates similar to dominant fish. Trout were observed in deep water more frequently than salmon. Also, trout spent comparatively less time touching the bottom than salmon. Dominant trout and salmon spent more time in deep water and off the bottom than subordinates.

**Conclusions:** The presence of a species sharing similar, but not identical, ecological preferences can create the opportunity for alternative behavioural strategies to be expressed, such as nonaggressive feeding by subordinate fish. The structure of dominance hierarchies can be dependent on the species assemblage.

**Reference:** Harwood, A.J., Metcalfe, N.B., Griffiths, S.W., and Armstrong, J.D. 2002b. Intra- and inter-specific competition for winter concealment habitat in juvenile salmonids. *Can. J. Fish. Aquat. Sci.* **59**: 1515-1523.

Species comparisons	Brown trout, Atlantic salmon
Fish age/size	Mean $\pm$ SE for salmon:= 65.5 $\pm$ 1.07 mm; brown trout =76.7 $\pm$ 1.62 mm
Source population	Wild
Type of study	Aquaria
Location	Glasgow, Scotland
Time of year	Experiment 1: 7 February to 8 March; experiment 2: 16 January to 4 March
Sample method	Visual observation
Spatial scale	1) 0.40 x 0.25 m arenas, 2) 2.25 x 0.60 m arenas,
Temporal scale	1) 10 observations in 45 minutes per day for 4 days x 8 replicates x 3 treatments 2) 14 observations during 7 hours x 8 replicates x 2 treatments
Water temperature	1) 6.9 – 10.3 °C 2) 4.3 – 6.1 °C

**Purpose:** 1) To quantify competition for shelter among conspecific and heterospecific pairs of Atlantic salmon and brown trout; and 2) examine the frequency of shelter sharing among allopatric groups of salmon and sympatric groups of Atlantic salmon and brown trout.

**Findings:** In sympatry, but not in allopatry, larger individual salmon and trout (in pairs) spent more time in shelter during the dawn period; shelter use by the larger fish did not differ between species. A prior resident effect was found both when shelter was limiting and available in excess. There was a positive relationship between the proportion of time spent foraging in deep water and shelter use in deep water, but the relative proportion of time spent foraging in the deep water was greater than the proportion of time sheltering in deep water. This suggests that fish were willing to move to find shelter or foraging habitat.

**Conclusions:** During winter, competition for refuges within and among salmon and brown trout may be intense if refuge availability is limited in the wild.

**Reference:** Heggenes, J., and Saltveit, S.J. 1996. Predicting fish habitat use to changes in water flow: modeling critical minimum flows for Atlantic salmon, *Salmo salar* and brown trout, *S. Trutta*. Regul. Rivers Res. Manag. 12: 331-344.

Species comparisons	Brown trout, Atlantic salmon
Fish age/size	Parr; salmon 7-12 cm, brown trout 5-12 cm
Source population	Wild
Type of study	Field / modeling
Location	Norway
Time of year	August and October 1987, June, August and November 1988
Sample method	Snorkeling
Spatial scale	5 x 50 m river sections with 6-13 transects per section (transect length not stated)
Temporal scale	2 years ( 5 sample periods)
Water temperature	Not provided

**Purpose:** 1) To quantify micro-habitat selection by brown trout and young Atlantic salmon over a range of habitat types and water flows, and include possible seasonal changes. 2) To quantify the available habitat over a range of water flows at a scale relevant to the fish.

**Findings:** Principal component analysis showed that variance in habitat use by salmon and brown trout was explained mostly by water velocities (surface, mean, snout) and water depth. Also important were height above bottom, substratum and cover. There was considerable overlap of niches between the two species, but there were differences in niche breadth. At mean water velocities, niche breadth (Levins index) was comparatively higher (0.452) for Atlantic salmon than for brown trout (0.333). Calculations of niche overlap suggested that the two species segregated most by water velocity (Horns index=0.87). Analysis of data on microhabitat use showed that brown trout (mean =16 m s<sup>-1</sup>, sd=15 m s<sup>-1</sup>) frequented considerably slower flowing waters than Atlantic salmon (Mean =34 m s<sup>-1</sup>, sd=25 m s<sup>-1</sup>); brown trout (mean=47 cm, sd=19 cm) also inhabited shallower areas than Atlantic salmon (mean =55 cm, sd=22 cm).

**Conclusions:** There is spatial niche overlap between brown trout and Atlantic salmon, suggesting competition. Fish habitat selection data combined with hydraulic modeling at a scale relevant to fish can be a useful tool in stream management.

**Reference:** Heggenes, J., and Traaen, T. 1988a. Daylight responses to overhead cover in stream channels for fry of four salmonid species. *Holarctic Ecology* **11**: 194-201.

Species comparisons	Brown trout, Atlantic salmon, brook trout (plus lake trout <i>Salvelinus namaycush</i> )
Fish age/size	Swim up stage with yolk sac absorbed and fry
Source population	Hatchery (# of generations not stated)
Type of study	Aquaria, artificial streams
Location	Norway
Time of year	Spring
Sample method	Observation
Spatial scale	2 channels (15 m x 0.2 m)
Temporal scale	One year, 2 trials, each approximately 2 hours x 6=12 hours
Water temperature	12.4-19.1 or 6.0-8.3 °C)

**Purpose:** To access the importance of overhead cover to four species of salmonid fry at the swim-up stage under different water temperatures and water velocities.

**Findings:** Salmon showed a strong preference for overhead cover, brown trout showed a moderate preference and brook trout did not consistently use overhead cover. Use of overhead cover by salmon and brown trout was highest and less variable in the lower water temperature trial. Salmon were noted to prefer the inlet and outlets of the streams, presumably where water velocities were relatively high. This preference was higher at high water temperatures. Brown trout and salmon fry, 2 weeks post yolk sac absorption, showed weaker preferences for overhead cover than swim-up fry. Inconsistent results were found for use of cover by the four species among the various water velocities (0.25, 0.50, 1.25, 2.00 l s<sup>-1</sup>).

