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Cohort strength and body size in co-occurring salmonids in a small stream network: variation in space and time

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Abstract: Trout and salmon commonly coexist in stream networks. Exploring similarities and differences among species can help explain coexistence and invasive ability. Here, we describe spatial distribution, cohort strengths and size-at-age of three co-occurring species in a small stream network. Spatial distributions varied dramatically among species; native brook trout (*Salvellinus fontinalis*) occupied all stream reaches, naturalized brown trout (*Salmo trutta*) were found in the mainstem and lower portions of tributaries and fry-stocked Atlantic salmon (*Salmo salar*) were limited to the mainstem. Size-at-age also differed among species, Atlantic salmon were consistently the smallest, brook trout were intermediate in size and brown trout were the largest. Despite size differences, mean lengths of brook trout and brown trout were highly correlated among years. Cohort strengths varied considerably across years but were also highly correlated for the two trout species, suggesting strong environmental control on cohort strength and a reduced role for species interactions. At low densities, we observed strong negative effects of density on body sizes and weaker effects otherwise. Overall, these results suggest differences in spatial distribution combined with similarities in response to environmental variation contribute to species coexistence in this small steam network.

Résumé : Des truites et saumons coexistent souvent dans des réseaux hydrographiques. L'examen des similitudes et différences entre espèces peut aider à expliquer cette coexistence et la capacité d'envahissement. Nous décrivons la répartition dans l'espace, la force des cohortes et la taille selon l'âge de trois espèces coexistant dans un petit réseau hydrographique. Les répartitions spatiales présentent des variations considérables entre espèces; les ombles de fontaine (*Salvellinus fontinalis*) indigènes occupent tous les tronçons, les truites brunes (*Salmo trutta*) naturalisées sont observées dans le cours d'eau principal et les cours inférieurs d'affluents et les saumons atlantiques (*Salmo salar*) ensemencés en tant qu'alevins se limitent au cours d'eau principal. La taille selon l'âge varie également d'une espèce à l'autre, la taille des saumons atlantiques étant uniformément plus petite, les ombles de fontaine étant de taille intermédiaire et les truites brunes présentant les plus grandes tailles. Malgré les différences de taille, les longueurs moyennes des ombles de fontaine et des truites brunes sont fortement corrélées au sein d'une même année. La force des cohortes varie considérablement d'une année à l'autre, mais est aussi fortement corrélée pour les deux espèces de truites, ce qui indiquerait que les conditions environnementales exercent un grand contrôle sur la force des cohortes et que les interactions des espèces jouent un rôle mineur. Nous observons de forts effets négatifs de la densité sur la taille du corps à de faibles densités, mais des effets plus faibles par ailleurs. Globalement, ces résultats indiqueraient que des différences sur le plan de la répartition spatiale combinées à des similitudes des réactions aux variations de conditions environnementales jouent un rôle dans la coexistence d'espèces dans ce petit réseau hydrographique. [Traduit par la Rédaction]

Introduction

Species responses to both extrinsic (environmental) and intrinsic (population dynamics) factors are key to understanding patterns of distribution and abundance. Co-occurring species frequently exhibit differences in habitat use across multiple spatial scales (Leibold and Tessier 1991). These differences can reduce the likelihood and intensity of negative interspecific interactions (Gotelli et al. 2010) and may contribute to long-term coexistence. When species show considerable overlap in spatial distribution and directly interact, differences in demographic responses to environmental variation are key to coexistence (Siepielski and McPeek 2010). This is a particularly important consideration for the many species that exhibit high annual variation in recruitment and cohort strength (relative abundance of a cohort). Cohort strength can often be directly attributed to environmental effects and may also influence age-structure and density-dependent population dynamics. Theory suggests that spatial and temporal variation in the availability of recruits can result in species coexistence in the absence of any intrinsic interspecific differences in habitat or resource use (Hubbell 2001; Leibold and McPeek 2006). Results of empirical studies have been mixed, however, and generally confined to relatively few systems (see Chave 2004 for a review). For stream fishes, the relative importance of

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species interactions vs. demographic and environmental variability in structuring assemblages has been a long-standing debate. A substantial body of literature suggests that the highly dynamic nature of stream habitats may reduce the likelihood of competitive exclusion and predictable niche differentiation (Grossman et al. 1982; Jackson et al. 2001). In contrast to this view, where patterns of species co-occurrence are largely determined by historical and stochastic factors and species-specific responses to habitats and disturbance regimes, others have suggested that stream fish species occupy distinct niches resulting in predictable and stable assemblage structure (Yant et al. 1984), with implications for species interactions and vulnerability to invasion from non-native species (Gido et al. 2004).

Stream salmonids (trout, salmon and their relatives) provide a good model for studying the factors involved in species persistence, co-occurrence and coexistence. Many co-occurring species show distinct and consistent patterns in spatial distribution at a range of scales (Armstrong et al. 2003), which has been suggested to mediate long-term coexistence. Most species also exhibit strong annual variation in recruitment (Kanno et al. 2016), which often determines cohort strength (Lobon-Cervia 2007; Bassar et al. 2016). The resultant variation in population size has a strong influence on individual somatic growth rates (Kanno et al. 2015), which can translate into density-dependent effects on individual body size and population size structure (reviewed in Grant and Imre 2005). In addition to interannual variation, recruitment and cohort strength often vary considerably along stream networks (Vincenzi et al. 2012), with similar effects on body size and size structure. In theory, spatial and temporal variation in cohort strength and body size, given the strong effect of body size on the outcomes of both intra- and interspecific interactions (Young 2004), may foster species coexistence, but this issue has not been directly addressed in previous studies. Specifically, few studies have collected data at sufficient resolution and for adequate duration to follow multiple cohorts for more than one sympatric species across their entire life history.

Understanding the link between population dynamics and coexistence is critical for conservation and management of stream salmonid fishes. Across their entire range, salmonids and the ecosystems they are part of have experienced a very large number of invasions (as both sources and recipients of invaders) (Krueger and May 1991) and extirpations (Katz et al. 2013), along with an increasing number of restoration and reintroduction initiatives (Fraser 2008). Interspecific interactions (competition and predation) between co-occurring salmonid species (native, invasive, and reintroduced) are clearly important in many cases (Dewald and Wilzbach 1992), but we still have challenges in forecasting when these interactions will lead to coexistence or extirpation. For example, brown trout (*Salmo trutta*) have been introduced and are well established as wild populations in many, but not all locations across the native range of brook trout (*Salvelinus fontinalis*) in the northeastern and north-central United States (Krueger and May 1991). In some cases, brown trout appear to have replaced native brook trout (Waters 1983; Wagner et al. 2013) but in others, relatively long-term coexistence has been maintained (McKenna et al. 2013) or brown trout establishment has not been successful over the long term (Hoxmeier and Dieterman 2019). Conversely, in a small number of cases in Western Europe, brook trout have established and been associated with local extirpation of native brown trout (Korsu et al. 2007, 2010). We currently have limited understanding of the mechanisms underlying alternative outcomes for these two species, which will become increasingly relevant in a nonstationary and in some cases rapidly changing environment (Wenger et al. 2011; Hitt et al. 2017).

To begin to address the potential roles of differences in spatial distribution, recruitment variation, and body-size responses to variation in cohort strength, we used a long-term intensive study of nonmigratory sympatric populations of brook trout and brown trout, with migratory juvenile Atlantic salmon (*Salmo salar*) present during part of the study period, to answer four fundamental questions:

1. Do these species exhibit distinct and consistent patterns in spatial distribution across the stream network?
2. Are body sizes changing over time? Are changes similar across species and the stream network?
3. What is the extent of variation in cohort strength for these co-occurring species and to what extent is this variation correlated across time and space?
4. What is the effect of cohort strength variation on body size for each species, and does it differ in different parts of the stream network?

Materials and methods

Field site

The study area is a small stream network in western Massachusetts, United States, consisting of a mainstem and three tributaries (Fig. 1) embedded in mixed hardwood forest with a dense canopy and light farming and residential areas. The entire watershed is 27.4 km^2 and contains a municipal reservoir at river km 6.6. Watershed area below the reservoir is 11.8 km^2 and is 15.7 km^2 above the downstream end of the reservoir. The study was conducted in a section of the stream network below the reservoir which consisted of four catchments that ranged in area from <1 to 12.4 km^2 (Table 1). The largest catchment was the West Brook, a 3rd-order stream with an average width of 7.4 m with a total stream length of 10 km below the reservoir, of which we sampled 1273 m (15%; Table 1). The West Brook streambed is mainly cobbles with sporadic bedrock and boulders. Stream habitat consists of mostly riffles with occasional glides and pools. A small, but passable waterfall defined the bottom of the study area and a large (4 m) impassable waterfall was located 3.5 km downstream of the study area (Fig. 1). The upstream boundary of the study area was open and fish could freely pass in either direction.

