

## Research Article

## Seasonal diet shifts and trophic position of an invasive cyprinid, the rudd *Scardinius erythrophthalmus* (Linnaeus, 1758), in the upper Niagara River

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### Abstract

Dietary shifts of invasive rudds *Scardinius erythrophthalmus* (Linnaeus, 1758) and food web structure of the upper Niagara River were examined. Stable isotope analysis (SIA) of liver tissue was used to test the hypothesis that rudds shifted their diets from piscivory during early spring months when macrophyte availability was low towards herbivory when macrophytes were abundant and warmer water temperatures facilitated digestion. Muscle tissue was used to evaluate the trophic position of rudds and other invasive species relative to native species. SIA revealed enriched  $\delta^{15}\text{N}$  and depleted  $\delta^{13}\text{C}$  in liver tissue of rudds during early spring months, suggesting a mostly piscivorous diet of pelagic origin when macrophyte availability was low, and depressed  $\delta^{15}\text{N}$  and elevated  $\delta^{13}\text{C}$  values during warmer summer months when littoral macrophytes were abundant. Analysis of muscle tissue from late summer indicated that rudds and other invasive fishes, including common carp *Cyprinus carpio* (Linnaeus, 1758) and goldfish *Carassius auratus* (Linnaeus, 1758), had similar trophic positions that may be attributed to their omnivorous feeding strategies. The ability of rudds to shift their diets from feeding on fishes of pelagic origin towards consuming littoral macrophytes is an adaptation that is likely to both facilitate invasion and create novel pathways of nutrient transfer among habitat types. Our results provide an increased understanding of the feeding ecology of the rudd and the role of this invasive species in the food web of the upper Niagara River.

**Key words:** omnivory, stable isotope analysis, liver tissue

### Introduction

The rudd *Scardinius erythrophthalmus* (Linnaeus, 1758) is a cyprinid native to Europe and western Asia, but humans have extensively expanded its distribution to include waters in Africa, North America, and New Zealand (Nico et al. 2014). During the late 19<sup>th</sup> century the rudd was purposely introduced to US waters as an ornamental species (Myers 1925) and later spread to other waters including the Great Lakes and their connecting channels due to its popularity as a bait fish (Crossman et al. 1992; Kapuscinski et al. 2012a, b). Though rudd populations are reported as low-density in many waters, Kapuscinski et al. (2012a) provided the first report of abundant rudd populations in Buffalo Harbor (eastern Lake Erie) and the upper Niagara River, where

rudds accounted for nearly half of the 14,130 fish captured in trap nets. A mark-recapture study conducted during 2012–2013 indicated that about 143,000 rudds (about 108 mt) were present in the upper Niagara River, at a density of about 32 rudds/ha or 0.024 mt/ha (Kapuscinski, unpubl. data).

Introductions of invasive freshwater fishes have had profound negative effects on aquatic ecosystem dynamics, so the unexpected abundance of rudds reported by Kapuscinski et al. (2012a) suggests possible need for future management actions. For example, the feeding behavior of introduced common carp *Cyprinus carpio* (Linnaeus, 1758) has been shown to negatively affect native aquatic macrophyte species through direct consumption, increased turbidity levels, and upheaval of nutrients originally deposited in

the benthos (Lougheed et al. 1998; Miller and Crowl 2006). Other invasive species like the round goby *Neogobius melanostomus* (Pallas, 1814) have been shown to displace native mottled scuplin *Cottus bairdii* from spawning habitat (Janssen and Jude 2001) and prey upon eggs, larvae, and adult life-stages of native fishes (French and Jude 2001). Rudds have contributed to undesirable changes in aquatic systems at both the community and ecosystem level. In New Zealand, abundant rudd populations altered aquatic macrophyte assemblages and promoted the spread of invasive macrophytes by selectively consuming native species (Lake et al. 2002; Hicks 2003). In addition, rudds may compete with native fishes for food resources like aquatic macroinvertebrates and fish, but rudds are also capable of supplementing their diet with algae and detritus (Garcia-Berthou and Moreno-Amich 2000)—food sources not commonly utilized by native fishes in north temperate North America. The rudd's ability to shift its diet based on food availability may be a substantial advantage over native species (Kolar and Lodge 2002; Shea and Chesson 2002; Marchetti et al. 2004), which may lead to declines in native species diversity and abundance. Furthermore, omnivorous species such as the rudd often translocate nutrients across habitat types (e.g., from pelagic to littoral areas; Vanni 2002), and the rudd's propensity to consume aquatic macrophytes creates novel trophic pathways in many of the ecosystems it invades, thereby liberating nutrients that would be otherwise sequestered in macrophytes or sediments. Acquiring knowledge about the feeding ecology of rudds will help resource managers understand how rudds affect invaded communities and implement an effective management framework. The objectives of this study were to (1) describe seasonal dietary shifts of rudds during May–October in the upper Niagara River, and (2) determine the trophic position and dietary carbon sources of common native and invasive species using stable isotope analysis (SIA).

