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BEHAVIORAL ECOLOGY –ORIGINAL RESEARCH

Effects of competition on fitness-related traits

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Abstract While interspecific competition is prevalent in natural systems, we do not yet understand how it can influence an individual's phenotype within its lifetime and how this might affect performance. Morphology and swimming performance are two important fitness-related traits in fishes. Both traits are essential in acquiring and defending resources as well as avoiding predation. Here, we examined if interspecific competition could induce changes in morphology and affect the swimming performance of two strains of juvenile Atlantic salmon (*Salmo salar*). We imposed competitive scenarios on the fish using artificial streams containing different combinations of four interspecific competitors. Exposure to interspecific competitors induced morphological changes over time, through the development of deeper bodies, whereas controls free of interspecific competitors developed more fusiform body shapes. Furthermore, swimming performance was correlated to fusiform morphologies and was weaker for Atlantic salmon in competitive scenarios vs. controls. This implies that interspecific competition has direct effects on these fitness-related traits in Atlantic salmon. To the best of our knowledge, this is the first time that morphology, an important fitness-related trait linked to swimming performance,

has been shown to be negatively impacted through interactions with an interspecific competitor.

Keywords Interspecific competition · Geometric morphometrics · Swimming performance · Atlantic salmon · *Salmo salar*

Introduction

All organisms interact with their neighbours, and sufficient resources and habitat heterogeneity can produce adaptive radiation among individuals with similar niches, over generations., Phenotypic plasticity in response to different environmental conditions can, however, reduce the costs of competition within an individual's lifespan (Schluter 2000; Tilman 1994; Wiens 1989). Populations composed of individuals that have some varying degrees of morphological variation and plasticity may differ in how they perform in competitive scenarios. The relationship between competition and morphological differentiation is poorly understood despite the prevalence of interspecific competition in natural systems (Connell 1983; Fausch 1988; Miner et al. 2005). Furthermore, it is unclear whether many of the morphological differences we observe in populations are due to adaptive phenotypic plasticity or simply due to adaptive divergence over time (Grether et al. 2009).

There are few studies that examine the effects of interspecific competition on fitness-related traits during the course of an individual's lifetime (Grether et al. 2009; Miner et al. 2005; Nislow et al. 2011). There is, however, a rich literature on ecological character displacement, where niche partitioning and adaptive radiation between two or more species living in sympatry have already occurred

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(Schluter 1994, 2000). For example, Melville (2002) surveyed two species of alpine lizards and found that the differences in their size and competitive ability were greater when living in sympatry, but not in allopatry and that the smaller of the two was forced into less favourable habitats. Similarly, Adams (2010) analysed the skull morphology of two species of terrestrial salamanders and found that both species had more robust skulls, characterised by differences in skull size, jaw length, and jaw thickness when living in sympatry but not in allopatry. Robust skulls were also correlated with aggressive behaviour and Adams hypothesized that both these traits should give a competitive advantage in interspecific interactions. The problem with this approach is that these character shifts may be masked when the phenotypic variation is associated with an environmental gradient or under spatial autocorrelation (Adams and Collyer 2007; Goldberg and Lande 2006). One way to overcome these potentially confounding factors is to manipulate competition in a controlled environment. The goal of this study was, therefore, to investigate if interspecific competition, in a controlled environment, could impact individual performance by modifying individual morphology within an individual's lifetime. We used an ecologically and economically important species for our investigation, the Atlantic salmon (*Salmo salar*).

Salmonids are good models for experimentation as they can rapidly respond to changes in the abiotic and biotic environment by adaptively modifying their behaviour, physiology, and development (Fausch 1998; Fraser et al. 2011; Hutchings 2004). Both morphology and swimming performance are important, easily measurable, traits for resource acquisition, territory defence, and predator avoidance and are good indices for fitness in fish (Álvarez and Metcalfe 2007; Colborne et al. 2011; Plaut 2001; Rouleau et al. 2010). Given that form follows function, morphology, and swimming performance which are tightly associated in salmonids (Blake 2004). For example, shallower, streamlined, and fusiform body shapes are important for juvenile Atlantic salmon as this hydrodynamic morphology reduces drag and the energetic costs of swimming. As juvenile Atlantic salmon preferentially establishes territories in fast flowing riffles, individuals with a fusiform body shape would have an advantage over individuals with less hydrodynamic morphologies (Finstad et al. 2011; Leavy and Bonner 2009; Taylor and McPhail 1985). Deeper body shapes, on the other hand, allows individuals to achieve greater acceleration, improved burst swimming performance, and greater manoeuvrability in complex habitats, all of which are essential for foraging and predator avoidance (Blake 2004; Domenici et al. 2008). Perceived body size is also a common predictor of competitive ability and dominance in fish. Individuals with deeper bodies and a larger profile will be perceived as having a greater size which may reduce antagonism from interspecific interactions regardless of actual size (Huntingford et al. 1990; Ward et al. 2006). Atlantic salmon also provides a good system for studies on interspecific interactions as they face severe competition from introduced non-native species in the North American Great Lakes. Atlantic salmon's main competitors in the Great Lakes include brown trout (*Salmo trutta*), rainbow trout (*Oncorhynchus mykiss*), Chinook salmon (*O. tshawytscha*), and coho salmon (*O. kisutch*) (Crawford and Muir 2007; Nislow et al. 2011). These non-native species are ecologically similar to Atlantic salmon but have not evolved together, and as such, have the potential to be strong competitors for similar resources and territory These competitors are also known to impact Atlantic salmon fitness by decreasing their social status, increasing their energy expenditure, and increasing their stress levels (Scott et al. 2005a, b; van Zwol et al. 2012a, b).

