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Seasonal abundance, diet, and energy consumption of round gobies (*Neogobius melanostomus*) in Lake Erie tributary streams

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Abstract – The invasive round goby (Neogobius melanostomus) is a benthic invertivore that has become established in many lake and river systems of Europe and the United States, especially within the Great Lakes basin. Multiple reports document its negative impact on benthic macroinvertebrates and fishes in lakes and recent studies show fish and invertebrate communities in streams are equally at risk. We assessed the seasonal abundance of round gobies and their summer diet composition in tributary streams to Lake Erie. Populations of round gobies in the lower reaches of two tributary streams peaked in abundance in early fall, were absent in late winter, and reappeared in early spring, suggesting a possible out-migration to the lake in winter. Population size distributions show a peak recruitment of young round gobies in July and low-level recruitment through October. In this study, round gobies obtained most of their energy from amphipods, chironomids, and caddisflies compared to other invertebrates, and midges were consumed in greater proportion than their availability suggesting a preference for these prey. As the stream lacked molluscs, large round gobies remained generalist invertivores without a diet shift to molluscivory as has been reported in lake studies. The observations on recruitment and abundance, and possible out-migration suggest the lower reaches of tributary streams may act as source populations for lake-bound round gobies. It may be possible to take advantage of this out-migration behaviour as a control strategy to capture large numbers of round gobies each winter.

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Introduction

The population size and range of the round goby, *Neogobius melanostomus* (Pallas 1814), in the Great Lakes watershed has grown substantially since their introduction in the early 1990s. Their population size recently was estimated at 9.9 billion fish in western Lake Erie alone (Johnson et al. 2005a). As lake populations have expanded, several studies have documented round gobies migrating into tributary streams in New York, Pennsylvania, Michigan, and Ontario (Phillips et al. 2003; Weimer 2003; Krakowiak & Pennuto 2008; Poos et al. 2009). Range expansion by this species also continues in many

European river systems (Copp et al. 2005; van Beek 2006). Tributary streams, rivers, and connecting canals are all potential pathways to inland lakes and reservoirs where, if introduced, round gobies are likely to have significant impacts on native fish and invertebrate communities (Jude et al. 1995; Charlebois et al. 1997; Kuhns & Berg 1999; Lederer et al. 2006; Krakowiak & Pennuto 2008; Poos et al. 2009).

Upstream migration of round gobies has implications for the ecology of streams and rivers. Krakowiak & Pennuto (2008) documented round gobies in four of eight Lake Erie tributary streams, and when present, round gobies constituted at least 50% of the fish caught. They reported streams with round gobies had reduced macroinvertebrate taxa diversity, macroinvertebrate richness, and nonDiptera:Chironomidae ratios compared to streams without round gobies. In the Great Lakes, Kuhns & Berg (1999) showed that when round gobies were excluded from zebra mussel beds, the density of nonmussel invertebrates was 44% higher than when round gobies were present. Additionally, Lederer et al. (2006) found that round gobies significantly reduced populations of zebra mussels, quagga mussels, isopods, amphipods, and snails in a study near Green Bay, Lake Michigan. Juvenile round gobies prey primarily upon macroinvertebrates, including both insect larvae and small crustaceans. As round gobies increase in size, they exhibit an ontogenetic diet shift at about 60-70 mm SL, switching to a predominantly mollusk-based diet (Jude et al. 1995; French & Jude 2001). This behaviour, in part, led Johnson et al. (2005b) to conclude that round gobies in Lake Erie's central basin were transferring significant new energy from the benthic zone to pelagic predators. Round goby impacts on stream macroinvertebrate communities and energy dynamics may be particularly significant since streams are devoid of dreissenid mussels.