## Methods

Rudds were captured from the upper Niagara River near the southern end of Grand Island using boat-electrofishing (Smith-Root boom shocking boat, pulsed DC, 500–1,000 V, 6–12 amps), provided by the New York State Department of Environmental Conservation. Three rudds were collected on each of seven dates, two dates during May (May 1 and May 28) and one date per

month during the rest of the sampling period (June 24, July 23, August 21, September 23, and October 21). Total length, weight, sex, and color (classified as olive or orange/gold) were recorded for each rudd. Water temperature was measured with a hand-held thermometer to the nearest 0.5 °C in the vicinity of where rudds were captured at about 0.3 m below the surface. Although these measurements did not capture fine-scale changes in water temperature, they were representative of the seasonal fluctuations occurring within the system and differed <1 °C from mean daily water temperatures recorded at five stations throughout the river (Kapuscinski, unpubl. data). Samples of emerald shiner *Notropis atherinoides* (Rafinesque, 1818; prey fish) and *Stuckenia pectinata* ([L.] Böerner, 1912; macrophyte) were collected during two different time periods to determine if isotopic values of putative, representative food items were stable over the sample period. Emerald shiners were collected near southern Grand Island by electrofishing on 20 June and by seining on 22 August, and *S. pectinata* was collected by hand on 10 July off the northern shoreline of Grand Island and on 22 August near southern Grand Island.

We used a variety of gears to collect three biological replicates of nine additional fish species (21–22 August), two macrophyte species (22 August), zebra mussels (*Dreissena polymorpha* [Pallas, 1771]; 22 August), and rusty crayfish (*Orconectes rusticus* [Girard, 1852]; 6 September) for food web analysis. Species were chosen to represent the most common native and invasive species from various trophic levels, and species-specific minimum length thresholds were used to ensure that adult specimens were collected. Fishes were collected near southern Grand Island using boat-electrofishing, except for emerald shiner and round goby, which were collected using a fine-mesh bag seine (9.4-m long and 1.6-mm mesh). Aquatic macrophytes (*S. pectinata* and *Vallisneria americana* [Michaux]) and zebra mussels were collected by hand while scuba diving near southern Grand Island, and baited minnow traps were used to collect rusty crayfish off the northwest shore of Grand Island. Larger specimens like common carp and river herring sucker *Moxostoma carinatum* (Cope, 1870) were processed immediately after collection, whereas all other specimens were stored individually in freezer bags and frozen for later processing. Liver tissue of rudds was dissected in a laboratory to remove the middle portion of the organ. Dorsal muscle tissue of fishes was removed from behind

the head and above the mid-line. To evaluate overall food web structure during late summer, SIA was conducted on dorsal muscle tissue of all fishes, tail muscle tissue of crayfish, fleshy tissue of zebra mussels, and stems and leaves of individual macrophytes. All samples were freeze-dried at  $-40^{\circ}\text{C}$  for 48–72 hours, homogenized using an agate pestle and mortar, and weighed out (typical mass  $\approx 1$  mg) into tin cups for SIA.

