

THE BENTHIC FEEDING ECOLOGY OF ROUND GOBY FRY

by

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ABSTRACT

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Larval and juvenile stage events play a dominant role in regulating the ultimate recruitment strength of fish populations. As such, the feeding ecology of early life stages are useful for interpreting the proximate causes of recruitment variability. This study provides the first targeted study of the early juvenile (“fry”) diet of the round goby (*Neogobius melanostomus*, Pallas 1814), a prominent Great Lakes invasive fish. Previous accounts of the diets of round goby fry in the Great Lakes have been based upon by-catch from nocturnal, pelagic studies. Alternatively, we sampled diurnally (day) in diverse benthic environments including open lake, embayment, and stream sites. It was typical for the local diet of round goby fry to feature a primary prey type which contributed >50% to the total diet. Primary prey varied between four types: harpacticoid copepods, chydorid cladocerans, chironomid larvae, or ostracods. An ontogenetic diet shift from harpacticoids to chydorids was suggested between 6 – 26 mm SL. The dominance of benthic prey types in the diet of round goby fry further supports the notion that dreissenid-induced benthification in the Great Lakes is beneficial for round gobies.

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Introduction

An understanding of early life history is essential for predicting the recruitment dynamics of a fish species (Hjort, 1914; Houde, 1987). Prey scarcity is one factor with the potential to limit recruitment by specifically limiting larval growth (Graeb et al., 2004; Welker et al., 1994) since growth rate forecasts recruitment strength of fish populations better than any single intrinsic variable (Letcher et al., 1996). Even slightly larger larvae capture prey more efficiently (Hunter, 1981), escape predators more successfully (Bailey, 1984; Blaxter, 1986), are more resistance to starvation (Hunter, 1981; Miller et al., 1988), and are capable of swimming faster (Blaxter and Staines, 1971). Therefore, knowledge of the diets of larval fish is valuable for interpreting the proximate causes of recruitment variability.

Only a handful of studies have been conducted on the early life history of the Laurentian Great Lakes invader, the round goby (*Neogobius melanostomus*, Pallas 1814), despite their prominent role in nearshore food-webs. The round goby is a small, benthic, Ponto-Caspian native which was inadvertently introduced into the Great Lakes basin in the ballast water of freighters (Hensler and Jude, 2007) sometime before their initial discovery in the St. Clair River in 1990 (Jude et al., 1992). Round gobies possess a number of traits which allowed them to thrive in the Great Lakes despite the presence of native species occupying a similar benthic niche (*Cottus bairdi*, *Etheostoma nigrum*, and *Percina caprodes*). Among these traits are a high reproductive output, tolerance of a wide range of environmental conditions, aggressive behavior, nest guarding by males, and large body size compared to interspecific rivals (Corkum et al., 1998; Jude, 1997). The near-simultaneous introduction of their native prey, dreissenid mussels (*Dreissena polymorpha* and *D. rostriformis bugensis*), may have likewise contributed to their

success in the Great Lakes (Jude et al., 1995; Jude et al., 1992). Round gobies are currently the second-most abundant prey fish species in Lake Michigan, behind alewife (*Alosa pseudoharengus*), based on a recent assessment of lake-wide biomass by USGS (Madenjian et al., 2012), and appear in the diets of most native piscivores (Johnson et al., 2005).

The offspring of round gobies typify a pattern of ontogenetic development described by Balon (1998) as direct development, which is common among livebearers and nest guarders. Eggs are large (3.4 – 3.8 mm) (Moskal'kova, 1989), and development within the egg is highly advanced (Moiseyeva, 1983); therefore, round gobies emerge functionally and morphologically similar to adults and, hence, lack a true larval stage (Marsden et al., 1996). Newly hatched round gobies are referred to in the literature as 'fry' (Marsden et al., 1996). In this study, the term 'fry' functionally describes round gobies in a size range of 6 – 26 mm SL.

Accounts of the diet of round goby fry in the Great Lakes have been based on few specimens, generally collected as by-catch during nocturnal, pelagic, larval fish studies (Hayden and Miner, 2009; McDonald et al., 2014). Round goby fry execute regular, nocturnal vertical migrations into the water column (Hayden and Miner, 2009; Hensler and Jude, 2007). Examination of nocturnal diets revealed that round goby fry forage during these pelagic migrations (Hayden and Miner, 2009; Jůza et al., 2015; McDonald et al., 2014). Upwards of 99% of the prey types in the diet of round goby fry in western Lake Erie were pelagic including, prominently: dreissenid eggs and veligers, cyclopoid copepods, daphnids and bosminids (Hayden and Miner, 2009).

Alternatively, McDonald et al. (2014) found evidence of benthic foraging by round goby fry at one site in the Detroit River. Harpacticoid copepods, which are interstitial, benthic

microcrustaceans (Fenchel, 1978), dominated the local diet (60% numerical abundance) at this site. A benthic diet component, including the harpacticoid copepod, *Moraria sp.*, the benthic chydorid, *Leydigia spp.*, oligochaetes and chironomid larvae, was likewise evident among round goby fry in a European Reservoir (Jůza et al., 2015). The presence of benthic organisms in the diet of round goby fry may reflect a pattern of diurnal, benthic foraging; or conversely, it may indicate pelagic foraging on tychoplankton, or “accidental plankton,” swept into the water column by currents or other disturbances of the benthic sediments.