Several studies have shown stream-dwelling round gobies have broad diets dominated by macroinvertebrates, especially chironomid larvae (Phillips et al. 2003; Weimer 2003; Carman et al. 2006) and amphipods (Copp et al. 2008). It is still unclear from these studies if round gobies are indiscriminant foragers, consuming prey based on its abundance in the habitat or exhibit some prey preference. Carman et al. (2006) showed diel shifts in diet composition of round gobies in the Flint River, Michigan which tracked activity patterns of the benthos. Similarly, Copp et al. (2008) showed a strong preference for amphipods in the River Danube. As many species of stream fishes such as rainbow trout (O. mykiss), darters (Etheostoma sp.), logperch (Percina caprodes, Rafinesque), or mottled sculpins (Cottus bairdi, Girard) rely on macroinvertebrates as their food source as well, round goby impacts on macroinvertebrate community composition may have detrimental effects on various stream fishes. Round gobies have already been implicated in the decline of mottled sculpins in the St. Clair River and southern Lake Michigan (Jude et al. 1995; Jude 1997), johnny darters (Etheostoma nigrum, Rafinesque) in Lake Michigan (Lauer et al. 2004), and rainbow darters in Lake Erie tributary streams (Krakowiak & Pennuto

Although several studies have examined round goby presence in tributary streams and rivers of the Great Lakes (Phillips et al. 2003; Weimer 2003; Carman et al. 2006; Krakowiak & Pennuto 2008; Poos et al. 2009), all studies to date were performed during the summer months. Very little is known about the presence of round

gobies during the colder months of the year. Round gobies in lake habitats are thought to undergo seasonal migrations, moving to deeper offshore areas during winter and residing in nearshore areas during the rest of the year (Charlebois et al. 1997; Sapota & Skóra 2005). It is unknown whether or not round gobies perform a similar migration in tributary streams, moving into deeper pool areas or even migrating back into the lakes during the colder months.

To better understand the potential impacts of round gobies in streams and rivers, we assessed their seasonal abundance and energy consumption in tributary streams to Lake Erie. The primary objectives of this study were: (i) to determine if round gobies were present in tributary streams throughout the year, (ii) to assess their seasonal size distribution, and (iii) to document their prey preference and energy consumption. Basic seasonal abundance and size distribution data will help resource managers understand whether round gobies are using tributary streams as reproductive areas or simply as travel corridors to inland waters. Knowledge of diet composition and energy content can provide insights into the likelihood of round goby diet competition with other invertivores and the likelihood of round gobies disrupting energy flow or transfer in stream ecosystems.

Methods

Seasonal abundance

Monthly fish sampling was performed on Eighteen Mile and Big Sister Creeks, New York (42°41.693°N; 78°56.015°W and 42°39.429°N; 79°02.155°W, respectively) between April 2006 and February 2007 to determine if round gobies inhabited the lower reaches of streams throughout the year. We sampled the same 100 m reach on each stream using a Coffelt Electronics BP-6 backpack electroshocker (170 V, 500 pps, DC-pulse) for up to 1000 s or until about fifty round gobies were collected. These fish tend to swim under the nearest rock when disturbed, making them very catchable during electrofishing bouts. Our technique entails shocking a rocky area and simultaneously lifting the larger rocks with the foot, allowing the current to wash stunned fish into the catch net (5-mm mesh, 35-cm wide D-net).

Sample sites were located upstream of any lake effects to prevent sampling within the drowned tributary mouth (Fig. 1). Sites sampled were approximately 2.0 and 1.0 km upstream from the Lake Erie shoreline at Eighteen Mile and Big Sister Creeks, respectively. At these locations, streams were of similar physicochemical condition (Table 1). Water temperature, dissolved oxygen, and conductivity levels were very similar in both streams in all months.

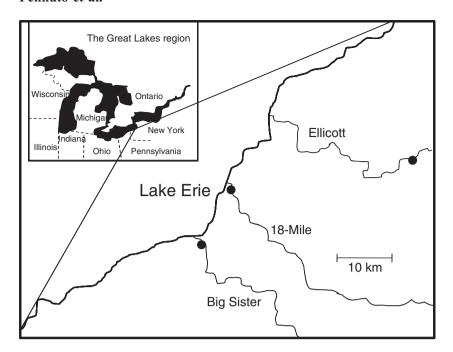


Fig. 1. Location of Lake Erie tributary streams sampled for round goby seasonal abundance (Eighteen Mile Creek and Big Sister Creek) and diet and energy consumption (Ellicott Creek).

Table 1. Midsummer (July) physicochemical characteristics of streams sampled for goby abundance and diets.

