

Growth rate differences between resident native brook trout and non-native brown trout

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Between species and across season variation in growth was examined by tagging and recapturing individual brook trout *Salvelinus fontinalis* and brown trout *Salmo trutta* across seasons in a small stream (West Brook, Massachusetts, U.S.A.). Detailed information on body size and growth are presented to (1) test whether the two species differed in growth within seasons and (2) characterize the seasonal growth patterns for two age classes of each species. Growth differed between species in nearly half of the season- and age-specific comparisons. When growth differed, non-native brown trout grew faster than native brook trout in all but one comparison. Moreover, species differences were most pronounced when overall growth was high during the spring and early summer. These growth differences resulted in size asymmetries that were sustained over the duration of the study. A literature survey also indicated that non-native salmonids typically grow faster than native salmonids when the two occur in sympatry. Taken together, these results suggest that differences in growth are not uncommon for coexisting native and non-native salmonids.

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INTRODUCTION

Introductions of brown trout *Salmo trutta* L. to North America have been implicated in the decline and displacement of native brook trout *Salvelinus fontinalis* (Mitchell) (Fausch & White, 1981; Waters, 1983; DeWald & Wilzbach, 1992). Non-native brown trout appear to have had a number of negative impacts on native brook trout. For example, brown trout may exclude brook trout from preferred resting positions (Fausch & White, 1981), prey on brook trout (Alexander, 1977), hybridize with brook trout, disturb the nests of brook trout (Witzel & MacCrimmon, 1983; Essington *et al.*, 1998) or displace brook trout into headwater tributaries (Waters, 1983). Some of these impacts probably stem from competitive interactions because (1) the two species overlap

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considerably in habitat preference, prey preference and diet (Nyman, 1970), and (2) they engage in intra- and interspecific interference competition for feeding stations (Fausch & White, 1981). Despite this evidence for negative impacts, the two species often coexist in apparent stability.

The effects of non-native brown trout on fitness-related traits of native brook trout is the focus of the present research programme. Previous work has demonstrated that seasonal survival rates are similar for equal-aged cohorts of the two species (Carlson & Letcher, 2003). Herein, relative growth rate is considered, which is related to fitness through its effects on body size (Roff, 1992; Stearns, 1992; Arendt, 1997; Blanckenhorn, 2000). Previous laboratory studies suggest that at 14° C, the growth rate of brown trout may exceed that of brook trout (DeWald & Wilzbach, 1992). Field data (Cooper, 1953; Fausch & White, 1986), however, are limited, particularly because no studies have examined individual growth across a realistic range of temperatures (*i.e.* across seasons).

Accounting for seasonal variation is important because environmental factors such as temperature and food availability influence growth rates. Indeed, the growth of stream residing salmonids is highly seasonal (Cooper, 1953; Jones *et al.*, 2002; Letcher & Gries, 2003) and tends to be concentrated during periods when food availability is elevated (Cada *et al.*, 1987; Filbert & Hawkins, 1995) and temperatures are optimal (Jensen, 1990; Filbert & Hawkins, 1995; Drake & Taylor, 1996). Most studies examining intra-population growth rate variation in salmonids have focused on a single season (Spalding *et al.*, 1995; Quinn & Peterson, 1996; Kahler *et al.*, 2001; Hesthagen *et al.*, 2004; Arnekleiv *et al.*, 2006), while those examining variation among seasons (Shetter, 1937; Cooper, 1953; Mortensen *et al.*, 1988; Lobón-Cerviá & Rincón, 1998; Utrilla & Lobón-Cerviá, 1999; Letcher & Gries, 2003) have largely ignored differences among species and cohorts, although there have been exceptions (Egglisshaw & Shackley, 1977; Whitworth & Strange, 1983). This is unfortunate because interactions among species, ages and seasons may be complex, and testing for the effect of one factor may require also assessing the others.

In the present study, the relative growth rates of sympatric brook and brown trout were investigated to determine whether growth rates consistently differ in a stream where the two species have long been sympatric. Allen & Hoekstra (1992) define three scale dimensions: (1) spatial extent, (2) temporal extent and (3) grain (*i.e.* the fine level of resolution often determined by sampling design). The present study was of intermediate spatial (a single stream reach encompassing 4778.4 m²) and temporal extent (2 years) and was fine-grained (multiple samples per year and individual fish marked and recaptured). This sampling scheme allowed a characterization of the seasonal growth pattern for two age classes of each species, and a test of whether growth rates differed between equal-aged brook and brown trout.

MATERIALS AND METHODS

STUDY SPECIES

Both brook and brown trout are iteroparous and can exhibit anadromy or non-anadromy. In the study site, all individuals of both species are non-anadromous. Both

species breed in the autumn (Witzel & MacCrimmon, 1983; Essington et al., 1998) and have embryos that incubate in the gravel for several months before hatching. Hatchlings ('alevins') then remain in the gravel for another month or so, during which time they absorb their yolk sac but do not feed exogenously. Free-swimming age 0 year fish ('fry') emerge from the gravel in the late winter or early spring and begin to feed on invertebrates. The fishes reached a size suitable for tagging (60 mm and 2 g) during the summer of their age 0 year.