Morphology and swimming performance are often plastic in a salmonid's lifetime, and variation in both of these traits is often associated with an abiotic environmental gradient, such as water velocity (Pakkasmaa and Piironen 2001; Peres-Neto 2004). While Atlantic salmon are plastic for a number of life-history traits (Klemetsen et al. 2003), and intraspecific competition has been studied extensively in this species, few studies have addressed how the biotic environment (e.g., interspecific competition) can induce a plastic response in fitness-related traits (Fausch 1998; Grether et al. 2009; Nislow et al. 2011). There is already some evidence that biotic interactions, such as predation, can induce plastic morphological responses in fishes. For example, developing a deeper body is a form of inducible morphological defence in prey fishes which are exposed to the risk of predation (Chivers et al. 2007). Not only will gape-limited predators preferentially eat shallow-bodied prey, they might also cause individuals to change their habitat use, removing them from the fast flowing water which induces fusiform body shapes in salmonids (Fu et al. 2013; Pakkasmaa and Piironen 2001). Similarly, this may put a great selective pressure for morphological plasticity on individuals to develop deeper body shapes in the presence of competitors and fusiform body shapes in the absence of competitors (Chivers et al. 2007; Grether et al. 2009; Harvell 1990; Leavy and Bonner 2009). While this change in morphology may be adaptive in the presence of competitors, it could result in a tradeoff with swimming performance as any change in morphology may have a strong effect on the hydrodynamic forces experienced by an individual (Blake 2004; Fu et al. 2013; Pettersson and Brönmark 1997). We hypothesize that strong interspecific competition can induce morphological plasticity which in turn will impact swimming performance. This relationship may be analogous to the morphological changes and swimming performance tradeoffs experienced by individuals

under the risk of predation (Grether et al. 2009; Relyea 2000; Van Buskirk and Relyea 1998).

To test for the effects of interspecific competition on fitness-related traits important in the early life of Atlantic salmon, we set out a comprehensive experiment to test whether the four aforementioned interspecific competitors could affect Atlantic salmon morphology and swimming performance in controlled artificial streams. Two strains of juvenile Atlantic salmon were compared during this study: the LaHave strain from Nova Scotia and the Sebago strain from Maine. An additional benefit to using these strains as our study species is that both are candidate strains for a Canadian government funded Atlantic salmon reintroduction program in the Great Lakes (Diamond and Smitka 2005; Huntsman 1944; Netboy 1968) and information regarding their performance when faced with competition is of great importance to the reintroduction effort. If interspecific competition with Atlantic salmon is able to influence these two traits, then individual fitness of these stocked strains will be impacted in the wild (Finstad et al. 2011), and impede self-sustaining populations from forming (Fausch 1988, 1998). We predicted that individual morphology would be influenced by interspecific competition and that this relationship would vary as a function of the interspecific competitor as they could impose different degrees of competitive pressure on Atlantic salmon. We also expected that swimming performance and morphology would be highly correlated, but that interspecific competition may impose a tradeoff that affects individual swimming performance.

Materials and methods

Subjects

Juveniles of all salmonid species were provided by the Ontario Ministry of Natural Resources (OMNR). Fertilised eggs from single-pair matings of wild LaHave (LaHave River, Nova Scotia, Canada: 44°14′N64°20′W) were received from 1989 to 1995, and captive generations were produced every year in Ontario starting in 1996. Fertilised eggs from single-pair matings of wild Sebago in Panther River (A tributary of Lake Sebago, Maine, U.S.S.: 43°53′N, 70°27′W), a hatchery-supplemented river, were received in 2006. Families for both strains of this experiment were produced in early November 2010 at the OMNR Harwood Fish Culture Station. For each strain, we randomly selected mature adults for a blocked full factorial 5 × 5 North Carolina breeding design (Lynch and Walsh 1988). Fertilised eggs were then transported the same day as fertilization to the OMNR Codrington Fisheries Research Facility for rearing.

Rainbow trout and brown trout were produced from hatchery parents derived from the Ganaraska River, Ontario. Chinook salmon and Coho salmon were produced from wild parents from the Credit River, Ontario. The fry of each species were kept in tanks (38 L, $n = 250$ fry) at the Codrington Facility until used in the artificial streams. Although the species differed slightly in the initial body length (LaHave 5.8 ± 0.4 cm; Sebago 5.6 ± 0.5 cm; brown trout 6.0 ± 0.7 cm; rainbow trout 6.0 ± 0.6 cm; Chinook salmon 8.2 ± 0.7 cm; Coho salmon 8.5 ± 1.0 cm), the juveniles of each species were the same age and thus representative of interspecific intra-cohort competition that would occur in a natural setting. Greater details on the non-native competitor populations can be found in Houde et al. (2015).

Experimental procedures

Artificial streams were constructed at the Codrington Facility, Ontario, Canada. The artificial streams measured 2.4 m long by 0.25 m wide, and the bottom was lined with gravel and pebbles creating a semi-natural environment The artificial stream was openly divided into a riffle section characterised by shallow, fast flowing water (1.60 m long, 0.25 m wide, and 0.40 m deep), and a pool section characterized by deeper, slower moving water (0.8 m long, 0.25 m wide, and 0.80 m deep). These were included in the design of the streams as they are the preferred habitats of juvenile salmonids (Arnold et al. 1991; Finstad et al. 2011). Natural stream water was actively pumped through the experimental streams at a flow rate between 0.41 m s^{-1} in the riffle section at the headwater and 0.27 m s^{-1} in the pool section downstream, measured using a 10 s average for each point using a digital flowmeter (Höntzsch, Germany);. Both stream velocities were representative of velocities experienced by juvenile salmonids in the wild (Keeley and Grant 1995). Fish were exposed to natural fluctuations in stream temperature and photoperiod. Throughout the experiment, the fish were fed commercial pellets once daily at a quantity of 3% total body mass. For more detailed information on the artificial streams and experimental setup, consult the supplementary material of Houde et al. (2015).

Individual LaHave and Sebago, as well as the competitor species, were randomly assigned to one of seven experimental treatments beginning in September 2011 and lasting for a total of 45 weeks, ending in August of 2012 (Table 1). Each treatment had two replicates which were run in tandem. Initial fish density was kept at a constant of 32 fish per stream. These higher than natural densities were used to encourage competitive interactions (Steingrímsson and Grant 1999).