It remains unclear if benthic foraging occurs consistently among round goby fry, nor is it clear whether the benthic component is related to a diurnal foraging cycle. Adult and older juvenile round gobies forage both day and night (Carman et al., 2006; Johnson et al., 2008). My study attempts to clarify the role of benthic and diurnal foraging in the early feeding of round gobies by collection at diverse habitats during the day.

The role of ontogeny on the diets of round gobies also requires further investigation. Round gobies experience one well-studied, major diet shift associated with ontogeny. Between 60 – 100 mm SL, juvenile round gobies in the Great Lakes transition from a diverse diet of aquatic arthropods (Chironomidae, Ephemeroptera, and Trichoptera), mesocrustaceans (0.2-20mm) (Amphipoda and Isopoda) and gastropods (Carman et al., 2006; French and Jude, 2001; Jude et al., 1995; Lederer et al., 2008, 2006) to an adult diet composed mainly of dreissenids (French and Jude, 2001; Janssen and Jude, 2001; Jude et al., 1995; Ray and Corkum, 1997). This ontogenetic shift correlates an important morphological development, the growth of pharyngeal molariform teeth, which are necessary for crushing the shells of dreissenids (Andraso et al. 2011; Ghedotti et al. 1995). The arthropod prey types of juvenile round gobies

(<60 mm) described above are generally too large for fry to consume. Thus there should be an earlier ontogenetic diet shift between hatchling and older juvenile diets.

Ontogenetic diet shifts are common within the larval stage of many pelagic fishes (Hunter, 1981). As larval fish increase in size, they generally select larger prey types (Juanes et al., 1994; Keast & Webb 1966; Persson, 1990; Popova, 1978, 1967) and subsequently benefit from improved growth rate and survival compared to conspecifics consuming smaller prey (Hunter, 1981, 1977). Among Great Lakes native fishes, the larvae of burbot (*Lota lota*) select sequentially larger prey types as they grow (3–15 mm), beginning with rotifers and progressing through stages where they prey upon cyclopoid nauplii, mature cyclopoids and mature calanoid copepods (Ghan and Sprules, 1993). While burbot are strictly pelagic during their larval stage (Clady, 1976; Ghan and Sprules, 1991), round goby fry are only nocturnally pelagic. I suspect that the evolutionary factors which drive pelagic fish larvae to select progressively larger prey may also apply to the fry of benthic fish like round gobies.

Round gobies are known to spawn in diverse riverine and lacustrine environments. The major objective of this study is to characterize the benthic, diurnal foraging ecology of early juveniles across a similarly wide range of environment types. To my knowledge the prey at first feeding, which occurs for round gobies between 6.0 and 6.2 mm TL (Logachev and Mordvinov, 1979), has not been assessed in any habitat type. An important result of an assessment of the diet of round goby fry may be to identify the first prey. And, as described previously, another objective is to quantify the timing of a predicted ontogenetic diet shift from the first-feeding diet to the juvenile diet.

Methods

Diet study

Round goby fry were collected from various locations in western Lake Michigan, Green Bay, and two tributaries of western Lake Michigan during the summers of 2013 and 2014. Sites were selected to represent a variety of habitats because the available potential first prey may vary among nursery areas. Ten sites were sampled across three environment types: open-water (6 – 8 m), natural and artificial embayments (< 2 m), and stream sites (Figure 1; Table 1). Three of the four embayments were within harbors, two in Milwaukee, WI and one in Port Washington, WI. Riley's Bay, a natural embayment on the eastern side of Green Bay, was also sampled. Two small tributaries, Pigeon River and Silver Creek, were each sampled at an upstream riffle and downstream pool, each within 3 km from Lake Michigan.

Sampling methods were varied to collect round goby fry in different environments because one method was not suitable for all sites. The Port Washington Marina and all stream sites were seined with a 2 m long net with 3 mm size mesh. Round goby fry at open-water sites (Bradford Beach and Milwaukee Breakwall) and one embayment (Riley's Bay) were collected by SCUBA divers or snorkelers wielding hand nets. Two embayment sites (Lorier Reef and Texas Rock) were sampled via ROV (remotely operated vehicle). This technique was effective at sampling round goby fry in complex benthic habitats (e.g., rocks and/or dense benthic algae) where fry were inaccessible via other sampling methods. The ROV was designed based on concepts from Bohm and Jensen (1997). It was outfitted with a suction sampler and a pair of electrodes (anode and cathode) designed to deliver a shock from an ETS ABP-3 Pulsed DC electrofishing

backpack unit. ROV electroshocking was used previously by Janssen (et al., 2006) to collect larval lake trout (*Salvelinus namaycush*) from a deep-water reef.

Where round goby fry were abundant, smaller individuals were selected preferentially to better represent the diet at first feeding. Total (TL) and standard length (SL) were measured for each fish to the nearest mm.

