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Round goby and zebra mussel interactions with darters in a warm-water stream community in southern Michigan, USA

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ABSTRACT

The non-indigenous round goby (*Neogobius melanostomus)* entered the Flint River, Michigan, USA around 1996 while zebra mussels (*Dreissena polymorpha)* invaded in late 1998. We wanted to identify if there were round goby or darter (*Etheostoma/Percina* spp.) diet or density alterations by comparing 1998 data with our 2002 data after mussel colonization. Chironomids dominated the round goby's pre-zebra mussel diet in August 1998 (89% by number), followed by hydropsychids (10%). After zebra mussels arrived, diets diversified; chironomids declined to 52%, hydropsychids stayed the same, gastropods were more prominent (22%) and 4% were zebra mussels. Data from a site upriver (with no round gobies or zebra mussels) showed darters consumed mostly chironomids (49%), mayflies (11%) and hydropsychids (9%), suggesting reliance on chironomid prey and other interactions compromised the ability of darters to coexist with round gobies downstream, since only one of three species present during 1998 was collected in 2002. Benthic assemblages on rocks changed dramatically (*R*-values $=0.95$) from 1998 to 2002. Blackside darter (*Percina maculata*) density in the presence of round gobies increased eightfold compared with 1998. We hypothesized zebra mussels fostered the growth of macrophytes, resulting in odonates composing 42% by volume of blackside darter diets in 2002 compared with 10% in 1998. Diet overlaps between small and large round gobies and blackside darters were high (Schoener Index $=0.55$–0.59, R-values $=0.11$–0.24), suggesting potential negative competitive interactions. Zebra mussel-mediated ecosystem changes may have decreased interspecific competition for food with blackside darters, allowing coexistence with round gobies. Native darters with varied diets feeding in mid-water, are most likely to coexist with round gobies, especially where dreissenids potentially mediate competitive interactions.

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Color versions of one or more of the figures in the article can be found online at www.tandfonline.com/tjfe.

1. Introduction

Round gobies (*Neogobius melanostomus*), native to the Black and Caspian seas, were first found in Michigan in 1990 (Jude et al. 1991) and are spreading throughout the Laurentian Great Lakes into Michigan's inland waterways and the Mississippi River where they can dramatically change aquatic food webs (Janssen and Jude 2001; Jude 2001; Poos et al. 2010). Similar range extensions have been documented in their native habitats in Europe (Charlebois et al. 1997). The round goby poses a threat to native fishes, since they can prey on native benthic fish larvae (Weimer and Sowinski 1999; French and Jude 2001) and have caused extirpation of some species, such as mottled sculpin (*Cottus bairdi),* Johnny darters (*Etheostoma nigrum*) and logperch (*Percina caprodes)* (Dubs and Corkum 1996; Lauer and McComish 2004; Balshine et al. 2005; Krakowiak and Pennuto 2008; Bergstrom and Mensinger 2009; Stauffer et al. 2016). They also can affect native unionid mussels through direct predation and reduction in mandatory fish hosts (Poos et al. 2010). As round gobies have become integrated into the Great Lakes and European ecosystems (e.g. Hensler et al. 2008), round goby proliferations have implications for modifying toxic substance bioaccumulation patterns in aquatic food webs (Johnson et al. 2005; Ng et al. 2008) and promoting Type E botulism by poisoning fishes and birds (Somers et al. 2003) because of their consumption of contaminated zebra mussels (*Dreissena polymorpha*) (Domske and Obert 2001; Yule et al. 2006). Since these non-indigenous species have also colonized river systems connected to the Mississippi River (Irons et al. 2006), which have a high diversity of darters, and are expanding in Europe with concomitant effects on their native fishes, information on warm-water river systems is essential to understand their interactions with small benthic fishes in river systems never exposed to these species (Kornis et al. 2013).