### Stable isotope analysis

Stable isotope analysis of liver tissue was used to examine seasonal dietary shifts of rudds because liver tissue has higher metabolic activity and turnover rate relative to muscle (Tieszen et al. 1983; Buchheister and Latour 2010). We assumed that the lipid content of rudd livers did not change substantially over the study interval, and therefore, did not adjust our observed isotope values using lipid-correction equations. Stable carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) isotope compositions of samples were measured at the Environmental Science Stable Isotope Laboratory at the State University of New York College of Environmental Science and Forestry using a Costech Elemental Analyzer coupled to a ThermoFinnigan Delta XL Plus stable isotope ratio mass spectrometer via a ThermoFinnigan Conflo III interface. Samples were analyzed in triplicate and accuracy and precision of the stable isotope measurements (expressed in the standard per mil notation relative to V-PDB for  $\delta^{13}\text{C}$  and atmospheric nitrogen for  $\delta^{15}\text{N} \pm \text{SD}$ ) were verified using National Institute of Standards and Technology RM8573 ( $\delta^{13}\text{C} = -26.4 \pm 0.1\text{‰}$  [ $n=38$ ],  $\delta^{15}\text{N} = -4.5 \pm 0.3\text{‰}$  [ $n=38$ ]), RM8574 ( $\delta^{13}\text{C} = +37.6 \pm 0.2\text{‰}$  [ $n=38$ ],  $\delta^{15}\text{N} = +47.6 \pm 0.3\text{‰}$  [ $n = 38$ ]), and RM8550 ( $\delta^{15}\text{N} = -29.8 \pm 0.1\text{‰}$  [ $n = 5$ ]). Daily precision of the instrument was verified by repeated analyses of internal laboratory standards including acetanilide ( $\delta^{13}\text{C} = -33.3 \pm 0.1\text{‰}$ ,  $\delta^{15}\text{N} = -1.1 \pm 0.1\text{‰}$  [ $n = 33$ ]), valine ( $\delta^{13}\text{C} = -10.6 \pm 0.1\text{‰}$ ,  $\delta^{15}\text{N} = -6.6 \pm 0.1\text{‰}$  [ $n = 7$ ]), and daphnia ( $\delta^{13}\text{C} = -24.5 \pm 0.1\text{‰}$ ,  $\delta^{15}\text{N} = +17.5 \pm 0.5\text{‰}$  [ $n = 7$ ]), during the sample runs.

### Data analysis

To examine seasonal dietary shifts of rudds, we separately compared  $\delta^{15}\text{N}$  values of liver tissue among sample dates and  $\delta^{13}\text{C}$  values of liver tissue among sample dates using one-way analysis of variance (ANOVA;  $\alpha = 0.05$ ; SAS 9.3, SAS Institute Inc., Cary, North Carolina) followed by

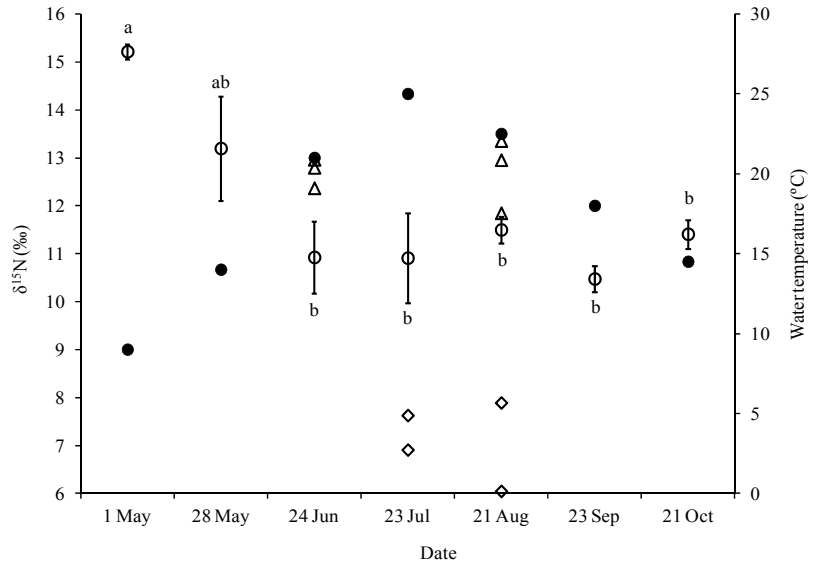
Tukey's Honestly Significant Difference test for multiple comparisons ( $\alpha = 0.05$ ). To determine food web structure of the upper Niagara River fish community, we compared  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values from muscle among species using two separate one-way ANOVAs followed by Tukey's Honestly Significant Difference test for multiple comparisons. Food web structure was visually evaluated using a stable isotope bi-plot based on mean  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values from the collected species. Mixing models were not used because the number of potential dietary sources was too large relative to the number of isotopes analyzed, and even use of Bayesian models would have yielded little useful information.