After collection, round goby fry were euthanized in an overdose of MS-222 and immediately stored in 90% ethanol to halt digestion. In the laboratory, digestive tracts were removed under a dissection microscope. Round goby fry lack a clearly defined stomach; therefore, the contents of the entire digestive tract were included in the diet results (Thomas, 1997). Prey in the gut contents were enumerated and identified to the lowest practical taxon. Degradation of prey items limited identification precision to the level of order or family in most cases. In cases where more accurate identification was possible, genus and species of prey items were recorded.

Electivity analysis

Electivity analyses compare the proportion of prey in stomach contents to the community composition of resident prey. The physical benthic habitat at most sites was too heterogeneous to adequately assess the relative abundance of resident prey. However, habitats at two sites, Texas Rock and Silver Creek mouth, were homogenous enough to allow such an assessment. Texas Rock is a Devonian limestone bedrock outcropping in Milwaukee's south harbor with an approximate area of 3000 m². When the assessment was conducted in 2014, the average depth was 1.5 m. The site was covered with a dense growth (5–15 cm length) of *Cladophora glomerata*. Silver Creek was physically separated from Lake Michigan at the time of sampling by

a sandbar. The area of the pool which formed behind the sandbar was approximately 900 m². Flow was negligible. It was fully exposed to sun and 1.5 m maximum depth. The benthic habitat at this site was characterized by sand substrate interspersed with benthic algae. Resident fauna were assessed from samples of substrate and benthic algae collected from several locations in the near vicinity of round goby fry sampling sites immediately after sampling was complete. Samples were pooled according to site and type prior to characterization. At Silver Creek mouth, substrate samples were scraped from the top 3 cm into a 1 L cylindrical plastic container. Containers were capped immediately underwater to trap resident fauna. Algal samples were collected at both sites. Algae were removed from their attachment points and placed in 1 L containers which were capped immediately underwater to trap resident fauna. Texas Rock lacked removable substrate and, therefore, resident fauna at this site was assessed from benthic algal samples only.

In the laboratory, supernatant water was drained from the sample containers through a 125 µm sieve to capture fauna. A wash bottle filled with 70% ethanol was used to rinse fauna from the sieve into a separate container. Sediment and benthic algae sample containers were subsequently refilled with 70% ethanol. Fauna from all samples were identified and counted under a dissection microscope.

Vanderploeg and Scavia's 'relativized index of electivity' (Vanderploeg and Scavia, 1979) was used to assess individual preference for, or avoidance of, certain prey types. The 'relativized index of electivity' equation is:

$$E^* = \frac{\left(W_i - \frac{1}{n}\right)}{\left(W_i + \frac{1}{n}\right)} \quad \text{where: } W_i = \frac{r_i}{\sum \bar{P}_i}$$

Where r_i is the numerical percent of prey i in the diet of an individual fish. P_i is the proportion of prey i in the prey community. n is the number of prey types included in the analysis. Prey types were included which appeared in both the diet and resident fauna. The E^* value is normalized to a 1 to -1 scale where positive numbers represent preference, negative numbers represent avoidance, and difference from 0 represents the strength of the relationship.

E^* was calculated for each prey type in the diet of individual fry. Fry with empty stomachs were excluded from the analysis. Sample mean E^* s were generated for each prey type. These were tested for significant difference using either a one-sample Student's t -test (H_0 : mean $E^* = 0$) (Alcaraz and Garcia-Berthou, 2007) or the Wilcoxon signed-rank test depending on whether data sets fit a normal distribution. For each site, sets of individual E^* s were tested for normality using the Shapiro-Wilk test.

Gape limitation

Gape was measured for a sample set of round goby fry ($n = 38$) in a size range of 9 – 25 mm SL. Gape was measured using an ocular micrometer with 30 μm precision. SL was measured to the nearest 500 μm with a dissection microscope. To confirm jaw position, fry were cleared and stained following the protocol of Potthoff (1984). Gape was experimentally defined as the longest distance between a fish's jaws with the jaws positioned at a 90° relative angle (Rowlands et al., 2006).

Ontogeny

At most sites, the majority of prey were of only one or two types. I searched for an ontogenetic diet shift by employing simple linear regression between round goby fry SL and the percent

abundance (%A) of prey types. Abundance values were logit transformed (Warton and Hui 2011). The logit transform is:

$$\text{logit}(p) = \ln\left(\frac{p}{(1-p)}\right)$$

Where 'p' is the percent abundance of a particular prey type among a pre-defined subset of the individual diet. To remove values of zero, the lowest observed non-zero %A value in the sample population was added to all %A values; except where values equal 1, or in the case that the addition of the lowest observed non-zero value causes the % A to reach or exceed 1 (Warton and Hui, 2011). The remove values of 1, the difference between 1 and the highest observed value was subtracted from all 1's (Warton and Hui, 2011). Fry with empty stomachs were removed from this analysis.

ANCOVA was used to compare parallel regression using percent abundance as the dependent variable, SL as the covariate, and site as the group variable. Pairwise comparisons of percent abundance between study sites were made using Tukey's Honest Significance Test.