In 1996, the round goby was found at two inland sites in Michigan: the Flint and Shiawassee rivers, which drain into the Saginaw River and eventually Saginaw Bay, Lake Huron. This was the first recorded appearance of this species at an inland site, far away from the Great Lakes and connecting channels. This finding prompted us to initiate this follow-up study, since relatively little was known about interactions with native, non-sport fishes in warm-water river systems. We only sampled the Flint River because (1) the only other inland river site with a known round goby invasion was the Shiawassee River and abundance was low there, (2) prior diet and density information was only available from this site (Carman et al. 2006) and (3) we had a unique opportunity to evaluate changes after zebra mussels colonized the site. Most studies since this one were conducted in tributaries either with or without zebra mussels; none made a comparison of changes before and after zebra mussel colonization. Carman et al. (2006) studied round goby diets in the Flint River during 1998, just as zebra mussels were observed upriver of our site (based on several canoe trips from the Holloway Dam to the study site (see Figure 1) and (Leonardi 2004). Colonization by zebra mussels of the study site after 1998 may have disrupted trophic dynamics. Zebra mussels were first found in the St. Clair River in 1988 (O'Niell and Dextrase 1994) and rapidly spread throughout the Great Lakes because their planktonic veliger offspring drifted in rivers and lakes and were transported by freighters. They are voracious filter feeders, removing algae from the water column, increasing water clarity and negatively affecting *Diporeia* in all the Great Lakes south of Lake Superior (Nalepa et al. 1998). They have been implicated in drastic trophic cascades in many of the Great Lakes especially Lake Huron, which resulted in the eventual loss of the salmon fishery there (Bunnell et al. 2014). Riverine round gobies in their native habitats prefer mollusks, especially zebra
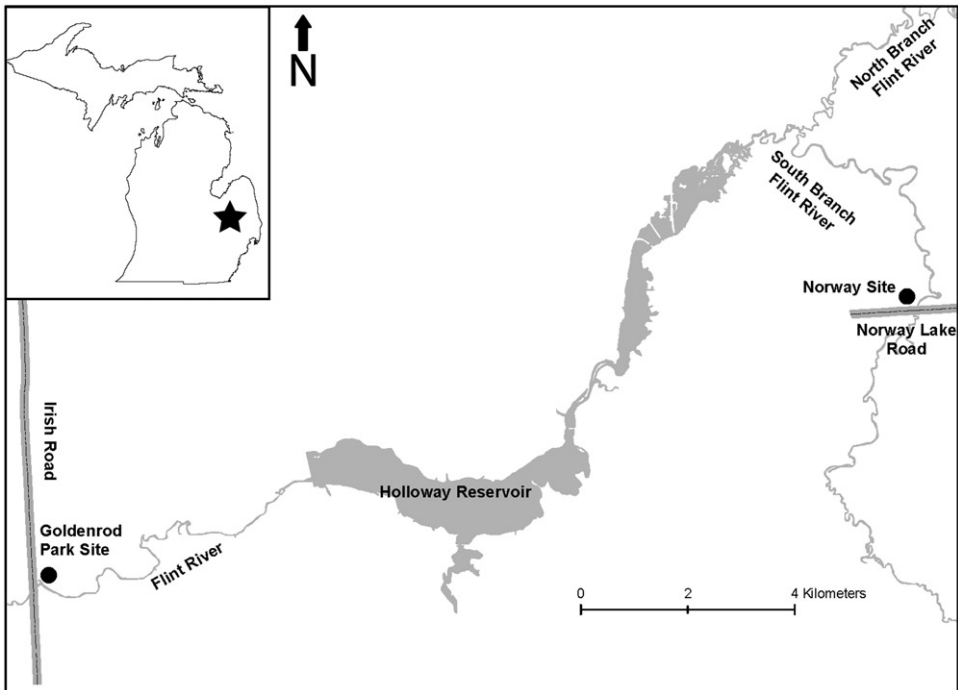
Figure 1. Map of the Flint River showing location in Michigan (black star) and the two sampling sites (black circles), Goldenrod Park (with round gobies and zebra mussels) and the Norway site (without round gobies and zebra mussels).

mussels where available (Charlebois et al. 1997). However, in some cases (see Carman et al. 2006; Diggins et al. 2002), they can be mostly insectivorous. Hence a shift toward zebra mussels as a primary food source was hypothesized for large round gobies in the Flint River. With this shift, food previously eaten by round gobies may have become available to native fishes, which could have reduced resource competition and changed food web dynamics. There is abundant evidence (Lederer et al. 2006; Brush et al. 2012) of the depressing effect of round gobies on benthos. We also wondered if round gobies would eat large quantities of fishes, as they have done in native habitats (3–42% of round goby diets was fish: Charlebois et al. 1997), thus harming native species, such as darters (*Etheostoma* and *Percina* spp.).

Because of information that round gobies have had detrimental impacts on benthic fishes (Reid and Mandrak 2008; Duncan et al. 2011), we focused on darters (*Etheostoma/Percina* spp.), since there were no mottled sculpins in our study area. We tested three hypotheses:

Hypothesis 1: round gobies compete with darters for resources causing diet overlap, which may have caused decreased abundance of darters.

Hypothesis 2: round gobies undergo a diet shift from being insectivorous to include more dreissenids, which may allow better survival of darters because of increased benthic prey and reduced resource competition and diet overlap.

Hypothesis 3: Availability of more dreissenids should reduce predation on small fishes by round gobies.

To test these hypotheses we documented predation, diet overlap and density changes from 1998 to 2002 for round gobies and darters, and elucidated predator selection of insect

prey to better understand potential impacts on benthos and potential competitive interactions between round gobies and darters, especially blackside darters (*Percina maculata*).

2. Methods

2.1. Study areas

This study was conducted in the Flint River, a warm-water stream in central Michigan, located in the Saginaw Bay, Lake Huron watershed (Figure 1, Leonardi and Gruhn 2001; Leonardi 2004). The Goldenrod Park study site was at the intersection of the Flint River and Irish Road in Genesee County (43°06′13.36″ N, 83°33′24.12″ W), 3.9 river-km downstream from Holloway Dam and 3.1 river-km upstream from Mott Dam. The study site was primarily riffle habitat with river depths to 1.2 m and a mean width of 30 m. Substrate was primarily cobble on sand. Water clarity was high during 2002 based on personal observations, photographs taken at the site in 1998 compared with 2002 and increases in Secchi disc readings in the reservoir above from 1998 to 2003 (Leonardi 2004). During 1998 there were very few macrophytes in the area we seined, while during 2002, there were extensive aquatic macrophyte beds (*Potamogeton crispus, P. filiformis* and *P. amplifolius*). Discharge at the Goldenrod Park site (data from a USGS gauging station number 04147500 2.8 km upstream) was 2.9 m^3/s during 29–30 August 2002, while it was 2.0 m^3/s during 23–24 August 1998, and was controlled by the upstream dam. This dam is operated by the city of Flint, Michigan for a water supply and operates in a run-of-the-river mode.

An upriver site (Norway—Figure 1), which was the nearest location in the Flint River to Goldenrod Park that contained no round gobies or zebra mussels, was upstream of Goldenrod Park and the Holloway Dam off Norway Lake Road, Lapeer County (43°08′42.77″ N, 83°21′12.28″ W). The site was composed of a riffle area similar to habitat found at Goldenrod Park; however, discharge was 0.7 m^3/s. Some sparse aquatic vegetation was observed.