**Conclusions:** There are among species differences in the use of cover with Atlantic salmon showing the strongest preference, brown trout showing intermediate preference and brook trout showing no preference. However, use of cover by fry of these species may be highly variable as the behavioural response to cover can be easily disturbed.



**Reference:** Heggenes, J., and Traaen, T. 1988b. Downstream migration and critical water velocities in stream channels for fry of four salmonid species. J. Fish Biol. 32: 717-727.

Species comparisons	Brown trout, Atlantic salmon, brook trout (plus lake trout <i>Salvelinus namaycush</i> )
Fish age/size	Swim up stage with yolk sac absorbed plus salmon (2 weeks older) and brown trout (8 weeks older)
Source population	Hatchery (# of generations not stated)
Type of study	Aquaria, artificial streams
Location	Norway
Time of year	11-18 June
Sample method	Observation
Spatial scale	2 channels (15 m x 0.2 m)
Temporal scale	One year (1986), 11 trials, each approximately 2.75 hours
Water temperature	12.4-19.1 or 6.0-8.3 °C)

**Purpose:** To determine whether salmonid fry, especially at the swim-up stage, were vulnerable to downstream displacement and eventually wash-out at comparatively low water velocities and, if so, to determine what water velocities the fry could withstand over short time intervals, and at what critical water velocities they were washed-out. An additional aim was to investigate the effect of temperature on critical velocities.

**Findings:** The swim-up fry of all four species withstood higher water velocities at higher temperatures. The maximum critical water velocities were slightly higher for brook trout ( $0.17 \text{ m s}^{-1}$ ) than brown trout or salmon (both:  $0.15 \text{ m s}^{-1}$ ) at 6.0-8.3 °C; all three species had maximum critical water velocities of  $0.19 \text{ m s}^{-1}$  at higher water temperatures (12.4-19.2 °C). At 19.2 °C, maximum critical velocity was higher for brown trout ( $0.24 \text{ m s}^{-1}$ ) than brook trout ( $0.22 \text{ m s}^{-1}$ ). Fry could withstand higher water velocities after two weeks of feeding exogenously. At 6.9 °C and 18.3 °C, maximum critical velocities of  $0.23 \text{ m s}^{-1}$  and  $24 \text{ m s}^{-1}$  respectively, were observed for brown trout (2 weeks). Maximum critical velocities tended to increase with temperature in salmon; rising from  $0.17 \text{ m s}^{-1}$  at 6.9 °C to  $0.19 \text{ m s}^{-1}$  at 8.3 °C and  $0.27 \text{ m s}^{-1}$  at higher temperatures approaching 19 °C.

**Conclusions:** Fry entering the free-feeding stage are most vulnerable to downstream displacement. The critical water velocity for displacement increases with fish size.

**Reference:** Höjesjö, J., Armstrong, J.D., and Griffiths, S. 2005. Sneaky feeding by salmon in sympatry with dominant brown trout. *Anim. Behav.* **69**: 1037-1041.

Species comparisons	Brown trout, Atlantic salmon
Fish age/size	Mean $\pm$ SE for salmon= 3.15 $\pm$ 0.15 g, 65.47 $\pm$ 0.96mm; trout = 5.29 $\pm$ 0.29 g, 77.4 $\pm$ 1.43mm.
Source population	Wild
Type of study	Aquaria
Location	Perthshire, Scotland
Time of year	May
Sample method	Visual observation
Spatial scale	80 x 2 x 2 m
Temporal scale	10 min observations x 2 per pair x 32 pairs=640 minutes
Water temperature	Not provided

**Purpose:** Test whether salmon are able to coexist with trout in flowing water by briefly invading a dominant trout's territory to catch food before returning to a periphery position.

**Findings:** Brown trout made more feeding attempts than salmon, but salmon fed more efficiently and the number of food items captured did not differ between the two species. Trout attacked salmon in 6 of 32 trials, but salmon attacked trout in only one of 32 trials. Trout were most frequently observed in the front or middle of the arena, while salmon tended to hold position on the bottom near the back of the arena.

**Conclusions:** Sneaky feeding appears to be an important means by which salmon can coexist with a species that would be deemed to be dominant on the basis of aggressive behaviours and the total time spent in high-quality feeding patches.

**Reference:** Hutchison, M.J., and Iwata, M. 1997. A comparative analysis of aggression in migratory and non-migratory salmonids. *Environ. Biol. Fish* **50**: 209-215.

Species comparisons	Brown trout, brook trout (plus other salmonids)
Fish age/size	Mean $\pm$ SE for brook trout = 9.558 $\pm$ 0.084 cm; brown trout = 8.405 $\pm$ 0.088 cm
Source population	Hatchery maintained?
Type of study	Aquaria
Location	Japan
Time of year	June-August, 1991 and June 1992
Sample method	Not applicable
Spatial scale	1 m <sup>2</sup> x 6 tanks
Temporal scale	29 hour total; 15 x 5 minute observations per species
Water temperature	9-10 °C

**Purpose:** To test whether intraspecific aggression in salmonids increases with duration of stream residence.

**Findings:** Non-anadromous brook trout were observed to nip conspecifics more frequently than any of the other 10 salmonids observed, with a mean ( $\pm$  standard error) nipping frequency of  $374.93 \pm 40.88$  nips hour<sup>-1</sup>. Brown trout nipped between 83 and 99 nips hour<sup>-1</sup>.

**Conclusions:** Duration of stream residence is an important and significant factor positively related to the degree of aggression in salmonid fishes.

**Reference:** Hvidsten, N.A. 1985. Mortality of pre-smolt Atlantic salmon, *Salmo salar* L., and brown trout, *Salmo trutta* L., caused by fluctuating water levels in the regulated river Nidelva, central Norway. J. Fish Biol. **27**: 711-718.

Species comparisons	Brown trout, Atlantic salmon
Fish age/size	0+
Source population	Wild
Type of study	Field
Location	River Nidelva, Norway
Time of year	Throughout year, 5 times in 1983, 9 times in 1984
Sample method	Observation
Spatial scale	Could not be determined
Temporal scale	Two years
Water temperature	Not provided

**Purpose:** To analyze the mortality of pre-smolt Atlantic salmon and brown trout caused by rapid fluctuations of the water level below a power station.