Table 1 Experimental design showing results for the means and standard deviations of the final mass and fork length taken for each strain and treatment group as well as the critical swimming speed (U_{crit}) and burst swimming speeds taken from a subset of these Atlantic salmon; ($n = 8$ per replicate)

Treatment	Ratio AS:competitor	Strain	Final mass (g)	Final length (cm)	U_{crit} (cm s^{-1})	Burst (m s^{-1})
Control	32:0	LaHave (16)	21.42 ± 7.34	11.98 ± 1.49	70.41 ± 26.10	1.25 ± 0.39
		Sebago (16)	22.26 ± 7.22	12.35 ± 1.60	95.89 ± 23.30	1.12 ± 0.45
Brown trout	16:16	LaHave (1)	14.91	10.95	56.01	1.05
		Sebago (6)	15.23 ± 4.11	10.50 ± 0.37	62.50 ± 24.07	1.30 ± 0.23
Rainbow trout	16:16	LaHave (12)	15.98 ± 4.57	10.86 ± 1.06	69.21 ± 16.77	1.43 ± 0.33
		Sebago (11)	15.94 ± 3.00	10.98 ± 0.90	54.49 ± 23.48	1.05 ± 0.30
Chinook salmon	16:16	LaHave (16)	20.35 ± 6.94	12.12 ± 1.73	57.15 ± 21.25	1.22 ± 0.19
		Sebago (16)	20.37 ± 7.41	12.31 ± 1.97	58.10 ± 23.27	1.19 ± 0.36
Coho salmon	16:16	LaHave (10)	23.61 ± 11.53	11.62 ± 1.45	57.15 ± 21.26	1.25 ± 0.43
		Sebago (14)	26.38 ± 13.07	11.83 ± 1.57	58.10 ± 23.24	1.29 ± 0.24
Mix	16:4:4:4:4	LaHave (3)	17.23 ± 7.56	10.95 ± 1.30	39.11 ± 24.62	1.02 ± 0.13
		Sebago (2)	28.33 ± 1.95	13.35 ± 0.21	[a]	[a]
LaHave-Sebago	16:16	LaHave (6)	25.46 ± 10.39	11.91 ± 1.66	67.53 ± 16.93	1.22 ± 0.35
		Sebago (6)	16.47 ± 7.59	11.88 ± 2.25	71.96 ± 17.51	1.40 ± 0.45

Numbers between parentheses are combined sample size for both replicates

[a] Mortalities

Table 2 Differentiation of morphologies across strains and treatments taken throughout the experiment

Samples	Strain		Treatment		Interaction	
	λ	P	λ	P	λ	P
Initial ($n = 240$)	0.40	<0.001	NA	NA	NA	NA
5 weeks later ($n = 240$)	0.35	<0.001	0.94	0.64	0.43	0.70
36 weeks later ($n = 442$)	0.47	<0.001	0.19	<0.001	0.29	<0.001
45 weeks later ($n = 312$)	0.55	<0.001	0.20	<0.001	0.32	<0.001

Partial warps were used as the response variables in a MANCOVA to test for differences across treatments and strains (NAs in the initial sample due to the fish being measured before being placed in a treatment)

Prior to being placed in the artificial streams in September, 2011, a subset of Atlantic salmon ($n = 240$) were lightly anesthetized (MS-222), removed from the water, weighed on a digital scale, and had their left sides digitally photographed next to a measuring scale immediately following this, the fish were placed in fresh stream water with an oxygen bubbler to recover. Once recovered and swimming freely, the fish were returned to the artificial streams. This was repeated another three times throughout the study (second sample after 5 weeks, third sample after 36 weeks, and fourth sample after 45 weeks; Table 2). As intraspecific and interspecific competition for refuges is high in the winter, measuring was avoided during this time so as not to further encumber survival (Harwood et al. 2002). Nineteen homologous landmarks (Fig. 1) were placed on each digital photograph using the tpsDig2 software (Rohlf and Marcus 2005). The homologous landmark coordinates were then analyzed using a generalised Procrustes analysis and subsequently transformed into partial warps which are used
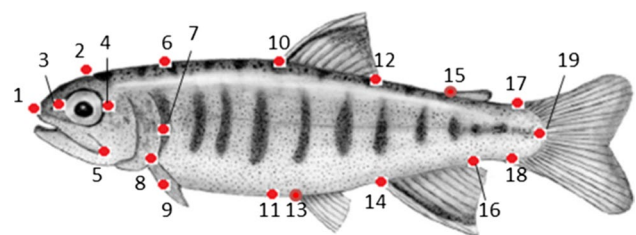

Fig. 1 Juvenile Atlantic salmon with 19 homologous landmarks which were used for geomorphometric analyses: *1* anterior lip of the upper jaw; *2* head at the midpoint of the eye; *3* most anterior point of the eye; *4* most posterior point of the eye; *5* base of the maxilla; *6* dorsal point of head at the posterior edge of the operculum; *7* posterior edge of the operculum; *8* insertion of the pectoral fin; *9* ventral point of head at the posterior edge of the operculum; *10* anterior dorsal fin insertion; *11* ventral point opposite of the anterior dorsal fin insertion; *12* anterior insertion of pelvic fin; *13* anterior insertion of anal fin; *14* posterior insertion of dorsal fin; *15* posterior insertion of the anal fin; *16* anterior insertion of adipose fin; *17* dorsal terminus of caudal flexure; *18* ventral terminus of the caudal flexure; *19* most anterior point of caudal peduncle

to compare morphologies using subsequent multivariate analyses (Zelditch et al. 2004). These shape variables were then contrasted across treatments and strains (see statistical analyses below).

We measured the critical swimming speed, an estimate of the maximum sustained speed which is an exclusively aerobic activity, and burst swimming speed, an anaerobic form of swimming, where the highest levels of exercise performance are attained (Beamish 1978; Domenici and Blake 1997; Peake et al. 1997; Peake 2008). Both were measured on the same subset of Atlantic salmon after 10 months of exposure to the interspecific competitors [$n = 135$; 8 per treatment; however, due to mortalities and individuals being set aside for a parallel study (Houde et al. 2015), some treatments had smaller sample sizes]. Each fish was measured first for burst swimming speed then after a >10-min recovery; the critical swimming speed was measured. Swimming performance was not measured multiple times in individuals to avoid stress and decrease the possibility of mortality. Burst swimming speed was measured in an acrylic raceway (25 cm × 23 cm × 150 cm), filled to a depth 15 cm of water. Individuals were confined to one end of the raceway with a plastic barrier and a shelter was placed at the other end to encourage directed swimming. After acclimating for 5 min, the barrier was removed and the individual was immediately exposed to a simulated predation event (golf ball being dropped from a distance of 50 cm directly overhead of the individual), causing a swimming escape response towards the far end of the raceway (Colborne et al. 2011; Lima and Dill 1990; Peres-Neto and Magnan 2004). Where fish were unresponsive to the golf ball stimulus, the handle of a fish net was used to gently probe the caudal fin to elicit swimming. If fish were still unresponsive to this stimulus, they were removed from the experiment but were still used in the critical swimming speed assay. Trials were recorded with a high-speed camera at 60 frames per second (Fastec Imaging) and video tracking software (Kinovea v. 0.8.15) was used to calculate the maximum burst swimming speed achieved. This was calculated as the maximum instantaneous velocity of the head of the fish between each frame in the video.