2.2. Fish collection and handling

During 2002, fishes were collected from the Flint River east of Flint, Michigan at Goldenrod Park, Genesee County, using a 5-m-long bag seine (Jude and DeBoe 1996) five times over a 24-h period on 29–30 August 2002: before dawn (06:20 h), mid-day (13:15 h), before dusk (19:00 h), after dusk (21:10 h) and mid-night (23:25 h). A before-dawn sample was also collected on 2 September 2002 at 04:00 h. We kick-seined and sometimes pulled the seine along the bottom until around 70–80 fish/period were captured. Sampling was done to replicate the Carman study, so as to provide direct comparisons of diet and densities before and after zebra mussel colonization. The Norway site upstream (Figure 1) was sampled at 15:20 h on 29 August 2002 once during the day, to provide information on darter ecology in a nearby site unaffected by round gobies and zebra mussels. Blackside darters were the only darter species we collected during 2002 at Goldenrod Park, but no diet data were available from blackside darters during 1998. To compare blackside darter diets between years, all blackside darters collected during August 1998 from the Carman study ($N = 13$) were analyzed for stomach contents.

The Carman et al. (2006) study site was identical to ours (Goldenrod park/downstream—see Figure 1); sampling occurred on 16 May, 28 June, 30 July and 22 August

1998. Fishes were collected seven times over a 24-h period, whereas we sampled only six times during this study. The same seine was used in both studies.

Area swept while seining was noted for samples collected during 1998 and 2002 so fish density could be estimated and compared. All round gobies and darters were preserved immediately in the field in ethyl alcohol. Other fishes were identified and their numbers estimated in the field before being released.

We only sampled during August 2002 and made our comparisons with similar 1998 August data (Carman et al. 2006). Our goal was to take advantage of this unique opportunity to demonstrate whether diet, density, or environmental changes had occurred after the dreissenid invasion. There is general support from the literature (French and Jude 2001; Carman et al. 2006) for the assertion that the diet of round gobies was mainly insectivorous, with a shift toward more mollusks (especially zebra mussels) with larger individuals, but with little change throughout the year. Therefore, we believed August data were adequate to demonstrate whether there were any major changes occurring in the area when compared with the Carman study.

2.3. Fish diet analysis

In the laboratory, fishes were identified to species, weighed to the nearest 0.1 g wet weight and measured (total length) to the nearest 1 mm. Stomachs were removed and their contents identified to the lowest taxonomic level, enumerated and volume measured using volumetric displacement (French and Jude 2001). When stomach contents were too small to measure, percent composition was estimated visually and volume was estimated to be 0.05 mL. All fishes, including those with empty stomachs (round gobies—14%, blackside darters—12%) were used in analyses. Carman et al. (2006) analyzed round goby diets using numbers of organisms consumed, so direct diet comparisons could only be achieved using numbers. We used volume for all other diet comparisons in this study, including the diet analyses for all blackside darters, because we believed volume provided a more valid estimation of diet.

2.4. Benthos collections

We collected three rocks (approximately 20×20 cm) each from the riffle areas of Goldenrod Park and Norway after seining on 30 August and four rocks on 27 September 2002 for a total of seven rocks sampled per site. Rocks were randomly selected and carefully removed into a 0.25-m-diameter, 363-micron-mesh plankton net placed downstream of the rock. All rocks, except four collected at the Goldenrod Park site on 27 September, were placed in a large white enamel pan and benthic organisms were removed on site and preserved in ethanol. The other four samples were taken to the laboratory and processed the next day. Insects were identified at least to family. Other methods for assessing benthos (e.g. Surber sampler) may have given a better representation of the benthos, but we chose methods that were consistent with the Carman study.

2.5. Data analysis

We divided round gobies into two size groups: small (<54 mm TL; $N = 371$, mean $= 36$, range 18–53, SE $= 0.4$) and large (≥ 54 mm TL; $N = 110$, mean $= 75$, range 54–104, SE $= 0.9$), based on previous research indicating that large round gobies consumed almost exclusively dreissenid mussels, while their smaller counterparts ate mostly insects (Jude

et al. 1995; French and Jude 2001; Andraso et al. 2011). Student's *t*-tests ($P = 0.05$) with Levene's tests for equality of variances were performed to determine diet differences for round gobies ≥54 mm TL between 1998 and 2002, and to detect changes in mean densities of round gobies and blackside darters at the Goldenrod Park riffle between 1998 and 2002. The Schoener Index (SI) (Schoener 1970) was used to assess diet overlap and species composition overlap of aquatic macroinvertebrates.

$$SI = 1 - \tfrac{1}{2}\left(\sum |P_{x,i} - P_{y,i}|\right)$$
$$i = 1, \ldots, n$$

Where $P_{x,i}$ and $P_{y,i}$ are the proportions of food category i in the diets of species X and species Y, respectively and N = number of food categories. This index measures diet similarity and ranges from 0 (no overlap, completely different) to 1 (identical diet). Values of 0.5 or greater indicate substantial overlap (Hartman and Brandt 1995; Zahn Seegert et al. 2014). The Strauss Index (Strauss L) (Strauss 1979) was used to calculate prey selectivity (diet composition versus abundance of insects on rocks) for round gobies and blackside darters using the formula: $L = r_i - p_i$ where r_i is the relative abundance (r) of food item (i) in the stomach and p_i is the relative abundance of food in the environment. The index ranges from –1 (strong avoidance) to +1 (strong preference).

We compared benthos results of Carman ($N = 135$ rocks sampled from May to August 1998—no significant differences among months) with 2002 data (Goldenrod site) and the Goldenrod site with the Norway site using *t*-tests with Bonferroni correction. Since there were different mean numbers of benthic organisms found per rock between 1998 and 2002, we standardized the counts to 100 organisms per rock. These data were also used to determine diet preferences of round gobies and darters.