Results

Primary prey selection

It was typical for the local diet of round goby fry to have a primary prey type which contributed >50% to the total diet (by number). Primary prey percent abundance ranged from 57—82.5% at open water and embayment sites (Table 2). Harpacticoid copepods were the primary prey of round goby fry at five of seven open water and embayment sites, including all of those sampled in 2013. At other sites, prey were dominated by either chydorid cladocerans (Lorier Reef in 2014) or ostracods (Riley's Bay).

The appearance of a locally dominant prey type was less consistent in two stream environments. The most abundant prey did not exceed 50% at two of five stream sites (Table 3). At three other streams sites, the abundance of primary prey types ranged from 64.4—87.6%. Chironomid larvae were either the first or second most abundant prey type at four of five stream sites. Chydorids were the primary prey at two stream sites including the pond-like mouth of Silver Creek, where they composed the largest component of any local diet (87.6%).

Electivity

Vanderploeg and Scavia's (1979) relativized electivity index indicated significant preference for chydorids by round goby fry at the Silver Creek mouth site ($E^*=0.55$, $p = 0.00$) (Table 4).

Chydorid percent diet abundance at Silver Creek mouth was 13x higher than their abundance in the resident fauna. Significant avoidance was reported at this site for harpacticoids ($E^* = -0.29$, $p = 0.02$) (Table 4) and four other prey types: chironomid larvae, chironomid pupae, cyclopoid copepods, and the cladoceran *Simocephalus sp.* which typically clings to vegetation.

Round goby fry at Texas Rock fed on harpacticoid copepods in proportion to their availability ($E^* = 0.17$, $P = 0.36$) (Table 4). Harpacticoids were the primary prey of round goby fry at this site (73.3% diet abundance) and the most numerically abundant prey type in the resident fauna (59.6%). Avoidance of chydorids by round goby fry was recorded at Texas Rock ($E^* = -0.50$, $p = 0.04$). General avoidance for most major prey taxa was recorded at both sites (Table 4).

Gape-length relationship

A strong linear relationship was established between gape (G) and SL (L) (regression equation: $G = 0.1015 * L - 0.0893$; $p < 0.001$; $R^2 = 0.81$, $n = 38$) (Figure 2). This equation was used to estimate gape for fish with known SL and unknown gape.

Ontogenetic diet shift among fry

An ontogeny-related diet shift from harpacticoid copepods to chydorids was suggested from the diet data pooled from the seven sites where either harpacticoids or chydorids were the primary prey (Figure 3). ANCOVA revealed no significant interaction between slopes ($F_{6, 108} = 1.14$, $P = 0.35$) despite the existence of a weak site effect ($F_{6, 108} = 2.23$, $P = 0.05$). This indicated that the regression between SL and chydorid percent abundance was relatively consistent between sites, and that these separate populations should be treated statistically as a single population. In this situation, Zar (1984) recommends pooling the sites to compute a common slope. Initial results of ANCOVA provided no evidence of a length effect on chydorid percent abundance in round goby fry diets ($F_{1, 108} = 1.77$, $P = 0.18$); but upon pooling the diet, chydorid percent abundance in the diet did significantly increase with fry length ($R^2 = 0.20$, $p = 0.00$, $n = 122$). Alternatively, regressions from individual sites produced no significant relationship ($R^2 = 0.01 - 0.17$, $p = 0.07 - 0.75$) (Figure 4); this could be due to low power due to low sample sizes per site ($n = 8 - 20$). Therefore, I conclude that chydorid percent abundance increases with fish length when harpacticoids and chydorids are common to the diet. However, the low R^2 value shows clearly that fish length describes little of the variability in chydorid consumption.

Post-hoc comparisons using Tukey's HST revealed that chydorid percent abundance varied significantly between sites in 12 of 21 pairwise comparisons including examples of year-to-year variability at the same site and variation between sites in close spatial proximity (<1km). Chydorid percent diet abundance at Lorier Reef differed significantly between study years: 2013 (median = 0.00, Q1 = 0.00, Q3 = 0.11) and 2014 (median = 0.61, Q1 = 0.50, Q3 = 0.74) ($p = 0.01$). Likewise, chydorid diet abundance varied significantly between Texas Rock (median = 0.00, Q1 = 0.00, Q3 = 0.25) and Lorier Reef in 2014 (median = 0.61, Q1 = 0.50, Q3 = 0.74) ($p = 0.00$). Both sites were sampled in 2014 but a few weeks apart (Table 1) and are physically separated by less than 1 km. Therefore, even if there is a trend related to ontogeny, the shift is likely overwhelmed by temporal and/or between-site heterogeneity in prey distribution. The existence of an ontogenetic trend should be validated with a follow-up experiment in a controlled, laboratory setting. In particular, work should focus on sensory mechanisms and prey handling specific to round goby fry.

Juvenile diet comparison

I did not observe a shift to the prey types commonly found in the diet of larger juvenile round gobies, such as aquatic insect larvae, mesocrustaceans or gastropods. Chironomid larvae composed 17.5% of the pooled diet of round goby fry, but they were the only prey common to the reported juvenile diet to contribute greater than 1% to the pooled diet. Chironomid percent abundance in local diets was highly variable but generally more abundant in the diet at stream sites (mean = 25.1%, range = 3.2 – 70.8%) compared to open water (mean = 14.9%, range = 10.5 – 17.0%) and embayment sites (mean = 7.2%, range = 2.7 – 18.6.)