Critical swimming speed was measured using an acrylic swim flume (Loligo Systems, Denmark). Following the burst swimming speed trial, the Atlantic salmon were then placed individually into the swim chamber and left to acclimate for 10 min. Water velocity was then increased by approximately 0.19 cm s^{-1} every 2 min until the fish showed signs of fatigue. Fatigue was defined as when a fish could no longer actively swim against the current and was swept back against the mesh at the back of the chamber even after a single, mild (5–10 V) electric pulse was administered to elicit movement. Critical swimming speed (U_{crit}) was calculated as $U_{crit} = U_i + (T_i/T_{ii} \times \times U_{ii})$ for each individual (Plaut 2001), where U_i is the highest velocity maintained for a full 2 min interval, T_i is the time of fatigue at last current velocity (minute), T_{ii} is the interval length (2 min), and U_{ii} is the water velocity increment (0.19 m s^{-1}). While many variations of this protocol exist, they are typically designed for adult fish, and so, shorter time intervals were used to better reflect the stream environment of juvenile Atlantic salmon where there are daily and seasonal fluctuations in water velocity (Peake 2008; Tierney 2011).

Statistical analyses

Two-way multivariate analysis of covariance (MANCOVA) was used to test for differences in partial warp scores (i.e., shape differences) across treatments and strains for each of the four sampling periods. Treatment and Atlantic salmon strain were used as fully interacting fixed effects in the model. Fish were not individually marked, so a repeated measures model was not feasible. Although partial warps, generated from a generalised Procrustes analysis, are standardized for scale, orientation, and position within the digital photograph, we also tested how final mass differed across treatments and strains as an additional estimate as to how interspecific competition could influence individual growth. We assessed this using a two-way ANOVA with treatment and strain as interacting fixed effects and artificial stream ID as a random effect.

To compare how treatments and strains differed in shape, we used discriminant function analysis (DFA) using the "MASS" package in R (Ripley et al. 2015; Venables and Ripley 2002), and thin-plate splines (Bookstein 1991). DFA was used to determine which shape variables (partial warp scores) predicted membership to a particular group (strain and treatment). We calculated the first two discriminant functions for each strain's morphology across treatments separately to focus on the effects of interspecific competition on morphology. We tested the significance of these relationships for each discriminant function using a one-way ANOVA with treatment as a fixed effect and post hoc pairwise t test with a Bonferroni correction. The main patterns of shape differentiation across treatments and strains were visualized using thin-plate splines produced by regressing each multivariate partial warp score onto each of the discriminant functions. Deformation grids were then produced using the tpsRegr software (Rohlf and Marcus 2005).

Two-way ANCOVAs were used to determine how burst swimming speed and critical swimming speeds differed across treatments and strains. As above, treatment and Atlantic salmon strain were used as fully interacting fixed effects in the model and mass was included as a covariate.

Fig. 2 a Plotted values of the discriminant functions (Sebago DF1 and DF2) of the partial warps describing body shape across the seven interspecific competition treatments for the Sebago strain. *1* Control (i.e. only Sebago) (*red*), *2* brown trout (*brown*), *3* rainbow trout (*light green*), *4* Chinook salmon (*dark green*), *5* coho salmon (*blue*), *6* Mix (*purple*), and *7* LaHave-Sebago (*magenta*). The scatter plot shows the first two discriminant function axes: DF1 and DF2 with 95% Confidence ellipses drawn into assist in distinguishing group differences. **b** Average Atlantic salmon morphology (*centre*), as well as the extreme morphologies along Sebago DF1 and DF2 visualized using thin-plate splines. DF1 and DF2 axes correspond to the scatter plot (**a**) (color figure online)
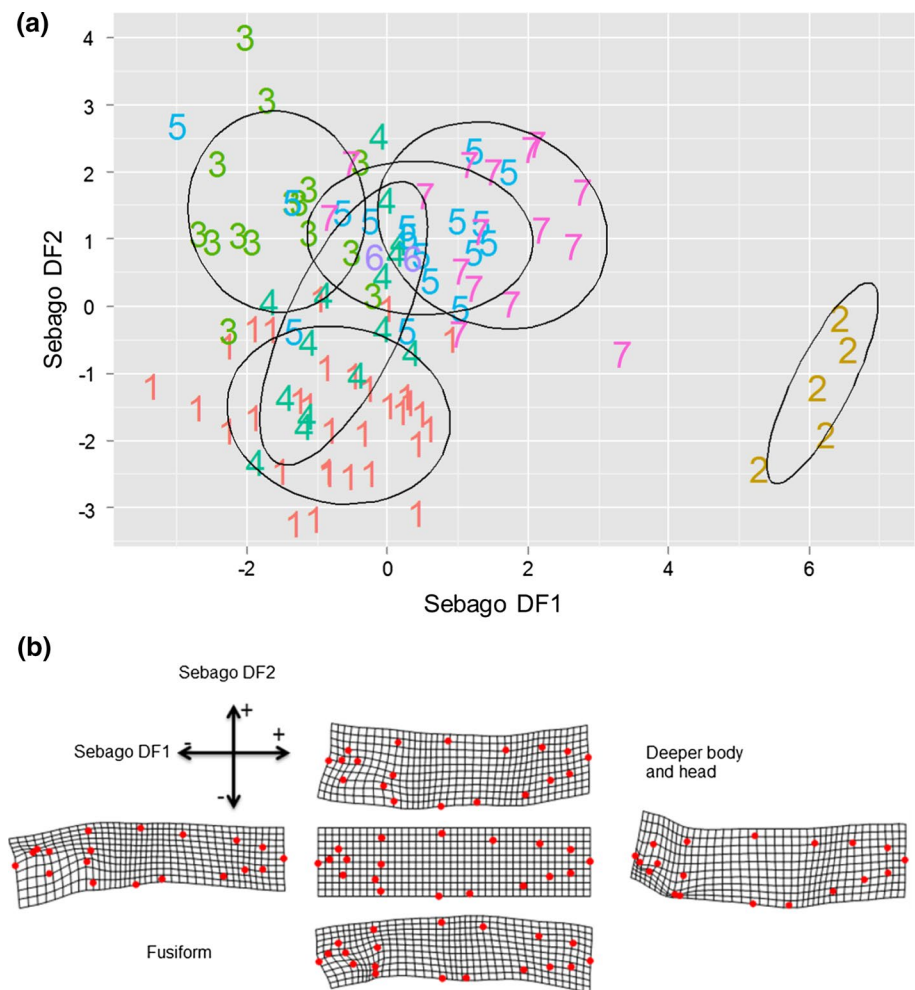
A post hoc Tukey test was then used to compare swimming performances among groups when statistical differences were found.

