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Examination of the influence of juvenile Atlantic salmon on the feeding mode of juvenile steelhead in Lake Ontario tributaries

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ABSTRACT

We examined diets of 1204 allopatric and sympatric juvenile Atlantic salmon (*Salmo salar*) and steelhead (*Oncorhynchus mykiss*) in three tributaries of Lake Ontario. The diet composition of both species consisted primarily of ephemeropterans, trichopterans, and chironomids, although juvenile steelhead consumed more terrestrial invertebrates, especially at the sympatric sites. Subyearlings of both species consumed small prey (i.e. chironomids) whereas large prey (i.e. perlids) made up a higher percentage of the diet of yearlings. The diet of juvenile steelhead at the allopatric sites was more closely associated with the composition of the benthos than with the drift, but was about equally associated with the benthos and drift at the sympatric sites. The diet of both subyearling and yearling Atlantic salmon was more closely associated with the benthos than the drift at the sympatric sites. The evidence suggests that juvenile steelhead may subtly alter their feeding behavior in sympatry with Atlantic salmon. This behavioral adaptation may reduce competitive interactions between these species.

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Introduction

Historically, Atlantic salmon (*Salmo salar*) were a major component of the Lake Ontario fish community and represented the world's largest freshwater population of salmon (Webster, 1982). Because of a combination of anthropogenic factors including overfishing, pollution, and the damming of natal streams (Huntsman, 1944), Atlantic salmon were extirpated in the Lake Ontario watershed by the late 1800s. Huntsman (1944) and Parsons (1973) suggest that of all the factors contributing to the decline and extirpation of Atlantic salmon perhaps the major factor may have been eliminating access to spawning and nursery streams. Since their extirpation, periodic efforts have been made to restore Atlantic salmon in Lake Ontario, but these have been unsuccessful (Parsons, 1973).

In the Lake Ontario watershed, and throughout the Great Lakes basin, Pacific salmonids including Chinook salmon (*Oncorhynchus tshawytscha*), Coho salmon (*Oncorhynchus kisutch*), and steelhead (rainbow trout) (*Oncorhynchus mykiss*) have been stocked beginning in 1873 (Parsons, 1973). However, it was not until control of sea lamprey (*Petromizon marinus*) was achieved in the Great Lakes that survival of stocked Pacific salmonids greatly increased. By the 1970s, natural reproduction of these migratory salmonid species had been documented throughout the Great Lakes basin (Carl, 1982; Johnson, 1980; Stauffer, 1972). Evidence of substantial natural reproduction of Pacific salmonids in Lake Ontario tributaries likely indicates that habitat conditions may also be suitable for Atlantic salmon natural reproduction (McKenna and Johnson, 2005).

Although the fact that Pacific salmonids are reproducing naturally in several Great Lakes tributaries may provide evidence of improved habitat conditions, it may also suggest that restoration of Atlantic salmon may prove more difficult because of potential for interspecific competition. Historically, within the Lake Ontario basin, native brook trout (*Salvelinus fontinalus*) would have co-existed with juvenile Atlantic salmon in streams. Although brook trout are still present in many Lake Ontario tributaries, most populations are restricted to headwaters or are located above impassible barriers inaccessible to Pacific salmonids (Johnson, 2008). Competition between Atlantic salmon and Pacific salmonids may occur at the adult stage for spawning habitat (Scott et al., 2005) or at the juvenile stage for territories (Raffenberg and Parrish, 2003). At the juvenile stage, because of similar life histories, including stream residence time and habitat preferences, steelhead are thought to pose a major competitive impediment to Atlantic salmon restoration in Lake Ontario tributaries (Johnson and Wedge, 1999). Juvenile steelhead currently represent the most abundant salmonid in Lake Ontario tributaries (McKenna and Johnson, 2005; Stanfield and Jones, 2003).

Although several aspects of competitive interactions between juvenile Atlantic salmon and steelhead have been examined in Lake Ontario tributaries (Coghlan and Ringler, 2005; Dietrich et al., 2008; Jones and Stanfield, 1993), potential competition for microhabitat or food resources has not been examined. A considerable amount of

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literature exists on the diet and feeding strategies of juvenile Atlantic salmon (Erkinaro and Erkinaro, 1998; Martinussen et al., 2011; Wankowski and Thorpe, 1979) and steelhead (rainbow trout) (Dedual and Collier, 1995; Johnson, 1985; Riehle and Griffith, 1993). Although some studies have compared the diet and feeding strategies of juvenile Atlantic salmon (Mookerji et al., 2004; Thonney and Gibson, 1989) and juvenile steelhead (Johnson, 2007; Johnson and Ringler, 1980) with other salmonid species in sympatry, there has been no examination of the diets of these species where they co-exist.

The purpose of this study was to determine if the presence of juvenile Atlantic salmon affected the feeding strategy of juvenile steelhead in Lake Ontario tributaries. Specifically, the study sought to examine if a detectable shift in the foraging mode (i.e. benthic versus drift feeding) of juvenile steelhead occurred in the presence of Atlantic salmon. Salmonid diets were examined at sympatric sites (both species) and allopatric sites (steelhead only). Available prey items (drift and benthos) were also quantified in order to determine if differences in steelhead diets between sympatric and allopatric sites were due to differences in available prey and also to determine the main feeding strategy of those species at each site.