**Findings:** Large losses of both salmon and brown trout were observed as a result of reduced discharges. Brown trout densities were comparatively lower than salmon, because brown trout tended to suffer higher mortalities due to their use of shallow waters near river banks, which makes them more susceptible to stranding.

**Conclusions:** Recruitment of brown trout on the River Nidelva was poor, while salmon recruitment was relatively stable. Brown trout had better growth rates than salmon, suggesting that stranding rather than competition with salmon causes low survival of trout.

**Reference:** Hvidsten, N.A., and Johnsen, B.O. 1992. River bed construction: impact and habitat restoration for juvenile Atlantic salmon *Salmo salar* L., and brown trout *Salmo trutta* L. Aquacult. Fish. Manag. **23**: 489-498.

Species comparisons	Brown trout, Atlantic salmon
Fish age/size	> 0+
Source population	Wild
Type of study	Field
Location	River Sjøya, Norway
Time of year	Various (April, November)
Sample method	Electroshocker
Spatial scale	Could not be determined
Temporal scale	1984-90
Water temperature	Not provided

**Purpose:** 1) To measure habitat preference among juvenile salmon (*Salmo salar* L.), and brown trout, (*Salmo trutta* L.), in natural and artificial weirs. 2) To analyze the effects of transported sediments on the densities and interspecific competition of downstream salmon and trout populations.

**Findings:** Densities of salmon > 0+ increased after the river bottom was covered with stones. Densities were lower (7 fish per 100 m<sup>2</sup>) before relative to after restoration (25-125 fish per 100 m<sup>2</sup>) and fish densities in control areas varied between 7 and 64 fish per 100 m<sup>2</sup>. Salmon densities were higher in restored locations where the entire width of the river was covered with stones than in control areas; similar trout densities were observed in these restored sites and control sites. Densities of both salmon and trout decreased downstream from the canalization area due to high sedimentation, which reduced the amount of suitable habitat.

**Conclusions:** Results were consistent with salmon using central parts of rivers and brown trout using areas near the river banks. Sedimentation impacted brown trout heavily, because hiding places near river banks were clogged. Properly maintained weirs may increase production of salmon in restored rivers.

**Reference:** Jones, M., Laurila, A., Peuhkuri, N., Piironen, J., and Seppä, T. 2003. Timing an ontogenetic niche shift: responses of emerging salmon alevins to chemical cues from predators and competitors. *Oikos* **102**: 155-163.

Species comparisons	Brown trout, Atlantic salmon
Fish age/size	Alevins-fry
Source population	Wild
Type of study	Aquaria
Location	Enonkoski, eastern Finland
Time of year	October - June
Sample method	Visual observations
Spatial scale	40 x 10 l buckets
Temporal scale	4 march – 23 June
Water temperature	1.4-12.5 °C

**Purpose:** To investigate whether there is flexibility in the timing of emergence of salmon alevins in response to chemical cues from two predators with different diel patterns of activity, as well as to cues from conspecific competitors.

**Findings:** Alevins in trials with brown trout tended (not significant) to emerge earlier than control fish; early emergent salmon were smaller (length) and had more yolk sac reserves than control fish. Alevins in trials with a known predator of salmon (burbot, *Lota lota*) emerged from the gravel significantly later than control fish.

**Conclusions:** Juvenile salmon are able to recognize chemical cues from predators while still in the gravel, but no response to cues from competitors was observed.

**Reference:** Kennedy, G.J.A., and Strange, C.D. 1986. The effects of intra- and inter-specific competition on the distribution of stocked juvenile Atlantic salmon, *Salmo salar* L., in relation to depth and gradient in an upland trout, *Salmo trutta* L., stream. *J. Fish Biol.* **29**: 199-214.

Species comparisons	Brown trout, Atlantic salmon
Fish age/size	Fry, parr older fish
Source population	Stocked salmon, wild brown trout
Type of study	Field
Location	Upland streams Northern Ireland
Time of year	Last 2 weeks of August and first week of September.
Sample method	Electroshocking
Spatial scale	31 sites: 11.3-76.7 m <sup>2</sup>
Temporal scale	2 years, 1981-82
Water temperature	Not provided

**Purpose:** Determine whether changes in the production of salmon fry is related to 1) changes in fry distributions in the absence of all other fish and 2) in the presence of

intra-specific competition from older salmon, but the continued absence of inter-specific competition from trout.

**Findings:** Interspecific competition from older trout restricted salmon fry to shallow water. Under sympatric conditions, trout and salmon fry were observed mostly in shallow waters with 1+ and older fish in deeper areas having lower water velocities; fry distributions changed to include deep areas when older trout were removed from streams and the habitats characterized by shallow water and high water velocity became least preferred. Evidence for intraspecific competition was found whereby older salmon reduced the growth and survival rates of salmon fry; no evidence was found for intraspecific competition in brown trout.

**Conclusions:** Salmon and brown trout in sympatry adjust the niches they occupy as a result of competition; their habitat preferences are different than when in allopatry.

**Reference:** L'Abée-Lund, J.H., and Heggberget, T.G. 1995. Density of juvenile brown trout and Atlantic salmon in natural and man-made riverine habitats. *Ecol. Freshw. Fish* 4: 138-140.

Species comparisons	Brown trout, Atlantic salmon
Fish age/size	0+, 1+
Source population	Wild
Type of study	Field
Location	River Guala, Norway
Time of year	Aug. and Oct.
Sample method	Electroshocker
Spatial scale	Area not provided (13 sample sites)
Temporal scale	One year, 1986
Water temperature	12.5 and 0.5 °C

**Purpose:** Determine whether use of erosion protected areas of streams differ between Atlantic salmon and brown trout during summer and autumn.

**Findings:** Densities of Atlantic salmon and brown trout (except 1+) age classes were higher in erosion protected areas than in natural areas. Brown trout tended to occur more often at man-made banks than at naturally stable/sheltered banks. Also, there was a seasonal shift in habitat use for both species. There were fewer brown trout in erosion protected areas in October compared to August. The number of salmon in natural areas fell between August and October, while numbers increased at erosion protected areas in October.