Non-chironomid insect larvae, including Ephemeroptera (0.7%) and Trichoptera (0.2%), and benthic mesocrustaceans (Amphipoda and Isopoda) (0.1%) made only marginal contributions to the pooled diet of round goby fry. The appearance of dreissenids was, likewise, rare. Veligers composed 0.4% of the pooled diet by numerical abundance. The nymphs of heptageniid mayflies were a significant prey type for round goby fry at the upstream riffle site on the Pigeon River, composing 11.2% of the local diet by numerical abundance. Greater than 75% of all non-chironomid insect larvae (Ephemeroptera and Trichoptera) in the pooled diet were found at this site.

Discussion

Benthic diet

Round goby fry sampled diurnally, in the benthos, fed almost exclusively on benthic prey types. Harpacticoid copepods, chydorid cladocerans, chironomid larvae, and ostracods composed the great majority of the pooled diet. Pelagic prey were rare. The two most dominant nearshore zooplankton according to Pothoven and Fahnenstiel (2014), *Diaptomus spp.* and *Bosmina longirostris*, did not appear in the diet at any open-water or embayment site (n=136). Likewise, *Daphnia spp.* (1.3%) and dreissenid veligers (0.8%), the two most abundant pelagic prey types to appear in the diet, made marginal contributions to total abundance.

These results contrast the results of two previous studies of the diet of round goby fry in the Great Lakes in which pelagic prey types composed between roughly 50% (McDonald et al., 2014) and 99% of the diet (Hayden and Miner, 2009). All previous diet studies sampled vertically migrating round goby fry using nocturnal ichthyoplankton tows (Hayden and Miner,

2009; Jůza et al., 2015; McDonald et al., 2014). My study was the first to directly sample round goby fry from the benthos, and the first to sample during the day.

I suggest that the disparity between my results and those previous is an indication that round goby fry may feed both day and night, as do larger individuals (Carman et al., 2006; Johnson et al., 2008). McDonald et al. (2014) found one site in the Detroit River where harpacticoid copepods dominated the diet (60% numerical abundance). Harpacticoids are an obligate interstitial organism; therefore, their presence in a nocturnal pelagic diet probably reflects a benthic component. Likewise, Jůza et al. (2015) found a significant portion of benthic prey in the diets of vertically migrating juvenile round gobies in the Biesbosch reservoirs of the Netherlands. Gut retention time for round goby fry is unknown, but is probably short. For larval fish of a similar size, gut evacuation rate has been measured between 1 – 8 hours (*Dorosoma*: Dettmers and Stein, 1992; *Gadus*: Canino and Bailey, 1995). A correlation is likely to exist between the incidence of benthic, or pelagic, prey types and the time of day. A diet study spanning both time frames would be helpful for testing this hypothesis.

The benthic diet of round goby fry increases the relevance of benthic meiofauna in the nearshore food web, especially given the increasing importance of round gobies as a forage fish (Dietrich et al., 2006; Hensler et al., 2008; Hirethota, 2015; Johnson et al., 2005; Steinhart et al., 2004). Benthic meiofauna have been historically understudied compared to their pelagic counterparts despite indications that their relative contribution to the nearshore microcrustacean community is substantial. Evans and Stewart (1977) found that chydorids, harpacticoid copepods and ostracods composed 16% of the pre-dreissenid nearshore microcrustacean community, and likewise, 37-40% of all microcrustaceans were contained

within the bottom 0.3 m of the water column. That said, major increases in benthic macroinvertebrate abundance have been observed in dreissenid-invaded systems associated with larger trends of benthification (Ozersky et al., 2011); and Evans and Stewart's pre-dreissenid community assessment may yet underestimate the current contribution of microcrustaceans and other meiofauna to the benthic component.

Juvenile diet comparison

It appears there is little overlap between the prey of round goby fry (6 – 26 mm SL) and those of larger juvenile round gobies (≥ 35 mm) (Carman et al., 2006; French and Jude, 2001; Jude et al., 1995; Lederer et al., 2008, 2006). Many common prey types of juvenile round gobies, including benthic mesocrustaceans (0.2-20mm), dreissenids, gastropods and trichopterans, contributed, collectively, 0–3.7% (mean: 0.3%) (by numerical abundance) to the local diets of round goby fry. Two exceptions, chironomid larvae and ephemeropteran nymphs, were notably important in the diets of both fry and larger juveniles. Chironomid larvae are commonly the most abundant prey type in juvenile round goby diets (Carman et al., 2006; French and Jude, 2001; Lederer et al., 2008, 2006); and were also an important component of the diet of round goby fry, especially for stream populations. Chironomid larvae were the dominant prey type at two stream sites (64.4% and 70.8%) and were the third most abundant prey type overall (17.5%). The relevance of chironomid larvae to both life stages is explainable by the wide size range of chironomid larvae which are available in the benthic environment. Chironomids progress through four benthic, larval instars during their development. *Chironomus riparius*, for example, ranges from 0.8 – 13.3 mm in length prior to pupation (Watts and Pascoe, 2000). Chironomid larvae appeared in the diet of round gobies as small as 8 mm SL and persisted throughout the

study size range (≤ 26 mm SL). Since $>95\%$ of round goby fry in this study were ≤ 20 mm SL, I conclude that the predicted ontogenetic shift from the diet of fry to the juvenile diet must occur after 20 mm SL.