Stream feature	Big Sister Creek	18 mile Creek	Ellicott Creek
Temperature (°C)	16.6	24.8	18.3
pH	8.2	7.8	8.1
Turbidity (NTU)	2.5	0.4	1.9
Conductivity (μ S·cm ⁻¹)	713	576	520
Mean width (m)	23.4	25	27.1
Mean velocity (m·s ⁻¹)	0.19	0.13	0.15
Mean depth (m)	0.43	0.22	0.14
% Canopy cover	26.5	0	0
% Bedrock and cobble bed	10	38	60

The turbidity levels in both streams were highest in the spring and declined through early fall (September).

Round gobies were weighed to the nearest 0.1 g using a portable field balance, measured (TL), finclipped (second dorsal fin removed), and returned to the stream. However, we obtained no recaptures over the duration of the field study, preventing us from estimating population sizes in these streams. Thus, monthly catch per unit effort (CPUE) and size distribution of round gobies were estimated and compared between streams. Fish total length was compared between streams and dates using a 2-factor ANOVA and monthly CPUE was compared using a 2-factor ANOVA without replication. All analyses were performed using SPSS 16.0 software.

Round goby diet

Round goby gut content composition was compared to benthic macroinvertebrate communities in Ellicott Creek. We targeted a different stream for this assessment to prevent impacting the monthly electrofishing study. The sample reach was located approximately 15 km upstream from the Niagara River (Fig. 1). Twenty-five round gobies were collected in July 2007 by electroshocking a 100-m stretch of stream. All round gobies were measured (TL), weighed, and preserved in 90% ethyl alcohol in the field and returned to the lab. The digestive track of each round goby was dissected out from mouth to anus and all of the contents were identified using a microscope at 40× magnification. Most items were identified to family level.

Ten replicate Surber samples (0.093 m², 0.5 mm mesh), were collected from riffle habitats where most round gobies were sampled. All macroinvertebrates and debris collected in the samples were preserved in 90% ethyl alcohol and returned to the lab. All macroinvertebrates were sorted and identified to genus, but later combined to the same taxonomic level as the gut content samples, typically family level. Invertebrates were identified using keys of Peckarsky et al. (1990) and Merritt & Cummins (1996).

Stomach contents of round gobies were compared to the community composition data generated from the Surber samples. A log-likelihood goodness-of-fit test (Manly et al. 1993) was used to examine if the occurrence of consumed prey differed from a random expectation based on the occurrence of the same taxa in the stream using $\alpha = 0.05$. Expected consumption was determined by calculation of 95% confidence intervals on consumed prey. A Bonferroni adjustment to the α level used in generating confidence intervals was made by dividing α by m, the number of prey

types used in the final goodness-of-fit test (Manly et al. 1993).

Energy consumption

Energy consumption by round gobies in Ellicott Creek was estimated using a Parr bomb calorimeter (Model 1356, Moline, Illinois). Macroinvertebrate prey were collected using kick nets (0.5-mm mesh) from riffle habitats where most round gobies were collected. Kick nets were used as we sought to maximise the number of invertebrates collected. Samples were placed in white sorting trays and picked live into individual vials with stream water. Samples were returned to the lab and a subset of individuals (n = 6-10, depending on availability) were blotted live on paper towels and placed in tared aluminium weigh boats to obtain wet weights (0.1 mg). These were then oven dried at 60 °C for 72 h to obtain dry weights. These samples were used to determine the mean biomass of live invertebrates for converting counts of items in round goby guts to energy equivalents. The remaining macroinvertebrates were placed in tared aluminium weigh boats by taxonomic group and dried at 60 °C for 72 h.

After drying, enough invertebrate sample was added to the calorimeter vessel to obtain a complete firing (~0.5 g dw). Sample sizes for the invertebrate groups analysed for calorimetric analysis ranged from 1 to 10, based on the availability of macroinvertebrates at the time of collection (Table 2). Dry weight caloric content (kJ·g⁻¹) was converted to wet weight caloric content based on % water determinations from the 10-organism subsample. Total energy available per taxon per m² was determined as the product of taxon caloric content (kJ·g⁻¹), mean benthic density obtained from the Surber samples, and mean weight per individual taxon. Round goby per capita daily energy consump-

Table 2. Field density and diet composition of the most common prey items found in the guts of round gobies from Ellicott Creek.