Three 2nd order tributaries flowed into the West Brook study area (Fig. 1). Drainage areas of the tributaries ranged from 1.06–2.46 km^2 and stream lengths ranged from 1.7 to 3.3 km (Table 1). The smallest tributary, Open Small (average width = 2.0 m), was open to immigration from the West Brook but a perched culvert (prior to 2013) restricted access during very low and high stream flows. Access to the Open Large (average width = 3.4 m) tributary was unrestricted and a 2-m-tall waterfall blocked access to the Isolated Large (average width = 3.0 m) tributary. The study length for each tributary was approximately 300 m (Table 1). At the upstream end of the study areas, either small (Isolated Large, 1 m) or very tall (Open Small, Open Large, >4 m) waterfalls blocked upstream migration. There were no brook trout present above the waterfall in Open Small, but trout were present above the waterfalls in Open Large and Isolated Large, resulting in proportions of occupied habitat sampled in each tributary = 1 for Open Small, = 0.09 for Open Large and = 0.19 for Isolated Large (Table 1).

Temperature loggers placed at the bottom of the West Brook and each tributary recorded stream temperature every 15 min, and we used a flow extension model to relate observed water depths from a pressure transducer (at the bottom of the West Brook study area) and a stage-discharge relationship to a nearby United States Geological Survey (USGS) stream gage (see Letcher et al. 2015 for details). Although we do not use stream temperature and flow data in our modeling, we provide a brief overview here to characterize the study area. Average stream temperatures varied across seasons (spring = 10.1 °C, summer = 16.0 °C, autumn = 8.2 °C, winter = 1.6 °C) and were similar across tributaries and the West Brook in the autumn and winter, but Open Small was about

Fig. 1. Map of the study area in Massachusetts, USA. The mainstem (West Brook) and tributary watersheds are colour-shaded and the tagging study area is shown with black and white dashes. Impassible (squares) and passable (circles) waterfalls are indicated on the stream network (blue lines). The map was made using ArcMap v10.8.1 and datasets included the National Hydrography Dataset (US Geological Survey 2020*a*), the National Elevation Dataset (US Geological Survey 2020*b*) and the National Hydrography Dataset Plus High Resolution Dataset for flow lines (US Geological Survey 2018).

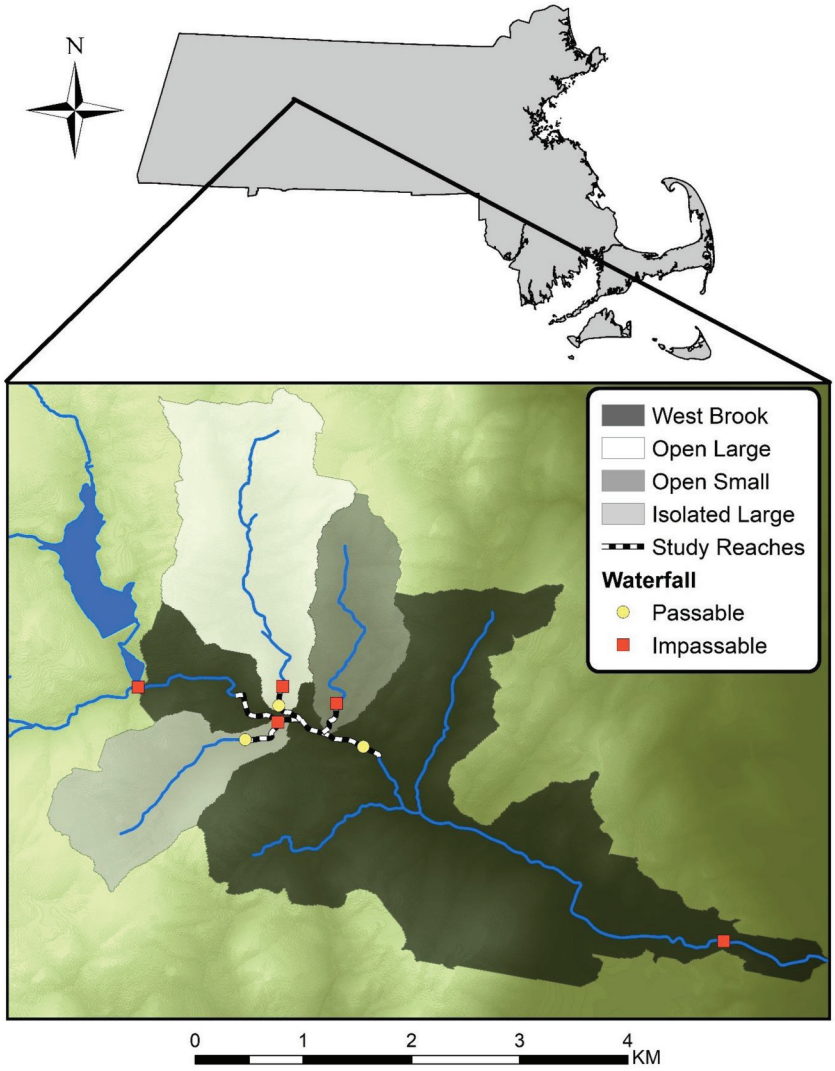


Table 1. Characteristics of the study area catchments and surrounding watershed (Fig. 1).

Catchment	Drainage area (km^2)	Average width (m)	Total steam length (km)	Proportion of steam length occupied by salmonids	Sampled study area stream length (m)	Proportion of occupied steam length sampled
West Brook	6.92	7.4	10.08	0.87	1273	0.15
Open Large	2.46	3.4	3.29	1.00	297	0.09
Open Small	1.06	2.0	2.00	0.16	320	1.00
Isolated Large	1.33	3.0	1.67	1.00	318	0.19

Note: West Brook drainage area and stream lengths are calculated from the mouth of the West Brook to the bottom of the reservoir and do not include the tributary areas or lengths.

1 degree warmer than the other tributaries in the spring and summer. Stream flow ($m^3 \cdot s^{-1}$) also varied across seasons (spring = 0.42 $m^3 \cdot s^{-1}$, summer = 0.12 $m^3 \cdot s^{-1}$, autumn = 0.24 $m^3 \cdot s^{-1}$, winter = 0.40 $m^3 \cdot s^{-1}$). All study locations contained naturally reproducing populations of brook trout, and West Brook, Open Large and Open Small (occasionally) contained naturally reproducing brown trout, which were introduced to the eastern US in the 1800s and are well established throughout the region. Both trout species spawned in the autumn (peak spawning for brook trout in October, with brown trout several weeks to a month later) and emerged in late winter – early spring. Atlantic salmon, which were native to the Connecticut River basin until their extirpation in the 1700s, were stocked as unfed fry (at yolk sac absorption) into the West Brook in spring from 1997 through 2004; juveniles were present in the system until 2007. Fry were part of the Connecticut River Atlantic salmon restoration program and were

obtained from the US Fish and Wildlife Service, White River hatchery (Bethel, Vermont). Details about Atlantic salmon stocking and life history can be found in Letcher and Gries (2003) and Sigourney et al. (2013). The only other fish species found consistently in the study area was blacknose dace (*Rhinichthys atratulus*), a common, native spring-spawning minnow, but densities were generally low and variable (West Brook: range 0–0.45 per m^2, mean = 0.068 per m^2; Open Small: range 0–0.25 per m^2, mean = 0.053 per m^2; Open Large: range 0–0.27 per m^2, mean = 0.053 per m^2; Isolated Large: mean = 0). Trout were not stocked in the study area and fishing pressure was very low.

Fish sampling

The study area was divided into 47, contiguous 20-m long sections in the West Brook and into 14 or 15 contiguous 20-m sections in the tributaries. Each section was sampled consecutively from downstream to upstream. Tributaries were typically sampled before the West Brook. Sampling in the West Brook consisted of isolating the study section with temporary block nets at the top and bottom of the section and conducting two-pass backpack electrofishing (300–400 V unpulsed DC). Owing to high capture rates in the tributaries (Letcher et al. 2015), we did not use block nets and conducted a single pass. Captured fish were anesthetized, measured for length (±1 mm, fork length), weighed (g, wet weight) and scanned for a tag. If no tag was present and the fish was >60 mm fork length and >2 g wet weight, the fish was tagged. We used 12-mm full-duplex passive integrated transponder (PIT) tags for individual fish identification (Biomark and then Digital Angel, St. Paul, Minnesota, USA). Tags were inserted through a thin abdominal slit made with a small scalpel (Gries and Letcher 2002). Tagging mortality was rare and tagging has minimal impact on fish growth and survival (Gries and Letcher 2002; Sigourney et al. 2005). Following recovery from anesthesia, fish were returned to the approximate center of the study section. All fish handling followed USGS, Eastern Ecological Science Center, Conte Research Laboratory Animal Care and Use guidelines. Although not reported here, we also took an anal fin clip sample for genetic analysis on first capture of each fish.

Sampling occurred four times per year, corresponding roughly with the winter and summer solstice, and spring and autumn equinox. Depending on the number of fish captured and weather, a sampling occasion took between seven and 12 sampling days. Longer sampling occasions typically resulted from floods causing unsafe and inefficient sampling conditions.