**Conclusions:** Between August and October, brown trout change behaviour, becoming more nocturnal while juvenile Atlantic salmon undergo a habitat shift to deeper waters (e.g., those provided by man-made river bank stabilization).

**Reference:** Liew, P.K.L. 1969. A study on the biology of brown trout, *Salmo trutta* Linn, from four different habitats on the Avalon peninsula, Newfoundland. M.Sc. Memorial University of Newfoundland. 186 p.

Species comparisons	Brown trout
Fish age/size	18cm-600cm
Source population	Wild
Type of study	Field
Location	Avalon Peninsula
Time of year	Summer
Sample method	Gillnets, beach seines
Spatial scale	Small ponds to large lakes
Temporal scale	1 season
Water temperature	N/A

**Purpose:** To investigate differences in general life history traits among populations of introduced brown trout and compare with literature from their native range.

**Findings:** Populations varying in life history traits, such as size-at-age and age-at-maturity. Additionally, populations differ markedly in growth rates. Windsor Lake population grew faster (from back calculated scales) than other investigated populations. Populations differed in dietary patterns; however, no attempt to quantify prey availability was conducted. No stream spawning was observed in Windsor Lake and it was concluded that spawning must occur along the shoreline. Spawning behaviour was different than expected based on the literature. The author was surprised to see a female fail to cover spawned eggs. Though there was little discussion of whether the laboratory conditions may have influenced this outcome

**Conclusions:** Life history traits of introduced brown trout populations vary among habitats. Traits such as growth rate, size at age and age at maturity may differ between introduced and native populations. It is unclear; however, whether these differences are the result of adaptive genetic differences or phenotypic plasticity.

**Reference:** Lura, H., and Sægrov, H. 1993. Timing of spawning in cultured and wild Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) in the River Vosso, Norway. *Ecol. Freshw. Fish* 2: 167-172.

Species comparisons	Brown trout, Atlantic salmon
Fish age/size	Mature
Source population	Wild and hatchery salmon, wild brown trout
Type of study	Aquaria
Location	River Vosso, Norway
Time of year	Autumn-spring
Sample method	Visual observations
Spatial scale	Not available
Temporal scale	Two year study, 5 Oct- 30 June
Water temperature	Not provided

**Purpose:** To investigate the time of spawning in cultured and wild Atlantic salmon and wild brown trout, and determine potential interactions between cultured salmon and brown trout during the spawning season

**Findings:** Spawning and subsequent hatching and first feeding occurred earlier in cultured (non-native) salmon than wild salmon. Brown trout tended to spawn earlier than wild salmon, but there was considerable overlap with cultured salmon. Hatching and first feeding occurred earlier (more than a month) in brown trout than either cultured or wild salmon due to faster growth rates of brown trout than salmon under observed water temperatures.

**Conclusions:** High numbers of cultured fish on the spawning grounds with brown trout may lead to increased hybridization and have a negative effect on brown trout populations in the long run.

**Reference:** Mackinnon, J.V. 1998. Observations on stream spawning brown trout, *Salmo trutta*, from Windsor Lake, Avalon Peninsula, Newfoundland. Honours thesis. Memorial University of Newfoundland. 62 p.

Species comparisons	Brown trout
Fish age/size	3-6 years
Source population	Wild
Type of study	Field
Location	Windsor Lake tributaries
Time of year	Fall
Sample method	Netting/hand capture
Spatial scale	2 small streams
Temporal scale	1 season
Water temperature	N/A



**Purpose:** To document the use of small streams for spawning by introduced brown trout.

**Findings:** Fish entered small tributaries of Windsor Lake following fall freshets and spawned between early October and end of November. Fish densities were high in both streams. Fish varied in amount of time in the stream and males tended to stay longer on the spawning grounds. Fish moved between systems, as evidenced by tagging.

**Conclusions:** Small streams of Windsor Lake are important spawning habitats for brown trout.

**Reference:** Matthews, M.A., Poole, W.R., Dillane, M.G. and Whelan, K.F. 1997. Juvenile recruitment and smolt output of brown trout (*Salmo trutta* L.) and Atlantic salmon (*Salmo salar* L.) from a lacustrine system in western Ireland. Fish. Res. **31**: 19-37.

Species comparisons	Brown trout, Atlantic salmon
Fish age/size	0+, 1+ > 1+
Source population	Wild with releases in system
Type of study	Field
Location	Western Ireland
Time of year	Summer-autumn
Sample method	Electroshocking and shore seines
Spatial scale	6 electroshocker sites (53.8-117 m <sup>2</sup> ), 22 seine sites (950 m <sup>2</sup> each)
Temporal scale	June 1991 –October 1995
Water temperature	Not provided

**Purpose:** Determine juvenile fish production from a lacustrine system in western Ireland.

**Findings:** Juvenile Atlantic salmon and brown trout use lacustrine areas extensively. Mean densities of 0.024 trout and 0.002 salmon m<sup>-2</sup> (Lake Bunaveela) and 0.010 trout and 0.010 salmon m<sup>-2</sup> (Lake Feeagh) were observed. There was considerable movement of 0+ and 1+ parr during the summer months and those parr entering lakes appeared to be in good condition (contrary to other studies). Trout production in rivers was dominated by 0+ and 1+ fish, with further growth occurring in lakes.

**Conclusions:** Brown trout and salmon may use lacustrine areas extensively which may reduce intra- and interspecific competition within streams.

**Reference:** O'Connell, M.F. 1982. The biology of anadromous *Salvelinus fontinalis* (Mitchill, 1815) and *Salmo trutta* (Linnaeus, 1758) in river systems flowing into Placentia Bay and St. Mary's Bay, Newfoundland, Memorial University of Newfoundland. 335 pp.