Taxon	Mean #·m ^{−2} in field (SE)	Mean # in guts (SE)	# Guts
Chironomidae larvae	1444.6 (31.6)	23.8 (6.7)	25
Chironomidae pupae	71.0 (11.2)	1.1 (0.1)	9
Mollusca	23.7 (0.8)	1.4 (0.2)	11
Amphipoda	88.3 (3.3)	2.7 (0.7)	22
Elmidae	1107.7 (37.7)	1.8 (0.5)	8
Hydropsychidae	17.3 (0.6)	1.2 (0.2)	6
Psephenidae	17.2 (0.6)	0	0
Isopoda	6.5 (0.6)	0	0
Turbellaria	15.1 (0.5)	0	0
Ephemeroptera	14.0 (2.6)	0	0
Simulidae	116.3 (5.4)	0	0
Other	17.0 (1.1)	1.9 (0.5)	15
Total	2933.3 (478.9)	33.9 (3.0)	

Field abundance estimated from 10 replicate Surber samples. The number of guts examined = 25.

tion per prey taxon (kJ·goby⁻¹·day⁻¹) was determined from the product of the caloric content per prev taxon and mean biomass per individual taxa in the gut. We did not weigh the gut contents of fish for energy estimates as items often were partially or nearly digested. Identification of prey was possible using undigested parts like chironomid head capsules. We used the mean weight of the 10-organism, calorimetry samples to estimate the biomass of each taxon within the gut. We assumed gut contents reflected consumption over the last 8 h based on gut analyses of round gobies in the Flint River by Carman et al. (2006). Thus, the initial value for per capita daily energy consumption was multiplied by 3 to obtain a 24-h value. To provide a rough estimate of round goby impact on stream energy flow, we divided per capita energy consumption by energy available per m².

Differences in energy content per invertebrate taxa were investigated using a one-way ANOVA with $\alpha = 0.05$. Only taxa with >1 bombed sample were included in the analysis. All data were $\log(x+1)$ -transformed to meet variance assumptions. An adjusted Bonferroni ($\alpha = 0.007$) was used to test for *post hoc* differences among means.

Results

Seasonal abundance

Eighteen Mile and Big Sister Creeks were sampled on a monthly basis during the open water season, between April 2006 and February 2007. Eighteen Mile Creek froze over in late December and was not sampled in January due to heavy ice cover. Big Sister Creek froze over in mid January and was not sampled in February. Peak water temperatures occurred in July in both of the streams and were lowest in January, before beginning to rise again (Fig. 2).

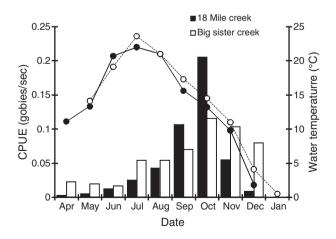


Fig. 2. Monthly abundance [catch per unit effort (CPUE)] of round gobies and water temperature in two Lake Erie tributary streams.

The total catch of round gobies increased from April to October in both streams and round gobies were more abundant in Big Sister Creek in all months except September and October (Fig. 2). The maximum CPUE (gobies·s⁻¹) in Eighteen Mile Creek was nearly double the maximum CPUE in Big Sister Creek (0.21 vs. 0.12, respectively). Populations peaked in October in both streams, declined most in Eighteen Mile Creek after water temperatures were below 15 °C, but did not decline in Big Sister Creek until temperatures were below 5 °C (Fig. 2). CPUE varied significantly by month ($F_{7,8} = 4.110$; P = 0.031), but not between streams ($F_{1.8} = 0.259$; P = 0.624).