We defined cohort for each fish based on size at first capture and species-specific size distributions. Size distributions for age-0+ fish were typically distinct from distributions for the other age classes (Letcher et al. 2015), but there was substantial overlap in body size among ages for older fish. Most fish (62%) were captured as age-0+ fish, limiting cohort assignment error. Based on the cohort assignments, we estimated cohort strength as the total number of individual fish captured from each cohort for each species. Cohort strength was further subdivided by "metapopulation", which separated the Isolated Large population from the connected West Brook, Open Large, Open Small network. For analysis, we scaled cohort strengths by subtracting mean values and dividing by the standard deviation for each population and species. We also used cohort assignments to estimate age in days from age-0+ January 1, using day-of-year + 365 × (year − cohort). Fish older than age-3+ were excluded from analysis to avoid smaller sample sizes of older fish. Finally, observations were coded by the presence of Atlantic salmon in the stream network (1 for cohorts <2005 and in the West Brook, 0 otherwise).

Field data summary

We present data from 62 sampling occasions from 2000–2015. Ice accumulation prevented winter sampling in 2002 in all locations, and additionally in 2005, 2007, 2012 and 2015 in the West Brook. Sampling was also incomplete in the West Brook in 2003 (completed 30 of 47 sections) and in 2004 (completed three of 47 sections).

Overall, we captured and tagged 11 707 brook trout, 5955 brown trout and 4219 Atlantic salmon (all captured fish were tagged (see Letcher et al. 2015), but we only use tagging data here for cohort assignment). We captured these individuals multiple times for a total of 23 526 (brook trout) and 11 884 (brown trout) observations for body size modelling.

Data analysis

Our goal was to explore size-at-age for seasonal data and to relate a measure of cohort strength to trout body size data. We were also interested in whether size trajectories were changing over time. Growth rate in the system is highly seasonal (Letcher et al. 2015), resulting in nonlinear body size trajectories within a year. Sample dates are also somewhat inconsistent within a season across years, suggesting a single categorical descriptor for sample seasonal date would not capture the variation in sample dates across years. Finally, both the nonlinear size trajectories and potential for nonlinear effects of cohort strengths suggest the need for a flexible modeling approach. For these reasons, we chose to model the size trajectories using general additive models (Wood 2006) which, by using smoothed functions (splines), address the issues outlined above. The splines capture the nonlinear size trajectories (size-at-age) and effects on the body sizes. We also included non-smoothed, parametric (categorical) variables in the model.

Our model selection approach was to use AIC to first determine inclusion of the parametric variables and then the inclusion of the smoothed variables. We ran separate models for each trout species (brook, brown) because brown trout were not present in all study catchments. Parametric variables included catchment (West Brook, Open Large, Open Small, Isolated Large) and presence–absence of salmon. Smoothed variables included age in days (ageDays, the number of days since 1 January (age-0+)), ageDays grouped by cohort, ageDays grouped by catchment, ageDays grouped by catchment and cohort, cohort grouped by catchment, brook trout cohort strength grouped by metapopulation, and brown trout cohort strength grouped by metapopulation. We used the "bam" function in the R package mgcv (Wood 2017) for model fitting to accommodate the large sample sizes. For all smoothed variables, we used cubic regression spline as the basis function and set the maximum dimension of the splines to four for all variables except ageDays, which had a maximum dimension of 10.

In addition to the central model described above, we also explored drivers of body sizes for age-0+ fish in the autumn across trout species, cohort and catchment with a simple one-way ANOVA. This analysis helps us understand body size drivers before the fish are big enough to tag in the autumn. We used the R package relimpo to estimate proportion of body size variance explained by the independent variables. We explored spatial distribution of species by simply counting the number of observations in each study catchment.

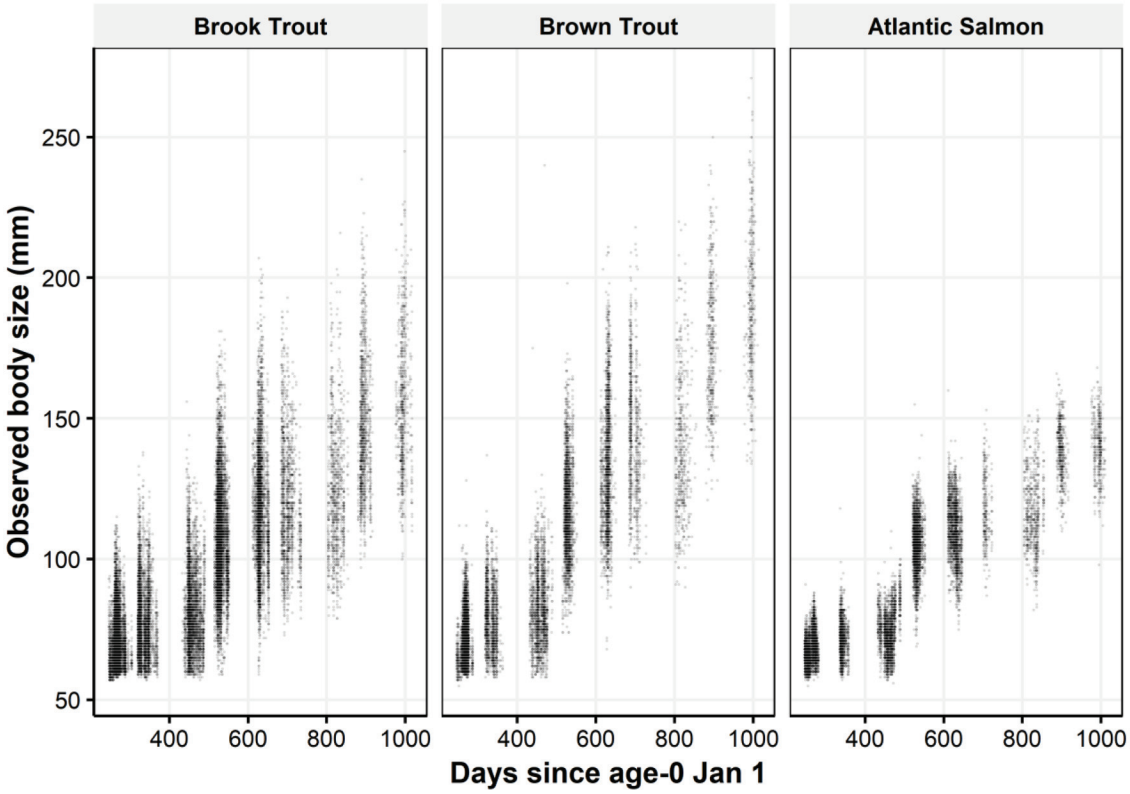
We tested for a relationship between brook trout and brown trout cohort strengths by running a simple linear regression with brown trout cohort strength as the dependent variable and brook trout cohort strength as the independent variable. We also tested for a relationship between brook trout cohort strengths in Isolated Large and the connected stream network with a similar regression.

Results

Body size

We observed wide body size distributions within each age–season combination, with increasing medians and ranges as fish aged (Fig. 2). Body sizes of Atlantic salmon were generally smaller than

Fig. 2. Observed lengths of individual fish as a function of age in days for three species of salmonids.



trout body sizes, and brook trout and brown trout body sizes overlapped substantially, except older brown trout tended to be larger than older brook trout (Fig. 2). For the first sampling occasion for each cohort, body size frequency distributions varied considerably across cohorts and catchments (Fig. 3), with 19.3% of the variation explained by cohort, 4.5% explained by catchment and 0.05% explained by species. Brook trout and brown trout mean lengths for the first sampling occasion for each cohort were positively correlated in the West Brook (Pearson correlation coefficient = 0.83) and Open Large (Pearson correlation coefficient = 0.59; refer to online Supplementary material, Fig. S1[1]). Correlation coefficients between brook trout and brown trout mean lengths for the remaining sampling occasions were consistently high in the West Brook (0.80–0.95, except for winter age-0+ = 0.6) and more variable in Open Large (−0.11–0.75; Supplementary Fig. S1[1]).

For both trout species, model selection for the fixed effects "catchment" and "presence of salmon" yielded delta AICs of >500 for additive models with both variables (results not shown), so these variables were retained for all subsequent model selection. Model selection for the spline model variables was also consistent between species, the model with all spline variables had the lowest AIC values (Table 2). The models explained 79.5% of the variation in brook trout and 87.9% of the variation in brown trout body sizes. QQ plots of residuals, histograms of residuals and observed vs. predicted observations all suggested that the model fit the data well (Supplementary Figs. S2, S3[1]), although body sizes of very small and very large fish were predicted less well than intermediate body sizes.

Spatial distribution

The three species were not evenly distributed across the stream network. Brook trout were observed in the mainstem and all three tributaries, brown trout were observed in the mainstem and the Open Large (occasional observations in Open Small) tributary and Atlantic salmon were observed primarily in the mainstem (occasional observations in Open Large; Fig. 4).

Fixed effect parameter estimates (Table 3) indicated that fish were on average 13 to 23 mm smaller in the tributaries compared to the mainstem and that fish were 7 (brook trout) or 9 (brown trout) mm larger early in the study when Atlantic salmon were present. Many of the spline variables were highly significant (Table 4). Notable exceptions include some "age in days × cohort" interactions for both species and the intraspecific effect of brown trout in the West Brook.