Finally, we used Pearson's correlation coefficient to test whether individual morphology (discriminant functions for each strain) were correlated to swimming performance and whether burst and critical swimming speeds were correlated. All morphological analyses were done with the tps software suite (Rohlf and Marcus 2005). All statistical tests were done with R v. 3.02 (R core Team 2014).

Results

Morphology

Morphologies differed significantly across the interspecific competition treatments. These differences appeared after 36 weeks but were also influenced by initial morphological differences between strains which were evident from before the beginning of the experiment. Differences

persisted to the final (45 weeks) sampling period where they were more accentuated (Table 2; Fig. 2). Due to the significant interaction term between strain and treatment observed during the final sampling period, we subsequently evaluated the morphology of each strain separately to concentrate the analyses on the influence of interspecific competition. For Sebago salmon, the first discriminant function (DF1–Sebago) described 39% and the second function (DF2–Sebago) described 29% of the morphological variation among treatments. For LaHave salmon, the first discriminant function (DF1–LaHave) described 38% and the second function (DF2–LaHave) described 29% of the morphological variation. Final LaHave morphology differed significantly across treatments (ANOVA—LaHave.DF1: $F = 66.00$, $n = 78$, $P < 0.001$; LaHave.DF2: $F = 39.19$, $n = 78$, $P < 0.001$). Final Sebago morphology also differed significantly across treatments (ANOVA—Sebago.DF1: $F = 47.61$, $n = 102$, $P < 0.001$; Sebago.DF2: $F = 27.20$, $n = 102$, $P < 0.001$). Both Sebago and LaHave salmon morphology varied similarly along the discriminant function axes. Control treatments tended towards more fusiform

Table 3 P values for post hoc pairwise comparisons with Bonferroni corrections of the discriminant functions (DF) describing shape variation across interspecific competitor treatments compared to controls

	Brown trout	Rainbow trout	Chinook salmon	Coho salmon	Mix	LaHave-Sebago
LaHave.DF1	<0.01	1.00	<0.01	<0.001	<0.01	<0.001
LaHave.DF2	1.00	<0.001	<0.001	1.00	<0.001	<0.001
Sebago.DF1	<0.001	0.23	1.00	<0.05	1.00	<0.001
Sebago.DF2	1.00	<0.001	<0.001	<0.001	<0.05	<0.001

Fig. 3 a Barplot of the discriminant function scores for the final sample (45 weeks), showing differences between the morphologies of the two strains of Atlantic salmon: LaHave and Sebago. **b** Thin-plate splines were used to visualize the differences in shape between the two strains
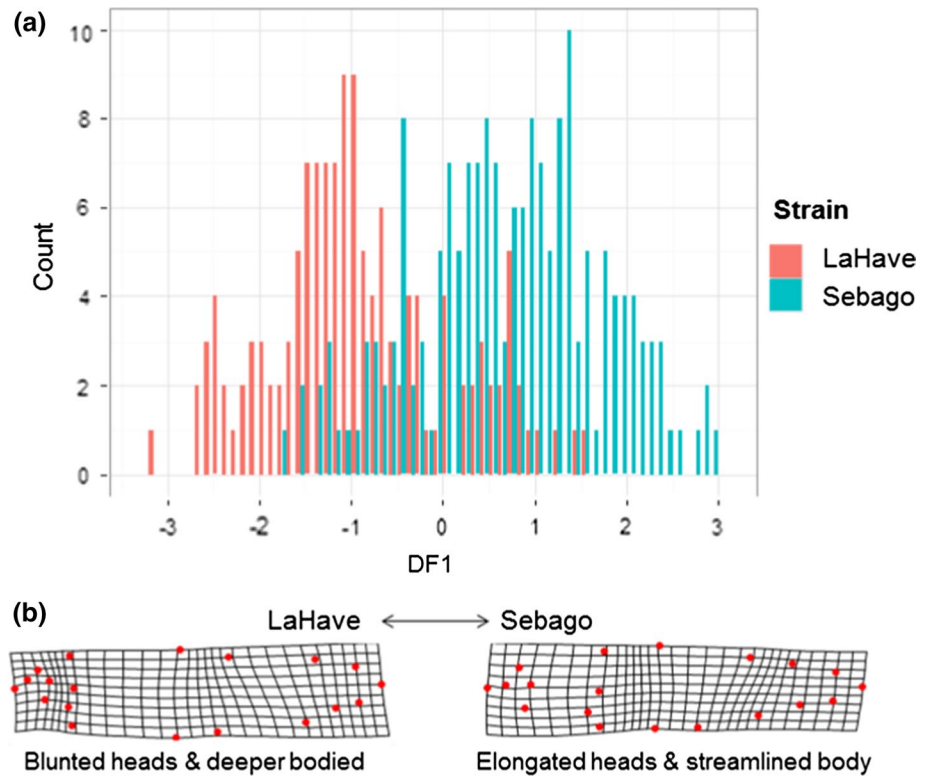
body shapes with more elongated heads and shallower bodies. In contrast, treatments with interspecific competitors had relatively deeper bodies, and blunted, deeper heads (Fig. 2; Table 3). Along the DF1–Sebago axis, fish morphology varied from shallower, elongated heads, shallower bodies, and shallower caudal peduncles to having shorter, deeper heads, lower attachment points for the pectoral fin, and slightly deeper bodies overall (Fig. 2b). Along the DF2–Sebago axis, fish morphology varied from having shallower, elongated heads and shallow bodies to having much deeper heads and bodies, as well as a higher attachment point for the pectoral fin (Fig. 2b).