The size of round gobies collected in both streams changed as a function of month $(F_{7.522} = 11.26;$ P < 0.001), and there was a significant date-by-stream interaction term in our ANOVA analysis of total length $(F_{7.522} = 2.19; P = 0.033)$, indicating that total length changed differently in the two streams per month. In May through August, the mean length of fish in Eighteen Mile Creek was less than the mean length in Big Sister Creek, whereas in September through December this pattern was reversed. Medium (40–59 mm) and large (≥60 mm) round gobies were the dominant size classes in both streams during May and June (Fig. 3). During July, an influx of small round gobies (<40 mm) indicated the recruitment of new young-of-the year (YOY). We observed egg-laden females in the June samples, supporting in-stream production of young. Within 1 month, the smallest round gobies were >40 mm and there was an absence of fish <40 mm in August. A second influx of small round gobies (<40 mm) appeared in September indicating a potential second spawning event. No fish were collected from Big Sister Creek in January (Fig. 3).

Diet composition

The number of items in the guts ranged from 6 to 181 (mean = 28.8) and no fish had an empty gut (Table 2). The gobies collected were separated into two size classes, small (<60 mm) and large (≥60 mm), representing the presumed length at which an ontogenetic diet shift should occur. The mean number of prey in the guts of the two size classes did not differ significantly (t = 1.27, d.f. = 23, P = 0.217). Large round gobies did not exhibit a diet shift to molluscs (gastropods or bivalves). There was no significant correlation between TL and number of items in round goby guts (r = 0.139; P = 0.508).

Invertebrate benthic density was nearly 3000 organisms·m⁻², with over half of the individuals (51.8%) belonging to the Chironomidae (Table 2). Elmid larvae and adults (Coleoptera: Elmidae) constituted the only other common taxa, representing nearly 38% of the benthic community (Table 2). There was a

significant difference between the field and gut content relative prey abundance ($X^2 = 61.93$, d.f. = 4, P < 0.001; Fig. 4). Chironomids were consumed in significantly greater proportion than their abundance in the field (P < 0.05), whereas elmids were consumed significantly less than their availability (P < 0.05). Amphipods, other Diptera, and 'other' invertebrates were consumed in equal proportions to their availability (Fig. 4).

Energy consumption

There was a significant difference in the energy content of invertebrates from Ellicott Creek $(F_{6.27} = 527.9, P < 0.001; Table 3)$. Round gobies obtained the highest amount of energy per goby per day from amphipods, but the lowest amount from water pennies (Psephenidae) (Table 4). Round gobies consumed only 0.014% of the energy available in riffle beetle tissue, whereas they consumed 0.809% of available energy in amphipod tissue. Although water pennies were moderately abundant in the stream (\sim 1% numerically) and represented an energetically profitable prey, they were not consumed by any gobies (Tables 2 and 4). Similarly, elmid beetles represented nearly 40% of the benthic community, contained the highest energy content of the prey taxa analysed, but constituted only $\sim 2\%$ of round goby gut contents. Round gobies consumed about 0.15% of the energy available in macroinvertebrate tissue per fish per m² per day (Table 4).

Discussion

Understanding the population dynamics and consumption patterns of round gobies will assist in predicting the potential impacts of this recent non-native fish in tributary streams and rivers around the world. We anticipate that the intimacy of connections and reciprocal interactions between streams and their watersheds, coupled with the aggressive nature and broad diet breadth of this fish, will lead to significant impacts on stream benthic macroinvertebrate and fish communities, as has recently been shown by Krakowiak & Pennuto (2008).

Our seasonal sampling data showed round gobies decreased in abundance with season and were absent from the sampling reaches in winter. This change in fish abundance could be due to several casual mechanisms including out-migration to Lake Erie, winter burial in soft sediments, or predation. Although the home range size of adult round gobies during the spawning season is on the order of m² (Ray & Corkum 2001), this behaviour breaks down in winter as round gobies migrate offshore to deeper waters (Skazkina & Kostyuchenko 1968; Charlebois