Predicted body sizes based on the selected model demonstrate highly seasonal patterns with most growth in the spring–early summer, a trend towards larger sizes for later cohorts and generally larger sizes in the West Brook compared to the tributaries (Fig. 5). Plotting the main effects of "cohort" for each species and catchment (Fig. 6) identified generally increasing body sizes, with increases of about 30 mm for both species in the West Brook and smaller increases (10–20 mm) in the tributaries.

Comparing predicted size trajectories among study catchments indicated that brook trout in West Brook were consistently largest over time, followed by Open Small, Isolated Large, and Open Large (Fig. 7). Brown trout in West Brook were slightly larger than brown trout in Open Large (Fig. 7). Sizes were similar among tributaries when brook trout were young and old but diverged in between (Fig. 7). Comparing predicted body sizes between species suggested that brook trout and brown trout sizes were similar when fish were young, but diverged for older fish in West Brook (Fig. 8). In contrast, brown trout in Open Large were consistently larger than brook trout in Open Large, with differences as great as about 25 mm (Fig. 8).

[1]Supplementary data are available with the article at https://doi.org/10.1139/cjfas-2020-0418.

Fig. 3. Frequency distributions for cohort-specific body sizes of fish at first possible capture (age-0+, autumn). Minimum length of collected fish was 60 mm. Cohorts (2000–2012) are indicated by shading (darker = earlier, lighter = later).

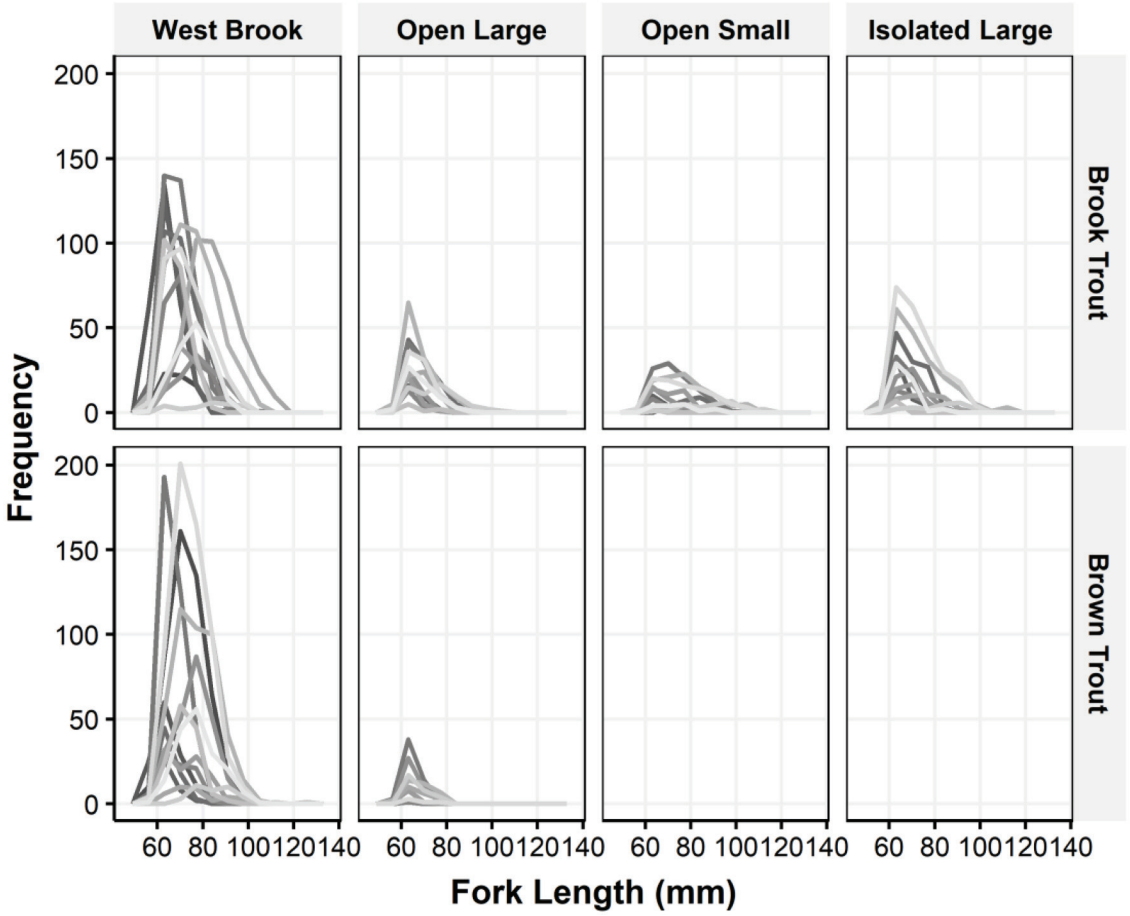
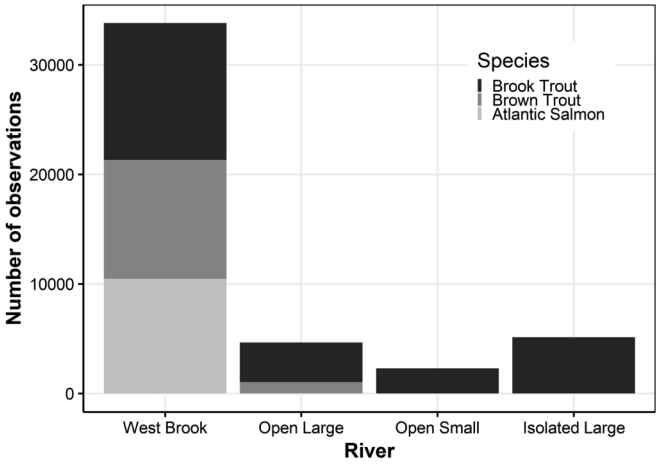


Table 2. Model selection table for the two species.

Age in days	Age in days by cohort	Age in days by catchment	Age in days by cohort and catchment	Cohort by catchment	Brook trout cohort strength by catchment	Brown trout cohort strength by catchment	df	AIC	ΔAIC
Brook trout									
x	x	x	x	x	x	x	153.9	188 634	—
x	x	x		x	x	x	92.2	189 181	547
x	x	x		x	x		82.0	189 329	696
x	x	x		x			72.0	191 540	2 907
x	x	x					55.6	193 270	4 636
x	x						48.4	194 682	6 048
x							15.0	196 672	8 038
							6.0	225 245	36 612
Brown trout									
x	x	x	x	x	x	x	84.5	94 948	—
x	x	x		x	x	x	69.5	95 022	74
x	x	x		x	x		63.3	95 076	128
x	x	x		x			57.4	95 681	733
x	x	x					50.4	96 400	1 451
x	x						45.1	96 512	1 563
x							13.0	98 180	3 232
							4.0	119 776	24 827

Note: All models include the fixed effects "catchment" and "presence of salmon".

Fig. 4. Number of individual observations by catchment for each species.



Cohort strength

Cohort strength varied considerably among cohorts with some consistent patterns among species and between brook trout populations (Fig. 9). Brook trout and brown trout cohort strengths were positively related (P value = 0.006, r = 0.71, slope = 0.75; Fig. 10, top panel). Brook trout cohort strengths in the two metapopulations were also positively related (P value = 0.002, r = 0.82, slope = 0.75; Fig. 10, bottom panel). We found no evidence for a relationship between cohort strength and body size of age-0+ autumn fish (Supplementary Fig. S2[1], but see below for cohort strength effects on size-at-age curves).

Effect of cohort strength on body size

Brook trout cohort strength had a negative effect on body size in most cases, with effect sizes of about 20 mm for both species in the West Brook, variable effects in Open Large (equivocal for brook trout, strongly positive for brown trout), and strongly negative effects at low cohort strengths for brook trout in Open Small and Isolated Large (Fig. 11). Brown trout cohort strength was related to decreased brook trout body sizes and had no effect on brown trout sizes in the West Brook, and, conversely, had a weak negative effect on brook trout sizes and a strongly negative effect on brown trout sizes in Open Large (Fig. 12).

Discussion

In this detailed long-term study encompassing annual and seasonal dynamics we observed distinct patterns in key aspects of spatial distribution, cohort strength, and body size of three co-occurring species of salmonid fishes within a small stream network. Brook trout were broadly distributed throughout the entire network including isolated tributary locations, juvenile Atlantic salmon were restricted to the mainstem, and brown trout occurred in the mainstem and in the large tributary with unrestricted access. Mean size-at-age also differed consistently between the three species (brown trout > brook trout > juvenile Atlantic salmon). However, the two trout species exhibited very similar and correlated patterns of annual variation in cohort strength, showed similar relationships between cohort strength and individual body size (clear increases in body size at low cohort strength, weaker evidence for decreases in strong cohorts, except for the effect of brook trout on brown trout sizes in the tributary), and were consistently larger at age in mainstem vs. tributary locations. Our results are consistent with spatial segregation between mainstem and tributaries as a potential mechanism allowing coexistence of salmonid species in small streams

Table 3. Fixed effect parameter estimates for both species.