To garner further support for benthos and diet assemblage differences, we used R–vegan (Oksanen et al. 2017) to calculate an Analysis of Similarity (ANOSIM). ANOSIM is a nonparametric permutation applied to a rank similarity matrix of samples (Clarke and Warwick 2001). Diet and benthos data were converted to proportions, square-root transformed using EXCEL and R created a Bray-Curtis similarity matrix which was used in the ANOSIM analysis. R-values from ANOSIM measure the absolute separation of diet and benthos assemblages in the site, year and fish comparisons we made and are usually more useful than *P*-values derived from the analysis (Clarke and Gorley 2001). R-values range between –1 and +1 with values <0.25 indicating little separation, those 0.5–0.75 indicating some overlap between groups and those >0.75 indicate clear separation between groups (Clarke and Gorley 2001).

3. Results

3.1. Fish density changes and community composition

Overall, 30 species of fishes were collected at the Norway and Goldenrod Park sites (data not shown); Leonardi and Gruhn (2001) collected 28 and 25 species respectively above and below Goldenrod Park in 1997, including five darter species. During 2002, round gobies and blackside darters accounted for 69% and 9%, respectively, of the fish community at Goldenrod Park ($N = 824$), while blackside darters and other darters (greenside *Etheostoma blennioides*, Johnny and rainbow *E. caeruleum* darters) represented 5 and 13% of the community at the upriver site ($N = 121$ fishes) during sampling in August and September 2002. Four darter species were present at Norwood during 2002, while at Golden Rod Park there were three darter species in 1998, which were reduced to one species found during 2002 (Table 1).

Table 1. Density (no./100 m^2) of darter species and round gobies at Goldenrod Park (1998 and 2002) in the Flint River, Michigan and at the Norway site upriver of the study site where round gobies and zebra mussels were absent.

	Goldenrod Park		Norway Site
Species	1998	2002	2002
Blackside darter	1.2	10.2	3
Greenside darter	0	0	2
Johnny darter	<1	0	6
Rainbow darter	<1	0	1
Round goby	29.0	77.5	0

Data from 1998 from Carman et al. (2006). Other fish species collected were excluded.

Blackside darter densities during August at the Goldenrod Park riffle increased nearly eight fold from 1998 to 2002 (1.2/100 m^2 versus 10.2/100 m^2); differences were significant ($p = 0.0092$, $t = 3.15$, d.f. $= 11$) (Table 1). Round goby abundance also increased significantly from 1998 to 2002 (29/100 m^2 versus 77/100 m^2—$p = 0.0225$, $t = 2.65$, d.f. $= 11$). Densities of blackside, greenside, Johnny and rainbow darters at the Norway site were 3, 2, 6 and 1 fish/100 m^2, respectively, much lower than those of either round gobies or blackside darters at the Goldenrod Park riffle.

Diets and diet overlaps of round goby and blackside darter

Large round goby diets in August changed substantially from 1998 to 2002 after zebra mussels invaded the Goldenrod Park site (Table 2), but diet assemblages showed minimal overlap (SI $= 0.27$) and little separation ($R = 0.15$—Table 3). Large round goby diets at Goldenrod Park during 2002 were more diverse than those of 1998 and were dominated by chironomid larvae and pupae (37% by number), hydropsychid larvae (9%), gastropods (22%), zygopterans (6%), ostracods (5%) and zebra mussels (4%) (Table 2). The large round goby diet during 2002 also contained fish (6% by volume) including juvenile spotfin shiners (*Cyprinella spiloptera)*, bluegills (*Lepomis macrochirus),* and pumpkinseeds (*Lepomis gibbosus).* In contrast, large round gobies from 1998 ate predominantly chironomids (89% by number) and hydropsychids (10%). Large round goby diets overlapped substantially with small round goby diets (SI $= 0.65$, $R = 0.15$—no separation—Table 3), and diets of both sizes of round gobies overlapped with blackside darters (SI $= 0.55$–0.59, $R = 0.11$–0.24—no separation—Table 3). Small round gobies ate more trichopterans by volume and almost twice as many chironomids as blackside darters, while blackside darters ate more ephemeropterans, plecopterans and three times as many odonates as the other two groups (Table 2). Large round gobies ate gastropods and zebra mussels (12 and 9% respectively of the diet), while blackside darters ate none.

During 2002, small round gobies ate more chironomids than did large round gobies (43 versus 19% by volume), while large round gobies ate more gastropods (22 versus 6%) (Table 2). Small and large round gobies during 2002 selected against hydropsychid prey (Strauss $L = -0.17$, -0.20), while large round gobies preferred gastropods and zygopterans ($L = 0.12$, 0.06).

To determine if blackside darter diets were influenced by the zebra mussel invasion at the study site, we compared their 2002 diets with 1998 diets. The change in blackside darter diets between 1998 and 2002, although pronounced, showed some overlap (SI $= 0.39$) but little separation ($R = 0.24$—Table 3). Blackside darters collected during 1998 at Goldenrod Park consumed mainly chironomids (53% by volume), ephemeropterans (32%)

Table 2. Percent composition by number (N) and volume (V) of diets of large (LG) and small (SM) round gobies (RG) *Neogobius melanostomus* and blackside darters (BD) *Percina maculata* collected during August 1998 and late August - September 2002 from the Flint River, Michigan at Goldenrod Park (GR) and the Norway site (NW).