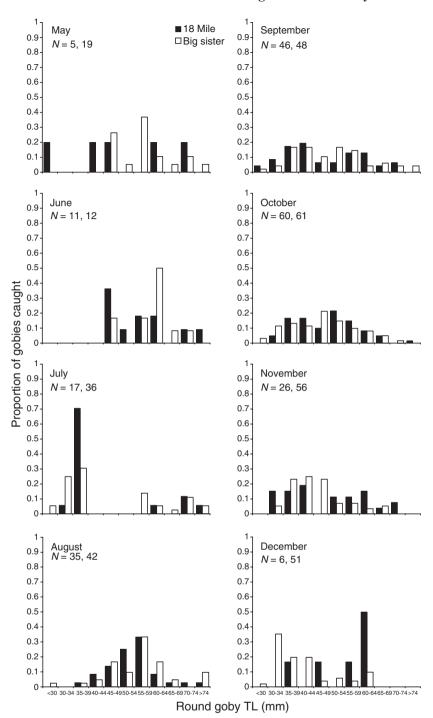


Fig. 3. Monthly size distribution of round gobies collected by electroshocking in two Lake Erie tributary streams sampled between April 2006 and January 2007. The sample sizes of gobies collected in Eighteen Mile Creek and Big Sister Creek, respectively, appear beneath the month on each graph.

et al. 1997; Sapota & Skóra 2005). Round gobies were present in both streams on the first sampling date in April, and CPUE steadily increased until October followed by a decline through December/January when no gobies were captured. This decline in fish abundance mirrors the seasonal decline observed by Sapota & Skóra (2005) in the Gulf of Gdansk, and represents the first observation of possible out-migration by stream-dwelling round gobies. However, these observations are not conclu-

sive evidence for out-migration since fish could have buried themselves within pool sediments (e.g., L. Corkum, U. Windsor, personal communication) or otherwise been uncatchable. As the substrate of both streams was composed mainly of cobble and bedrock, it is unlikely that round gobies could have buried themselves within the sediments. Additionally, our sample sites were within 2 km of the stream mouth, making out-migration a relatively short distance downstream to the lake plausible.

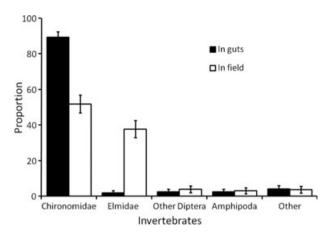


Fig. 4. Relative abundance of select macroinvertebrates in round goby guts and the field from Ellicott Creek. Error bars on each proportion represent 95% confidence intervals after Manly et al. (1993).

Table 3. Mean energy content (kJ·g $^{-1}$ ww) of macroinvertebrates from Ellicott Creek, July 2007.

Taxon	N	Mean energy content (SE)
Elmidae (riffle beetles)	9	10.61 (0.31) ^a
Psephenidae (water pennies)	2	6.74 (0.10) ^b
Hydropsychidae (net-spinning caddisflies)	5	6.28 (0.19)b
Chironomidae (nonbiting midges)	2	4.10 (0.05) ^c
Amphipoda (sideswimmers)	10	3.28 (0.04) ^d
Tipulidae (craneflies)	3	1.96 (0.12) ^e
Gastropoda (snails, shell included)	3	0.92 (0.06) ^f

Different letter superscripts indicate significant differences based on an adjusted Bonferroni *post hoc* test ($\alpha = 0.007$). N =number of calorimetry samples.

The winter decline in CPUE also may be due to increased predation, increased mortality, or other losses from the system like accidental catch by anglers. Steelhead trout begin their spawning migration into tributary streams in late September or early October. However, it is unlikely that spawning trout

reduced the abundance of round gobies in these tributary streams. Steelhead are known to use both Eighteen Mile and Big Sister Creeks during fall spawning runs, but the peak of the runs occurs about a month prior to the observed decline in goby CPUE and the runs are not particularly large in either stream (William Culligan, NY Dept. of Conservation, personal communication). These salmonids, in general, do not feed much during spawning runs (Rand et al. 1993) and we are not aware of any studies on steelhead diets in these tributary streams since the arrival of the round goby. A detailed assessment of the movement pattern of radio-tagged round gobies would be useful to confirm the degree of out-migration by fish from reaches of tributary streams near their lake mouths. As part of another study, electrofishing at a site on Ellicott Creek ~15 km upstream from the Niagara River (the nearest likely source population for round gobies) confirmed the presence of this species in January 2008 (Pennuto, unpublished data). Thus, proximity to the lake may be an important factor in determining seasonal out-migration behaviour by round gobies in tributary streams, if it occurs.