## Results

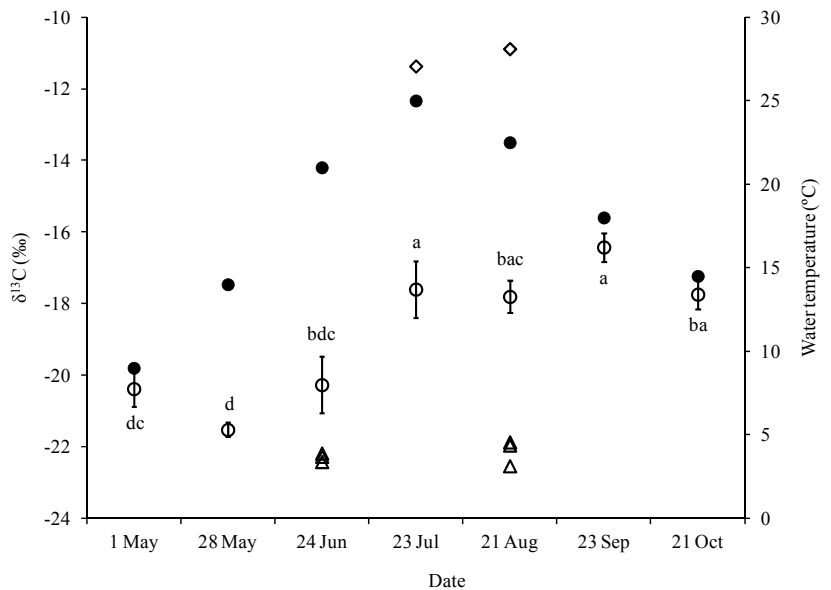
### Liver tissue analysis

The  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values of 21 rudd liver tissue samples (three samples from seven dates) were measured. Mean  $\delta^{15}\text{N}$  values ranged from a low of 10.9‰ in June to a high of 15.2‰ in early May (Figure 1). Mean  $\delta^{15}\text{N}$  values (ANOVA,  $df = 20$ ,  $F = 6.68$ ,  $P = 0.0015$ ) differed among months; Tukey's Honestly Significant Difference test determined that mean  $\delta^{15}\text{N}$  samples from May 1 were greater than those from the months of June through October, while samples from May 28 did not differ from other dates (Figure 1). Mean  $\delta^{15}\text{N}$  values were negatively correlated with water temperatures (Pearson's Correlation Coefficient =  $-0.7953$ ,  $P = 0.0325$ ; Figure 1). Mean  $\delta^{13}\text{C}$  values ranged from a low of  $-21.5\text{‰}$  in May to a maximum of  $-16.4\text{‰}$  in September (Figure 2) and differed among months (ANOVA,  $df = 20$ ,  $F = 12.05$ ,  $P < .0001$ ). In general, the  $\delta^{13}\text{C}$  values became more positive as the season progressed and water temperatures increased (Figure 2), but the correlation between mean  $\delta^{13}\text{C}$  values and water temperatures was not statistically significant (Pearson's Correlation Coefficient =  $0.4731$ ,  $P = 0.2836$ ). Mean  $\delta^{15}\text{N}$  values of emerald shiner (representative prey fish) did not differ between June (mean  $\delta^{15}\text{N} = 12.7 \pm 0.2$  SE) and August (mean  $\delta^{15}\text{N} = 12.7 \pm 0.5$  SE; paired t test,  $df = 2$ ,  $P = 0.977$ ), nor did mean  $\delta^{13}\text{C}$  values differ between June (mean  $\delta^{13}\text{C} = -22.3 \pm 0.1$  SE) and August ( $\delta^{13}\text{C} = -22.1 \pm 0.2$  SE; paired t test,  $df = 2$ ,  $P = 0.595$ ). Similarly, mean  $\delta^{15}\text{N}$  values of *S. pectinata* (representative macrophyte) did not change between July (mean  $\delta^{15}\text{N} = 7.3 \pm 0.4$  SE) and August (mean

**Figure 1.** Mean ( $\pm$  standard error)  $\delta^{15}\text{N}$  values of rudd liver tissue samples (open circles) and observed water temperatures (closed circles) from seven collection dates during 2013. Mean liver tissue values sharing the same letter are not statistically different. Note: open triangles represent observed  $\delta^{15}\text{N}$  values of emerald shiner dorsal muscle (representative prey fish) and open triangles represent  $\delta^{15}\text{N}$  values of *Stuckenia pectinata* (representative macrophyte).