Species	Parameter	Estimate	SE	t value	P value
Brook trout	Intercept	104.91	1.55	67.89	<2E-16
	Catchment: OL	−13.68	1.89	−7.25	4.26E-13
	Catchment: OS	−22.86	5.91	−3.87	0.000111
	Catchment: IL	−13.01	1.61	−8.09	6.2E-16
	Salmon presence	6.53	0.94	6.96	3.5E-12
Brown trout	Intercept	103.05	0.52	198.11	<2E-16
	Catchment: OL	−18.13	3.00	−6.04	1.62E-09
	Salmon presence	9.20	1.21	7.59	3.53E-14

Note: The intercept contained the mainstem (West Brook) and salmon presence = 0. Catchment estimates indicate average deviations from mainstem sizes. OL, Open Large; OS, Open Small; IL, Isolated Large.

(Korsu et al. 2007). In contrast, while density-dependent effects observed for both trout species may contribute to population resilience, our data were likely insufficient to distinguish intra- vs. interspecific effects of density and cohort strength on individual body size. We conclude that although in many respects, there may be substantial overlap in the ecological roles and responses of brook trout and brown trout in small streams, the ability of both species to recover from low densities and weak cohorts, combined with some degree of spatial segregation at the network scale, may prevent species replacement, at least in the near term. Applying the analytical framework we have developed over longer time series across multiple study systems, potentially coupled with manipulative approaches is likely necessary to elucidate the factors fostering long-term population persistence and species coexistence.

Longitudinal zonation of fish species assemblages is a fundamental characteristic of streams and rivers. This has been observed for stream salmonids in a wide range of studies (Bozek and Hubert 1992; De La Hoz Franco and Budy 2005; Korsu et al. 2007). As found previously, the two trout species were distributed further upstream and in smaller tributaries than salmon (De La Hoz Franco and Budy 2005), likely associated with both habit requirements and in some cases restrictions on upstream movement and possibly stocking location (mainstem only). This segregation, along with the potential differences in microhabitat use (Armstrong et al. 2003; Nislow et al. 2010), likely reduces local spatial overlap and direct interaction between juvenile Atlantic salmon and either brook or brown trout in this system. This spatial segregation is also consistent with our failure to detect any compensatory response to the loss of Atlantic salmon from the system (small, positive effect of Atlantic salmon presence in the models), even though juvenile Atlantic salmon accounted for over half the total salmonid biomass in the first five years of the study. Brook trout and brown trout regularly used tributaries over the course of the study, but this was much more common for brook trout, where nearly half of all individual observations occurred in tributaries, compared to less than 10% for brown trout. Preferential upstream distribution of brook trout relative to other salmonids (including brown trout) has been previously demonstrated in a number of other studies (Bozek and Hubert 1992; Korsu et al. 2007; Öhlund et al. 2008). However much of this work has been at larger spatial scales and encompasses substantial differences in fundamental habitat characteristics such as water temperature, acidity, forest cover, and slope–elevation. Differential distribution of brook and brown trout in our study is not associated with major differences in these factors. It is unclear whether the patterns we observed are due to intrinsically poorer performance of brown trout and (or) superior performance of brook trout in small tributaries, but these differences may help mediate long-term coexistence in our study system and perhaps more generally.

In addition to distinct patterns of longitudinal distribution, the three species also showed consistent differences in size-at-

Table 4. Estimated degrees of freedom (edf), degrees of freedom (df), *F* values and *P* values for the spline effects.

Effect	edf	df	*F*	*P*	
Brook trout					
Age in days	7.95	8.00	502.74	**<2E-16**	***
Age in days × cohort 2000	0.89	0.98	0.05	8.18E-01	
Age in days × cohort 2001	1.98	2.00	3.76	**2.16E-02**	*
Age in days × cohort 2002	2.84	2.94	7.77	**5.83E-04**	***
Age in days × cohort 2003	1.00	1.01	0.13	7.17E-01	
Age in days × cohort 2004	2.60	2.86	10.81	**1.18E-06**	***
Age in days × cohort 2005	1.01	1.01	8.67	**3.14E-03**	**
Age in days × cohort 2006	2.88	2.98	14.56	**1.33E-09**	***
Age in days × cohort 2007	1.01	1.02	3.64	5.51E-02	
Age in days × cohort 2008	2.96	3.00	24.96	**6.92E-16**	***
Age in days × cohort 2009	2.98	3.00	44.36	**<2E-16**	***
Age in days × cohort 2010	2.94	2.99	19.63	**1.71E-12**	***
Age in days × cohort 2011	1.83	1.95	19.17	**1.20E-07**	***
Age in days × cohort 2012	1.00	1.00	0.00	9.92E-01	
Age in days × cohort 2013	1.00	1.01	0.00	9.52E-01	
Age in days × catchment WB	1.01	1.01	274.37	**<2E-16**	***
Age in days × catchment OL	2.56	2.82	15.83	**1.80E-08**	***
Age in days × catchment OS	1.01	1.02	40.88	**1.34E-10**	***
Age in days × catchment IL	2.84	2.95	39.50	**<2E-16**	***
Cohort × catchment WB	2.99	3.00	238.95	**<2E-16**	***
Cohort × catchment OL	2.79	2.95	85.52	**<2E-16**	***
Cohort × catchment OS	2.95	3.00	184.56	**<2E-16**	***
Cohort × catchment IL	2.17	2.58	14.59	**2.08E-08**	***
Cohort strength brook trout × catchment WB	2.99	3.00	217.52	**<2E-16**	***
Cohort strength brook trout × catchment OL	2.99	3.00	73.17	**<2E-16**	***
Cohort strength brook trout × catchment OS	2.98	3.00	50.05	**<2E-16**	***
Cohort strength brook trout × catchment IL	2.95	2.99	158.51	**<2E-16**	***
Cohort strength brown trout × catchment WB	2.38	2.64	38.24	**9.69E-10**	***
Cohort strength brown trout × catchment OS	2.88	2.98	25.17	**4.11E-15**	***
Brown trout					
Age in days	7.94	8.00	436.58	**<2E-16**	***
Age in days × cohort 2000	0.95	0.99	0.02	9.00E-01	
Age in days × cohort 2001	0.01	0.02	0.03	9.84E-01	
Age in days × cohort 2002	0.01	0.01	0.12	9.71E-01	
Age in days × cohort 2003	2.59	2.86	2.14	5.89E-02	
Age in days × cohort 2004	1.01	1.02	0.87	3.52E-01	
Age in days × cohort 2005	1.01	1.03	0.09	7.66E-01	
Age in days × cohort 2006	2.26	2.58	1.09	3.48E-01	
Age in days × cohort 2007	2.84	2.97	4.38	**3.38E-03**	**
Age in days × cohort 2008	2.49	2.76	3.92	**8.45E-03**	**
Age in days × cohort 2009	1.02	1.03	0.62	4.35E-01	
Age in days × cohort 2010	2.97	3.00	28.05	**<2E-16**	***
Age in days × cohort 2011	2.90	2.99	9.09	**1.31E-05**	***
Age in days × cohort 2012	1.01	1.01	0.05	8.31E-01	
Age in days × cohort 2013	1.02	1.03	1.89	1.68E-01	
Age in days × catchment WB	1.00	1.00	32.35	**1.31E-08**	***
Age in days × catchment OL	1.99	2.35	21.47	**5.75E-11**	***
Cohort × catchment WB	2.98	3.00	237.10	**<2E-16**	***
Cohort × catchment OL	2.84	2.95	37.07	**<2E-16**	***
Cohort strength brook trout × catchment WB	2.89	2.99	155.62	**<2E-16**	***
Cohort strength brook trout × catchment OL	1.66	1.91	24.50	**6.10E-11**	***
Cohort strength brown trout × catchment WB	1.86	2.10	1.08	2.75E-01	
Cohort strength brown trout × catchment OL	2.23	2.48	25.79	**1.71E-13**	***

Note: The large number of cohort × catchment interactions were omitted for brevity. *P* values < 0.05 are in bold and number of asterisks indicate relative strength of the *P* values. Catchment abbreviations: WB = West Brook, OS = Open Small, OL = Open Large, IL = Isolated Large.

age with brown trout largest and Atlantic salmon smallest in age-specific body length. Based on our size-at-age modeling, we observed that brook trout were slightly longer than brown trout in their first year, but that brown trout surpassed brook trout with faster age-1+ and age-2+ growth in spring resulting in a ~15% size advantage for brown trout by age-2+ summer in the West Brook and a ~30% size advantage in the large tributary. This switching of size rank of the two species over time contrasts with the intraspecific maintenance of size rank observed for brook trout in our study system (Letcher et al. 2011) and suggests some

Fig. 5. Predicted sizes for cohorts (lines), catchments (columns) and species (rows). Dashed vertical lines represent 1 January.