Heptageniid mayfly nymphs were a locally important prey type (11.2% A) for round goby fry at the furthest upstream, riffle site in the Pigeon River (3.0 km from Lake Michigan). Carman et al. (2006) also found heptageniids in the diets of juvenile and adult (54–82 mm SL) round gobies in the Flint River and predation on heptageniids in the Flint River was nocturnal. This pattern reflects the nocturnal foraging habit of heptageniids (Elliott, 1968; Lyman, 1945). Consequently, the occurrence of heptageniids in the diets of round goby fry suggests nocturnal foraging.

Ontogenetic diet shift among fry

A tenuous ontogenetic diet shift from benthic harpacticoids to benthic chydorids was suggested by analysis of the round goby fry diet (Figure 3). In general, benthic-foraging fry in shallow, nearshore environments fed primarily on harpacticoid copepods at the switch to exogenous feeding. Harpacticoids served as the primary prey until an early-life ontogenetic diet transition to benthic cladocerans, specifically chydorids from the genera *Alona*, *Chydorus*, and *Eurycerus*, which occurred between 6 – 26 mm SL.

An ontogenetic shift from harpacticoids to chydorids may constitute as a shift to larger prey types based on size measurements of prey from stomach contents which indicated that chydorids were generally larger (two-sample $t(32) = 7.07$, $p < 0.01$) and displayed a greater range in size. Harpacticoids in the stomachs of round goby fry averaged 120 μm wide ($n = 9$, $SD = 26 \mu\text{m}$), while chydorids averaged 237 μm wide ($n = 28$, $SD = 37 \mu\text{m}$) (Figure 2). Hunter (1981) demonstrated that slight increases in width among prey types can produce large

increases in mass. For instance, an increase of 2.5X in copepod width can increase mass by an order of magnitude (Hunter, 1981). It is highly advantageous for larval fish with the capacity to capture larger prey to do so to speed growth (Hunter, 1977). Larval growth rate produces a greater effect on survival than any other intrinsic variable (Letcher et al., 1996).

The results of electivity analysis may be interpreted as support for the observed ontogenetic shift. Round goby fry at Texas Rock, which were smaller than at any other site (mean = 9.2 mm SL, range = 6 – 14 mm SL), fed on harpacticoids in proportion to their environmental availability, but significantly avoided chydorids. Conversely, at the mouth of Silver Creek, round goby fry were nearly twice as long (SL) on average compared to Texas Rock (mean = 17.6 mm SL, range = 13 – 26 mm SL) and displayed a significant preference for chydorids and significant avoidance of all other prey taxa including harpacticoids (Table 4). Mechanisms underlying field observations such as this are best studied in controlled laboratory experiments.

Natural variation and heterogeneity

While I found evidence of a general ontogenetic shift, the low R^2 value associated with the trend demonstrates that fish size actually describes little of the variation in round goby fry prey selection. At sample size ≤ 20 , the trend was not statistically resolved, meaning that the correlation between SL and prey percent abundance was not significant at any single site. This is likely explainable by low statistical power due to small sample size, but also by heterogeneity in the benthic environment. Variability among individual round goby fry could be due to prey patchiness, which we did not investigate, and/or the variability of chydorid size. This would be best resolved in a laboratory environment by specifically testing for prey handling and prey detection.

Diet heterogeneity reflects both environmental heterogeneity and individual specialization. Benthic microcrustacea are commonly distributed contagiously (Fenchel, 1978). Substrate type (McLachlan and Brown, 2010) and food resources (Carman and Thistle, 1985) are known to be aggregating factors. Patch sizes are typically small for chydorids: patches of *Alona*, *Chydorus*, *Eurycercus* and others have been measured on the order of 1 – 18 m² and can vary between adjacent 1 m² quadrats by >360 individuals (Whiteside, 1974). Therefore, local abundances of benthic copepods or cladocerans are largely unpredictable. Additionally, search volume is tiny for pelagic fish larvae in a similar size range to round goby fry (Hunter, 1981). Pilchard (*Sardina pilchardus*), plaice (*Pleuronectes platessa*), and anchovy (*Engraulis mordax*) in a 5-10 mm size range search between 0.1 - 1.8 L / hr. (Blaxter and Staines, 1971; Hunter, 1972). Search volume has not been measured for a species with benthic larvae but is likely comparable. Therefore, I conclude that environmental heterogeneity has the potential to obscure the influence of ontogeny on prey selection at small sample size.