Species comparisons	Brown trout, brook trout
Fish age/size	0-8+, 100-400 mm
Source population	Wild
Type of study	Field
Location	Multiple rivers near Placentia and St. Mary's Bay
Time of year	Summer-autumn
Sample method	Fykes, gillnets, electroshocking
Spatial scale	Large rivers and small creeks and estuaries, quantified areas not given
Temporal scale	1976 –1977 (two years of sampling)
Water temperature	8.8-17.5 °C

**Purpose:** To study life history traits among and within populations. Also to determine whether smolt size/age had an adaptive basis.

**Findings:** Smolt migration occurred from April to June and upstream migration occurred during July-August. However, up and downstream movement may occur throughout the year. There was evidence of homing. Movements were concurrent between species. Smolt age for both species was highly variable from 1-7 for brook trout to 8+ for brown trout. Spawn timing differed among systems, varying from October to November. No spawn timing for brown trout was determined (no spawners found). Anadromous brook trout tended to be dominated by females and anadromous and non-anadromous fish spawn together. Patterns of sex and anadromy were not consistent for brown trout; in some cases the sex ratio among sea-going migrants was approximately 50:50, other times male biased, other times female biased. Interestingly, the majority of upstream migrating fish (of both brook trout and brown trout) were not maturing. Females tended to be alternate year spawners. Diet was fairly consistent among species. Most of brown trout introduced were suspected to be of a British non-anadromous form.

**Conclusions:** Relatively "slow" spread of brown trout could be related to straying rate, slow growth, and alternate year spawning. It was not possible to conclude whether competitive exclusion occurred, though a number of native fish declined while numbers of exotics increased. Declines were suspected to be due in part to a combination of differential angling catchability, angler preference and changes in management (timing of angling season).

**Reference:** Økland, F., Jonsson, B., Jensen, A.J., and Hansen, L.P. 1993. Is there a threshold size regulating seaward migration of brown trout and Atlantic salmon? J. Fish Biol. **42**: 541-550.

Species comparisons	Brown trout, Atlantic salmon
Fish age/size	All
Source population	Wild
Type of study	Field
Location	Norway
Time of year	Summer and autumn
Sample method	Electroshocker, gillnets, rod and line
Spatial scale	4 rivers; 9, 31, 59 66 km
Temporal scale	1949-1990
Water temperature	Not provided

**Purpose:** Determine whether there is a threshold size for smolting.

**Findings:** Smolt age was more variable for brown trout (2-7 years) than Atlantic salmon (2-6 years). Also, smolt age of both species was more variable in northern than southern rivers. The authors conclude that there is no threshold size for smolts and that smolt age may depend on growth rate.

**Conclusions:** Relative to Atlantic salmon, brown trout exhibited higher variability in size and age of smolting, which may be linked to brown trout being under comparatively less intense selection pressure to migrate to the sea.

**Reference:** Orpwood, J.E., Griffiths, S.W., and Armstrong, J.D. 2003. Effects of body size on sympatric shelter use in over-wintering juvenile salmonids. J. Fish Biol. **63**: 166-173

Species comparisons	Brown trout, Atlantic salmon
Fish age/size	0+, 1+
Source population	Wild
Type of study	Aquaria
Location	Scotland
Time of year	November to December
Sample method	Observations
Spatial scale	80 x 2 x 2 m aquaria
Temporal scale	1 year 2002 (29 observations)
Water temperature	Mean=6.2 °C (range: 3.5-7.5 °C)

**Purpose:** 1) Determine whether the degree of shelter dominance in Atlantic salmon and brown trout increases with the size differential between heterospecific pairs. 2) Determine whether shelter dominance is correlated with aggression (accounting for size differential).

**Findings:** Body size, irrespective of species, determined use of winter shelters. In heterospecific pairs, single use of shelters increased with the size differential between the two fish. Some sharing of shelters was observed and this was not related to the size differential between fish. Brown trout initiated more aggressive interactions, and generally, aggression occurred when both fish in a trial were similar in size. The authors postulate that a higher growth rate (and hence a larger size differential prior to winter) experienced by brown trout during summer may give them a competitive advantage over salmon for winter shelters.

**Conclusions:** The fitness consequences of high growth performance (growth rate and longer growth period) of brown trout relative to salmon during summer are likely to be evident during winter as shelter dominance increases with fish size.

**Reference:** Ottaway, E.M., and Clarke, A. 1981. A preliminary investigation into the vulnerability of young trout (*Salmo trutta* L.) and Atlantic salmon (*Salmo salar* L.) to downstream displacement by high water velocities. *J. Fish Biol.* **19**: 135-145.

Species comparisons	Brown trout, Atlantic salmon
Fish age/size	Alevins: salmon means = 26.3, 31.0 mm; brown trout means = 23.1, 24.2, 25.5 mm
Source population	Not stated
Type of study	Artificial stream
Location	Northumberland, Great Britain
Time of year	Spring
Sample method	Observation
Spatial scale	4 channels, each 3 x 1 x 0.47 m deep
Temporal scale	One year; 5 replicates, each 15 days
Water temperature	4.0-11.2 °C

**Purpose:** To assess how fry movement was related to changes in water velocity in a natural setting with shelter available.

**Findings:** Both salmon and brown trout experience flow sensitive periods following emergence, but the timing of these periods differ among species. Overall, comparatively more salmon than trout were displaced in the trials. The salmon that moved were larger individuals and movement occurred at the lower water velocities tested. No size specific pattern of brown trout movement was observed. In two of two trials with brown trout, displacement downstream increased with increasing water velocity.

**Conclusions:** Young brown trout and Atlantic salmon pass through short flow sensitive periods post emergence. These periods are on the temporal scale of a week or two. Changing flow rates influence brown trout and salmon differently, with brown trout being displaced by high water velocities and Atlantic salmon actively moving downstream at low water velocities.

**Reference:** Peake, S., McKinley, R.S., and Scruton, D.A. 1997. Swimming performance of various freshwater Newfoundland salmonids relative to habitat selection and fishway design. *J. Fish Biol.* **51**: 710-723.