Whether round gobies out-migrate or overwinter in streams has potential implications for stream energy dynamics and communities. Unlike anadromous salmon which translocate and deposit enormous quantities of marine-derived nutrients to headwater streams via their upstream spawning migration and eventual death (Bilby et al. 1996; Merz & Moyle 2006), round gobies may act more like nutrient and energy robbers, removing nutrients and energy from stream systems and translocating them to the lakes in winter. We require further information on in-stream energy budgets and secondary production in these streams to more fully understand if the possible translocation is significant at the system scale.

Round gobies are able to reproduce several times during a single spawning season, typically between

Table 4. Energy content of select invertebrates from Ellicott Creek and consumption estimates for round gobies.

Taxon	Mean # in guts	Mean biomass in guts (mg ww)	Energy content (kJ·g ⁻¹ ww)	Energy consumed per goby per day (kJ)†	Benthic biomass (g·m ⁻²)	Benthic energy available (kJ·m ⁻²)	% of available energy per m² consumed per goby per day
Chironomidae	24.1	3.6	4.10	0.044	2.29	9.39	0.469
Elmidae	0.5	4.8	10.61	0.153	103.79	1101.21	0.014
Amphipoda	2.4	118.6	3.28	1.177	44.37	145.54	0.809
Hydropsychidae	0.2	6.1	6.28	0.115	4.34	27.26	0.422
Ephemeroptera	0.04	0.4	5.06	0.007	0.70	3.54	0.198
Psephenidae	0	0	6.74	0	4.42	29.79	0
Mollusca	0.4	23.5	0.92	0.065	12.66	11.65	0.558
Other‡	1.4	22.9	1.92	0.132	2.56	4.92	2.683
Total	29.1	179.8		1.693	175.13	1333.30	0.127

†Energy consumed per day was estimated by assuming the mean biomass in the gut reflected consumption over an 8-h period. The energy consumed per day is the product of energy content (kJ·g⁻¹) and mean biomass in the gut multiplied by 3. ‡'Other' includes: Isopoda, Annelida, Hydracarina, Tipulidae, and zooplankton combined.

May and August (Charlebois et al. 1997; MacInnis & Corkum 2000). May and June appeared to be a period of growth for round gobies in both streams since there were few, if any, small (<40 mm) round gobies collected during these months. Monthly size distribution data indicate that peak recruitment occurred in the streams in July, with low-level recruitment sustained into September and October. This coincides with stream temperatures in excess of the minimum spawning temperature of 12 °C reported by Moiseyeva & Rudenka (1996). Thus, these tributary streams appear to be sites of reproduction. Egg-laden females were observed during July gut content assessments, supporting the possibility of in-stream production. It is also possible that the influx of small gobies in our sampling data represents in-migration of lake-spawned YOY. However, migration upstream against strong currents may be beyond the physical capability of YOY gobies. Laboratory flume trials (Hoover et al. 2003) suggest juvenile round gobies tire sooner, and remain in station-holding position for a shorter duration relative to adults. An understanding of YOY swimming performance might reveal limits on the current velocity which they can overcome, and shed more light on the likelihood of the lower stream reaches as reproduction sites.

The overall size of round gobies in these stream populations was small relative to lengths observed in lake habitats. Johnson et al. (2005b) and Simonović et al. (2001) provide estimates of round goby length at age. Using their age/length relationships, nearly all the gobies we captured in these stream habitats would be age 0+ and 1+. Interestingly, round gobies from river habitats (Danube and upper Detroit River) exhibit slower growth rates and are thus smaller at each age class than their open water counterparts from the Caspian and Azov Seas (MacInnis & Corkum 2000; Simonović et al. 2001). However, round gobies from Central Lake Erie show roughly the same size/age relationship as gobies from the Danube River (Johnson et al. 2005b). MacInnis & Corkum (2000) indicated that round gobies from the Detroit River matured sooner and at a smaller size than round gobies from their native range. They documented an egg-laden female round goby as small as 43 mm SL. If we use this size as a lower limit for reproduction, then these stream populations have large proportions of potentially reproductive females.