The habit of round goby fry to select a primary prey type is likewise reflective of a predator foraging in a patchy environment. Local diets of round goby fry included a single prey type which exceeded 50% of the total diet abundance among 10 of 12 sampled populations (Table 2). This result is illustrative of both the patchy distribution of prey and the foraging behavior of round goby fry. The Marginal Value Theorem (Charnov, 1976) predicts that predators in patchy environments will actively seek to improve net energy intake by restricting travel between prey patches to maximize time spent consuming prey. Even in cases where the distribution of two or more prey types overlap, planktivorous fish improve capture rate and capture success by focusing on a single prey type (Persson, 1985). Attempting to simultaneously exploit two prey

types with different evasion maneuvers lowers feeding efficiency (Persson, 1985). Therefore, the potential energetic gains of selecting a larger prey must be weighed against the cost of searching for it. The results of this study suggest that availability and distribution of prey must necessarily trump preference in patchy benthic environments.

Marine and freshwater fish larvae

As a marine fish currently inhabiting a freshwater system, the round goby provides a potential opportunity for research on the dichotomy between marine and freshwater fishes described by Houde (1994). Houde argued that mean survivorship to metamorphosis is much higher (average about 44x) for the larvae of freshwater fishes compared to marine fish larvae. Houde attributes this disparity, in part, to large differences in hatchling body size between the two groups associated with a clear split in reproductive and developmental strategies. Houde argued that freshwater fishes generally spawn demersally and produce relatively few, large eggs and large offspring, while marine fishes commonly spawn pelagically and produce many, small eggs and similarly small larvae. Smaller larvae are, among other detriments, more vulnerable to starvation due to unsubstantial energy reserves and high metabolic demands (Hunter 1981). The high rates of mortality which are intrinsic to small body size are theoretically compensated by the sheer abundance of offspring produced by marine fishes; however, Houde contends that freshwater fish larvae should also benefit from an environment which is decidedly more hospitable compared to the marine environment. The offspring of freshwater fishes spend more time in shallow, productive waters compared to marine fish larvae which are subject to potential adverse transport to unproductive offshore waters.

What makes the round goby potentially interesting in this context is that it will undergo a diel vertical migration into the pelagia but is also benthic. It may be that the relative benefit of pelagic feeding vs. benthic feeding, and the round goby's diel feeding cycle, may depend on local conditions and, over time, there may be regional phenotypical and even microevolutionary variation in its first feeding.

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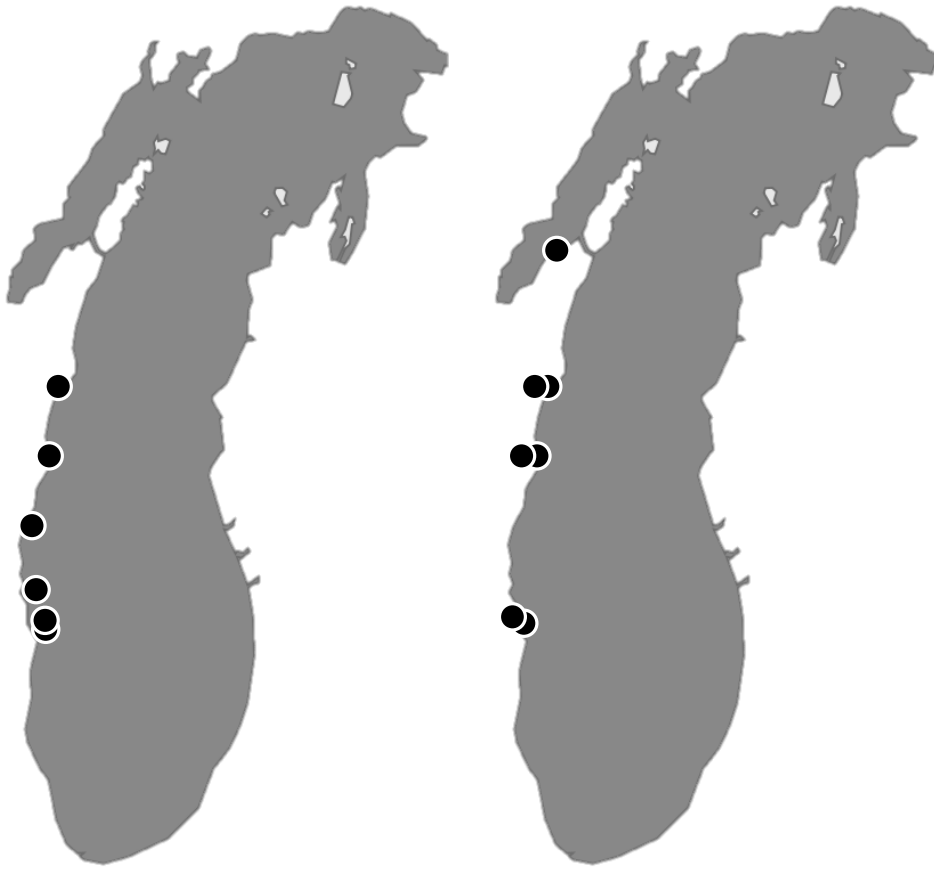


Figure 1. Experimental site locations in Lake Michigan, Green Bay and Lake Michigan tributaries from 2013 (left) and 2014 (right).

Table 1. Experimental site summary.

Study sites are listed chronologically with their given abbreviations. GPS coordinate locations for each site are likewise listed. Sampling was repeated in the second year of the study at Lorier Reef and Pigeon River.