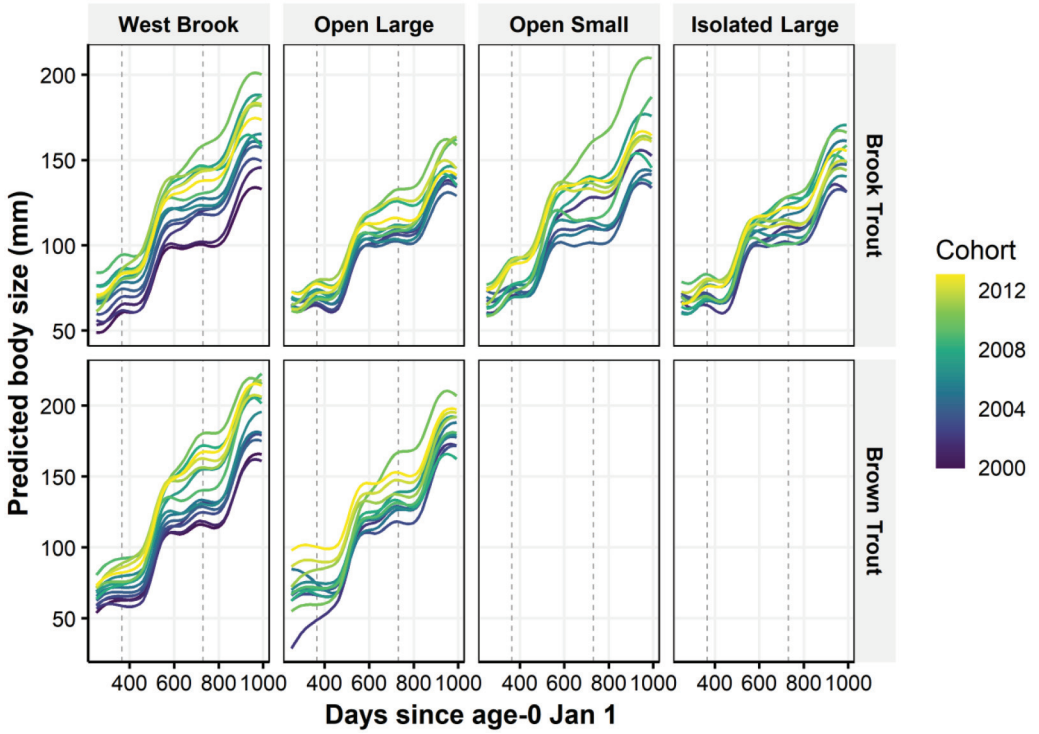
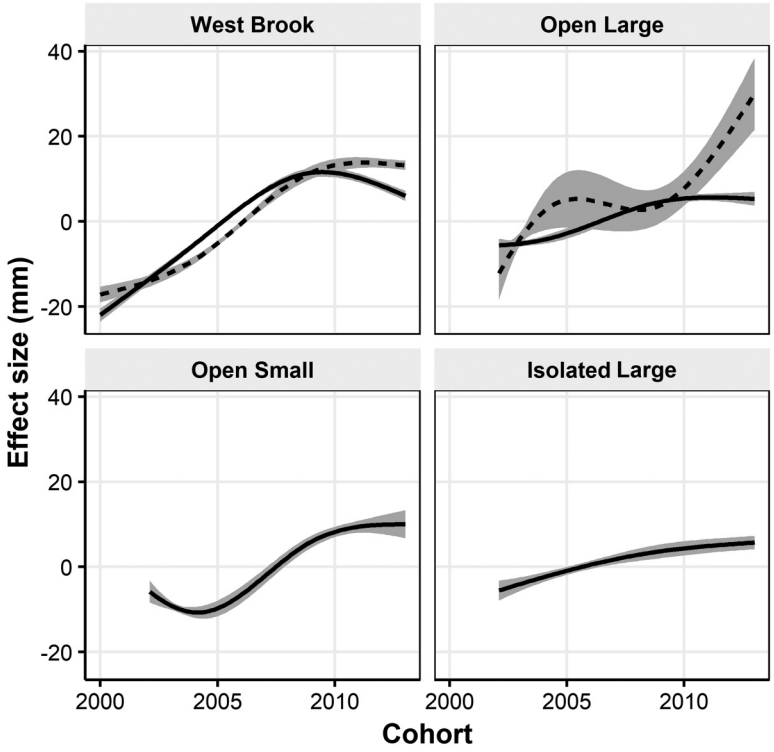


Fig. 6. Cohort main effects on size-at-age curves for each catchment (panels) and species (brook trout: solid line, brown trout: dashed line). Grey shading around lines represents 95% confidence intervals.



intrinsic potential differences between the species. The early size advantage for brook trout could stem from earlier brook trout spawning and emergence (Witzel and Maccrimmon 1983; Essington et al. 1998). The later size advantage for brown trout is consistent with laboratory (Dewald and Wilzbach 1992; Hitt et al. 2017), enclosure (Korsu et al. 2009) and field (Cooper 1953; Zorn and Nuhfer 2007; Öhlund et al. 2008; Hoxmeier and Dieterman 2013) observations that superior brown trout competitive ability can lead to

Fig. 7. Predicted body sizes across catchments (line colours) and species (rows). Predictions are for the 2006 cohort and values of salmon presence–absence, and brook trout and brown trout cohort strengths were set to 0.

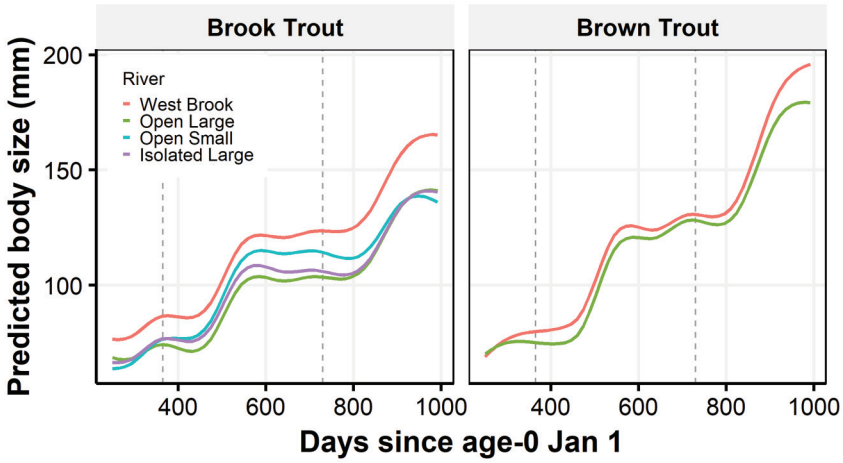
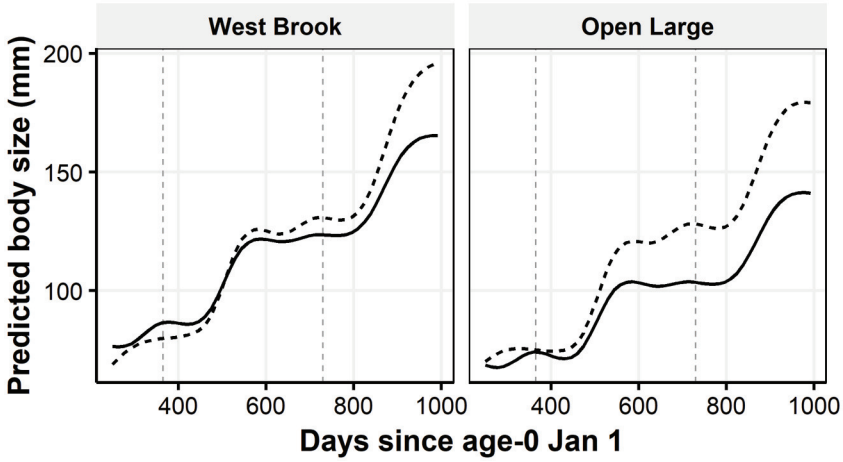


Fig. 8. Predicted body sizes for brook trout (solid lines) and brown trout (dashed lines) and catchments (panels) where the species coexist. Predictions are for the 2006 cohort and values of salmon presence–absence, and brook trout and brown trout cohort strengths were set to 0.

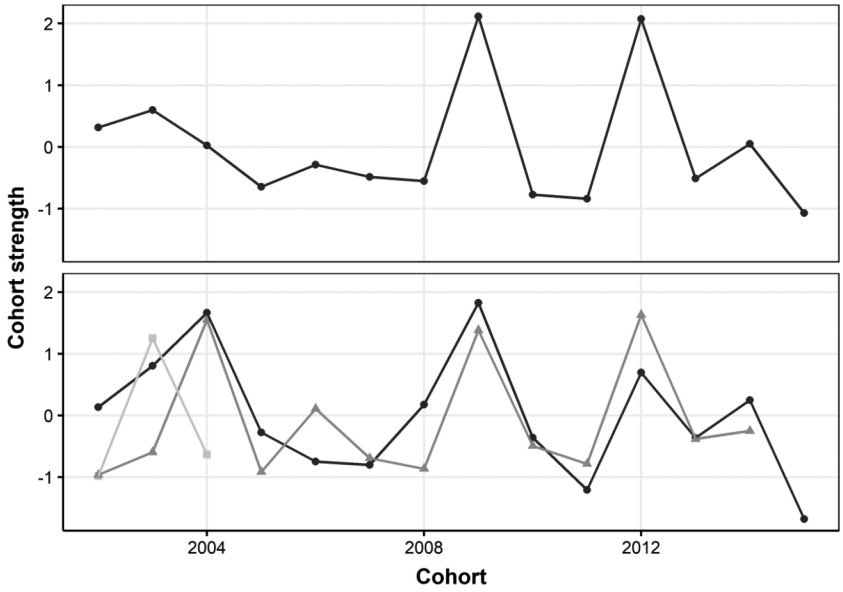


larger body size. It is also possible that the higher temperature for maximum growth of brown trout compared with brook trout (Childress and Letcher 2017) could lead to larger sizes as stream temperatures increase. In addition, competitive ability can reinforce size differences, as competitively dominant individuals have been shown to monopolize favorable foraging locations and access to shelters (Harwood et al. 2003). Consistent with this perspective, the larger body size differential between the species we observed in the tributary compared to the mainstem suggests that brown trout may have dominated the advantageous feeding sites that are likely at a premium in the smaller tributary. Finally, the suggestion that brown trout competition limited brook trout body size in the large tributary is reinforced by the observation that brook trout in the smaller tributaries without brown trout were larger than brook trout in the large tributary that contained brown trout.