The diet breadth of round gobies in Ellicott Creek was similar to the breadth reported in other round goby diet composition studies (French & Jude 2001; Phillips et al. 2003; Weimer 2003; Carman et al. 2006). Like other stream studies, macroinvertebrates were an important prey item for round gobies and gobies did not feed randomly on available macroinvertebrates. The Chironomidae were consumed in greater

proportion than their occurrence and represented the numerically dominant prey item. Hydropsychidae (Trichoptera), and Amphipoda were also important prey items of round gobies in this study. Carman et al. (2006) showed that gobies fed primarily on chironomid and hydropsychid larvae during the day, which is very similar to the findings in this study. Weimer (2003) and Phillips et al. (2003) also found that chironomid larvae made up the majority of prey items consumed by round gobies. There were very few molluscs (mostly gastropods) available as prey, forcing gobies >70 mm to consume other invertebrates. Thus, whereas lake round gobies tend to exhibit a diet shift to molluscivory at this size (French & Jude 2001), stream gobies remain generalist invertivores. Copp et al. (2008) documented a similar reliance on nonmolluscan prey by large round gobies in the River Danube. At least one invertebrate group, riffle beetles, was very abundant in Ellicott Creek, but not common in the guts. These beetles are typically found within patches of moss or filamentous algae on the upper surfaces of rocks in stream riffle habitats. It is possible that the upper stone surfaces are a predation refuge from these benthic fish. Alternatively, elmids are rather slow moving insects, and simply may be undetected by foraging round gobies.

Stream-captured gobies held large numbers of prey in their guts, though generally guts did not appear 'full'. We estimate that these fish consume, on average, 0.54 g of invertebrate prey per day. This consumption value is lower than most published laboratory or field studies done on round gobies from lake habitats. Lee & Johnson (2005) predicted a 10-g round goby would consume 1.75 g day⁻¹. If we scaled our mean round goby mass up to 10 g, and apply our fish mass-to-prey count relationship, our estimate of daily food consumption (0.76 g·day⁻¹) is still well below that of Lee & Johnson (2005). Our estimates are also below those reported for a laboratory study by Ray & Corkum (1997), who suggest a daily intake of 1.02 g per day for 7.0-8.4 cm round goby. We suspect our numbers are consistently low in this study because of our assumption that the observed gut contents represented consumption over the last 8 h. Most prey items showed signs of digestion, especially chironomids, indicating consumption over a time period. As we do not know the actual digestion time for these invertebrate prey, the 8-h consumption 'rule' could be conservative and these fish were consuming greater numbers of prey. Overall, round gobies consume \sim 1.7 kJ of energy per goby per day, which represents $\sim 0.15\%$ of the energy available per m², a significant amount of energy. As our estimates of energy consumption were generated in July, they may not be reflective of consumption patterns at other times of the year.

This work represents the first examination of the seasonal patterns in round goby occurrence and

reproduction in tributary stream habitats. Population size distribution data and the occurrence of egg-laden females suggest tributary streams are spawning sites, making streams a contributory source habitat for round gobies in the Great Lakes. We suggest this species may exhibit annual stream-to-lake winter migrations with a return to tributary habitats in the spring. Annual winter offshore migrations with a return to the nearshore have been documented for round gobies in lake habitats (Sapota & Skóra 2005), suggesting this may be a robust behaviour with the potential for invasion management. It may be possible to take advantage of this migration behaviour as a management tool by collecting large numbers of out-migrating gobies, thus reducing winter recruitment into adjacent lakes.

During their residence in tributary streams, these fish consume a broad array of invertebrates and exhibit a nonrandom feeding pattern leading to a diet dominated by midge larvae. However, other invertebrate groups potentially account for a larger percent of the energy consumed by this fish species. Collectively, we estimate these invertivorous benthic predators consume a significant portion of the available benthic energy in tributary streams, though we do not know just how significant this proportion is in terms of other in-stream demands. Further research on tagged fish and at sites well inland from the lakes will provide needed information on seasonal migration patterns across the range of this non-native species. Additionally, seasonal population estimates performed in conjunction with seasonal gut and benthic analyses will reveal the full potential impacts of energy consumption by round gobies.

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