**Figure 2.** Mean ( $\pm$  standard error)  $\delta^{13}\text{C}$  values of rudd liver tissue samples (open circles) and observed water temperatures (closed circles) from seven collection dates during 2013. Mean liver tissue values sharing the same letter are not statistically different. Note: open triangles represent observed  $\delta^{13}\text{C}$  values of emerald shiner dorsal muscle (representative prey fish) and open triangles represent  $\delta^{13}\text{C}$  values of *Stuckenia pectinata* (representative macrophyte).



$\delta^{15}\text{N} = 7.0 \pm 0.9$  SE; paired t test,  $df = 1$ ,  $P = 0.689$ ), nor did mean  $\delta^{13}\text{C}$  values differ between July (mean  $\delta^{13}\text{C} = -10.5 \pm 0.9$  SE) and August ( $\delta^{13}\text{C} = -10.1 \pm 0.8$  SE; paired t test,  $df = 1$ ,  $P = 0.126$ ).

#### Food web analysis

Mean  $\delta^{15}\text{N}$  (ANOVA,  $df=40$ ,  $F=50.39$ ,  $P<.0001$ ; Table 1) and  $\delta^{13}\text{C}$  values (ANOVA,  $df=40$ ,  $F=24.55$ ,  $P<.0001$ ; Table 1) from dorsal muscle of fishes, tail muscle of crayfish, soft tissue of

zebra mussel, and stem and leaves of macrophytes differed among species; Table 2 lists statistically significant differences among pairs of species as determined by Tukey's Honestly Significant Difference test. An isotopic bi-plot of mean  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values indicated that rudds (1) occupied a trophic position slightly above that of a primary consumer (higher  $\delta^{15}\text{N}$  value), similar to native brown bullhead *Ameiurus nebulosus* (Lesueur, 1819), emerald shiner, pumpkinseed sunfish *Lepomis gibbosus* (Linnaeus, 1758), and river redhorse sucker, and invasive common carp,

**Table 1.** Mean total length and standard error (SE) of fishes and crayfish, and mean, minimum, and maximum  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values from muscle of fishes and crayfish, soft tissue of zebra mussel, and stem and leaves of aquatic macrophytes. Three biological replicates of each species were collected from the upper Niagara River during 21 August–4 September 2013.

Species	Length (mm)		$\delta^{15}\text{N}$		$\delta^{13}\text{C}$	
	Mean	SE	Mean	Min, Max	Mean	Min, Max
Rudd	368	9	12.7	12.4, 13.4	-16.7	-17.4, -15.8
Common carp	627	15	11.6	11.5, 11.8	-16.9	-17.0, -16.8
Emerald shiner	60	2	12.7	11.8, 13.4	-22.1	-22.5, -21.9
Goldfish	207	9	12.2	11.8, 12.4	-15.7	-16.1, -15.4
Redhorse sucker	399	18	13.2	12.8, 14.0	-19.8	-22.6, -17.5
Round goby	111	2	13.3	13.2, 13.5	-17.0	-17.4, -16.6
Brown bullhead	246	8	12.8	12.3, 13.1	-16.9	-17.7, -16.3
Largemouth bass	353	12	15.9	15.4, 16.5	-18.8	-19.2, -18.3
Pumpkinseed	178	2	12.7	12.1, 13.5	-15.7	-16.1, -14.8
Yellow perch	219	9	15.2	14.6, 15.9	-18.9	-19.8, -17.8
Crayfish	77	3	10.5	9.4, 11.6	-14.7	-16.9, -11.4
Zebra mussel	–	–	8.9	8.6, 9.0	-22.0	-22.2, -21.9
<i>Stuckenia pectinata</i>	–	–	7.0	6.0, 7.9	-10.1	-10.9, -9.3
<i>Vallisneria americana</i>	–	–	7.1	6.8, 7.4	-10.0	-10.9, -9.5

**Table 2.** Pairwise comparisons of mean  $\delta^{15}\text{N}$  (above diagonal) and  $\delta^{13}\text{C}$  (below diagonal) for 14 species sampled from the upper Niagara River as determined by two separate one-way ANOVAs ( $\alpha = 0.05$ ) and Tukey’s Honestly Significant Difference Tests ( $\alpha = 0.05$ ). Note: \* denotes a statistically significant difference, whereas NS denotes a non-significant difference. SP = *Stuckenia pectinata*, VA = *Vallisneria americana*, ZM = zebra mussel, RC = rusty crayfish, RG = round goby, EMS = emerald shiner, GF = goldfish, CC = common carp, RRS = river redhorse sucker, BBH = brown bullhead, PS = pumpkinseed, YP = yellow perch, LMB = largemouth bass.