STUDY SITE AND DATA COLLECTION

The study was conducted in the West Brook, a third order stream in the Connecticut River basin, Massachusetts, U.S.A. (42°25' N; 72°40' W). The specific study site is 955 m in length and, during low summer flow conditions, is 4778.4 m² in total surface area. A logger recorded water temperature every 2 h from which the daily averages over the study period were calculated [Fig. 1(a)]. A stage and discharge relationship was

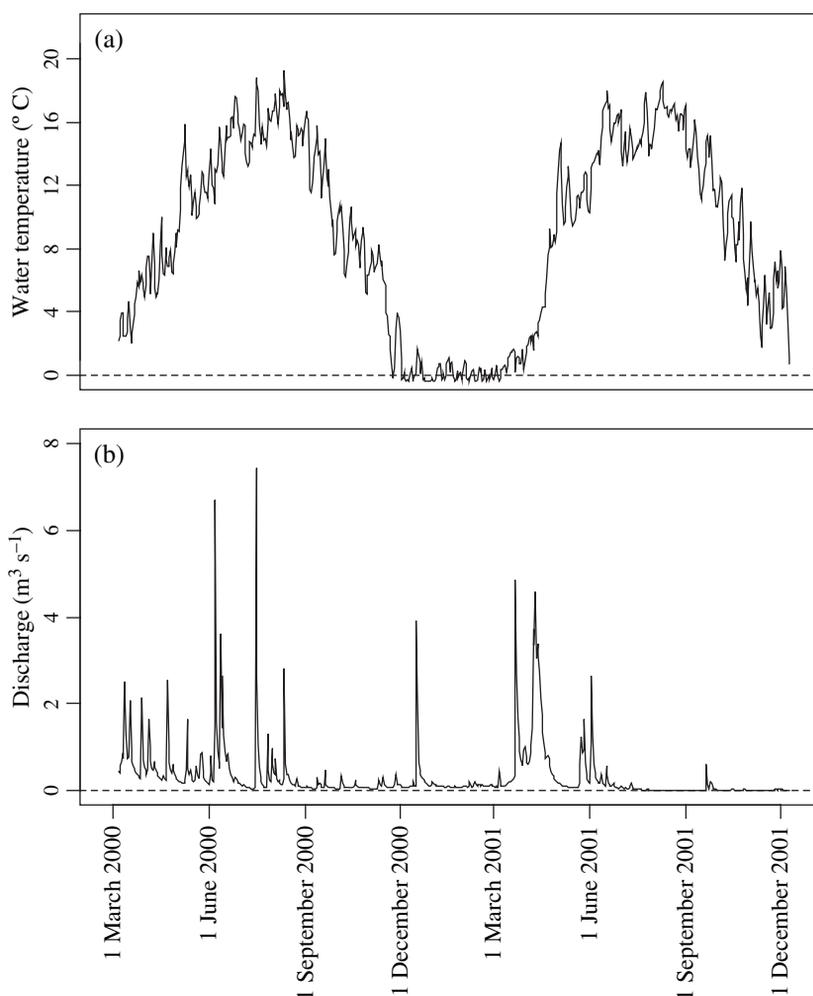


FIG. 1. (a) Average daily water temperature and (b) discharge in the West Brook, MA, U.S.A. from March 2000 to December 2001.

used to generate the average daily discharge during the study period [Fig. 1(b)]. The West Brook contains self-sustaining populations of brook and brown trout (Carlson & Letcher, 2003; Carlson *et al.*, 2004) and is artificially stocked each spring with juvenile Atlantic salmon *Salmo salar* L. The date of brown trout introduction to the West Brook is unknown. The three salmonids are the only fish species present, except for an occasional black-nosed dace *Rhinichthys atratulus* (Hermann). For the 1999 cohort, which emerged from the gravel during the spring of 1999, data were obtained on the age 1 to age 2 year period (second spring of life to the third autumn of life). For the 2000 cohort, which emerged during the spring of 2000, data were obtained on the age 0 to age 1 year period (first summer of life to second autumn of life).

The entire study site was sampled 11 times between March 2000 and December 2001 (Table I). Three sampling techniques were employed: day electrofishing (unpulsed direct current at 400 V), standard night seining (Gries & Letcher, 2002) and a modified night-seining technique that included the use of torches and hand-held aquarium nets to capture fishes along the stream margins. The last two techniques were employed only during low summer flow conditions, when night seining is most efficient. Regardless of sampling technique, a 20 m section was enclosed with block-nets and two-pass removal was performed. This procedure was repeated in an upstream direction until the entire site was sampled, which usually required 7–11 days.

The programme 'MARK' (White & Burnham, 1999) was used to estimate the probability of capturing an individual if it was alive and present in the study site during the main sampling period. The sample-specific estimates and CI are provided in Carlson & Letcher (2003). The averages of these estimates is $P = 0.71$ (brook trout, 1999 cohort), $P = 0.69$ (brown trout, 1999 cohort), $P = 0.53$ (brook trout, 2000 cohort) and $P = 0.48$ (brown trout, 2000 cohort). Capture probabilities were therefore similar between equal-aged brook and brown trout, minimizing bias in the growth estimates.

