Trophic niche overlap and abundance reveal potential impact of interspecific interactions on a reintroduced fish

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Abstract

Conceptually trophic niche overlap and species abundance can describe the strength and number of interspecific trophic interactions to determine the competitive impact on reintroduced species or other ecosystem changes. We use an example with young-of-year (YOY) Atlantic salmon (*Salmo salar*) reintroductions to determine if trophic niche overlaps and abundances limit restoration success. Using seasonal stable isotopes and abundance estimates for invertivorous fishes in three Lake Ontario tributaries, we assessed community isotopic structure, trophic niche overlap, and the impact of the niche overlap by incorporating relative abundance. Brown trout (*Salmo trutta*) YOY could be a strong competitor with a high trophic niche overlap with Atlantic salmon YOY but at lower abundances relative to Atlantic salmon minimizes impact. Stream resident fish communities appeared to partition resources across seasons such that abundant species had low trophic niche overlap to minimize overall competition with Atlantic salmon YOY given available resources, indicating niche complementarity. Through joint consideration of trophic overlap and abundance using our conceptual model, the competitive impact of community composition on a reintroduced species could be assessed.

Key words: stable isotopes; streams; salmonids; restoration; competition; Lake Ontario

Introduction

In aquatic systems, stocking fish to supplement wild populations and enhance fisheries occurs globally, and it is important to determine any limitations to stocking success (Minckley 1995; Brown and Day 2002; Molony et al. 2003). Removal of threats and having suitable habitat and food requirements are key factors to successful reintroductions (Harig et al. 2000; Cochran-Biederman et al. 2015). However, understanding a reintroduced species' interspecific interactions through potential competition can help determine biotic limitations to reintroduction success (Ewen and Armstrong 2007; Jachowski et al. 2016). The composition of the resident fish community may also influence the success of salmonid reintroductions (Harig et al. 2000; Scott et al. 2003; Cochran-Biederman et al. 2015). Not only can non-native species have negative influences on reintroduced species (Levin et al. 2002; Scott et al. 2003; Coghlan et al. 2007a) but so too can native species (Ward et al. 2008; Robinson and Ward 2011). Thus, existing resident species may be strong competitors with stocked species for food resources and/or habitat (Griffith et al. 1989; Schooley and Marsh 2007; Ward et al. 2008) and influence the outcome of the stocking.

The extent to which species overlap in trophic niches can indicate the degree of sharing of resources and potential interspecific competition (Hutchinson 1957), yet the intensity or impact of resource sharing and competition may in part be related to the abundance of the species involved, particularly in resource limited situations. Niche complementarity suggests that species co-exist by utilizing different resources (MacArthur and Levins 1967; Schoener 1974). However, few studies have assessed both niche partitioning and abundances simultaneously (e.g., Sugihara et al. 2003; Mason et al. 2008). When combining niche complementarity with abundance, there is evidence that abundant species would have low trophic niche overlap with each other, thereby minimizing competition for resources and enhancing ecosystem function (Sugihara et al. 2003; Mason et al. 2008). However, we do not know whether this holds true during ecosystem disruptions such as the addition of new species and estimating the potential competitive impact on a species may be important for ecosystem management and understanding community structure.

We provide a conceptual framework to estimate the potential competitive impact on a species of interest by combining the strength of interaction based on the degree of trophic niche overlap with the number of interactions from the other species' abundance (Figure 1). In our conceptual framework, both trophic niche overlap and relative abundances are on a continuous scale from low to high, however, we considered the relative abundance of species in a community to be high if it is greater than the relative abundance of the species of interest. If trophic niche overlap among species is low, then the strength of the interspecific interactions are weak (Figure 1, bottom quadrants) and although the potential number of interactions with an abundant species can be high or frequent, it would be an example of niche complementarity and the resident species would have low impact on the introduced species (Figure 1 – bottom, right quadrant). The lower the relative abundance of the resident species with low trophic niche overlap the lower the impact on the introduced species (Figure 1 – bottom, left quadrant), while less abundant species with high trophic overlap would have a low impact due to the limited, but strong interactions with the introduced species (Figure 1 – top, left quadrant). However, if an introduced species has a high trophic niche overlap with an abundant species (Figure 1 – top, right quadrant), then it implies strong, frequent interactions with a species, and therefore potential competition for resources and a strong impact which could be a limitation on the success of introduction. Incorporating the abundance of the species present in the system can influence our interpretation of the importance of a high trophic niche overlap.

Trophic niche overlap is frequently assessed using stable isotopes as they provide better estimates of trophic niches than stomach contents in describing longer term community or population structure (Peterson and Fry 1987; Layman et al. 2007; Jackson et al. 2011). Isotopic or trophic niche overlap has been previously used to assess diet partitioning between species and potential indicator for competition (Wang et al. 2018; Ogloff et al. 2019). Similarly, metrics have been used to describe the isotopic structure of the community (e.g., Layman metrics) and whether it varies among communities with different interspecific diet partitioning and trophic diversity (Layman et al. 2007; Sagouis et al. 2015). However, species abundance has yet to be incorporated into conventional trophic niche evaluations which leaves a gap in understanding the overall impact that the lack of diet partitioning may have on a species. Our conceptual framework (Figure 1) provides a way in which the number of interactions based on other species' abundances can be used in combination with the strength of isotopic trophic overlap to determine the resulting impact to a species. This framework can be applied to various scenarios in which changes in an ecosystem may warrant a better understanding of the trophic interactions and resulting potential competitive impacts to a species by including abundance, such as ecosystem disturbances or the addition of a species (e.g., native or invasive). Here, we use an example with a reintroduced species to assess conventional isotopic analyses with niche overlap and isotopic structure with resident species. We also incorporate species abundance with niche overlap to better understand the overall impact of the community on the reintroduced species.