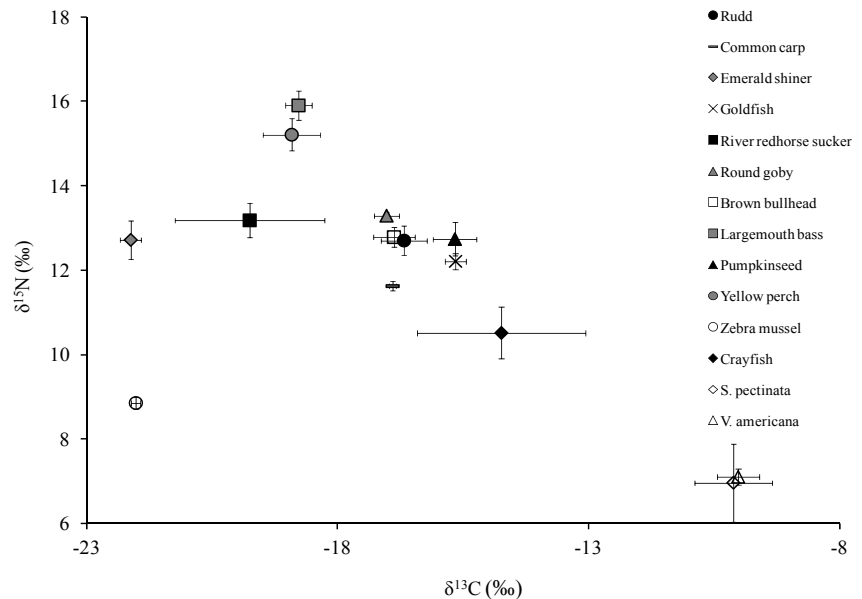
	RUDD	CC	EMS	GF	RRS	RG	BBH	LMB	PS	YP	ZM	RC	SP	VA
RUDD	-	NS	*	NS	NS	NS	NS	*	NS	*	*	NS	*	*
CC	NS	-	*	NS	NS	NS	NS	*	NS	*	*	NS	*	*
EMS	NS	NS	-	NS	NS	*	NS	*	NS	*	NS	*	*	*
GF	NS	NS	*	-	NS	NS	NS	*	NS	*	*	NS	*	*
RRS	NS	NS	NS	*	-	NS	NS	*	NS	*	NS	*	*	*
RG	NS	NS	NS	NS	NS	-	NS	*	NS	*	*	NS	*	*
BBH	NS	NS	*	NS	NS	NS	-	*	NS	*	*	NS	*	*
LMB	NS	NS	NS	NS	NS	NS	NS	-	NS	NS	NS	*	*	*
PS	NS	NS	*	NS	*	NS	NS	*	-	*	*	NS	*	*
YP	NS	NS	NS	NS	NS	NS	NS	NS	NS	-	NS	*	*	*
ZM	*	*	*	*	*	*	*	*	*	*	-	NS	*	*
RC	*	NS	*	NS	*	*	*	*	*	*	*	-	*	*
SP	*	*	*	*	*	*	*	*	*	*	NS	*	-	NS
VA	*	*	*	*	*	*	*	*	*	*	NS	*	NS	-

goldfish, and round goby, and (2) rudds utilized dietary carbon sources similar to the native brown bullhead and the invasive common carp and round goby (Figure 3). Although rudds occupied a trophic level below that of largemouth bass *Micropterus salmoides* (Lacépède, 1802) and yellow perch *Perca flavescens* (Mitchill, 1814), it should be noted that the rudds sampled were too large to be preyed upon by largemouth bass and yellow perch.

## Discussion

Our results from analysis of liver tissues indicate that rudds in the upper Niagara River may have shifted their feeding strategy from being mostly piscivorous in spring ( $\delta^{15}\text{N} = 15.2$  on 1 May) to being mostly herbivorous as the season progressed (mean  $\delta^{15}\text{N} = 11.0$  during 24 June–21 October). High  $\delta^{15}\text{N}$  values of liver tissues from early-season fish indicate that rudds fed at a higher

**Figure 3.** Isotopic bi-plot showing trophic position (mean  $\pm$  standard error  $\delta^{15}\text{N}$ ) and dietary carbon source (mean  $\pm$  standard error  $\delta^{13}\text{C}$ ) values of representative species from the upper Niagara River community during 21 August–4 September 2013. Three replicate of each species were collected, and samples were taken from muscle of fishes and crayfish, soft tissue of zebra mussel, and stem and leaves of aquatic macrophytes.