Parameter	GR: 1998		GR: 2002				NW:2002			
	BD (V)	RG (N)	BD (V)	SM RG (V)	LG RG (N)	LG RG (V)	BD (V)	GD (V)	JD (V)	RD (V)
Anisoptera			6	2	1	3				
Amphipoda							20	55		15
Chironomidae	53	89	21	43	37	19	40	45	97	
Corixidae							20			
Dreissena polymorpha										
Ephemeroptera	32		4	2	4	9				45
Gastropoda				4	3	4				
Heptageniidae				6	22	12				25
Hydrophychidae	2	10	12	10	9	6	20		2	15
Ostrocoda			1	8	6	1				
Plecoptera			3	2	1	3				
Trichoptera	2		2	3	5	6				
Zygoptera	10		42	5	6	11				
Unidentified food			9	7	3	11			1	
Miscellaneous	2	3	1	7	3	15				
Sample size	13	70	64	371	110	110	6	3	11	2
Mean length (SE)	59 (2.3)	75 (1.0)	57 (1.2)	36 (0.4)	75 (0.9)	75 (0.9)	52 (2.0)	77 (2.0)	68 (1.9)	72 (2.8)
Range TL (mm)	46–75	51–97	41–74	18–53	54–104	54–104	40–70	74–82	63–73	68–76

Also included were diets of blackside, Johnny (*Etheostoma nigrum*) (JD), greenside (*E. blennoides*) (GD), and rainbow (*E. caeruleum*) (RD) darters collected at the Norway (NW) site. Trichoptera includes all families except Hydropsychidae. For Norway darter diets, Ephemeroptera excluded Heptageniidae, while for remaining fish, Heptageniidae was included in Ephemeroptera. Miscellaneous food included: Bluegill; brachycentrids; coleopterans; corixids; *Daphnia* spp; Diptera pupae; dytiscids; elmids; *Gammarus* spp.; harpacticoid copepods; heptageniids; *Helisoma* spp.; hydracarinids; isopods; lepidopterans; *Lepomis* spp.; limnephilids; limpets; spotfin shiners; simuliids; *Sialis* spp; tipuliids; unidentified amphipods, insects, pupae, fish and plants. Samples include fishes with empty stomachs. Percentages may not sum to 100% due to rounding error. Also included is mean length (SE) and range of fishes collected.

Table 3. Schoener Index (SI - diet overlap) and Analysis of Similarity (ANOSIM) values for various comparisons of benthos data on rocks (ANOSIM values only) and diet of round gobies (RG) and blackside darters (BD) of different sizes and from different years. GR = Goldenrod Park, LG = large, SM = small, na = not applicable.

Comparison	SI	R - p	R -statistic
GR Benthos: 1998 versus 2002	na	0.001	0.95
Benthos: GR versus Norway	na	0.001	0.92
LG RG 1998 versus LG RG 2002	0.27	0.001	0.15
BD 1998 versus BD 2002	0.39	0.007	0.19
SM RG 2002 versus LG RG 2002	0.65	0.001	0.15
BD 2002 versus SM RG 2002	0.55	0.001	0.24
BD 2002 versus LG RG 2002	0.59	0.001	0.11

and zygopterans (10%) (Table 2). Blackside darters during 2002 consumed almost five-fold more odonates (zygopterans plus anisopterans) (48 versus 10% by volume) than in 1998, fewer chironomid larvae and pupae (21 versus 53%), fewer mayflies (4 versus 32%), but more hydropsychid larvae (12 versus 2%). Using the Strauss Index comparing benthos on rocks with diet, which may have missed pulses of prey in the water column or bottom, it was still clear that like round gobies, blackside darters selected against hydropsychid and also chironomid prey at the Goldenrod Park riffle ($L = -0.15$, -0.29), despite the fact that hydropsychids increased almost ninefold on the rocks compared with 1998 values (Table 4). Odonates, mostly zygopterans, appeared to be preferred prey, since they made up 48% by volume of the blackside darter diets during 2002 ($L = 0.37$—high preference), while composing 4.7% of the benthos on rocks. However, some may have been eaten from macrophytes skewing this comparison. Blackside darters at Goldenrod Park demonstrated no strong selection for or against other prey items.

At the Norway site, diets of darters were exclusively invertebrates; diets varied by species, with blackside and rainbow darters having more diverse diets than greenside and Johnny darters (Table 2). Blackside, rainbow and greenside darters ate ephemenopteran and trichopteran larvae and chironomids in similar amounts; whereas, Johnny darter diets were composed of 97% chironomids by volume. Rainbow darter was the only darter species to eat Heptageniidae. Norway-site blackside darters ate almost twice as many chironomids and hydropsychids than at Goldenrod Park. In addition, Norway-site blackside darters uniquely ate amphipods and corixids, while Goldenrod Park fish ate more odonates. Blackside darters at Norway showed positive selection for amphipods ($L = 0.20$), chironomids ($L = 0.32$), corixids ($L = 0.20$) and selected against heptageniids ($L = -0.15$), hydropsychids ($L = -0.32$) and trichopterans ($L = -0.17$). Blackside darter diets at the Norway site were most similar to those of strongly benthic greenside darters (SI $= 0.60$, significant), less similar to diets of Johnny darters (SI $= 0.42$) and least similar to their mid-water-form counterpart rainbow darters (SI $= 0.30$). Greenside darters ate more trichopterans and plecopterans by volume than blackside darters.

3.2. Benthos data

Seventeen taxa (pooled into 11 taxonomic groups) of benthic invertebrates were collected during 2002 at Goldenrod Park from the seven rocks sampled with a mean number of 98 per rock (Table 4). Chironomids were the most abundant taxa composing 50% of benthic organisms found, while Hydropsychidae composed 27%. Zebra mussels were not very abundant on rocks, since only ca. 7/rock (7%) were observed. A comparison of benthic groups on rocks from 1998 with 2002, showed clear separation of benthic assemblages between years (R-value $= 0.95$—Table 3). Chironomidae declined significantly (without the

Table 4. List of the mean number of benthic organisms (standardized to 100/rock) found on rocks during 1998 ($n = 135$, pooled data over 4 months) (Carman et al. 2006) and 2002 ($n = 7$ per site, this study). Rocks were removed from Goldenrod Park (Goldenrod) and the Norway site upriver in the Flint River, Michigan. Rocks from 2002 were collected on 30 August ($n = 3$ per site) and 27 September 2002 ($n = 4$ per site) and data pooled.