In contrast to consistent differences in spatial distribution and size-at-age for the three species, cohort strength of brook trout and brown trout was highly correlated. This pattern was driven by interannual variation in recruitment (as measured by population size in the September age-0 sample), with the same years producing either high recruitment or low recruitment for both trout species. Population size and cohort strength in stream salmonids has been observed to be recruitment-dependent in a number of species, often determined within the first months after emergence from their redds (Elliott 1994; Armstrong and Nislow 2006; Kanno et al. 2016). In our study system and over most of their geographical range, both brown trout and brook trout spawn in autumn and emerge in spring (Witzel and Maccrimmon 1983; Essington et al. 1998) and are therefore subject to similar environments during the first few months of life. Previous studies have suggested that environmental conditions during this period can drive variation in cohort strength. In particular, high flow events during winter and spring (and in southern European populations of brown trout, low flows during summer) appear to result in low recruitment and weak cohorts for both brook (Kanno et al. 2015; Blum et al. 2018) and brown trout (Spina 2001; Nicola et al. 2009). In addition, neither brook trout nor brown trout cohort strength was influenced by the presence of juvenile Atlantic salmon, despite the large proportion of salmonid biomass accounted for by Atlantic salmon when they were present. Our results are therefore consistent with a common density-independent early life mechanism similarly affecting abundance of both trout species.

In addition to correlated variation in cohort strength, we observed correlated patterns of seasonal, interannual, and among-cohort variation in individual body size and size-at-age. Brook trout, brown trout

Fig. 9. Scaled cohort strength across cohorts, for Isolated Large (top panel) and the metapopulation (West Brook, Open Large, Open Small). Lines and symbols depict species (brook trout: black circles, brown trout: grey triangles, Atlantic salmon: light grey squares).



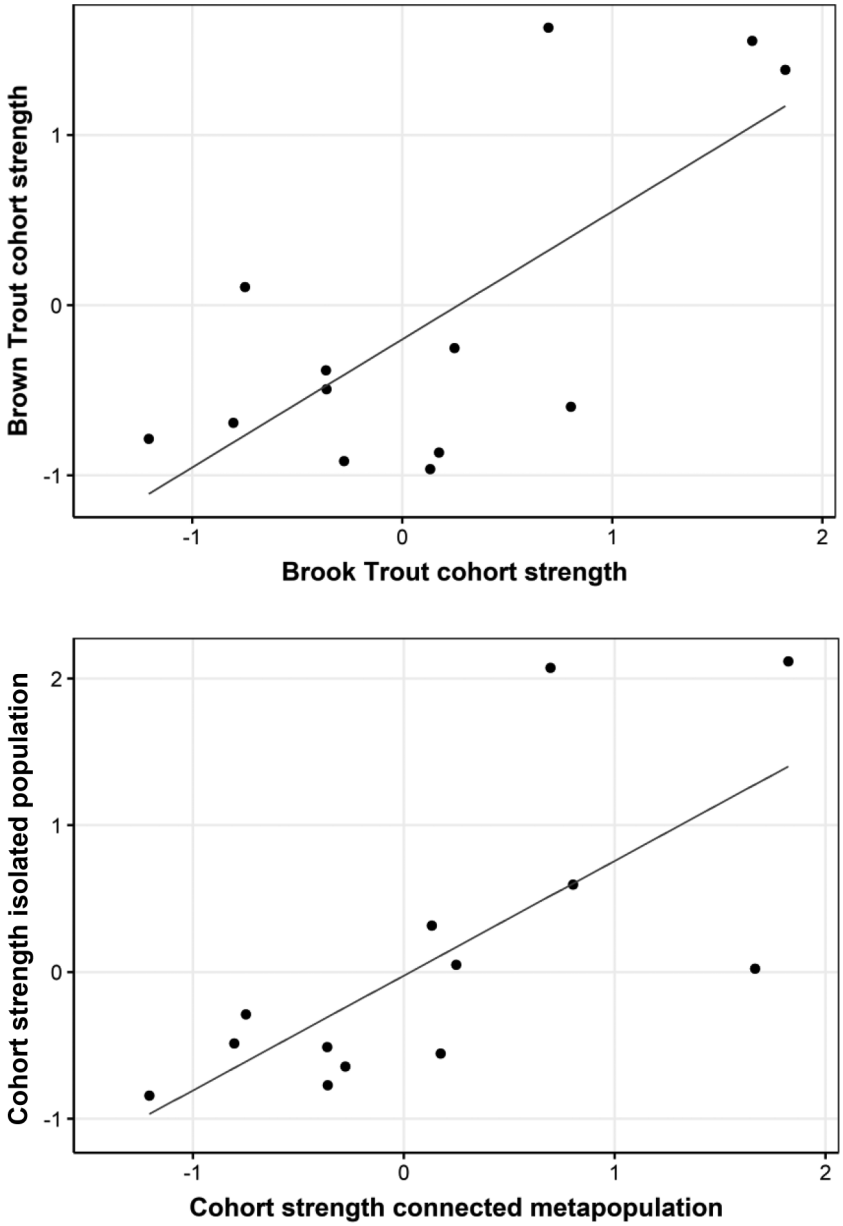
and Atlantic salmon all exhibited maximum increases in individual body size during the spring and early summer. Other studies with sufficiently frequent sampling have also demonstrated strong seasonal growth in both brook trout (Cooper 1953, 1961; Whitworth and Strange 1983; Utz and Hartman 2009) and brown trout (Beyerle and Cooper 1960; Egglishaw and Shackley 1977; Mortensen 1982). Although the extent and specific timing of seasonal growth varies among studies, all found that growth in spring and early summer was faster than growth in other seasons and that rapid growth can even be constrained to just two months of the year (Cooper 1961; Utz and Hartman 2009). Slower summer growth, often despite stream temperatures near growth optima, suggests that summer food limitation or seasonal behavioral changes limit summer growth. In the West Brook, food availability changes dramatically over the year, with relatively high densities of drifting invertebrates in the spring (Grader and Letcher 2006), and lower densities in the summer and winter, a pattern observed in other studies (Sweka and Hartman 2008; Wagner et al. 2014), particularly in streams draining woodlands dominated by deciduous vegetation. Associated with high growth rates, all three species of salmonids in the West Brook feed mainly on aquatic-derived drifting invertebrates in the spring, suggesting a lack of resource limitation during this season. In the summer as the availability of these prey resources decrease, brook trout, and to a lesser degree brown trout shift their foraging to terrestrial-derived surface drift, a diet shift observed in several other studies (Sweka and Hartman 2008; Wagner et al. 2014). It also appears that brook trout may generally adopt a low-risk, low energy use strategy as flows decrease seasonally in small streams (Sotiropoulos et al. 2006), suggesting that a combination of low prey availability, low stream flows and behavioral choices limit growth in summer and autumn. Further, it has been shown that salmonids become more risk averse as they get older and closer to reproductive age (Reinhardt and Healey 1999). This general principle is consistent with seasonality of growth being most pronounced for age-1+ and older stream salmonids, while age-0+ fish often show relatively high growth rates in summer and autumn (Cooper 1961; Mortensen 1982; Letcher et al. 2015).

In common with many other studies (e.g., McFadden 1961; Petty et al. 2005; Hoxmeier and Dieterman 2013), we observed very wide body size distributions for both species that varied among years. Cohort-specific mean size for age-0 autumn occasion was highly correlated between brook trout and brown trout in the West Brook. Correlation was present but weaker between the species in the tributary where the species overlapped (Open Large). This correlation suggests similar mechanisms driving early body size distributions for brook trout and brown trout, which are both autumn spawners. Mechanisms promoting variation in early body size for this population were not examined here, but possibilities include differences in spawn timing among females, temperature-dependent development rates while in the gravel, or early pre-capture growth rates. Observed increasing stream temperatures in the study area in the spring, summer and autumn, but not the winter (B. Letcher, unpublished data), suggest that changes in spawn timing or early growth rates, but not development rates in gravel, are likely explanations for larger age-0 fish over time in the autumn. While density-dependent size and growth have been frequently observed in stream salmonids (Grant and Imre 2005), it has been suggested that in some situations high early mortality may drive densities to such low levels that growth is driven largely by density-independent factors (Armstrong and Nislow 2006; Lobon-Cervia 2007).