trophic level during the months of April and May, since enriched  $\delta^{15}\text{N}$  values are indicative of higher trophic positioning (DeNiro and Epstein 1981; Vander Zanden and Rasmussen 1999). The 4.2‰ difference in  $\delta^{15}\text{N}$  values of rudd livers from 1 May vs. 24 June–21 October is indicative of a shift of two trophic levels, since liver tissue of fishes is typically enriched by about 1.5‰ relative to the diet (Pinnegar and Polunin 1999). This shift of about two trophic levels is consistent with a change from piscivory to herbivory, occurring on the order of weeks to months, due to the faster turnover of liver tissues (Buchheister and Latour 2010). Gut content analysis of rudds collected in 2009 from the upper Niagara River (Kapusinski et al. 2012b) showed that diets included about 4% fish by weight during June and 5% during November; macrophytes and algae accounted for the remainder of their diets. In our study, the mean  $\delta^{15}\text{N}$  value of rudd muscle tissue (12.7‰) was 5.7‰ higher than the mean  $\delta^{15}\text{N}$  value of 7.0‰ observed for two macrophyte species. On average, bone-collagen and muscle tissue of herbivorous fishes exhibits a trophic-level discrimination ( $\Delta^{15}\text{N}$ ) of 4.78‰ (Mill et al. 2007), so rudds were slightly more than one trophic level above macrophytes in August. A difference of slightly greater than one trophic level between rudds and macrophytes in August may have resulted from rudds consuming fish or

other animal matter, or a time-lagged signal of spring piscivory by rudds due to the slower turnover time of  $\delta^{15}\text{N}$  in muscle tissue (Buchheister and Latour 2010). Furthermore, corresponding  $\delta^{13}\text{C}$  values of rudd liver tissues were depleted in spring, indicative of consumption of pelagic prey (France 1995a; France 1995b; Vander Zanden and Rasmussen 1999), such as emerald shiner and spottail shiner *Notropis hudsonius* (Clinton, 1824). Emerald shiner and spottail shiner, which consume pelagic zooplankton (Hartman et al. 1992; Pothoven et al. 2008), are abundant in the upper Niagara River during spring and readily consumed by rudds (M. Guinan, personal observation). Our results suggest that the contribution of higher trophic level prey, like fishes, may be particularly important to rudd growth, particularly in the spring months prior to a transition to a more herbivorous diet.

Mean  $\delta^{13}\text{C}$  values of rudd liver (-17.8‰) and muscle (-16.7‰) tissues indicated a mixed diet of pelagic (mean  $\delta^{13}\text{C}$  of emerald shiner = -22.1‰) and littoral (mean  $\delta^{13}\text{C}$  of *S. pectinata* and *V. americana* = 7.0‰) food sources. This was unexpected given the dominance of macrophytes previously observed in rudd guts (Kapusinski et al. 2012b), but may have resulted from rudds consuming small amounts of fish or other animal matter and time-lagged signals of spring piscivory due to the turnover time of  $\delta^{13}\text{C}$  in liver (50% at 20 d and 95% at 72 d) and

muscle (50% at 49 d and 95% at 298 d) tissues (Buchheister and Latour 2010). Decreases in mean  $\delta^{15}\text{N}$  values and corresponding increases in  $\delta^{13}\text{C}$  values indicate rudds transitioned to a littoral-based herbivorous diet (DeNiro and Epstein 1981; France 1995b; France 1995a; Vander Zanden et al. 1997) towards the end of May, which continued until at least our last sample date on 21 October. Isotopic values of emerald shiner (representative prey fish) were similar in June and August, as were isotope values of *S. pectinata* (representative macrophyte) in July and August, so changes in the isotopic values of rudd livers were most likely caused by dietary shifts rather than isotopic changes in food sources.