Captured fishes were anaesthetized (clove oil: 30 mg l^{-1}), weighed (mass, M ; $\pm 0.1 \text{ g}$), measured (fork length, L_F ; $\pm 1 \text{ mm}$), sampled for scales (to determine age) and checked for maturity (expression of milt indicated a mature male). All fishes $>60 \text{ mm } L_F$ and $>2.0 \text{ g } M$ were tagged in the peritoneal cavity with a 12 mm passive integrated transponder tag (PIT tag; Digital Angel, St Paul, MN, U.S.A.). Any previously tagged fishes had their tag numbers recorded. The anal fin was clipped on all fishes to serve as a secondary mark. The percentage of fishes captured which had lost their tag (*i.e.* had an anal fin clip but no PIT tag) was 1.1% for brook trout and 1.0% for brown trout.

STATISTICAL ANALYSES

The value of M was compared between brook and brown trout for each combination of cohort and sampling period with t -tests. In the case of unequal variances (*i.e.* Levene's test for equality of variances; Zar, 1999), means were compared using Welch's approximate t (Zar, 1999). Growth rates were then compared with ANCOVA, where the dependent variable was the natural logarithm of final mass over an interval ($\ln M_2$), the independent variable was the natural logarithm of initial mass over the interval ($\ln M_1$), and the fixed grouping factor was either season or species. Mass data were \ln transformed to remedy non-linearity and non-constant variance issues (Zar, 1999). This method was effective in removing confounding effects of initial size on growth rate, a problem that afflicts the use of specific growth rates. The first step in each ANCOVA was to test for heterogeneity in the slopes of lines relating final size to initial size (*i.e.* the interaction term). If this term was not significant, it was removed and the model was fitted again, revealing the effect of the grouping factor (season or species) and allowing comparisons of line elevations (*i.e.* final sizes at a common initial size). These are standard procedures for statistically removing the effects of covariation with body size (Huitema, 1980). If the interaction term was significant, it could not be removed. In these cases, it was concluded that the groups being compared differed in growth when the final sizes of the one group were consistently above or below final sizes of the other group (*i.e.* if the final sizes for one group fell above or below those of the other group across the entire range of initial sizes).

TABLE I. Intervals during which growth was measured, average interval length, density (total number of fish captured divided by total area of the study site) and number of individuals which were captured in the beginning sample of an interval and the number of these that were subsequently included in the growth analysis (caught again during the ending sample of an interval). The starting sample and ending sample number defining each interval are presented below each interval designation. Data are reported by cohort (1999 or 2000) and species (brook or brown trout). Intervals correspond to those reported in Carlson & Letcher (2003) and Carlson *et al.* (2004). Fishes were captured by electrofishing during all samples except samples 3 and 4, where night seining was employed

Interval (starting sample–ending sample)	Average starting date (range)	Average ending date (range)	Average number of days in interval	Species of trout	Cohort (age designation, years)	Density starting sample (fish m ⁻²)	Number captured in starting sample	Number captured in both starting and ending sample
Spring 2000 (1–2)	14 March (6–22 March)	25 May (18 May to 1 June)	72	Brook Brown	1999 (age 1) 1999 (age 1)	1.17 1.00	56 48	32 20
Early summer 2000 (2–3)	25 May (18 May to 1 June)	9 July (5–13 July)	45	Brook Brown	1999 (age 1) 1999 (age 1)	1.36 1.70	65 81	8 6
Summer 2000 (3–4)	9 July (5–13 July)	24 August (20–29 August)	46	Brook Brown	1999 (age 1) 1999 (age 1)	0.46 0.23	21 10	7 3
Late summer 2000 (4–5)	24 August (20–29 August)	27 September (22 September to 2 October)	34	Brook Brown	2000 (age 0) 2000 (age 0)	0.96 1.05	46 50	13 2
Autumn 2000 (5–6)	27 September (22 September to 2 October)	8 December (1–15 December)	72	Brook Brown	1999 (age 1) 1999 (age 1)	0.29 0.27	14 13	11 8
				Brook Brown	2000 (age 0) 2000 (age 0)	1.49 2.60	71 124	22 58
				Brook Brown	2000 (age 1) 2000 (age 1)	0.69 1.00	33 47	10 15
				Brook Brown	2000 (age 0) 2000 (age 0)	1.40 9.96	67 476	18 128

TABLE I. Continued

Interval (starting sample–ending sample)	Average starting date (range)	Average ending date (range)	Average number of days in interval	Species of trout	Cohort (age designation, years)	Density starting sample (fish m ⁻²)	Number captured in starting sample	Number captured in both starting and ending sample
Winter 2000– 2001 (6–7)	8 December (1–15 December)	13 March (8–19 March)	95	Brook	1999 (age 1)	0.54	26	3
				Brown	1999 (age 1)	0.54	26	10
				Brook	2000 (age 0)	1.30	62	19
Spring 2001 (7–8)	13 March (8–19 March)	9 June (5–14 June)	88	Brook	2000 (age 0)	5.38	253	62
				Brook	1999 (age 2)	0.17	8	4
				Brown	1999 (age 2)	0.31	16	8
Early summer 2001 (8–9)	9 June (5–14 June)	25 July (20–30 July)	46	Brook	2000 (age 1)	1.11	53	26
				Brown	2000 (age 1)	4.69	223	67
				Brook	1999 (age 2)	0.15	7	3
Late summer 2001 (9–10)	25 July (20–30 July)	9 September (4–14 September)	46	Brook	1999 (age 2)	0.31	17	11
				Brown	1999 (age 2)	2.28	109	52
				Brook	2000 (age 1)	5.06	240	101
Autumn 2001 (10–11)	9 September (4–14 September)	6 December (3–10 December)	88	Brook	1999 (age 2)	0.10	5	3
				Brown	1999 (age 2)	0.36	18	12
				Brook	2000 (age 1)	2.18	104	66
				Brook	2000 (age 1)	5.11	243	136
				Brook	2000 (age 1)	2.39	114	32
				Brown	2000 (age 1)	4.29	203	100