Species comparisons	Brown trout, brook trout, Atlantic salmon (anadromous and land-locked)
Fish age/size	Parr, smolts; anadromous salmon: 4.8-13.1 cm, land-locked salmon: 9.1-23.7 cm, brook trout: 6.2-40.5 cm, brown trout: 5.1-26.0 cm
Source population	Wild
Type of study	Aquaria
Location	Newfoundland, Canada
Time of year	June –October
Sample method	Blazka-type swimming flume
Spatial scale	6, 40, 120 l volumes
Temporal scale	Approximately 2.5-3 hours
Water temperature	6 °C

**Purpose:** 1) To compare performance of sympatric anadromous salmon parr and brook trout to determine if current speed is important in segregating the two species. 2) To determine whether land-locked and anadromous populations of salmon have diverged with respect to swimming ability. 3) To derive models that describe the swimming ability of each species so that fishways and culverts in Newfoundland can be designed to optimize fish access to habitat upstream from man-made and natural obstructions.

**Findings:** Generally, anadromous salmon parr did not swim; they remained close to the bottom of the flume, using their pectoral and anal fins to hold position, usually until the trial ended. When swimming was observed, fatigue occurred quickly (< 5 min). Anadromous smolts swam actively in the flume, maintaining position indefinitely at relatively low speed. At relatively high speeds, most fish fatigued quickly. Landlocked salmon tended to swim indefinitely, or for only a short period. Brook and brown trout swam actively and fatigue times of up to 150 minutes were observed. Sustained swim speed and prolonged/burst swimming/holding speed for brook trout was significantly lower than that for the other species tested. Also, land-locked salmon had lower sustained swim speeds than anadromous forms. Prolonged swimming /holding did not differ between brown trout and land-locked or anadromous salmon parr, but differences were observed in all other comparisons. Note that brown trout used in this study were from a different system than the other fish.

**Conclusions:** Atlantic salmon smolts are stronger swimmers than brown trout, which may aid in segregating species by water velocity. Brown trout may compete with Atlantic salmon parr and brook trout because their swimming abilities are similar.

**Reference:** Pickering, A.D., Griffiths, R., and Pottinger, T.G. 1987. A comparison of the effects of overhead cover on the growth, survival and hematology of juvenile Atlantic salmon, *Salmo salar* L, brown trout, *Salmo trutta* L, and rainbow-trout, *Salmo gairdneri richardson*. *Aquaculture* **66**:109-124.

Species comparisons	Brown trout, Atlantic salmon (plus rainbow trout)
Fish age/size	0+
Source population	Wild salmon parents, farmed parents for brown trout
Type of study	Aquaria
Location	Great Britain
Time of year	July – Nov.
Sample method	Observation
Spatial scale	8 tanks, 3.14 m <sup>2</sup>
Temporal scale	One year, 1986
Water temperature	6.7-17.1 °C

**Purpose:** Determine whether overhead cover increases growth and survival rates of fish in aquaria and whether physiological stress in fish is reduced by cover.

**Findings:** No effect of overhead cover on the growth rate of brown (or rainbow) trout, but Atlantic salmon grew faster with cover. Between July and September, salmon without cover grew to 1.5 g while those in covered treatments grew to 4.0 g. Also, in tanks with cover, there were more fish in the upper size mode (38%) compared to uncovered tanks (22%). Thrombocyte and lymphocyte counts were lower in salmon from uncovered tanks, indicating chronic stress toward the end of the experiment when fish density was high. These physiological changes were not observed in either trout species (covered or uncovered).

**Conclusions:** Overhead cover may increase the growth rate of underling salmon and result in increased numbers of one year old smolts. Also, cover may reduce chronic stress in salmon. Cover may not influence stress levels or influence the growth rates of brown trout.

**Reference:** Quist, M. C., Hubert, W.A., and Isaak, D.J. 2004. Fish assemblage structure and relations with environmental conditions in a Rocky Mountain watershed. *Can. J. Zool.* **82**: 1554-1565.

Species comparisons	Brown trout, brook trout
Fish age/size	Not size based
Source population	Wild
Type of study	Field
Location	Salt River, Idaho and Wyoming, USA
Time of year	July-mid September
Sample method	Electroshocker
Spatial scale	110 reaches (mean=194.2 m length, 4.6 m width)
Temporal scale	1996-1997
Water temperature	10.9 °C (range: 5.2-17.9 °C)

**Purpose:** To determine the fish assemblage structure with respect to environmental and habitat characteristics of a mountain watershed.

**Findings:** Brook trout were grouped with cutthroat trout (*Oncorhynchus clarki*) and mottled sculpin (*Cottus beldingi*); this assemblage was observed at higher elevations where there was a high proportion of pool habitats. Brown trout were grouped into a diverse assemblage with many species. This assemblage was observed at lower elevations, where pools were common, the gradient was low and summer temperatures were relatively warm.

**Conclusions:** Results were consistent with other studies, finding that both brook trout and brown trout use pool habitats, but that brook trout may use cooler water temperatures at the upper reaches of systems that brown trout can not tolerate. Therefore, brook trout may not compete with brown trout in cooler head waters.

**Reference:** Saltveit, S.J. 1993. Abundance of juvenile Atlantic salmon and brown trout in relation to stocking and natural reproduction in the River Lærdalselva, western Norway. *North Am. J. Fish. Manage.* **13**: 277-283.

Species comparisons	Brown trout, Atlantic salmon
Fish age/size	30-160 mm; age 0-2
Source population	Wild and stocked
Type of study	Field
Location	Norway
Time of year	Spring to fall
Sample method	Electrofishing
Spatial scale	1018, 847, 1133, 1286 m <sup>2</sup>
Temporal scale	1982-1990
Water temperature	Not provided

**Purpose:** To compare stocking with natural reproduction in the River Lærdalselva, Norway.

**Findings:** There was no increase in brown trout densities following a reduction in salmon densities that occurred when salmon stocking activities ended.

**Conclusions:** Stocking of Atlantic salmon does not appear to be detrimental to resident brown trout production or to the fishery.

**Reference:** Saltveit, S.J., Bremnes, T., and Lindas, O.R. 1995. Effect of sudden increase in discharge in a large river on newly emerged Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) fry. *Ecol. Freshw. Fish* 4: 168-174.