Relative to controls, each of the treatments with interspecific competitors developed significantly different morphologies along at least one of the discriminant functions describing shape variation (Table 3). Compared to control treatments of both strains, fish paired with brown trout had the deepest body shapes of all (Fig. 2a). Individuals paired with Chinook salmon or rainbow trout were the most similar in morphology to the control

treatments, having more fusiform body shapes as opposed to deeper body shapes. Atlantic salmon paired with coho salmon, the multispecies mixed treatment, and the intraspecific competition treatments (LaHave and Sebago) were slightly less fusiform than the control treatment.

We also compared how strains differed in their overall morphology, using thin-plate-splines and deformation grids and observed that LaHave salmon had shorter, blunted heads, whereas Sebago salmon had more elongated heads resulting in a more streamlined, fusiform body shape (Fig. 3a, b) (Blake 2004; Fraser et al. 2007). These differences in morphology between strains were apparent from the beginning of the experiment (MANCOVA: Wilks $\lambda = 0.40$, $n = 240$, $P < 0.001$) and persisted throughout all the other sampling periods (Table 2).

The final masses of Atlantic salmon also differed across treatments (ANOVA: $F = 7.00$, $n = 317$, $P < 0.001$), but not strains ($F = 0.86$, $n = 317$, $P = 0.43$), and there was no significant interaction between these two factors ($F = 2.15$, $n = 317$, $P = 0.08$). Post hoc Tukey tests showed that
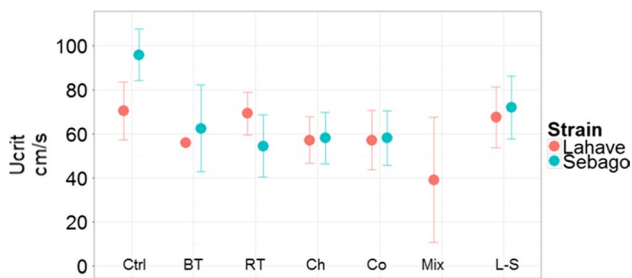
Fig. 4 Means and 95% confidence intervals for the critical swimming speeds (U_{crit}) of Atlantic salmon by strain and treatment. *Ctrl* control, *BT* brown trout, *RT* rainbow trout, *Ch* Chinook salmon, *Co* coho salmon, *Mix* all four interspecific competitors, and *L-S* LaHave-Sebago. ANCOVAs were used to test for differences among treatments. Statistical significance is indicated by *asterisk*. Mortalities in the LaHave-Brown trout, and Sebago-Mix treatments prevented means and confidence intervals from being calculated

treatments, where Atlantic salmon was paired with either rainbow trout or brown trout, had a significantly lower mass relative to controls (Table 2). Mortalities were also very low, occurring only after the 36-week point in treatments containing rainbow trout or brown trout.

Swimming performance

Burst swimming speeds (1.23 ± 0.35 cm s^{-1}; Table 1) did not differ significantly between treatments (ANCOVA: $F = 0.47$, $P = 0.83$) or strains ($F = 1.34$, $P = 0.25$). Mass only marginally predicted burst swimming speed ($F = 3.94$, $P = 0.05$). Finally, burst swimming speed was not correlated to mass ($r = 0.17$, $P = 0.07$) or critical swimming speed ($r = 0.12$, $P = 0.18$).

When controlling for individual mass, there were significant differences in critical swimming speeds across treatments (ANCOVA: $F = 6.28$, $P < 0.001$) but not between strains (ANCOVA: $F = 0.24$, $P = 0.63$). There was, however, a significant interaction between strain and treatment (ANCOVA: $F = 2.89$, $P < 0.05$). Mass also significantly predicted U_{crit} ($F = 17.95$, $P < 0.001$). Greater critical swimming speeds (higher U_{crit}) (Table 1) were also correlated to mass ($r = 0.27$, $P < 0.01$). Considering both strains together, control groups had a mean critical swimming speed of 83.15 vs. 55.09 cm s^{-1} in treatments with interspecific competitors. Given the morphological differences between strains (Fig. 2) and the interaction between strain and treatment, LaHave, and Sebago salmon were once again treated separately for subsequent analyses. We observed no significant differences in critical swimming speeds among treatments for LaHaves, suggesting that interspecific competition did not seem to affect swimming

performance (ANCOVA, $F = 1.19$, $n = 64$, $P = 0.32$; Fig. 4). On the other hand, critical swimming speeds did differ significantly among treatments for Sebago (ANOVA, $F = 7.48$, $n = 75$, $P < 0.001$; Fig. 4). A post hoc Tukey–Kramer test for critical swimming speeds of Sebagos showed that control treatments of Sebago had significantly greater critical swimming speeds than all other Sebago treatments with an interspecific competitor (Fig. 4a). Swimming performance did not depend on which species of competitor was present. Critical swimming speed in the intraspecific competition treatment was significantly different from controls for LaHave but not for Sebago, although their critical swimming speeds were both lower when compared to controls (LaHave control 70.41 ± 26.10 cm s^{-1} vs. intraspecific competition 67.53 ± 16.93 cm s^{-1}; Sebago control 95.89 ± 23.30 cm s^{-1} vs. intraspecific competition 71.96 ± 17.51 cm s^{-1}).