These ANCOVA require that similar lengths of time have passed for the groups being compared. This was not a problem when comparing species, because the average length of a given sampling interval differed by at most 1 day between equal-aged brook and brown trout. Seasonal comparisons, however, were problematic. For the 1999 cohort, no combination of samples yielded intervals of similar length, which precluded a direct comparison of growth using ANCOVA. For the 2000 cohort, however, it was possible to compare four 'seasons' of approximately equal length: winter 2000–2001 (8 December 2000 to 13 March 2001, 95 days), spring 2001 (13 March 2001 to 9 June 2001, 88 days), summer 2001 (9 June 2001 to 9 September 2001, 92 days) and autumn 2001 (9 September 2001 to 6 December 2001, 88 days).

RESULTS

A total of 965 brook trout and 1393 brown trout were tagged and released during this study. The number of individuals for which growth could be measured (Table I) was a sub-set of the total because growth rate estimation required that an individual be captured in both the starting and ending sample of an interval. On average, 40% of the individuals captured in the starting sample defining an interval were also captured in the ending sample (Table I).

BODY MASS

For the 1999 cohort, brown trout were significantly larger than brook trout from December 2000 to September 2001 [Fig. 2(a)]. They were also larger, although not significantly so, in August and September 2000 [Fig. 2(a)]. This broadly consistent size difference arose because average brook trout M , but not brown trout M , decreased during their age 1 year winter [Fig. 2(a)]. The exceptions to this general pattern were that brook trout were significantly larger in March and May 2000 and non-significantly larger in July 2000 [Fig. 2(a)]. For the 2000 cohort, brown trout were larger than equal-aged brook trout in eight of nine samples (from August 2000 to December 2001), significantly so in all but one sample [December 2000; Fig. 2(b)]. The sole exception to this pattern was that brook trout were non-significantly larger during July 2000 [Fig. 2(b)].

GROWTH VARIATION AMONG SEASONS

Growth was highly seasonal for both species, with the period of rapid M gain confined to the spring and early summer (Fig. 2). For the 2000 cohort (1999 could not be analysed in this way), the interaction term ($\ln M_1 \times \text{season}$) was significant for both species, precluding a direct ANCOVA comparison of differences in regression line elevation. Fortunately, plots of $\ln M_2$ and $\ln M_1$ clearly show that growth is substantially greater for both species during the spring than during the other seasons (Fig. 3) because the regression line representing the spring sample falls above the regression lines representing the other samples across the range of x -values (*i.e.* initial sizes). Thus, ANCOVA, which accounts for variation in initial size (Fig. 3), yielded the same conclusion as the comparison of seasonal size trends (Fig. 2), growth rates were elevated in the spring relative to the other seasons, which did not differ from each other (Fig. 3).