A species that may be negatively influenced through trophic interactions with resident taxa is Atlantic salmon (*Salmo salar*) in Lake Ontario. Since Atlantic salmon extirpation in the

1890s, Pacific salmonids (*Oncorhynchus* spp.), among other species, have been introduced into Lake Ontario and elsewhere in the Laurentian Great Lakes, and different fish communities exist in the streams where Atlantic salmon young-of-year (YOY) are currently being reintroduced (Christie 1974; Crawford 2001). Studies have shown that non-native juvenile brown trout (*Salmo trutta*) and rainbow trout (*Oncorhynchus mykiss*; Stanfield and Jones 2003; Coghlan et al. 2007b) and native sculpin spp. (Gabler and Amundsen 2006) reduced growth and/or survival of Atlantic salmon YOY and can therefore be considered competitors with Atlantic salmon YOY and were a priori hypothesized to be potential competitors in Lake Ontario tributaries. Streams selected for Atlantic salmon reintroduction in the Lake Ontario watershed were chosen based on quality of suitable habitat (Stanfield and Jones 2003) but few studies have assessed the impacts of the local fish communities for potential competition for food resources (Johnson and McKenna 2015; Houde et al. 2016). Interspecific trophic competition may influence the growth, survival, and ultimately success of Atlantic salmon reintroductions in Lake Ontario. Thus, the stocking of Atlantic salmon YOY in Lake Ontario tributaries make for an ideal system to assess trophic interactions of a reintroduced species and the influence of the resident community.

Atlantic salmon YOY primarily consume aquatic macroinvertebrates (Keeley and Grant 1997; Coghlan et al. 2007a; Johnson 2013a, 2013b). By using stable isotopes to describe Atlantic salmon YOY diets, we can repeatability sample with non-lethal fin tissue (Sanderson et al. 2009; Hette-Tronquart et al. 2012) and determine how the trophic niche overlaps with the existing fish community of the same trophic guild. Dietary overlap with other salmonid and sculpin species may generate potential competition with Atlantic salmon YOY, and thus the degree of trophic niche overlap or trophic structure of different fish communities may influence Atlantic salmon reintroduction success. Diets within the fish community may also change seasonally depending on food availability. Convergences in diet may occur during times in which food resources are more limited, such as overwinter as seen with YOY rainbow trout, brown trout, and Atlantic salmon (Johnson et al. 2017). Yet fish can also converge in diets during times with greater prey abundances and resource subsidies, such as terrestrial arthropods falling into streams in the summer (Nakano et al. 1999; Kawaguchi et al. 2001). Thus, seasonal variation in isotopic niche overlap may further influence the competitive impacts on Atlantic salmon.

In this study, we examine whether the potential success of a reintroduced fish species in streams may be limited by a strong overlap in food resources with other species (interspecific competition), in particular abundant species. The objective of this study was to determine the degree of food resource overlap and potential competition within three different invertivore fish communities seasonally by assessing species abundance, the communities isotopic trophic structure, and trophic niche overlap with Atlantic salmon YOY stocked into Lake Ontario tributaries. We hypothesized that 1) streams with more potential competitors (e.g., YOY brown trout, rainbow trout, and adult sculpin spp.) would have greater niche overlap with Atlantic salmon YOY and a smaller, condensed isotopic trophic structure, and 2) the greatest overlaps/smaller, condensed isotopic trophic structure would occur overwinter due to limited food resources and in summer due to abundance of terrestrial inputs. Lastly, we would determine whether Atlantic salmon were impacted (by having high niche overlap with abundant species) by resident fish species, in particular by potential competitors. These results will help determine the trophic interactions and relative impact with a reintroduced species over time and whether they may pose limitations to the successful reintroductions of Atlantic salmon in Lake Ontario.

Methods

Study area

The trophic niches of the invertivore fish community were assessed in three tributaries of Lake Ontario after being stocked with Atlantic salmon YOY by the Ontario Ministry of Natural Resources and Forestry (OMNRF). The study sites - Cobourg Brook (44.0315° N, 78.1453° W), Credit River (43.8024° N, 79.9959° W), and Duffins Creek (43.9483° N, 79.0802° W) – have similar cobble, gravel, and boulder dominated sediments and forested riparian vegetation, yet different flows, stream widths, as well as variation in fish communities at each site (Table S1). The OMNRF has stocked these sites in previous years and some Atlantic salmon that did not smolt in the spring may still be present as yearlings. All three sites have salmonids present, however, in terms of the presence of literature-based potential competitors (i.e., YOY brown trout, YOY rainbow trout, and adult sculpin spp.), Cobourg Brook had the most with brown trout YOY, rainbow trout YOY and adult slimy sculpin (*Cottus cognatus*), Credit River was intermediate with brown trout YOY and adult mottled sculpin (*Cottus bairdii*), and Duffins Creek had no potential competitors present.

Field Sampling

Between May 3 - 16 of 2017 Atlantic salmon YOY were stocked by OMNRF Normandale Fish Culture Station (Turkey Point, ON Canada) throughout the length of the three sites. Ten Atlantic salmon YOY from Normandale Fish Culture Station were euthanized and frozen for later stable isotope analyses to establish hatchery stable isotope values. Following stocking, at each field site, sampling occurred four times: 3 weeks post-stocking (spring – May/June 2017), summer (July/August 2017), fall (October 2017), and early spring the following year (overwinter – March 2018). Stream width (m) and water velocity (m/s) were measured at a representative location for each sampling event. Sampling consisted of using a 3-pass electrofishing removal method to estimate fish community abundances throughout the entire stocking site. Using a backpack electrofisher (settings: 40 Hz, 250-450 V; make: Halltech Aquatic Research, Guelph, ON, Canada) and two netters, each pass started at the downstream end and worked upstream in a zigzag pattern, sampling all habitat types. All captured individuals were processed and held in aerated coolers with stream water until all three passes were complete prior to release. Fish processing involved identifying and counting all fish for each pass, and a subset of fish per species ($n < 20$) were measured for fork length (± 1 mm) and mass (± 0.1 g) and a small fin clip was taken from the upper caudal fin and stored frozen for later stable isotope analyses. We used fin as a non-lethal alternative tissue to muscle for stable isotope analyses to minimize impacting abundances through repetitive lethal sampling on small fishes over the seasons (Sanderson et al. 2009; Hette-Tronquart et al. 2012). Small freshwater fishes tend to have a strong linear relationship between fin and muscle, however, variation can exist across species (Sanderson et al. 2009; Hette-Tronquart et al. 2012; Hayden et al. 2017). Only potential invertivorous species with >5 individuals within a stream and occurring in at least two seasons were further analyzed (with one exception, brook trout (*Salvelinus fontinalis*) YOY in Duffins Creek that was only sampled in the fall). Species deemed to be primarily piscivores or herbivores as determined in the literature (Scott and Crossman 1998) were not included for further analyses.