Increasing water temperature and more abundant macrophyte growth are the likely mechanisms that cued the transition to herbivory by rudds. Behrens and Lafferty (2007) suggested that a positive relationship exists between assimilation of plant material by omnivorous fishes and increased water temperatures. Fishes, including the rudd, typically lack organs for the fermentation of cellulose by microorganisms, so herbivory may only be energetically beneficial at elevated water temperatures when cellulolytic activity is at its peak in aquatic ecosystems (Niederholzer and Hofer 1979). Prejs (1984) concluded that macrophytes should comprise >50% of the diet of rudds when water temperatures are above 16 °C, and Kapuscinski et al. (2012b) reported that  $\geq 78\%$  of the diet of rudds was composed of macrophytes when water temperatures were >16 °C in the Niagara River, whereas only 36% of the diet was macrophytes in May when the water temperature was 14 °C. Our results indicate that the onset of herbivory by rudds in the Niagara River corresponded with water temperatures increasing from 14 °C in late May to 21°C in June. Colle et al. (1978) similarly reported reduced feeding intensity by herbivorous grass carp *Ctenopharyngodon idella* (Valenciennes, 1844) when water temperatures were below 14 °C. The abundance and growth of macrophytes increases with increasing water temperatures during spring and early summer in the upper Niagara River, so the presence of new macrophyte growth may also induce rudds to shift to a mostly herbivorous diet. Furthermore, rudds may have shifted to a mostly herbivorous diet to avoid predation by piscivorous fishes, such as northern pike *Esox lucius* (Linnaeus, 1758) and muskellunge *E. masquinongy* (Mitchill, 1824; Eklöv and Hamrin 1989), or to

avoid competition with other fishes for invertebrate food resources (Johansson 1987). A lack of prey fish should not have induced the shift to herbivory, as age-0 fishes are abundant in the upper Niagara River during July and August (Kapuscinski and Farrell 2014).

Kapuscinski et al. (2012b) provided evidence that rudds in the Niagara River fed intensely on aquatic macrophytes throughout the summer and fall, but results of our SIA of muscle indicates that rudds occupied a slightly higher trophic position in August than would be expected for a strict herbivore, and consumed some food from pelagic origins. As discussed above, the observed isotope values may have resulted from incomplete or inconsistent diet shifts by rudds (i.e., continued consumption of fish or other animal matter) or lag time in turnover of  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  in muscle tissue following a diet transition (Perga and Gerdeaux 2005; Buchheister and Latour 2010; Feiner et al. 2013). Regardless, it appears that rudds are (1) consuming prey fishes, thereby reducing the amount of prey fishes available to native piscivores, and (2) consuming prey from pelagic origins and translocating acquired nutrients to the upper Niagara River. Based on our results from SIA of liver and muscle tissues, it is apparent that the shorter turnover time of liver tissue provides a more accurate assessment of trophic position over short time intervals, making analysis of liver tissue valuable in the study of fishes that exhibit seasonal dietary shifts.

Our  $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$  bi-plot provides an indication of the food web structure in the upper Niagara River, in which rudds shared similar niche spaces with other abundant invasive fishes, such as common carp and goldfish. The success of these species in establishing populations can, in part, be attributed to their generalist feeding strategies (Marchetti et al. 2004; Feiner et al. 2013). Like rudd, common carp and goldfish are omnivorous (Garcia-Berthou 2001; Lorenzoni et al. 2007) and may demonstrate dietary shifts depending on availability of resources. In addition to the wide breadth of diet of these species, their ability to exploit resources not commonly utilized by native species (e.g., aquatic macrophytes) and occupy niches that avoid competition facilitates their successful invasions (Shea and Chesson 2002). Further research is warranted to elucidate how these invasive, omnivorous fishes alter or create novel trophic pathways and affect nutrient fluxes, e.g., by translocating nutrients across habitat types or liberating nutrients from macrophytes and sediments (Vanni 2002).

The negative effects of invasive common carp on water quality, macrophytes, and macroinvertebrates have been well documented (Lougheed et al. 1998; Parkos et al. 2003; Miller and Crowl 2006), as have the negative effects of invasive round goby on native fishes (Jansen and Jude 2001; Bergstrom and Mensinger 2009). In contrast, little attention has been given towards examining the effects of goldfish or rudds on invaded ecosystems in North America, despite their extensive human-induced range expansions. For example, an abundant rudd population may be capable of negatively altering aquatic macrophyte communities through selective feeding (Wells 1999; van Donk and Otte, 1996; Lake et al. 2002; Kapuscinski et al. 2014), and potentially hinder native fish populations by reducing availability of suitable spawning and nursery habitat. The potential effects of rudd in the upper Niagara River may be substantial given the relatively large abundance of the population (Kapuscinski, unpublished data). Research that elucidates the effects of this invasive population on ecosystem structure and function will be critical to the protection, restoration, and management of native fishes and their habitats.

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