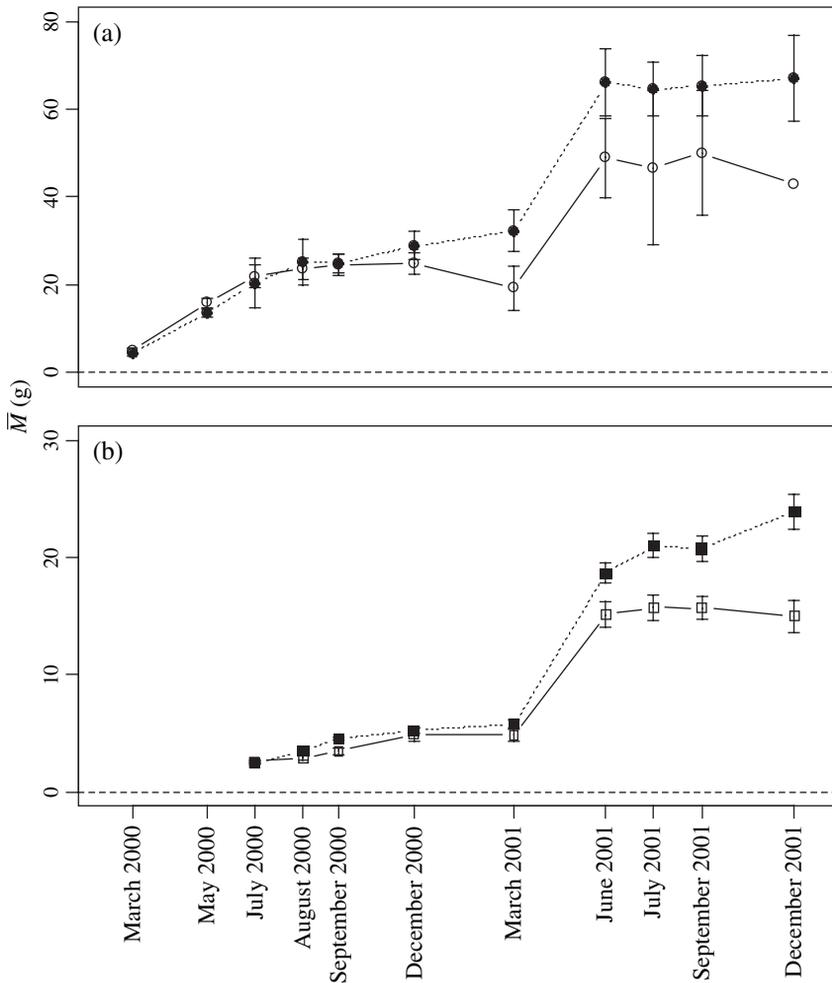


FIG. 2. Mean mass (\bar{M}) \pm 95% CI for brown (●, ■) and brook (○, □) trout from the (a) 1999 and (b) 2000 cohorts.

GROWTH VARIATION BETWEEN SPECIES

For the 1999 cohort, sample sizes were small (Table I), but the data spanned a sufficient range of initial sizes to warrant analysis (supported by a highly significant covariate, $\ln M_1$, in all but one interval; Table II). For this cohort, the interaction between initial size ($\ln M_1$) and species was not significant (Table II) in eight of nine intervals. Removal of the interaction term revealed that brown trout of the 1999 cohort grew faster than equal-aged and equal-sized brook trout during three intervals (age 1 year early summer, age 2 year spring and age 2 year early summer), whereas the two species grew at similar rates during the remaining five intervals (Table II). In the interval for which slopes differed (age 1 year winter), M_2 for a given M_1 showed considerable overlap between the species, suggesting that growth rates did not differ significantly.

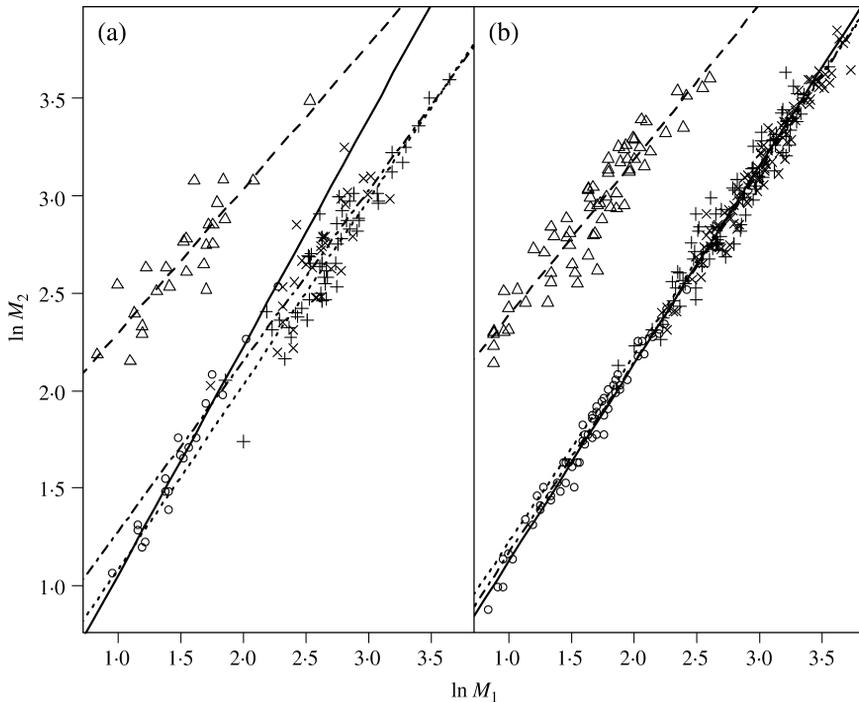


FIG. 3. Seasonal growth comparison for the 2000 cohort (a) brook and (b) brown presented as the \ln final mass ($\ln M_2$) and \ln initial mass ($\ln M_1$) of individual fishes plotted over specified seasons: winter 2000 (\circ), spring 2001 (\triangle), summer 2001 (\times) and autumn 2001 (\times). The curves were fitted by: (a) winter 2000 $y = 1.1719x - 0.1184$ ($r^2 = 0.962$, $P < 0.001$), spring 2001 $y = 0.7389x + 1.5577$ ($r^2 = 0.792$, $P < 0.001$), summer 2001 $y = 0.9485x + 0.1345$ ($r^2 = 0.883$, $P < 0.001$), autumn 2001 $y = 0.8748x + 0.4023$ ($r^2 = 0.700$, $P < 0.001$) and (b) winter 2000 $y = 1.0117x + 0.1186$ ($r^2 = 0.978$, $P < 0.001$), spring 2001 $y = 0.7974x + 1.5909$ ($r^2 = 0.890$, $P < 0.001$), summer 2001 $y = 0.9607x + 0.2658$ ($r^2 = 0.922$, $P < 0.001$) and autumn $y = 0.9781x + 0.1927$ ($r^2 = 0.959$, $P < 0.001$).