Morphology and swimming

Differences in morphology between strains and treatments were also significant within the subset of fish that were measured for swimming performance (MANCOVA: Treatment: Wilks $\lambda = 0.47$, $n = 133$, $P < 0.001$; Strain: Wilks $\lambda = 0.03$, $n = 133$, $P < 0.001$; Interaction: Wilks $\lambda = 0.05$, $n = 133$, $P < 0.001$). Considering both strains together, we found that across all treatments, critical swimming speed (U_{crit}) was correlated with morphology. More specifically, the first discriminant function describing shape across treatments (DF1 treatment, representing 42% of shape variation) was significantly correlated with greater swimming performance indicated by a high U_{crit} ($r = 0.30$, $P < 0.001$) but not the second discriminant function (DF2 treatment, representing 23% of shape variation; $r = 0.11$, $P = 0.19$). Burst swimming speed, however, was not correlated to shape (DF1 treatment: $r = 0.07$, $P = 0.43$; DF2 treatment: $r = -0.05$, $P = 0.56$).

Due to a significant interaction term between strain and treatment for predicting critical swimming speeds (ANCOVA: $F = 4.12$, $P = 0.04$), we analysed the relationship of each strain's morphology to swimming performance separately. We found that Sebago morphology (DF2–Sebago but not DF1–Sebago), which ranged from a deeper bodied morphology to a more shallow, fusiform morphology (Fig. 2b), was correlated to critical swimming speed ($r = 0.48$, $P < 0.001$), but not to burst swimming speed ($r = 0.48$, $P < 0.001$. On the other hand, LaHave morphology (DF1–LaHave or DF2–LaHave), despite showing similar variation to Sebago morphology, was correlated to the swimming performance measures.

Discussion

To the best of our knowledge, this is the first time anyone has directly sought to experimentally measure the effect of interspecific competition on individual morphology and performance in fish. Our results indicate that interspecific competition can induce morphological differentiation in juvenile Atlantic salmon within a matter of months and that this, in turn, impacts swimming performance. These results are similar to studies which examined trait-mediated indirect interactions in multispecies food webs. While these studies focused primarily on how the presence of a predator could induce morphological change in prey species, they also unexpectedly found that in the absence of predation, competition between the two prey species, or two morphs of the same species, could still lead to changes in morphology. These morphological changes led to tradeoffs between their competitive ability and their vulnerability to predation (Harvell 1990; Werner and Peacor 2003). For example, Van Buskirk and Relyea (1998) found that in the absence of predators, tadpoles of the wood frog (*Rana sylvatica*) that had shorter bodies and deeper tails (inducible defenses against predation) were poorer competitors and had poorer survival when compared to individuals that did not develop that morphotype. Similarly, in the absence of predators, competition between wood frog and leopard frog (*R. pipiens*) tadpoles resulted in changes in mouth width and tail length when housed together but not when reared separately. This could lead to differential foraging success between the two species and supports the idea that competition can alter morphology (Relyea 2000). Along with our own results, these studies support the argument that competition can induce a generalised, plastic, morphological response (Grether et al. 2009).

In this study, interspecific competition induced a deeper, less fusiform morphology as well as a lower U_{crit}, indicative of a poorer swimming performance (Tierney 2011), in juvenile Atlantic salmon. Fusiform morphologies were correlated to swimming performance, implying that there was a cost to developing a deeper body shape in response to competition. Our results are similar to the changes in morphology observed across a wide variety of taxa when inducible defences are developed by prey species in response to the risk of predation (Chivers et al. 2007; Harvell 1990). This further suggests a generalised morphological response to antagonistic interactions with other species (Grether et al. 2009). As opposed to a direct antagonistic interaction, the interspecific competitors could be causing a shift in habitat use in the Atlantic salmon which could have exposed them to different environmental factors, such as slower water currents. Faster water currents found in riffles, the preferred habitat of juvenile Atlantic salmon is known

to induce fusiform body shapes in salmonids (Fu et al. 2013; Pakkasmaa and Piironen 2001). It is unclear whether developing a deeper morphology would be advantageous in a natural environment with interspecific competitors present, but it is clear that swimming performance is impacted through the development of a deeper body. These results are, therefore, important in understanding how Atlantic salmon reintroductions in streams, where non-native competitors are present can potentially impact the swimming performance of individuals, and could lead to a decrease in fitness.

Interspecific competition was sufficient to induce morphological change in Atlantic salmon, because the differences in morphology across treatments that we observed developed due to prolonged exposure to the interspecific competitors. Furthermore, Atlantic salmon developed different morphologies as a function of the interspecific competitor with which they were paired. Brown trout and rainbow trout appeared to induce the greatest departure from control treatments where fusiform body shapes were the norm, though both these species induced different morphologies in Atlantic salmon. Each treatment of Atlantic salmon in competition treatments differed significantly in at least one of the discriminant functions describing shape variation from control morphologies. Not only did morphology vary across treatments but the difference in final masses among groups relative to controls suggests that interspecific competitors had a negative impact on Atlantic salmon. The interspecific competitors could have influenced Atlantic salmon mass by either acquiring more food resources themselves or directly impeding the Atlantic salmon from feeding. Indeed, interference competition whereby the non-native competitors antagonize Atlantic salmon and keep them from directly acquiring resources could explain why the final masses of Atlantic salmon in treatments containing brown trout and rainbow trout were significantly smaller (Houde et al. 2015). Indeed, the groups with a greater number of mortalities are those containing brown trout and rainbow trout, suggesting that the smaller individuals that remained may have been able to avoid antagonistic interactions (or predation) by taking refuge in the interstitial spaces provided by the rocky substrate of the artificial streams, which the larger individuals could not do (Harwood et al. 2002). This makes sense as both brown trout and rainbow trout have negative effects on the fitness of Atlantic salmon (Nislow et al. 2011; Scott et al. 2005a, b).

The differences in body shape that we observed between strains were present from the onset of the experiment. This result is consistent with other studies which have observed differences between the morphologies of different

populations of salmonids. For instance, Solem and Berg (2011) were successfully able to correctly discriminate between eight populations of juvenile Atlantic salmon from three different regions in Norway as well as the river of origin by looking at morphology. Since both strains were raised in the same environmental conditions from birth, and are several generations removed from wild populations, these divergent morphotypes could represent variation for morphological plasticity between these Atlantic salmon strains in response to their environments (Fraser et al. 2011). For example, wild populations of salmonids found in the same river vary in morphology as a function of the distance they have to migrate. Populations with greater distances to migrate tend to be more fusiform than populations with shorter distances to travel. This hydrodynamically streamlined morphology could be adaptive as it would reduce the costs of locomotion (Fraser et al. 2007; Taylor and McPhail 1985).