Stable Isotopes Analyses

All fin clips were freeze-dried at -48°C for 48 h and cut to the appropriate size for weighing (600 – 800 µg) into tin capsules. Stable isotope analyses were completed using a Delta Plus isotope-ratio mass spectrometer (Thermo Finnigan, San Jose, CA, U.S.A.) coupled with an elemental analyzer (Costech, Valencia, CA, U.S.A.). Standard delta notation (δ) was used to express stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope ratios in parts per thousand (‰)

differences from a standard reference material as the following equation: $\delta^{13}C$ or $\delta^{15}N$= $[(R_{sample}/R_{standard} - 1)] \times 1000$ where R = $^{13}C/^{12}C$ or $^{15}N/^{14}N$, respectively. Atmospheric nitrogen and Vienna Pee Dee Belemnite carbonate were the standard reference materials for ^{15}N and ^{13}C, respectively. Precision was assessed by the standard deviation of replicate analyses of four standards (NIST1577c, internal lab standard (tilapia muscle), USGS 40 and Urea (n=125 for all)), which measured ≤0.22‰ for $\delta^{15}N$ and ≤0.22‰ for $\delta^{13}C$ for all the standards. Accuracy was based on the certified values of USGS 40 (n=125 for $\delta^{13}C$ and $\delta^{15}N$) analyzed throughout runs and not used to normalize samples, which showed a difference of -0.01‰ for $\delta^{15}N$ and -0.02‰ for $\delta^{13}C$ from the certified value. All stable isotope analyses were completed by the Chemical Tracers Laboratory at the University of Windsor's Great Lakes Institute for Environmental Research, ON, Canada.

Data were corrected for lipids since the elemental carbon-nitrogen (C:N) ratios in this study were above ≥ 3.4 for 94% of samples and ≥ 4 for 5% of samples. All samples with a C:N ratio >3.4, were lipid corrected using the Kiljunen et al. (2006) non-linear mathematical lipid normalization model with the Post et al. (2007) percent lipid calculation as recommended by Skinner et al. (2016).

Data Analyses

Age classes (YOY, yearling, adult) were assigned to salmon and trout based on length distribution curves in which distinct length-age classes were seen (generally YOY were <125 mm, yearlings were >150 mm and <250 mm, and adults were >250 mm but this changed throughout the seasons). Brook trout was the only species with adults included in the analysis, as diet can include macroinvertebrates while other adult salmonids either had too few samples to be included (e.g., rainbow trout) or were considered primarily piscivorous which was confirmed with elevated $\delta^{15}N$ (e.g., brown trout). Each lifestage for salmonid species were kept separated for analyses as YOY and yearlings can potentially be feeding on different items based on ontogenetic diet shifts (Keeley and Grant 1997; Mittelbach and Persson 1998).

To compare isotopic niche breadth between potential competitors (consumers of aquatic macroinvertebrates) and Atlantic salmon, we calculated the standard ellipse area for each species-lifestage in each stream and season using the SIBER (Stable Isotope Bayesian Ellipses in R) package in R (Jackson et al. 2011). We used the corrected version of the standard ellipse area (SEA_C), which contains ~40% of the isotopic data, thereby representing the core isotopic niche of each group while correcting for variable sample sizes (Jackson et al. 2011).

Using the maxLikOverlap function in SIBER, we estimated the maximum likelihood proportional isotopic niche overlap of Atlantic salmon YOY on species-lifestages (and species-lifestages niche overlap on Atlantic salmon YOY) within the same stream and season using species-lifestage-specific SEA_C. This provides two estimates of overlap depending on who is overlapping whom. For example, Atlantic salmon YOY could have 100% overlap with blacknose dace (*Rhinichthys atratulus*) whereas blacknose dace may only have 22% overlap with Atlantic salmon YOY depending on the position and size of each species-lifestage SEA_C. We included both overlap estimates to assess for trends. Spring was excluded from the seasons when comparing overlaps with Atlantic salmon YOY as the isotopic signature had not equilibrated to the stream diet at this time (i.e., isotopes reflected hatchery feed; see Supplementary Materials). This was to be expected as the isotopic value of fin can take approximately 2-3 months to equilibrate to their diet (or 4-5 tissue turnover half-lives) for rapidly growing, juvenile fishes (McIntyre and Flecker 2006; Heady and Moore, 2013). The log(x+1)-transformed proportion Atlantic salmon YOY overlaps onto species-lifestages (and vice versa) were compared among streams and season (excluding spring) with a two-way ANOVA without an interaction term as we were only interested in the main effects.

For each stream by season, the relative abundance of each species-lifestage was calculated by the catch per unit effort (CPUE; number captured per electrofishing seconds) divided by the total fish CPUE over the sampling event. To assess for any trends in the catches, both the total fish CPUE and the relative abundance of Atlantic salmon YOY were compared across streams and seasons using a two-way ANOVA (without an interaction). The relative abundance of each species-lifestage was then plotted by the trophic niche overlaps with Atlantic salmon YOY and each species-lifestage. Proportional trophic niche overlaps greater than 0.5 were considered high. Any species-lifestage relative abundances that were greater than the minimum relative abundance of Atlantic salmon YOY from all sampling events (0.12) was considered high. The relative competitive impact of each species-lifestage on Atlantic salmon YOY was estimated depending on where the species-lifestage falls relative to the conceptualized framework quadrants.

Using the species-lifestages mean δ^{13}C and δ^{15}N values, community-level niche space metrics (also known as Layman's metrics) were calculated for each stream by season following Layman et al. (2007) and adopting a Bayesian approach implemented by Jackson et al. (2011) using the laymanMetrics function in SIBER. The community (stream by season) was considered significantly different for a metric when the 95% Bayesian credible intervals did not overlap another stream by season. The following metrics were used: the total area of the convex hull, the mean distance to the centroid, the range of carbon and nitrogen (δ^{13}C range and δ^{15}N range, respectively), the mean nearest neighbour distance, and the standard deviation (SD) of the nearest neighbour distance. An in-depth description for each metric can be found in Layman et al. (2007). These metrics were used to indicate the total extent of carbon and nitrogen resources exploited by the community and the distribution of species-lifestages within the isotopic space.