For the 2000 cohort, the interaction between initial size and species was not significant in six of seven intervals (Table II). Removal of the interaction term revealed that brown trout of the 2000 cohort grew faster than equal-aged and equal-sized brook trout during four intervals (age 0 year late summer, age 1 year spring, age 1 year early summer and age 1 autumn), slower during one interval (age 0 year autumn) and similarly during one interval (age 1 year late summer; Table II). In the interval where slopes differed (age 0 year winter), M_2 for a given M_1 showed considerable overlap between the species, suggesting that growth rates did not differ (as in the 1999 cohort).

DISCUSSION

This study yielded several salient results. First, both species showed high growth in the spring, followed by low growth thereafter (Figs 2 and 3), a pattern

TABLE II. ANCOVA results for effect of species with ln final mass (M_2) as the dependent variable and ln initial mass (M_1) as the covariate for each interval reported by cohort*. Subscripts denote d.f. associated with the F -statistics. Because only two brown trout from the 2000 cohort were captured in both the starting and ending samples for the summer 2000 interval (see Table I), no ANCOVA was performed for the 2000 cohort during the summer 2000 interval

Interval	Starting sample	Ending sample	Cohort	Age designation (year)	Full Model				Species exhibiting fastest growth	Model r^2
					Species (F)	ln M_1 (F)	Interaction (F)	Adjusted mean (F)		
Spring 2000	1	2	1999	Age 1	0.008 ^{1,48}	152.967 ^{1,48}	0.037 ^{1,48}	0.231 ^{1,49}	Brown	0.773
Early summer 2000	2	3	1999	Age 1	0.041 ^{1,10}	62.926 ^{1,10}	0.002 ^{1,10}	5.836 ^{a,11}		0.882
Summer 2000	3	4	1999	Age 1	0.220 ^{1,6}	91.884 ^{c,6}	0.216 ^{1,6}	0.005 ^{1,7}		0.972
Late summer 2000	4	5	1999	Age 1	0.304 ^{1,15}	128.698 ^{c,15}	0.261 ^{1,15}	0.289 ^{1,16}		0.896
Autumn 2000	5	6	1999	Age 1	0.307 ^{1,21}	161.084 ^{c,21}	0.153 ^{1,21}	3.761 ^{1,22}		0.894
Winter 2000-01	6	7	1999	Age 1	7.819 ^{a,1,9}	230.662 ^{c,1,9}	7.964 ^{a,1,9}	Int.		Int.
Spring 2001	7	8	1999	Age 2	0.008 ^{1,8}	146.846 ^{c,1,8}	0.056 ^{1,8}	30.900 ^{c,1,9}	Brown	0.975
Early summer 2001	8	9	1999	Age 2	0.214 ^{1,10}	21.792 ^{b,1,10}	0.135 ^{1,10}	5.143 ^{a,1,11}	Brown	0.787
Late summer 2001	9	10	1999	Age 2	0.091 ^{1,11}	2.849 ^{1,11}	0.093 ^{1,11}	0.206 ^{1,12}		0.942
Late summer 2000	4	5	2000	Age 0	0.190 ^{1,76}	287.622 ^{c,1,76}	0.242 ^{1,76}	12.867 ^{b,1,77}	Brown	0.832
Autumn 2000	5	6	2000	Age 0	4.750 ^{a,1,142}	1061.772 ^{c,1,142}	0.436 ^{1,142}	33.386 ^{c,1,143}	Brook	0.939
Winter 2000-01	6	7	2000	Age 0	9.220 ^{b,1,77}	1911.484 ^{c,1,77}	10.289 ^{b,1,77}	Int.		Int.
Spring 2001	7	8	2000	Age 1	0.070 ^{1,89}	388.585 ^{c,89}	0.562 ^{1,89}	17.958 ^{c,90}	Brown	0.879
Early summer 2001	8	9	2000	Age 1	1.715 ^{1,149}	2940.690 ^{c,1,149}	0.011 ^{1,149}	114.165 ^{c,1,150}	Brown	0.960
Late summer 2001	9	10	2000	Age 1	1.894 ^{1,198}	4398.157 ^{c,1,198}	1.674 ^{1,198}	0.507 ^{1,199}		0.965
Autumn 2001	10	11	2000	Age 1	1.196 ^{1,128}	676.172 ^{c,1,128}	2.103 ^{1,128}	8.364 ^{b,1,129}	Brown	0.934

Int., the interaction term was significant and could therefore not be removed from the model precluding comparisons of adjusted means.

*The Species, ln M_1 and Interaction columns show statistics for the full model (including the interaction term to test for homogeneity of the slopes). For traits in which the slopes did not differ among species ($P > 0.05$), the interaction term was removed to calculate the adjusted mean F (species comparison at a common initial size) and model r^2 (last two columns).

^a $P < 0.05$; ^b $P < 0.01$; ^c $P < 0.001$.

that probably reflected increased flow (Fig. 1) and food availability during the spring. For example, Grader & Letcher (2006) found that the density of invertebrate drift in the West Brook peaked in the spring and was much reduced during the remainder of the year. Additionally, the West Brook is fed by a reservoir from which little water is released during the summer, leaving the stream essentially spring-fed. This general pattern may also reflect seasonal differences in feeding motivation (Metcalf *et al.*, 1986). These results therefore support previous studies in showing that salmonid growth in streams is highly seasonal (Cooper, 1953; Whitworth & Strange, 1983; Letcher & Gries, 2003).