Our observed values for critical swimming speeds fell within the published ranges documented for the species at the parr life stage (Peake 2008). Our results suggest that while falling within accepted norms for the species and life stage (Peake 2008), critical swimming speeds in Atlantic salmon were lower in the presence of interspecific competitors. If interspecific competitors were directly antagonising Atlantic salmon, then Atlantic salmon may have been shifting their habitat use and spending more time taking refuge to reduce the costs of competition (Schluter 2000). Taking refuge in the rocky substrate could alter Atlantic salmon's morphology by limiting the development of their musculature associated with swimming (Kieffer 2010; Palstra and Planas 2011; Webb 1984). This could happen through a reduced exposure to higher water velocities, which are known to induce streamlined, fusiform body shapes through exercise (Pakkasmaa and Piironen 2001), and less access to food (Currens et al. 1989; Leavy and Bonner 2009; Pakkasmaa and Piironen 2001; Peres-Neto and Magnan 2004). We did not detect differences in burst swimming speed between strains or treatments; however, this may be due the naiveté of hatchery-reared fish to predation risk from above (Álvarez and Nicieza 2003). We noted that most many individuals were unresponsive to stimuli from above and it took several attempts to initiate the burst swimming behaviour. Therefore, we cannot draw any strong conclusions about the effects of interspecific competition on this mode of swimming.

Morphology has an intricate relationship with function in fish (Blake 2004). The streamlined, energy efficient morphotype characteristic of salmonids is an adaptation to prolonged swimming but may vary in function of the life-histories and the physical environmental constraints imposed on different populations (Taylor and McPhail 1985). Here, we provided support that a correlation exists between critical swimming speed and a streamlined body shape but that this relationship varies as a function of the interspecific competitor present. Only Atlantic salmon in the control treatments developed significantly streamlined body morphologies. This is even more apparent in the control treatments of Sebago salmon, where critical swimming speed was not only significantly greater over all other treatments but was also highly correlated to a streamlined body shape. This may also be a result of their more elongated head, contributing to a more streamlined shape when compared with the LaHave. Interestingly, Pakkasmaa and Piironen (2001) reported that juvenile brown trout (*Salmo trutta*) developed streamlined bodies when reared in fast flowing water but not juvenile Atlantic salmon which instead developed deeper bodies. Although they also reported that they were both longer and had more elongated heads than salmon reared in low water velocity, which could nonetheless be interpreted as a streamlined morphotype (Pakkasmaa and Piironen 2001).

Developing deeper bodies may be adaptive for individuals faced with interspecific competition (Grether et al. 2009) and may give them a competitive advantage in interactions with interspecific competitors (i.e., it may give the impression of having a larger body size, a common sign of dominance in fish; Huntingford et al. 1990; Ward et al. 2006). This appears to be at the cost of swimming performance. We cannot, however, conclude that the deeper bodied morphology gives a competitive advantage through burst swimming performance as burst swimming did not vary between treatments and was not correlated with morphology. This is likely due to the naiveté of hatchery-reared fish towards predation (Álvarez and Nicieza 2003; Pakkasmaa and Piironen 2001). Alternatively, interspecific interactions may be forcing Atlantic salmon into sub-optimal territories in the artificial streams. This may result in reduced access to resources and to faster-flowing water, a factor known to induce streamlined body shapes in salmonids (Finstad et al. 2011; Fu et al. 2013). This is plausible as these interspecific competitors have been shown to affect Atlantic salmon habitat use (Houde et al. 2015). Either way, the deeper bodied morphotype, induced by the presence of interspecific competition, led to a decrease in swimming performance which could have negative impacts on individual fitness in the wild. Juvenile Atlantic salmon prefer territories with faster water velocities (riffles) and fish with lower critical swimming speeds would not be able to hold this territory (Armstrong et al. 2003; Pakkasmaa and Piironen 2001).

The changes in morphology induced by competition that we observed in individuals' lifetimes may eventually result in an ecological character shift of stocked populations in the wild when competitors are present (Schluter 2000). Competition produced two distinct morphotypes

(fusiform or deep-bodied) which performed differently, and this could reflect differences in the amount of exercise and thus development of musculature that individuals experienced (Johnston et al. 2011; Lailvaux and Husak 2014; Palstra and Planas 2011). In the wild, this induced shape change in the presence of interspecific competition may result in individuals that are mismatched with regard to their preferred habitat (fast flowing riffles which are associated with high levels of invertebrate drift) which require a greater swimming performance to exploit (Finstad et al. 2011). Stream flow strongly influences the spatio-temporal distribution of fish and consequently, morphology and swimming performance limit the territories that individuals can occupy (Leavy and Bonner 2009; Peres-Neto and Magnan 2004). In the wild, Atlantic salmon with deeper bodies and consequently poorer swimming performance could be marginalised to poorer quality habitats and forced to switch to lower quality resources rather than incur injury through competition (DeWitt et al. 1998; Milinski 1982). Deviation away from this optimal habitat might then result in decreased fitness (Sih et al. 1985). To increase the fitness of Atlantic salmon in the wild and the success of stocking programs, interactions with competitors need to be minimised to ensure that morphology and swimming performance are optimised to the local environment (Diamond and Smitka 2005). This is particularly important in the case of Lake Ontario Atlantic salmon reintroductions which face competition from these non-native interspecific competitors. Information on factors that impede the establishment of a self-sustaining population of Atlantic salmon will aid in understanding the factors contributing to their successful reintroduction and re-establishment of a historical top aquatic predator in the Great Lakes.

Author contribution statement ADS carried out the data acquisition, data analysis, participated in the design of the study, and drafted the manuscript; ALSH participated in data acquisition and participated in the design of the study; BDN and PRPN both conceived and participated in the design of the study. All authors gave the final approval for publication.

Compliance with ethical standards

Conflict of interest We have no competing interests.

Ethics This study was approved by Université du Québec à Montréal's ethics committee.

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