| | 1998 | 2002 | |
Taxa	Goldenrod	Goldenrod	Norway
Amphipoda	0	0.3	0.5
Anisoptera	0	0	0.2
Chironomidae	82.99	49.7	7.8
Coleoptera*	0	0.6	1.1
Corixidae	0.05	0	0
Diptera*	0.05	0.4	0.3
Dreissenidae	0	6.7	0
Elmidae	0.2	1.5	1.4
Ephemeroptera*	3.1	4.7	2.9
Heptageniidae	0.2	1.5	14.8
Hydropsychidae	3	27.4	52.5
Megaloptera	0.1	0	0
Oligochaeta	0	0	0.2
Orthoptera	0.05	0	0
Planaria	0	0	0.3
Plecoptera	0.05	0	0
Psephenidae	0	0.4	0
Sphaeriidae	0	0	0.3
Tipulidae	0	0	0.5
Trichoptera*	10.19	2.2	17.1
Zygoptera	0.05	4.7	0.2
Total no. rocks	135	7	7
Mean total no.	43	98	90

*Diptera taxa exclude Chironomidae, Ephemeroptera taxa exclude Heptageniidae, Trichoptera taxa exclude Hydropsychidae and Coleoptera taxa exclude Elmidae.

Bonferroni correction, but not with it) from 82% in 1998 to 50% during 2002 ($p = 0.0035$, $t = 3.1549$, d.f. = 140), Odonata significantly increased from 0.1 to 4.7% ($p = 0.0003$, $t = 4.0420$, d.f. = 140), while remaining comparisons were not significant. Comparing Goldenrod Park benthic groups during 2002 with the Norway site assemblage showed clear separation (R – value $= 0.92$—Table 3). Odonates were significantly (without the Bonferroni correction, but not with it) more abundant at Goldenrod Park (4.7%) than at Norwood (0.4%) ($p = 0.0154$, $t = 2.8229$, d.f. = 12). Remaining groups were not significantly different from each other, although Heptageniidae (10-fold), Hydropsychidae (2-fold) and Trichoptera minus Hydropsychidae (8-fold) were all higher at Norwood compared with the Goldenrod site. Two of these comparisons were almost significant.

4. Discussion

4.1. Diet overlap of round gobies with darters

We hypothesized resource competition as a possible negative interaction of round gobies with native darters and studies (Kuhns and Berg 1999; Raby et al. 2010) have shown round gobies can severely depress benthic organisms. Since round gobies composed around 70% of the riffle fish community during 1998 and 2002, their impact on native species of fishes and invertebrates was hypothesized to be great. As evidence of this, diets

of blackside darters and round gobies at Goldenrod Park overlapped, since the diet of small and large round gobies was composed of 35% by volume Chironomidae, while blackside darter diets were 21% chironomids and even higher (40%) at the Norway site. Wynes and Wissing (1982) reported that blackside and rainbow darters in an Ohio stream did not feed on the drift (because most drift occurred at night), but were almost obligate, daytime bottom feeders. This would place them in potential direct competition with round gobies, especially small ones that also concentrated their feeding in this ben-thic zone.

Diet information for Johnny and greenside darters at the Norway site was only a single sampling bout to provide data on what they would eat in the absence of round gobies. These data, along with literature data, suggest there would be a substantial diet overlap with round gobies, since darter diets were 97 and 45% chironomids by volume, respect-ively, a staple of round gobies. However, rainbow darters at the upstream site had a varied diet consisting of only 15% chironomids, suggesting they may be able to obtain alternate food resources if chironomids were in limited supply (see Stauffer et al. 2016 who found this), as blackside darters apparently have, in areas where round gobies were present. Darters are known to feed extensively on chironomids in other environments (Turner 1921; Hlohowskyj and White 1983). Since round gobies ate odonates in low quantities (9% of the diet) and the majority of odonate consumption occurred at night, we presume this predation was opportunistic while searching for chironomids. Conversely, blackside darters consumed large quantities of odonates (48% by volume of their diet) at the Goldenrod Park riffle mostly during the day, probably by picking resting or feeding odo-nates from rocks and plants. Most damselflies eaten were *Argia* spp., which are cryptic, day-active and common residents of riverine environments, especially in the presence of macrophytes. Benthos data showed odonate (mostly damselflies) percent composition on rocks was much lower in 1998 (<1%) than during 2002 (4.7%). Thus, blackside darters, whose population increased dramatically with appearance of macrophytes, appeared to be able to evade interspecific competition with round gobies by apparently feeding more at mid-levels in the water column, something noted for blackside darters by Greenberg (1991). Additional support was provided by Malone (2016), who studied tributaries to Lake Michigan with and without round gobies. They showed that blackside darters had similar densities in invaded and round goby-free tributaries.

Zebra mussels were less important in round goby diets than expected, but they appear to have caused extensive ecological changes in the Flint River. We observed proliferation of aquatic macrophytes, apparently induced by zebra mussels clearing the water column (Effler and Siegfried 1998; Schloesser and Manny 2007). Zebra mussels were first found in Holloway Reservoir above our site during 1995 and from 1998 to 2003, Carlson's Trophic State Index increased, there was lower total phosphorus and chlorophyll a, and higher Secchi disc readings (Leonardi 2004). These changes were reflected at our river site and promoted greater sunlight penetration (Skubinna et al. 1995; Horgan and Mills 1999; Vanderploeg et al. 2002), which was followed by an increase in macrophytes, odonates and blackside darters. Blackside darters prefer clear to slightly turbid water (Becker 1983) and increased abundance of macrophytes is also ideal habitat for odonates. More odonates were found at the study site in 2002 on rocks than were found in 1998. One of the major food items for blackside darters at Goldenrod Park was odonates, which was not the case in 1998, nor were they important at the Norway site, where chironomids were predomin-antly eaten. Because odonates thrive in macrophytes, this may represent not only an ideal prey for blackside darters, but also a habitat shift allowing them to flourish in the pres-ence of round gobies. Blackside darters are known to use vegetation for shelter (Becker

1983) and are midwater-dwelling fish (Trautman 1981). DeVanna et al. (2011) proposed that *Dreissena* acted as ecosystem engineers and facilitators, with the Flint River ecosystem an example, since changes that occurred appear to have allowed expansion of blackside darters. This is exceptional, since other major studies in tributaries have found that round gobies depressed all darters (Phillips et al. 2003; Krakowiak and Pennuto 2008; Poos et al. 2010) except rainbow darters (Stauffer et al. 2016), but these systems did not have zebra mussels present.