Second, growth often differed between the species. Specifically, brown trout showed significantly faster growth than brook trout in seven of 16 intervals (Table II) and were consequently larger for much of the age 0+ to age 2+ year period (Fig. 2). Brook trout showed significantly faster growth in only one interval (age 0 year autumn). Only two studies have compared growth rate between sympatric brook and brown trout in natural streams. Cooper (1953) found that brook trout cohorts increased in average size faster than brown trout cohorts, but these comparisons confounded individual growth with differential mortality. This was problematic because mortality owing to sport fishing was higher for brook trout than for brown trout (Cooper, 1953). In contrast, Fausch & White (1986) found that age 0 year brook and brown trout emerged from the gravel at a similar size and grew at a similar rate during their first summer but growth information from other seasons was not reported (Fausch & White, 1986). In the present study, the brook trout were significantly larger than brown trout during the first sample in which they were captured (age 0 year July), but this size advantage was reversed by the next sample (age 0 year August) after which brown trout maintained their size advantage throughout the duration of the study [Fig. 2(b)].

Third, species differences in growth were largest when overall growth was greatest in the spring. Growth differed between brook and brown trout in eight of 16 intervals and five of these differences were associated with spring and early summer growth intervals (Table II). Divergence of growth rates during periods of rapid mass gain resulted in differences in size that were sustained throughout the duration of the study (Fig. 2).

POSSIBLE CAUSES OF GROWTH DIFFERENCES

The observed species differences in growth might arise through at least four non-exclusive mechanisms. First, species may differ in optimal temperatures for feeding or growth. Many authors have reported that brook trout are usually found farther upstream, where the water is cooler, than are brown trout (Waters, 1983). This suggests that brook trout may be more cold tolerant, but Elliott (1981) found that brown trout have a slightly wider range of temperatures suitable for feeding (4–19° C) than do brook trout (8–20° C). In the study sites within the West Brook, the two species coexist in a zone of sympatry, suggesting that they should experience similar thermal conditions. Moreover, temperatures during the spring period, when most mass is gained, are well within the feeding range of both species (Fig. 1). Whether local adaptation

in thermal ecology (Jensen *et al.*, 2000) drives the observed growth differences between the two species remains to be tested.

Second, the two species may differ in aggression, which may drive differences in microhabitat use. Stream resident salmonids aggressively defend territories (Kalleberg, 1958) and some studies have shown that differences in aggression or dominance are related to growth rate (Fausch, 1984) although exceptions have been demonstrated (Vøllestad & Quinn, 2003). In the most relevant study, Fausch & White (1981) found that brown trout excluded equal-sized brook trout from advantageous stream positions, which should lead to a growth advantage for brown trout. Indeed, Fausch (1984) showed that juvenile salmonids quickly establish dominance hierarchies, and that individuals exhibiting the fastest growth were those holding the optimal positions (*i.e.* positions that provided 'maximum profit' in terms of energy expenditure and energy acquisition). Lower growth of brook trout than brown trout in the West Brook may thus reflect displacement of the former by the latter from optimal positions.

Third, differences in past growth might maintain or exacerbate differences in current growth. This positive feedback might occur because the ability of salmonids to defend preferred stream positions is a function of their body size. For example, Young (2004) found that the larger size of juvenile coho salmon *Oncorhynchus kisutch* (Walbaum) than juvenile steelhead trout *Oncorhynchus mykiss* (Walbaum) allowed the coho salmon to exclude the steelhead trout from mutually preferred habitat. For the West Brook, the growth of brown trout exceeded that of equal-aged brook trout during the spring, and the resulting size-asymmetry was maintained thereafter (Fig. 2). In fact, the two species continued to diverge in size, owing to continued faster growth by the brown trout. A similar pattern of increasing divergence in size has been documented for brook trout and rainbow trout (*O. mykiss*) (Whitworth & Strange, 1983). These size asymmetries probably give the larger fishes access to the most profitable stream positions, thereby enhancing their subsequent growth (Fausch, 1984). Of course, the invocation of past growth to explain current growth cannot explain how growth diverged in the first place.

Fourth, differences in the density of conspecifics and heterospecifics might influence growth rate differences. For instance, Byorth & Magee (1998) found that growth rates differed between Arctic grayling *Thymallus arcticus* (Pallas) and brook trout. The species exhibiting the higher growth rate, however, was also the species making up a lower proportion of the total biomass within a given enclosure. Intraspecific interactions thus seemed more important in determining growth than did interspecific interactions. The growth of brown trout is a negative function of conspecific density at densities similar to those observed in the present study (Jenkins *et al.*, 1999; Lobón-Cervía, 2007), and brown trout densities exceeded those of brook trout in the West Brook (Table I). It might therefore be expected that brown trout were more growth limited than brook trout, which was not the case. Perhaps growth differences might have been more pronounced if the densities of the two species were more equal, or perhaps, resource limitation is different for the two species; for example, brook trout use a resource that is less abundant and so a lower density still has greater effects.