Species comparisons	Brown trout, Atlantic salmon
Fish age/size	Emergent fry
Source population	Wild
Type of study	Field
Location	River Suldalslagen, western Norway
Time of year	Late April – mid June
Sample method	Drift net
Spatial scale	1 m diameter
Temporal scale	3 years; 5 replicates in 1 hour, 1991 (day sampling) 1992-93 (day-night sampling), 7 visits total; each visit 3-10 days
Water temperature	~ 4-7.5 °C

**Purpose:** To determine the downstream migration of juvenile salmonids in a large river.

**Findings:** Salmon, but not trout, were observed to drift more at night than during the day. When flow increased (regulated river) in May, brown trout were already feeding externally and displacement downstream increased (both day and night) with the increased water velocity. Salmon emerged later than trout. More salmon were displaced at night than during the day, suggesting that salmon emerge (during high flow) at night, then move downstream to establish new territories.

**Conclusions:** Emergent fry of Atlantic salmon and brown trout react differently to water flow, with salmon actively moving to new areas at low flow rates and brown trout being passively displaced by high flows.



**Reference:** Sandeman, L.M., and Pippy, J.H.C. 1967. Parasites of freshwater fishes (salmonidae and coregonidae) of insular Newfoundland. J. Fish. Res. Board Can. **24**: 1911-1943.

Species comparisons	Five species of salmonids and coregonids
Fish age/size	N/A
Source population	Wild
Type of study	Field/Parasitology
Location	Insular Newfoundland systems
Time of year	Summer
Sample method	Gillnet/angling
Spatial scale	N/A
Temporal scale	N/A
Water temperature	N/A

**Purpose:** To document frequency of occurrence of freshwater parasites among salmonids and whitefishes of insular Newfoundland and to, if possible, identify host specificity.

**Findings:** Overall rates of infection were high for all species, yet variable. Two new parasite species were described.

**Conclusions:** Small sample sizes preclude direct evidence of host specificity, yet variation in occurrence of parasites in hosts indicated the possibility that this was so.

**Reference:** Scott, R.J., Judge, K.A., Ramster, K., Noakes, D.L.G., and Beamish, F.W.H. 2005. Interactions between naturalized exotic salmonids and reintroduced Atlantic salmon in a Lake Ontario tributary. Ecol. Freshw. Fish **14**: 402-405.

Species comparisons	Brown trout, Atlantic salmon (plus chinook and coho salmon)
Fish age/size	Atlantic salmon females: mean=60.7 cm, males: mean=54.3 cm
Source population	Hatchery supplied Atlantic salmon, wild brown trout
Type of study	Field
Location	Wilmot Creek, Ontario, Canada
Time of year	October –December 2000
Sample method	Visual observation from stream bank
Spatial scale	1.5 km by 6.32 m wide=9480 m <sup>2</sup>
Temporal scale	860 minutes of observation, 20 minutes each, between 5 Nov. and 8 Dec.
Water temperature	Not provided

**Purpose:** To determine the frequency and impact of previously observed interactions between reintroduced Atlantic salmon and other species present on spawning sites in natural Ontario streams

**Findings:** Of the 48 female and 17 male Atlantic salmon monitored during this study, only one interaction between Atlantic salmon and brown trout was observed. One brown trout male was observed to court an Atlantic salmon female. Most (7 of ten) interactions observed were between Chinook salmon and Atlantic salmon and included courting and aggressive behaviour.

**Conclusions:** Introduced salmonids, including brown trout, may impact negatively on efforts to reintroduce Atlantic salmon to Lake Ontario.

**Reference:** Sosiak, A.J. 1982. Buoyancy Comparisons between juvenile Atlantic salmon and brown trout of wild and hatchery origin. *Trans. Am. Fish. Soc.* **111**: 307-311.

Species comparisons	Brown trout, Atlantic salmon
Fish age/size	Salmon: hatchery mean =74 mm (58-94 mm) and 139 mm (118-171mm), wild mean=92 (77-103 mm); brown trout: hatchery mean = 75 mm (57-97 mm), 143 ( 115-172 mm), wild 132 mm (116-146 mm)
Source population	Hatchery and wild
Type of study	Desiccating jars
Location	Sweden
Time of year	August – November
Sample method	Observation
Spatial scale	4 jars with diameters of 21, 25.5, 30.5 and 31 cm
Temporal scale	One year study, approximately 3 days per trial
Water temperature	7.1 -18.0 °C

**Purpose:** Buoyancies of hatchery-reared and wild brown trout were compared to determine whether domestication influences buoyancy. Also, buoyancies of hatchery-reared Atlantic salmon were related to the results above.

**Findings:** Hatchery-reared brown trout were relatively more buoyant than wild fish, suggesting that domesticated brown trout may be comparatively less competitive than wild fish in fast moving water where remaining near the bottom is advantageous. Hatchery-reared Atlantic salmon (both 0+ and 1+) were less buoyant than brown trout (0+ and 1+) in moving water, but salmon adjusted their buoyancy to equal that of brown trout (hatchery-reared) in still water. These findings support the idea that Atlantic salmon may have a competitive advantage over brown trout in habitats with high water velocities.

**Conclusions:** Age 0 and 1 Atlantic salmon are less buoyant than brown trout, which may help salmon to remain closer to the substratum; hence salmon may inhabit areas with higher velocities than brown trout.

**Reference:** Taniguchi, Y., Rahel, F.J., Novinger, D.C., and Gerow, K.G. 1998. Temperature mediation of competitive interactions among three fish species that replace each other along longitudinal stream gradients. *Can. J. Fish. Aquat. Sci.* **55**: 1894-1901.