4.2. Feeding behavior and invertebrate prey susceptibility

It is important to understand the functional feeding behavior of darters and round gobies and the behavior of their invertebrate prey to ascertain potential competitive interactions and mechanisms of potential impact among these groups (Matthews 1998). The round goby is a benthic species that feeds mainly on invertebrates and can affect any species with a similar niche, such as darters, madtoms *Noturus* spp., sculpins (Krakowiak and Pennuto 2008) and logperch (Stauffer et al. 2016). Round gobies can severely depress benthic populations (Djuricich and Janssen 2001; Ratti and Barton 2003; Pennuto et al. 2010). When we compared the overall diet composition of round gobies and blackside darters during 2002 with the overall benthos composition on rocks, we showed that zygopterans were preferred prey, very abundant at Goldenrod Park (almost 5% of the benthos population on the rocks and they were probably much more abundant in the macrophytes, which did not exist in 1998), and composed 5–7 and 42% by volume of the diets of round gobies and blackside darters respectively at Goldenrod Park.

Between 1998 and 2002, hydropsychids and odonates showed increased abundances on rocks. Round gobies and blackside darters generally increased their consumption of these two groups, showing availability is an important component of diet for both species.

Blackside darters may be more capable of partitioning resources in the presence of round gobies than other darters. One exception was rainbow darters, which seem to co-exist with round gobies (Burkett and Jude 2015; Stauffer et al. 2016). Many other studies have shown darters to be detrimentally affected by round gobies (summarized by Poos et al. 2010). Blackside darters in this study appeared to be an exception, since they had a more diverse diet in the presence of round gobies and zebra mussels than they did at the Norway site, possibly due to: (1) differences in habitat—Norway site was a riffle with cooler water, fewer macrophytes and lower discharge, and (2) differences in feeding mode (feeding higher in the water column) perhaps in response to predation (Schlosser 1987), competition with round gobies, or insect availability. Blackside darters forage mostly in mid-water during the day (Keast and Welsh 1968; Thomas 1970). As a result they are able to partition their food and habitat resources (Schoener 1974) with a presence in the upper water column and a more diverse diet than most other darters (and round gobies), which have no air bladders, have more prominent sub-terminal mouths and feed on the bottom (Smart and Gee 1979; Paine et al. 1982). Further evidence for mid-water feeding by blackside darters was their consumption of corixids and zooplankton. Corixids are usually associated with vegetation and can be found in the water column, a finding also noted by Smart and Gee (1979). *Daphnia* spp. and harpacticoid copepods were found in the diet of large, but not small round gobies during 2002, which was also noted by Carman et al. (2006) and Weimer and Sowinski (1999). Zooplankton apparently originated from the Flint River upstream impoundment, which documents that large round gobies and blackside darters fed on drifting zooplankters. Chironomidae usually pupate at

dusk and during the night (Palmen 1955) making them susceptible to predation during dusk, when blackside darters fed heavily on these dipterans.

Zebra mussels in low volumes were found in diets of small round gobies and were eaten in larger volumes (9% by volume) by large round gobies. This pattern is similar to findings in other studies (Jude et al. 1995; French and Jude 2001); however, zebra mussels made up substantially higher percentages of the diets in these studies than what we measured. We attributed this to the Flint River being in the early colonization period by zebra mussels and the smaller maximum sizes apparently reached by round gobies in small streams compared with those found at other Great Lakes sites. Once round gobies reached sizes of >100 mm they eat almost exclusively dreissenid mussels (Jude et al. 1995). Therefore, a diet shift toward zebra mussels may not yet be complete, or round gobies may prefer soft-bodied prey in this river system when they have a choice.

4.3. Impact of round gobies

Before round gobies became established in the Flint River, there were five species of darters (blackside, greenside, Johnny, fantail *Etheostoma flabellare* and rainbow) inhabiting the river in the immediate area (Leonardi and Gruhn 2001). The one closest station sampled by MDNR during 1997 was 8 km east of our site. They collected 27 species, 507 fishes and three different species of darters: blackside, Johnny and greenside. By 1998, after round gobies had invaded, three darter species remained at the Goldenrod Park site (blackside, Johnny and rainbow) (Carman et al. 2006), while during our study in 2002, only the blackside darter was captured at Goldenrod Park. However, it should be noted that effort was comparatively low during 2002 compared with 1998 resulting in the capture of 824 fish with sampling occurring six times at one site over a 24-h period.