POSSIBLE CONSEQUENCES OF GROWTH DIFFERENCES

The immediate consequence of disparate growth rates between ecologically similar species is a divergence in body size (Fig. 2). This size-structure probably minimizes direct overlap in resource use possibly facilitating their stable coexistence. To the degree that this is true, growth rates should often differ between native and non-native salmonids when they coexist (and, more generally, between coexisting stream resident salmonids). To test this prediction, results were compiled from previously published studies comparing the growth of native and non-native salmonids in natural streams, artificial stream enclosures or laboratory studies (Table III). In all but one comparison, growth differed between pairs of co-occurring native and non-native salmonids (10 of 11 studies; Table III). Interestingly, the growth of the non-native salmonid often exceeded that of the native salmonid (eight of 10 studies in Table III). Of course, the studies included in Table III represent cases where the non-native salmonid has established a self-sustaining population. Whether this result holds for cases of unsuccessful introductions or invasions remains unknown.

Together, these results suggest that sympatric native and non-native salmonids often differ in growth rate, suggesting that differences in growth may facilitate coexistence of ecologically similar species. This effect may occur for several reasons. First, differences in growth may reduce niche overlap and increase resource partitioning (Nyman, 1970). For instance, a size difference may lessen the degree of interference competition for preferred resting positions, because body size is often related to microhabitat choice (Fausch & White, 1981). Second, the expected fitness benefits of faster growth may be offset by equivalent fitness costs (Arendt, 1997; Blanckenhorn, 2000). For example, rapid growth can increase the risk of predation (Munch & Conover, 2003). Native and non-native salmonids may therefore achieve similar fitness despite differences in growth, which should facilitate their stable coexistence. Indeed, previous work in the West Brook has shown that equal-aged brook trout and brown trout survive at similar rates (Carlson & Letcher, 2003). Thus, despite the faster growth of brown trout, their survival rates do not exceed those of equal-aged brook trout suggesting that growth rate is not the only factor determining success in this system. Future work designed to elucidate the causes of mortality are necessary to understand how brook trout survive at similar rates as brown trout despite their relatively slower growth.

In the present study, growth often differed between native trout and the non-native trout, and the differences in growth were concentrated during the spring and early summer when overall growth was most rapid. Differences in growth during periods when the opportunity for growth is high can lead to sustained size differences, which presumably reduces niche overlap, increases the partitioning of available resources, and in so doing creates favourable conditions for coexistence. Interestingly, it appears that the growth rates of non-native salmonids often exceed those of native salmonids when they occur in sympatry. Future work is necessary to test whether these growth differences are a cause or consequence of coexistence.

TABLE III. Growth comparisons between co-occurring native and non-native salmonids

Author	Growth advantage		Setting	Conclusion
	Native species	v. Non-native species		
Whitworth & Strange (1983)	Brook trout (BKT)	≤ Rainbow trout (RBT)	Natural stream	Growth rates of BKT and RBT were equal until the spring of their second year of life when RBT grew faster than BKT and then maintained the size-at-age difference throughout the duration of the study
Fausch & White (1986)*	Brook trout	< Coho salmon	Natural stream	Age 0 year coho salmon were larger than BKT during the summer (but emerged earlier and larger)
Rose (1986)	Brook trout	= Brown trout (BNT)	Natural stream	Age 0 year brook and brown trout emerged at a similar size and had similar growth rates during their first summer
Beall <i>et al.</i> (1989)	Brook trout	< Rainbow trout	Natural stream	Growth of age 0 year BKT decreased after emergence of RBT
Héland & Beall (1997)	Atlantic salmon (ATS)	< Coho salmon	Stream enclosures	Growth of age 0 year ATS was reduced in sympatric treatments relative to allopatric treatments
Byorth & Magee (1998)	Atlantic salmon	< Coho salmon	Stream enclosures	Age 0 coho year (between the ages of 3 and 6 months) were larger than ATS. Growth of ATS was inversely related to coho densities
	Arctic grayling (ARG)	? Brook trout	Stream enclosures	Result depended on density of conspecifics but not heterospecifics (<i>e.g.</i> ARG grew faster when their densities were low irrespective of BKT densities, a similar result was obtained for BKT)

TABLE III. Continued

Author	Growth advantage		Setting	Conclusion
	Native species	v. Non-native species		
Magoulick & Wilzbach (1998)	Brook trout	> Rainbow trout	Laboratory stream channels	Juvenile BKT growth exceeded that of RBT at both 13 and 18° C
DeWald & Wilzbach (1992)	Brook trout	< Brown trout	Laboratory stream channels	BNT growth exceeded BKT growth when held together at 14° C; neither species gained mass in single-species trials indicating they may have been stressed
Isely & Kempton (2000)	Brook trout	< Rainbow trout	Laboratory raceways	Young-of-the-year (YOY) hatchery produced RBT growth exceeded that of YOY hatchery produced BKT when held in sympatry (but BKT growth > RBT growth when held alone)
Gunckel <i>et al.</i> (2002)	Bull trout (BLT)	< Brook trout	Stream enclosures	In mixed species treatments, BKT were more aggressive and grew significantly faster than BLT

*Fausch & White (1986) also conducted comparisons of growth in controlled laboratory situations but both brook and brown trout grew poorly confounding interpretations of growth comparisons between the species.

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