Estimating size-at-age for separate cohorts allowed us to characterize body size variation over time by exploring size-at-age curve differences among cohorts (year classes). We found that both brook and brown trout body sizes-at-age increased over the course of the study. Interestingly, even though cohort body size switching was possible in our flexible GAM model, cohorts generally maintained rank order in estimated body sizes, especially in the mainstem, suggesting that body size differences among cohorts were set when fish were young, i.e., before fish were large enough to capture (autumn, age-0+). An earlier analysis of brook trout tagging data in the study area (Letcher et al. 2011) also suggested that individual body size trajectories were mainly determined early in life, based on the observation that individual fish generally maintain body size rank (repeatability of individual body size = 0.73) and that compensatory growth was weak. Maintenance of individual size ranks likely contributed substantially to the generally observed maintenance of among-cohort size ranks for both trout species.

Our relatively simple body size analysis involved several assumptions that may have varying levels of effect on results. First, size-

Fig. 10. Brook trout cohort strength vs. brown trout cohort strength for the connected metapopulation (top panel) and connected metapopulation vs. isolated population for brook trout (bottom panel).



dependent processes (losses or gains) could influence size-at-age curves by either removing small or large fish (losses, mortality or emigration) or adding small or large fish (gains, immigration). In this analysis we assume that size-dependent losses or gains occur but that the magnitude and direction of effects are consistent across cohorts. We have observed negative size-dependent survival across locations in brook trout (Letcher et al. 2015), but the variation among years is unknown. We also assume that the tributary of capture represents actual fish location in the sampling interval prior to sampling. We have estimated brook trout movement among tributaries and most movement is out of Open Small to the mainstem (Kanno et al. 2014; Letcher et al. 2015), but timing of movements relative to sampling occasions is unknown as is the extent of variation among years. In addition, we estimated density effects as total cohort strengths. This single number may not represent actual, experienced density at a local spatial scale for individual fish or over the course of time for fish in each cohort, but we assume that the estimated cohort strength characterizes average densities across fish and years.

These results help inform our understanding of stream salmonid assemblage structure, which in turn has implications for conservation and management. Perhaps most clearly, it appears that the ability of brook trout to use the smallest perennial tributaries in the system may promote persistence with co-occurring species. Effective use by brook trout of these spatially constrained and relatively unproductive habitats may be associated with a suite of characteristic traits including risk-averse foraging strategies (Sotiropoulos et al. 2006), use of terrestrial derived prey resources (Sweka and Hartman 2008), tolerance of low effective population sizes (Letcher et al. 2007; Whiteley et al. 2017), and early sexual maturation at small body sizes (Wilson et al. 2003; Letcher et al. 2007). Independent of the specific mechanisms,

Fig. 11. Brook trout cohort strength effects on size-at-age-curves for each catchment (panels) and species (brook trout: solid line, brown trout: dashed line). Grey shading around lines represents 95% confidence intervals.

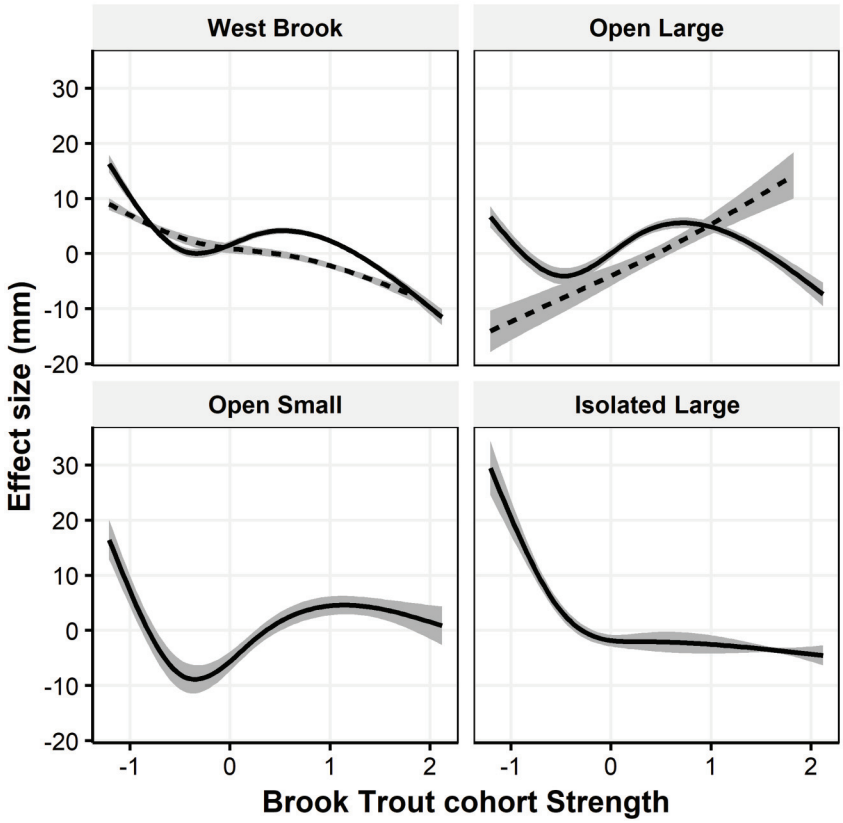
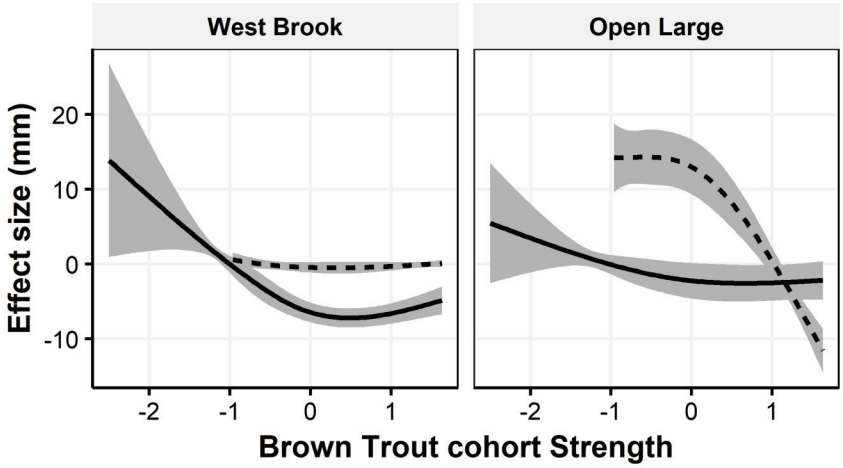


Fig. 12. Brown trout cohort strength effects on size-at-age curves for each catchment (panels) and species (brook trout: solid line, brown trout: dashed line). Grey shading around lines represents 95% confidence intervals.



occupancy of small tributaries allows a substantial proportion of the population to occupy "enemy-free space" (Jeffries and Lawton 1984), potentially balancing the size-advantage possessed by brown trout in this and likely other systems. Not only does the ability to effectively use small tributaries contribute to coexistence, it may be a key attribute in determining vulnerability to invasion by brook trout in small streams outside of the species' native range. In terms of restoration, our results support efforts to maintain and restore connectivity between mainstem and tributary habitats with the goal of maintaining resilient and diverse stream salmonid assemblages. While in some systems (Fausch et al. 2008) maintaining or erecting barriers to stop the upstream spread of non-native species and protect native headwater populations has been suggested or implemented, our results indicate that these may not be necessary or even helpful for brook trout coexisting with non-native brown trout in small stream networks.

Hybridization with invasive species can also affect persistence of native populations (Hitt et al. 2003; Muhlfeld et al. 2009). During our study, we observed fewer than five (phenotypically based) hybrids between brook trout and brown trout, indicating low risk of introgressive hybridization. Of course, results may be specific to our study area and additional studies will be necessary to evaluate the generality of results. In general, connectivity is particularly relevant given previous studies indicating the importance of network connectivity and access to productive mainstem habitats for native brook trout population resilience and life history diversity (Letcher et al. 2007; Huntsman et al. 2016).

Our results also have implications for our general understanding of the factors structuring stream fish assemblages. In the West Brook, brook trout and brown trout abundances were highly correlated, and the two species appeared to respond as functional equivalents with respect to effects of seasonal and annual variation in environmental conditions on size and growth. This similarity and potential niche overlap should in theory increase the strength of species interactions. However, in a highly stochastic environment which produces substantial interannual variation in abundance and body size, neutral community theory (Hubbell 2001) predicts that subtle interspecific advantages may be too weak to result in species replacement. These considerations could be broadly applicable to stream fish assemblages where highly variable environmental conditions produce strong recruitment-dependence (Peres-Neto 2004). Along these lines, competitive exclusion and species replacement may be more likely in more constant environments that produce less variation in cohort strength and body size (e.g., Hoxmeier and Dieterman 2019; Miller et al. 2019). Testing these and other fundamental hypotheses will require extension of these kinds of analytical approaches across a broad range of conditions. Given the fairly basic data needs of these analyses, the large body of monitoring data on stream salmonid populations may provide a powerful way to assess the importance and the outcomes of species interactions and assemblage structure.

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