All analyses were conducted in R version 3.6.1 (R Core Development Team, 2019) and significance was assessed at $\alpha = 0.05$ or whether 95% credible intervals did not overlap. Values are reported in mean ± SD. Assumptions of normality and homoscedasticity were visually assessed using qqplot and fitted versus residual plots.

Results

A total of 688 samples were analyzed for stable isotopes from the three tributaries collected between May 2017 to March 2018 over four sampling events. Atlantic salmon YOY sizes ranged from a minimum mean fork length of 55 ± 5 mm (Duffins Creek, May 2017) to a maximum mean fork length 117 ± 10 mm (Credit River, March 2018; Table S2). Atlantic salmon YOY were generally the most abundant fish in each stream for every season, followed by either slimy sculpin (Cobourg Brook), mottled sculpin (Credit River), or longnose dace (*Rhinichthys cataractae*; Duffins Creek; Table S2). The total CPUE did not vary by stream ($F_{2,6} = 5.139$, $P = 0.050$) but differed across seasons ($F_{3,6} = 19.133$, $P = 0.002$) in which total CPUE was lower overwinter ($P < 0.01$) than any other season ($P > 0.05$; Figure 2; Table S2). Further, the relative abundance of Atlantic salmon YOY did not vary by stream or season ($F_{2,6} = 3.595$, $P = 0.0941$; $F_{3,6} = 3.856$, $P = 0.0751$, respectively; Figure 2). The standard ellipse areas (SEAc) for each species-lifestage by stream and season showed a distinct separation of the initial spring Atlantic salmon YOY from all other fish from the same stream community and was fairly similar to hatchery conspecifics (Figure 3). However, by summer (fall for Cobourg Brook), Atlantic salmon YOY ellipses had isotopic signatures aligned with the stream community (Figure 3). Otherwise, no distinct patterns were evident (Figure 3).

The proportion of Atlantic salmon YOY isotopic niche overlapping with other species-lifestages niches within the same stream and season (excluding spring) ranged from 0 to 1 (Table S2). However, Atlantic salmon YOY overlaps with species-lifestages was not significantly different among streams ($F_{2,40} = 0.891$, $P = 0.418$) or seasons ($F_{2,40} = 0.724$, $P = 0.491$; Figure 4). The isotopic niche overlap of other species-lifestages onto Atlantic salmon YOY also ranged from 0 to 1 (Table S2). Similarly, species-lifestages overlapping with Atlantic salmon was not significantly different among streams ($F_{2,40} = 0.730$, $P = 0.488$) or seasons ($F_{2,40} = 0.721$, $P = 0.492$; Figure 4). Across all co-occurrences with Atlantic salmon YOY (with either Atlantic salmon YOY overlapping species-lifestages or vice versa), 28% ($n = 13$ of 45) had a high niche overlap (proportion > 0.5) with Atlantic salmon YOY, which primarily occurred in Credit River ($n = 6$) and Cobourg Brook ($n = 5$; Table 1). Atlantic salmon yearlings, blacknose dace, brown trout YOY and yearlings, rainbow trout YOY, and rainbow darter (*Etheostoma caeruleum*) all had a high niche overlap with Atlantic salmon YOY in at least one co-occurrence, and brown trout YOY had the greatest proportion of occurrences with a high niche overlap with Atlantic salmon YOY (Table 1). Brook trout adults and YOY, longnose dace, mottled and slimy sculpin, and white sucker (*Catostomus commersonii*) had low or no niche overlap with Atlantic salmon YOY (Table 1; Table S2).

When comparing the proportion of trophic niche overlap (Atlantic salmon YOY overlapping species-lifestages, and vice versa) to relative abundance of the species-lifestages, there was an absence of species-lifestages that had a high overlap with Atlantic salmon and high relative abundance (proportion > 0.12), aside from rainbow darter from Duffins Creek in which the relative abundance of Atlantic salmon in the same season (fall) was 0.4 (Figure 4; Figure 5). The majority of species-lifestages had low niche overlap with and low relative abundance to

Atlantic salmon YOY with a few instances with high niche overlap and low relative abundance or low niche overlap and high relative abundance (Figure 5).

When assessing the Bayesian Layman metrics among streams and seasons, there was a relatively consistent pattern difference in which spring for all three streams had higher $\delta^{13}C$ range and mean distance to centroid than the other seasons within the same stream. The mean nearest neighbour distance and SD of the nearest neighbour distance also showed the similar pattern with higher values in spring than the other seasons but it was not significantly different for Duffins Creek (Figure 6). The total convex hull area had high values in spring but it was not significantly different from at least one other season within the same stream. The $\delta^{15}N$ range did not show any apparent distinction between seasons or streams (Figure 6). There were no significant differences between stream communities for any of the Layman metrics.

Discussion

We assessed the trophic niches of stocked Atlantic salmon YOY in multiple streams over seasons to determine whether potential competition with resident fishes may be occurring in Lake Ontario tributaries. Streams with greater or fewer a priori hypothesized potential competitors such as brown trout, overall did not appear to influence the isotopic niche space of Atlantic salmon YOY in any season. Using conventional stable isotope analyses, brown trout YOY strongly overlapped with Atlantic salmon YOY, however, with the inclusion of their low abundance it would not be perceived to have a large impact on Atlantic salmon YOY population growth or survival, as seen in our conceptual model. Combining abundance with stable isotope analyses revealed the impact of trophic interactions on a reintroduced species and provided insights on potential competition. Stream fish communities partitioned available resources such that trophic interactions were reduced with the stocked Atlantic salmon YOY, as evidenced by the low isotopic niche overlap with abundant species. The low abundance of species-lifestages with a high niche overlap with Atlantic salmon YOY also indicates that there would be a low competitive impact to Atlantic salmon YOY populations. Further, there were no seasonal patterns (from summer to overwinter) in the relative overlap or niche size that would influence trophic interactions nor any changes in the relative abundance of Atlantic salmon YOY within the community. However, overwinter had the lowest total CPUE across streams due to low temperatures/conductivity which made electrofishing less effective. Across streams, the spring season had increased trophic niche breadth in the isotopic structure via Layman metrics, however, that was related to the isotope signatures of the stocked Atlantic salmon YOY not yet reaching dietary equilibrium with the stream from previous hatchery food. Our study suggests potential dietary competition from the invertivorous fish communities should not impact juvenile Atlantic salmon populations in these streams, particularly if juvenile Atlantic salmon are stocked in high abundances.