Species comparisons	Brown trout, brook trout (plus creek chub <i>Semotilus atromaculatus</i> )
Fish age/size	107-165 mm fork length
Source population	Wild
Type of study	Artificial stream + wild
Location	Wyoming, USA
Time of year	Not provided
Sample method	Observation
Spatial scale	Oval channel=3.7 x 2.4 m with a stream width and depth of 0.6 m
Temporal scale	One year, 29 trials, each trial= 2 hours of observations per day for 6 days
Water temperature	3, 6, 10, 20, 22, 24, 26 °C

**Purpose:** 1) To test the hypothesis that brook trout would be the competitively superior species at cold water temperatures, brown trout would be competitively superior at moderate water temperatures and creek chub (*Semotilus atromaculatus*) would be competitively superior at warm water temperatures. 2) To examine whether the competitive inferiority of a species at a particular temperature was due primarily to appetite loss or to interactions with other species.

**Findings:** During the acclimation period, when fish were held individually, no fish died at temperatures of 3-22 °C. Two of ten brook trout died during acclimation to 24 °C; all brown trout survived this trial. All brook trout and four of ten brown trout died during acclimation to 26 °C. At temperatures between 3 °C and 24 °C, there were no differences in the number of aggressive acts initiated by brook and brown trout. Brook trout increased food consumption when dominant brown trout were removed from trials at temperatures <24 °C; food intake did not change when brown trout were removed from the 24 °C trial. Brown trout generally consumed more food items than brook trout in all trials below 26 °C. In all trials at temperatures between 3 °C and 24 °C, brown trout ate more food items when competitively dominant fish were removed from trials. In three of four trials at 26 °C, brown trout did not eat and were considered to be under physiological stress in allopatry or sympatry with chub or brook trout.

**Conclusions:** Brown trout are comparatively more tolerant of higher water temperatures than brook trout. At water temperatures below 26 °C, there are no differences in aggression between brown trout and brook trout.

**Reference:** Waters, T.F. 1983. Replacement of brook trout by brown trout over 15 years in a Minnesota stream: production and abundance. Trans. Am. Fish. Soc. **112**: 137-146.

Species comparisons	Brown trout, brook trout (plus rainbow trout)
Fish age/size	All ages
Source population	Wild
Type of study	Field
Location	Valley Creek, Minnesota
Time of year	April and September or March, July and November
Sample method	Mark-recapture - electrofishing
Spatial scale	0.181 hectare (0.4 km long, average 4 m wide)
Temporal scale	15 years; 1965-79
Water temperature	3-26 °C

**Purpose:** To document the changes of trout species composition in terms of density, standing stock and annual production and second, to attempt to relate these changes to possible causative factors.

**Findings:** Over a 15 year period, percentage of trout species in the study site (Valley Creek) changed from 100 % brook trout (although brown trout were known to occur in the system) to 70% brown trout, 15 % brook trout and 15 % rainbow trout. Following two years of relatively high siltation in 1971-72, brook trout numbers and annual production gradually declined, while brown trout numbers began increasing up to 1980.

**Conclusions:** Habitat factors in combination with behavioural differences between brook and brown trout were largely responsible for the species changes (replacement) that occurred.

**Reference:** Witzel, L.D., and MacCrimmon, H.R. 1983a. Embryo survival and alevin emergence of brook charr, *Salvelinus fontinalis*, and brown trout, *Salmo trutta*, relative to redd gravel composition. Can. J. Zool. **61**: 1783-1792.

Species comparisons	Brown trout, brook trout
Fish age/size	Mature
Source population	Wild
Type of study	Aquaria
Location	Ontario, Canada
Time of year	Autumn-winter
Sample method	Observations
Spatial scale	18 incubators
Temporal scale	Two years (406-514 degree days)
Water temperature	10.0-11.1 °C

**Purpose:** Assess potential alevin production from stream redds and to select for appropriate gravel compositions for use in the creation or enhancement of spawning areas.

**Findings:** Survival to hatch, size and developmental condition of both brook and brown trout alevins increased with gravel size and decreased with percent sand composition. Survival of both species was poor in fine sediments. Brown trout embryos hatched approximately 52 degree days before brook trout embryos. Brown trout were comparatively larger (length and weight) at emergence than brook trout; yolk sac reserves were also larger in brown trout. The authors note that in Ontario, brook trout usually spawn earlier, develop faster (cooler water temperatures than in the laboratory) and emerge earlier than brown trout in the wild.

**Conclusions:** Redd gravel size and sand loading are instrumental in the determination of survival, timing and duration of emergence, and size and developmental condition of brook and brown trout.

**Reference:** Witzel, L.D., and MacCrimmon, H.R. 1983b. Redd-site selection by brook trout and brown trout in southwestern Ontario streams. *Trans. Am. Fish. Soc.* **112**: 760-771.

Species comparisons	Brown trout, brook trout
Fish age/size	Mature fish, age classes 1+ to 5+; brook trout: female averages: 12.6 - 25.8 cm, male averages: 13.7-26.2 cm; brown trout: female averages: 20.0-54.5 cm, male averages: 23.7-53.3 cm
Source population	Wild
Type of study	Field
Location	Southwestern Ontario, Canada
Time of year	Autumn-November
Sample method	Coring
Spatial scale	95 cm <sup>2</sup> x 114 cores=10830 cm <sup>2</sup>
Temporal scale	August -November
Water temperature	3-13 °C

**Purpose:** To document comparative observations on the reproduction of brook and brown trout under allopatric and sympatric conditions in representative southern Ontario watersheds.

**Findings:** Spawning by brown trout usually began one week later than brook trout. Spawning overlapped by three weeks in sympatric conditions (brook trout spawned over 3-5 weeks, brown trout spawned over 2-4 weeks). Intraspecific reuse of redds by brook and brown trout occurred at seven of the eight sites studied and the only interspecific reuse of redds observed was by small brown trout that reused redd sites of brook trout (and other species). Brook trout spawned exclusively in areas with groundwater seepage while brown trout spawned in areas both with and without groundwater seepage. The average water velocity at brook trout redds was less than half that at brown trout redds, but water depths did not differ. The sediment size (geometric mean) of redd sites used only by brook trout was smaller than that of redds used only by brown trout.

**Conclusions:** There was little evidence of interaction between brook and brown trout during the breeding season in southern Ontario, although there was considerable overlap in spawning times of the two species in sympatry.