Methods

Three streams were selected for study; Orwell Brook, Trout Brook, and Little Sandy Creek. These three streams are excellent spawning and juvenile nursery streams for migratory salmonids ascending from Lake Ontario (McKenna and Johnson, 2005; Wildridge, 1990). In each stream two representative sites were chosen for sampling: an allopatric site (juvenile steelhead only) and a sympatric site (both juvenile steelhead and juvenile Atlantic salmon present). The allopatric site was located higher (1–3 km) than the sympatric site in each stream. Stream characteristics at sympatric and allopatric sites were similar in terms of substrate (mostly gravel and cobble), gradient, pool/riffle ratio, and riparian over story. Stream temperatures during summer seldom exceed 21 °C in any of the three tributaries.

The Atlantic salmon were stocked as fry in early May during the year prior to this investigation (Orwell Brook and Little Sandy Creek only) and again the following May. Fish were collected during July and August 2009 using a back pack electrofisher at both sites in each stream. Concurrent with juvenile salmonid collections, aquatic invertebrates were also sampled in each stream. Collections of aquatic invertebrates were made with drift nets (aperture 30.5 × 30.5 cm; mesh size 0.60 mm) and Surber samples (0.092 m^2; mesh size 0.75 mm) in order to represent all available prey and identify foraging behavior (i.e. drift versus benthic). At both sympatric and allopatric sites, five drift net samples and five Surber samples were taken at approximately the same time (i.e. 1000 h–1600 h) that fish collections were made. Drift nets were usually set 2–3 h before fish collections began and the nets sampled the entire water column. Both drift net and Surber samples were taken in riffle and run habitats. Upon collection, juvenile salmonids were preserved in 10% buffered formalin and Surber and drift net samples were each placed in one container containing 70% ethanol.

Juvenile salmonids were measured (total length in mm) before their stomachs were examined. Taxonomic identification of prey found in stomachs and in the drift and Surber samples was generally to the Family level for aquatic invertebrates and Order for terrestrial invertebrates. For the purpose of examining feeding strategies, emergent aquatic insects were considered to be terrestrial insects since they occurred mainly in the drift. Salmonid diets and the composition of the drift and Surber samples were quantified on the basis of dry weight (taxa dried at 105 °C for 24 h).

Similarity in the composition of benthic samples and drift samples between allopatric and sympatric sites in each stream, between the diet of juvenile salmonids, and between salmonid diets and the composition of the drift and benthic samples was determined using the equation of Morisita (1959) as modified by Horn (1966). Zaret and Rand (1971) consider values ≥0.60 to be indicative of significant biological overlap. To facilitate the comparison of differences between prey items of juvenile steelhead at the allopatric and sympatric sites, we grouped the identified taxa into aquatic and terrestrial categories. Percent composition was arcsin square root transformed to normalize the data set prior to analysis. We used paired *t*-tests (Statistix 8.0, Analytical Software, Tallahassee, FL) to examine if grouped taxa were different within each stream. An alpha value of $p < 0.05$ was set to represent statistical significance.

Results

A total of 1204 juvenile Atlantic salmon and steelhead were examined for diet analysis in the three streams (Table 1). Atlantic salmon fry had not been stocked in Trout Brook the previous year so only subyearling salmon, released during spring, were present when the study was carried out.

Available prey

Ephemeropterans (mainly baetids) were the major benthic taxa collected in the Surber samples in Orwell Brook and were closely followed by trichopterans (mainly hydropsychids) (Fig. 1). At both allopatric and sympatric sites in Trout Brook ephemeropterans and trichopterans were co-dominant in the Surber samples (Fig. 2). In Little Sandy Creek the primary benthic taxon collected was trichopterans (mostly hydropsychids) (Fig. 3).

Terrestrial invertebrates were the dominant component (46.6%–76.1%) of the drift samples at all six sites (Figs. 1–3). The major aquatic invertebrate taxon in the drift was ephemeropterans (11.5%–34.5%) which was dominated by baetids (5.5%–29.1%). There was a higher similarity in the composition of the benthos between allopatric sites and sympatric sites in the same stream ($\overline{x} = 0.85$) than in the composition of the drift ($\overline{x} = 0.67$) (Table 2) but both values exceeded the level that suggests biological significance.

Diet composition

Subyearling steelhead

Ephemeropterans and trichopterans were the two major prey groups consumed by subyearling steelhead at all sites. The contribution of ephemeropterans in the diet ranged from 24.2% (Trout Brook sympatric site) to 42.0% (Orwell Brook allopatric site). Baetids were the major family of ephemeropterans consumed by subyearling steelhead at all six sites and their contribution in the diet ranged from 24.0% (Trout Brook sympatric site) to 41.7% (Orwell Brook allopatric site). The other two prey groups that consistently ranked third and fourth in the diet of steelhead among the sites were terrestrial invertebrates and chironomids. Terrestrial invertebrates made up 14.3% (Little Sandy Creek allopatric site) to 25.0% (Trout Brook sympatric site) of the diet. Chironomids were generally the fourth ranked prey in the diet contributing from 13.8% (Orwell Brook allopatric site) to 22.6% (Orwell Brook sympatric site) (Figs. 1–3).

Yearling steelhead

Terrestrial invertebrates were the major prey of yearling steelhead at both allopatric (30.2%) and sympatric (36.4%) sites in Trout Brook and were consumed at all six sites (Figs. 1–3). Trichopterans were the chief prey (allopatric site 36.2%, sympatric site 40.1%) in Orwell Brook (Fig. 1) and Little Sandy Creek (allopatric 54.8%, sympatric 53.7%) (Fig. 3). Although hydropsychids were the main trichopteran family consumed by yearling steelhead in Orwell Brook, odontocerids contributed 36.7% (allopatric site) and 40.6% (sympatric site) of the diet in Little Sandy Creek (Figs. 1 and 3). With one exception (Orwell Brook sympatric site), perlids were consistently important (14.9%–23.6%) in the diet of yearling steelhead. Chironomids occurred in the diet at all six sites