Isotopic niche overlap was not greater and isotopic structure was not smaller/condensed overwinter or summer relative to other seasons as hypothesized. Temporal reductions in food availability, like in winter, can increase niche overlap between species of the same trophic guild (Shustov et al. 2014; Sánchez-Hernández et al. 2016). Similarly, periods of high food availability, like in summer, can increase trophic niche overlap when species feed on similar abundant resources (Kawaguchi et al. 2001; Chen et al. 2011). With the abundant stocking of Atlantic salmon in streams, resources were likely limited during all seasons as abundant species-lifestages had distinct trophic niches and partitioned resources. Resource limitation in all seasons may explain the lack of seasonal differences in niche overlaps and isotopic structure.. Macroinvertebrate communities also change seasonally (Giller and Twomey 1993; Fierro et al.

2015), which will influence prey availability if fish species have certain prey preferences, and therefore degree of overlap with other fish may also be seasonally variable. As isotopes reflect a longer-term diet relative to stomach contents, as was seen during the post-stocking spring when Atlantic salmon YOY isotopes had yet to reflect stream isotopes, this method may not have been the most effective to capture shorter-term within season changes in diet. Instead investigating the stomach contents of invertivorous fish with the abundance and seasonality of macroinvertebrate can confirm resource limitation and further understand the seasonality of trophic niche overlaps with Atlantic salmon YOY.

Of the few species with high overlap with Atlantic salmon YOY, brown trout YOY had a high niche overlap with Atlantic salmon (and vice versa) for most of their co-occurrences. There may be competition for food resources with Atlantic salmon and brown trout YOY in Lake Ontario tributaries, however, it did not always occur in all seasons for some streams (e.g., Credit River – fall). Brown trout had more co-occurrences of high overlap with Atlantic salmon YOY than rainbow trout, potentially indicating that rainbow trout is not as frequent a competitor with Atlantic salmon YOY. Neither sculpin species had a high overlap with Atlantic salmon YOY suggesting they are not trophic competitors, as has been seen in other systems (e.g., Gabler and Amundsen 2006). Across multiple studies, when co-occurring, brown trout consistently reduced Atlantic salmon growth in artificial streams, while rainbow trout had variable results (Van Zwol et al. 2012; Houde et al. 2015a, b, 2017). Brown trout YOY have been shown to strongly compete with Atlantic salmon YOY for habitat resources (Armstrong et al. 2003) and feed on similar aquatic invertebrates (Dineen et al. 2007; Johnson and McKenna 2015). However, brown trout may feed more heavily on terrestrial invertebrates in Lake Ontario tributaries (Johnson and McKenna 2015), which may explain the one instance in which brown trout YOY did not highly overlap with Atlantic salmon and they fed on different seasonal prey. Our study indicates that competitive interactions between Atlantic salmon and brown trout likely exist, yet unlike other studies with equal abundances of both species (e.g., Van Zwol et al. 2012; Houde et al. 2015a, b, 2017), our systems had low relative abundance of brown trout YOY and high relative abundance of Atlantic salmon YOY such that the overall impact of any potential competition with Atlantic salmon YOY would be low.

Together, trophic niche overlap and abundance can reveal instances where resource sharing could infer competition and the resulting level of impact on a species. We used the example with Atlantic salmon YOY to show how combining trophic niche overlap and abundance indicated that there was no high impact towards reintroduction success. Abundance has not been utilized in conjunction with stable isotopes, however, by doing so one can infer the potential level of impact through competition for food resources that conventional analyses may not reveal. In all three streams, abundant species did not have a strong niche overlap with the abundant Atlantic salmon YOY, similar to the niche complementarity hypothesis, where abundant species have different niches (Mason et al. 2008). In our study, most species had relatively low abundance and low niche overlap or few, weak interactions, thereby partitioning resources and having no impact on Atlantic salmon (Figure 1 – bottom, left quadrant). Having a highly diverse prey community may result in such low levels of competition among species-lifestages (Sánchez-Hernández et al. 2017). A few species-lifestages, like brown trout YOY, had high trophic niche overlap yet low relative abundance and thus strong, but limited interactions and thereby minimal impact to Atlantic salmon (Figure 1 – top, left quadrant). Isotopic niche partitioning has been seen in other systems between fish from the same trophic guild (Dromard et al. 2015; Britton et al. 2018), however, inclusion of relative abundance may show that niche separation is greater between abundant species, as suggested with niche complementarity (Mason et al. 2008). Our methods and conceptual model for combining abundance and trophic niches can be applied in various circumstances in which an ecosystem exhibits a disturbance or addition of a new species (reintroduced or invasive) and could be applied towards other conservation related issues. More studies should incorporate abundance estimates into trophic studies to better understand the impact of interspecific relationships, as we showed here.

All three stream communities had similar community isotopic structure and species-lifestage niche overlaps with Atlantic salmon YOY, regardless of having greater or fewer potential competitors. Although there were more instances of co-occurring species-lifestages having high niche overlap with Atlantic salmon YOY in the streams with moderate and high potential competition (Credit River and Cobourg Brook, respectively) than the stream with no potential competitors (Duffins Creek), the overall mean niche overlap of the streams were similar across streams and seasons. From a fish community perspective, the isotopic structure was quite similar across all streams and seasons (excluding post-stocking spring). Thus, there was consistent partitioning of resources among invertivorous fish in the community across seasons and streams, even though the fish communities were different, implying some resource limitation was also occurring. Similar species occurring across streams (e.g., blacknose dace), may have different trophic niche overlaps with Atlantic salmon YOY, yet species partitioned food resources to minimize competition by having either low abundance and high niche overlap (Figure 1 – top, left quadrant) or high abundance and low niche overlap (Figure 1 – bottom, right quadrant). From a community perspective, each stream showed niche complementarity and responded similarly to the addition of Atlantic salmon YOY, regardless of the individual species present. Determining trophic niches and abundance relationships among species may help determine how species organize themselves within communities regarding resource partitioning of the more abundant species and changes in niche space, as well as ecosystem functions and resilience to change.