Round gobies have already been implicated in the local extirpation of mottled sculpins (Janssen and Jude 2001), greenside darters (Jude 2001; Poos et al. 2010) and Johnny darters (Lauer et al. 2004; Krakowiak and Pennuto 2008). Logperch were detrimentally affected in the field (Stauffer et al. 2016) and in laboratory studies (Balshine et al. 2005). Round gobies may also detrimentally affect darters by eating their larvae (Weimer and Sowinski 1999; Abbett et al. 2013) and eggs, which was believed to have happened for greenside darters (Jude 2001), which are known to spawn on vegetation and algae and guard their nests (Winn 1958; Balon et al. 1977) in Lake Erie. Logperch also spawn on sand (Becker 1983) and have been extirpated locally on near shore Lake Erie reefs (Jude 2001, Stauffer et al. 2016). On the other hand, rainbow darters, which deposit their eggs on sand, seem to co-exist with round gobies in the St. Clair River in Michigan, as their population numbers remained unchanged after round gobies invaded that system in the early 1990s (French and Jude 2001), but populations were diminished, but not eliminated during a study comparing the 1994 populations with 2011 (Burkett and Jude 2015). Stauffer et al. (2016) also found rainbow darters co existed with round gobies. Krakowiak and Pennuto (2008) showed fish communities in streams with round gobies contained no rainbow darters, even though they were present prior to the round goby invasion. Johnny darters lay their eggs on the undersides of rocks in small crevices (Balon et al. 1977), which may be too small for spawning round gobies. However, they have still been extirpated in other locations, suggesting a different mechanism for their elimination (Lauer et al. 2004; Poos et al. 2010).

We hypothesized that fish consumption by round gobies would decline after zebra mussels colonized the river and acted as a buffer. Fish consumption by round gobies has been rarely observed in the Great Lakes region (French and Jude 2001), but does occur in

their native Caspian Sea area (3–42% of diets were fish: Charlebois et al. 1997). However, Vâsek et al. (2014) found no field evidence to support round goby fish predation in the Danube Basin. During this study, after zebra mussel colonization, large round gobies ate three species of fish (pumpkinseed, bluegill, spotfin shiner and unknown fish which composed 0.2% by number and 6% by volume of the diet, while Carman et al. (2006) found them eating a stonecat (*Noturus flavus)* and a round goby (<1% by number). In other studies, Burkett and Jude (2015) found fish made up 3% by volume of round goby diets and Poos et al. (2010) discussed fish predation as a threat. Abbett et al. (2013) documented consumption of larval fish thought to be fantail darters, which composed 11.2% of the round goby diet (dry weight). Jude (2001) reported consumption of a large trout-perch (*Percopsis omiscomaycus*) in the St. Clair River and fathead minnows (*Pimephales promelas*) used as bait were found in Lake Michigan round gobies. A few eggs were eaten by round gobies in Lake Michigan (Mychek-Londer et al. 2013), while lake trout eggs and fry were eaten in a laboratory setting (Chotkowski and Marsden 1999). Fish predation has important ecological consequences, as it establishes that round gobies, when given an opportunity, will eat small fishes (and eggs) and opens another avenue, predation, to their ability to impact native species (see Ross 1991). More opportunity for predation may exist in warm-water environments, since they are more productive with generally higher species diversity, than most of the Great Lakes. The apparent disappearance of four species of darters documented during this study does not appear to be related to predation by round gobies, but by changing environmental conditions induced by zebra mussels or competition from round gobies for benthic prey, which is consistent with other studies (Krakowiak and Pennuto 2008; Poos et al. 2010).

Similar effects observed elsewhere and the Flint River may likewise be expected to occur in the Mississippi River watershed, since round gobies have already become established in the Illinois River (Irons et al. 2006) and are likely to spread downstream quickly, because their larvae exhibit diel vertical migration behavior (Hensler and Jude 2007). Their continued success will likely be enhanced, because of the presence of a diverse invertebrate fauna, including many mollusks, and because zebra mussels are already present along the length of the Mississippi River and in many of its tributaries. We expect round gobies may inflict the same types of ecological instabilities documented on Flint River native fish and invertebrate assemblages. However, presence of dreissenid mussels along the Mississippi River may buffer some negative impacts of round gobies on native benthic fishes by providing an alternative food source instead of native benthos and creating increased water clarity fostering macrophyte growth and more odonate prey. These changes would favor darters that feed higher in the water column, as we have found with blackside darters in the Flint River.

The Flint River is a typical, warm-water river in Michigan and demonstrates the effects that zebra mussels and round gobies could have on other inland waterways in the Great Lakes Basin and beyond. Loss of natural biodiversity spurred by these non-indigenous species can make ecosystems more difficult to manage. Already dreissenids have been implicated in sport fish (Francis et al. 1996) and invertebrate (Nalepa et al. 1998) declines, including a trophic cascade in Lake Huron (Evans et al. 2011).

In our case the blackside darter and perhaps other darters were probably depressed by colonization of the river by round gobies in 1996, but this effect appeared to be ameliorated for blackside darters after zebra mussels invaded. Because round gobies are known to penetrate tributaries (Phillips et al. 2003; Kornis and Vander Zanden 2009; Jude, unpublished data) and along with dreissenids are transported easily from one body of water to another, they are likely to become established in many lotic ecosystems with

favorable habitats. Here they would be expected to depress invertebrate populations and displace or extirpate darter and other benthic fish species that are susceptible to round goby impacts or cannot utilize the mid-water environment to find prey, as we documented on the Flint River.

Disclosure statement

There have been no financial interests or other benefits that derived from the conducting or publishing of this research.

Notes on contributors

David Jude, PhD is a fishery biologist and limnologist and a retired emeritus research scientist in the School of Natural Resources and Environment at the University of Michigan. He has over 40 years of Great Lakes research and teaching experiences. His research interests include invasive species (he discovered the first round gobies in North America), toxic substances, wetlands and fish population studies with emphasis on early life history stages. He has been down in a research submarine, the Johnson Sea Link II, worked with remotely operated vehicles, and participated in over 100 Great Lakes cruises aboard several ships, including the EPA's Lake Guardian and the University of Michigan's R/V Laurentian.

Steven Hensler has a BS degree from Ohio State University and a MS degree from the University of Michigan where he worked on yellow perch and round goby early life history. He has done extensive research on the Great Lakes, worked for the U.S. Fish and Wildlife Service studying invasive species in the Great Lakes from 2006 to 2016, and more recently became executive director of a research foundation, the Cerulean Center, located in Traverse City, Michigan.

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