There were some limitations to this study largely related to sampling logistics. With assessments restricted to the post-stocking period, albeit repeatedly over the year, the community may have already shifted to reach a new equilibrium with the reintroduced species, and any response to strong competition (e.g., species with both high overlap and high abundance) had already dissipated. Future research should include a pre- and post-stocking assessment to better quantify how community structure changes or reorganizes following species introduction. Further, due to previous stocking in the streams, the fish community may have already shifted to a new equilibrium prior to this study. Assessing the competitive impact on streams which are stocked with Atlantic salmon YOY for the first time may provide insight on how communities shift with novel disturbances and the duration it may take to reach a new steady state. Using stomach content analyses could also determine immediate community changes with species disruptions, and whether there are stronger competitive impacts upon the disturbance but with lethal sampling could not determine changes over time. Improving upon the methodology of our study will further inform us on the ecological structure and resilience of communities with species reintroductions, among other ecological perturbations.

By sampling more streams, we could have assessed a more continuous gradient of community compositions, including an unstocked stream without Atlantic salmon. Although we tried to assess streams with different resident fish communities, and across seasons, some could argue only three sites to be a limitation. All three streams had similar species-lifestage niche overlaps with Atlantic salmon YOY and community isotopic structure, which indicates consistency across streams in response to a reintroduction. These streams also have similar habitat characteristics typical of those stocked with Atlantic salmon YOY (e.g., cold-water streams with gravel, cobble-boulder streambeds) across Lake Ontario (McKenna and Johnson 2005; Coghlan et al. 2007; Johnson 2013b). Thus, the streams assessed represented conditions Atlantic salmon YOY encounter across Lake Ontario. Future studies could try to incorporate more streams to determine if there are any community composition or habitat-related trends related to niche overlaps with Atlantic salmon and competitive impacts, as well as increase statistical power for different analyses. More importantly, this methodology of determining competitive impact was successfully applied to three different streams and will be beneficial towards assessing community changes with a new species or other disturbances.

In conclusion, we used Lake Ontario Atlantic salmon as an example to show how the inclusion of abundance estimates with trophic niche interactions can be used to assess the competitive impact of the resident community on a reintroduced species. Conventional stable isotope analyses alone may have concluded that brown trout YOY have a high impact on Atlantic salmon YOY, however, the impact was low when abundance was considered. As fish stocking will remain an important management tool, understanding the community impact on the reintroduced species is essential for managing reintroduction success. Our analysis suggests current practices of stocking Atlantic salmon YOY at higher density than resident salmonids is minimising potential competitive impact and thus not limiting the reintroduction of the species. Incorporating abundance improves our understanding of trophic interactions and potentially ecosystem functioning within the community. The stream fish communities assessed supported niche complementarity with low niche overlap among abundant species and Atlantic salmon YOY. Thus, our framework could be applied to other circumstances beyond species reintroductions such as to better understand potential competitive impacts on other species of interest, and determine whether these impacts influence community structure. It is important to understand species' interspecific interactions through potential competition to determine any biotic limitations that could affect community structure and resource partitioning, particularly with ecological disturbances and species additions.

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Tables

Table 1. The number of times a species-lifestage was captured simultaneously (or co-occurring) with Atlantic salmon young-of-year (YOY) across seasons (excluding spring) and the number and proportion of the 40% isotopic niche overlaps that were greater than 0.5, grouped by location and species-lifestages. Trophic niche overlaps refers to either Atlantic salmon YOY overlapping a species-lifestage or vice versa and was counted once per co-occurrence (e.g., if both methods of overlap were > 0.5 it was only counted once).

Location	**Co-occurrences**	**Overlaps > 0.5**	**Proportion of overlaps > 0.5**
Cobourg Brook	16	5	0.31
Credit River	16	5	0.31
Duffins Creek	13	2	0.15

Species-lifestages	**Co-occurrences**	**Overlaps > 0.5**	**Proportion of overlaps > 0.5**
Atlantic Salmon – Yearling	8	2	0.25
Brook Trout – YOY	1	0	0.00
Brook Trout – Adult	1	0	0.00
Brown Trout – YOY	4	3	0.75
Brown Trout – Yearling	2	1	0.50
Rainbow Trout – YOY	3	1	0.33
Rainbow Trout – Yearling	3	0	0.00
Blacknose Dace – Adult	6	3	0.50
Longnose Dace – Adult	5	0	0.00
Rainbow Darter – Adult	5	2	0.40
Mottled Sculpin – Adult	3	0	0.00
Slimy Sculpin – Adult	3	0	0.00
White Sucker – Adult	1	0	0.00

Figure captions

Figure 1. Conceptual interspecific interaction-abundance impact model based on trophic niche overlap between species X and other species in the community, and the relative abundance of other species in the community. Grey scale indicates potential level of impact to species X based on interaction strength of the niche overlap and number of potential interactions from other species' relative abundance if greater or lesser than relative abundance of species X, where light grey indicates negligible impact, grey is low to moderate impact, and dark grey is high impact.

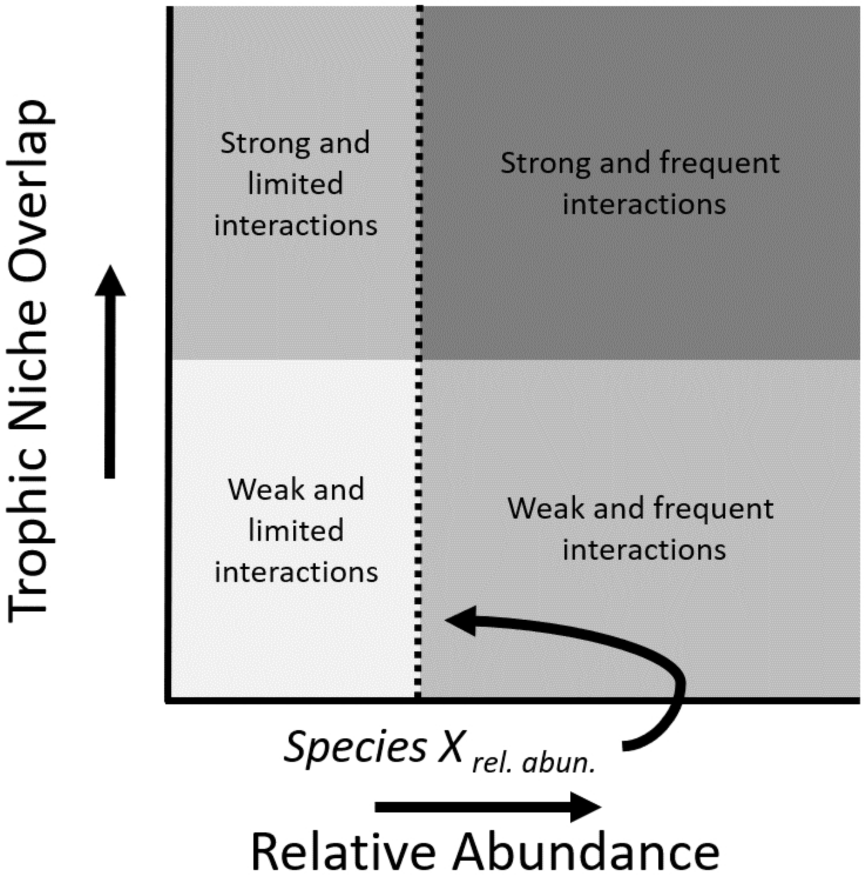
Figure 2. The A) total and species-lifestage catch-per-unit-effort (CPUE; number captured per electrofishing seconds) and B) relative abundance of species-lifestage in each stream (Co = Cobourg Brook; Cr = Credit River; Du = Duffins Creek) and season (Sp = spring; Su = summer; Fa = fall; Ow = overwinter). Stream barplots are segregated by black lines.

Figure 3. Stable isotope bi-plot of the isotopic niches of species-lifestages of invertivores in the fish community by season and location. Thick circles enclose standard (40%) ellipse areas for each species-lifestages. Hatchery Atlantic Salmon signatures are portrayed in spring for each location for reference.

Figure 4. Mean ± SE of the proportion overlap of the standard ellipse area with A) Atlantic salmon young-of-year (ATLS) overlapping species-lifestages (SL) and B) SL overlapping ATLS, by stream and season.

Figure 5. The proportion overlap of the standard ellipse area with A) Atlantic salmon young-of-year (ATLS) overlapping species-lifestages (SL) and B) SL overlapping ATLS by the relative abundance of SL. Grey scale indicates the potential level of impact to ATLS based on interaction strength of the niche overlap as depicted in Figure 1. High niche overlap is considered > 0.5, and the lowest relative abundance of ATLS across sampling events was 0.12.

Figure 6. Density plots showing the isotopic structure or Bayesian Layman's metrics (TA = total convex hull area; CD = mean distance from the centroid; NND = mean nearest neighbour distance, SDNND = standard deviation of the nearest neighbour distance) for the fish community in each stream (Co = Cobourg Brook, Cr = Credit River, Du = Duffins Creek) and season (Sp = spring, Su = summer, Fa = fall, Ow = overwinter). The black dots represent the mode and boxed areas reflect the 95, 75 and 50% credible intervals.



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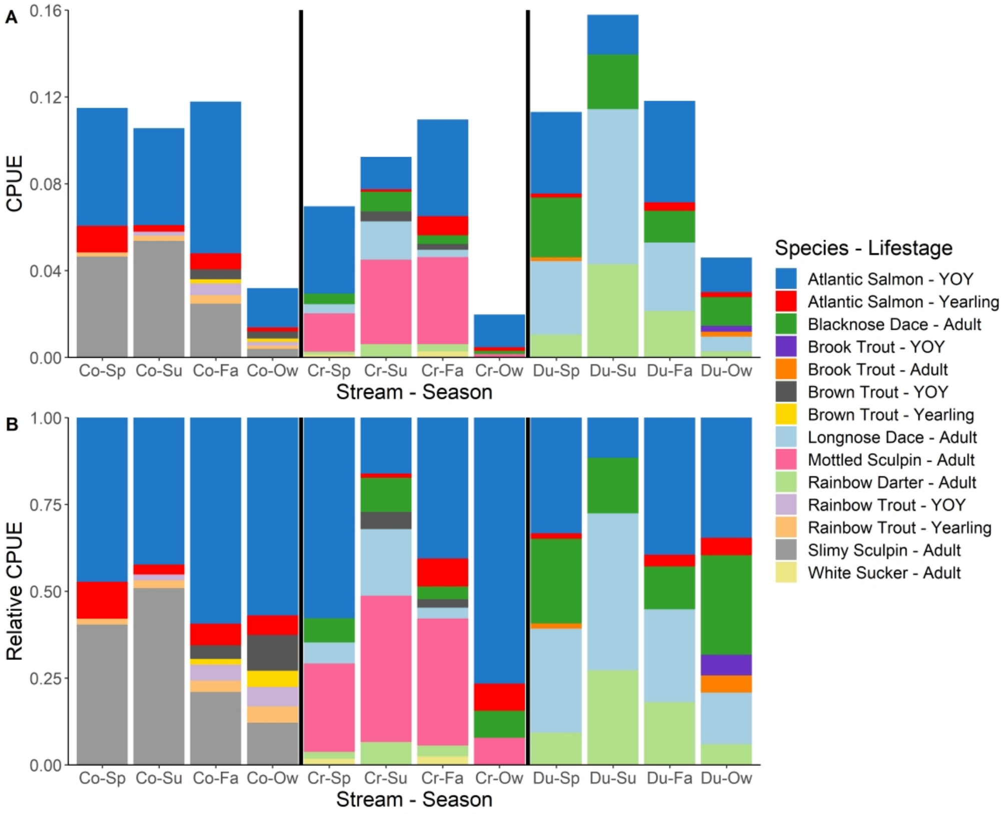

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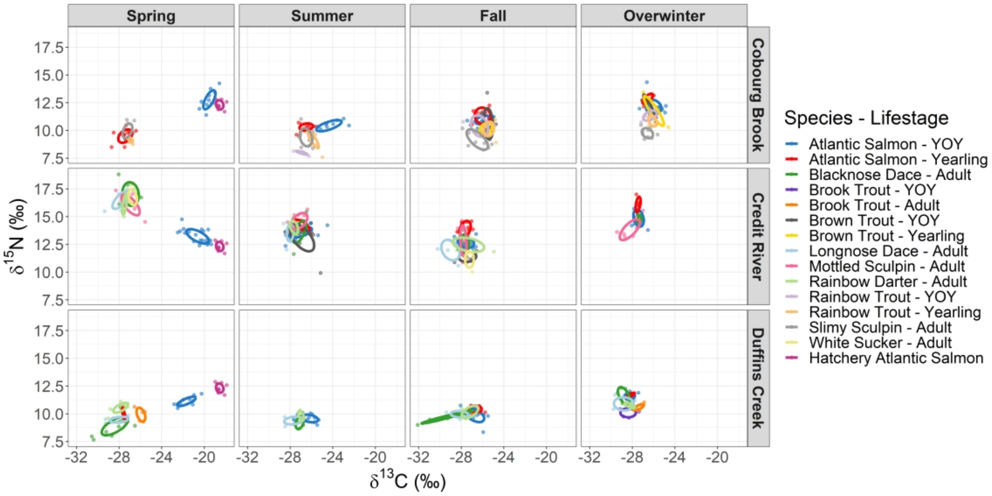

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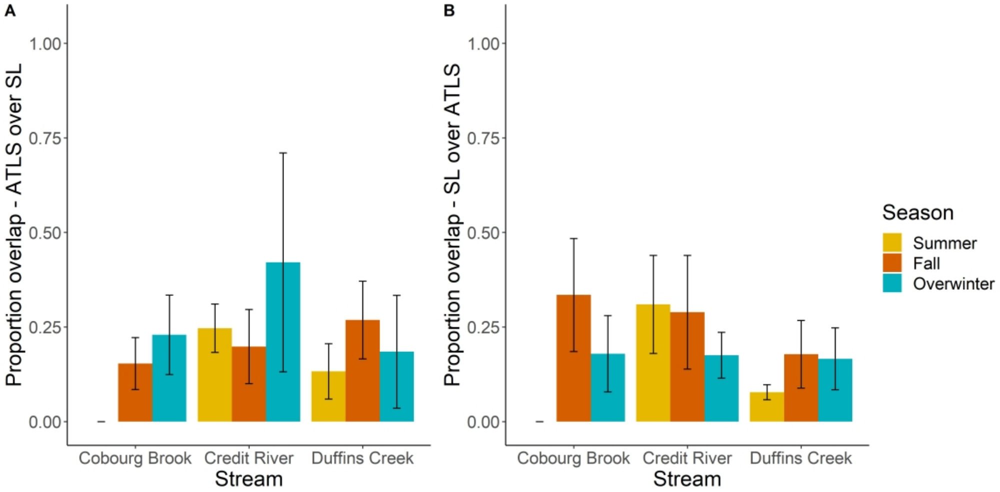

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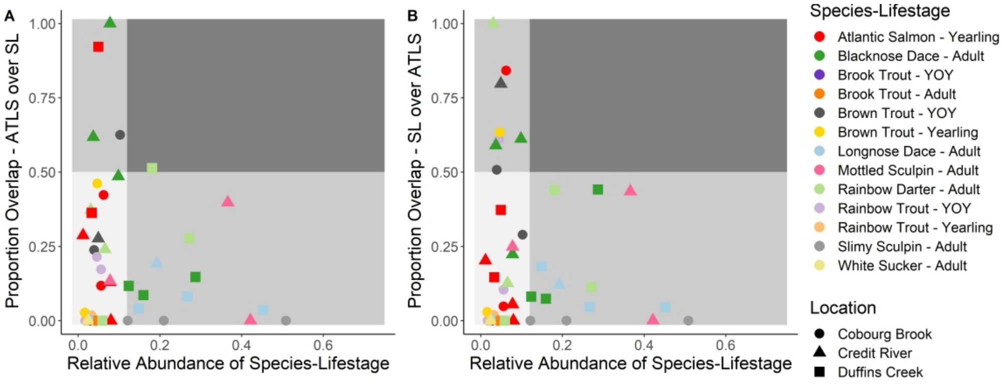

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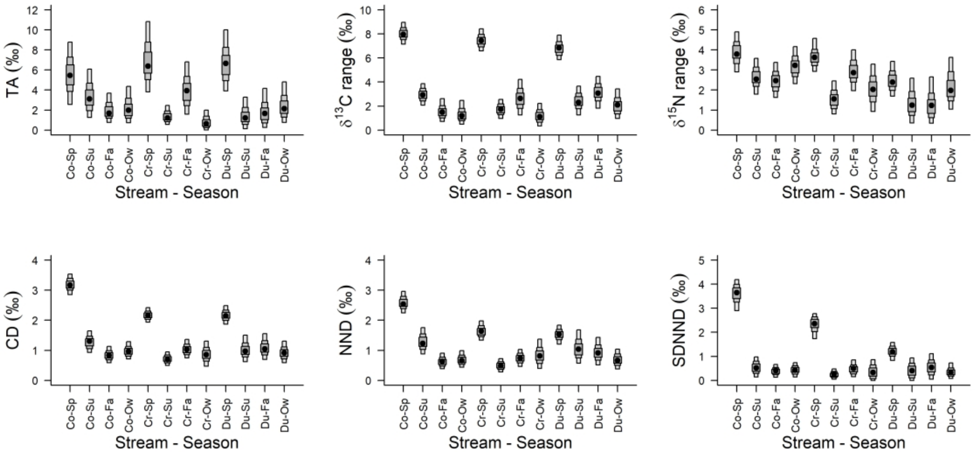

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