Study Site	Location		Date
Lorier Reef	42° 59.13'	87° 51.46'	01-Aug 2013
Milwaukee Breakwall	42° 59.12'	87° 51.41'	15-Aug 2013
Pigeon River	43° 47.13'	87° 43.41'	23-Aug 2013
Port Washington Marina	43° 23.23'	87° 51.52'	27-Aug 2013
Bradford Beach	43° 03.47'	87° 51.40'	29-Aug 2013
Texas Rock	42° 59.27'	87° 52.24'	08-Aug 2014
Silver Creek (riffle)	44° 03.49'	87° 39.22'	21-Aug 2014
Silver Creek (mouth)	44° 03.42'	87° 39.13'	21-Aug 2014
Pigeon River	43° 47.13'	87° 43.41'	21-Aug 2014
Pigeon River (riffle)	42° 46.52'	87° 44.51'	21-Aug 2014
Riley's Bay	44° 50.59'	87° 31.02'	25-Aug 2014
Lorier Reef	42° 59.13'	87° 51.46'	27-Aug 2014

Table 2. Primary prey types of round goby fry at embayment (< 2m) and open-water (10m) sites in western Lake Michigan in 2013 and 2014. Percent abundance reflects the numerical abundance of primary prey types relative to the total number of prey in the local diet. RGF standard length (range and mean) are listed for each site, as well as corresponding sampling dates.

	2013		2014		
Embayments (< 2m)	P. Washington Marina	Lorier Reef	Lorier Reef	Texas Rock	Riley's Bay
Primary prey type	Harpacticoid	Harpacticoid	Chydorid	Harpacticoid	Ostracod
% abundance	57.0	67.4	65.4	73.3	69.5
SL (mm): range (mean)	10 – 18 (14.5)	7 – 19 (13.8)	10 – 17 (13.9)	6 – 14 (9.2)	8 – 15 (11.0)
Date	Aug. 21	Aug. 1	Aug. 27	Aug. 8	Aug. 25
Open-water (6-8m)	Bradford Beach	Milwaukee Breakwall			
Primary prey type	Harpacticoid	Harpacticoid			
% abundance	65.3	82.5			
SL (mm): range (mean)	9 – 18 (13.3)	9 – 15 (12.1)			
Date	Aug. 29	Aug. 15			

Table 3. Primary prey types of round goby fry in two small tributaries of Lake Michigan in 2013 and 2014. Percent abundance reflects the abundance of primary prey types relative to the total number of prey in the diet. Local size range and mean size are listed, as well as corresponding sampling dates. Abbreviations given for chydorids (CHY), chironomid larvae (CL), and harpacticoid copepods (HC).

Streams	2013	2014			
	Pigeon River	Pigeon River	Pigeon River (riffle)	Silver Creek (riffle)	Silver Creek (mouth)
Primary prey type	CL	CHY / CL	CL	HC / CL	CHY
% abundance	70.8	46.4 / 33.2	64.4	46.0 / 44.8	87.6
SL mm: range (mean)	10 – 19 (13.6)	12 – 18 (15.2)	10 – 28 (16.6)	16 – 22 (18.3)	13 – 26 (17.6)
Date	Aug. 23	Aug. 21	Aug. 21	Aug. 21	Aug. 21

Table 4. Summary of round goby fry feeding electivity based on the composition of local diets and ambient fauna. Texas Rock is a shallow reef in Milwaukee's south harbor. Silver Creek is a small tributary on Lake Michigan's western side. Vanderploeg and Scavia's relativized index of electivity was used to produce E*s for individual RGF. Mean E*s were subsequently calculated for each prey type. Percent abundance reflects the numerical abundance of primary prey types relative to the total number of prey in the local diet. Percent ambient fauna, likewise, reflects the numerical abundance of a given prey type compared to the total numerical abundance of all fauna. Frequency of occurrence is the percent of RGF where a given prey appeared in the diet.

	Harpacticoid Copepods	Cyclopoid Copepods	Chydorids	<i>Simocephalus</i> <i>sp.</i>	Chironomid Larvae	Chironomid Pupae	<i>Hydracarina</i> <i>sp.</i>
Silver Creek mouth							
<i>Mean SL: 17.6 mm</i>							
Mean E* (p-value)	-0.29 (0.02)	-0.95 (0.00)	+0.55 (0.00)	-0.76 (0.00)	-0.88 (0.00)	-0.93 (0.00)	-----
% diet abundance	5.2	0.5	87.6	3.0	3.5	0.1	-----
% ambient fauna	4.5	11.6	6.6	15.7	52.1	2.5	-----
Freq. of occurrence (%)	85.0	20.0	95.0	45.0	50.0	5.0	-----
Texas Rock							
<i>Mean SL: 9.2 mm</i>							
Mean E* (p-value)	+0.17 (0.36)	-----	-0.50 (0.04)	-----	-0.71 (0.04)	-----	-0.85 (0.02)
% diet abundance	73.3	6.7	10.0	-----	6.7	0.0	3.3
% ambient fauna	59.6	0.0	13.4	-----	13.8	0.9	11.1
Freq. of occurrence (%)	88.9	11.1	33.3	-----	22.2	0.0	11.1

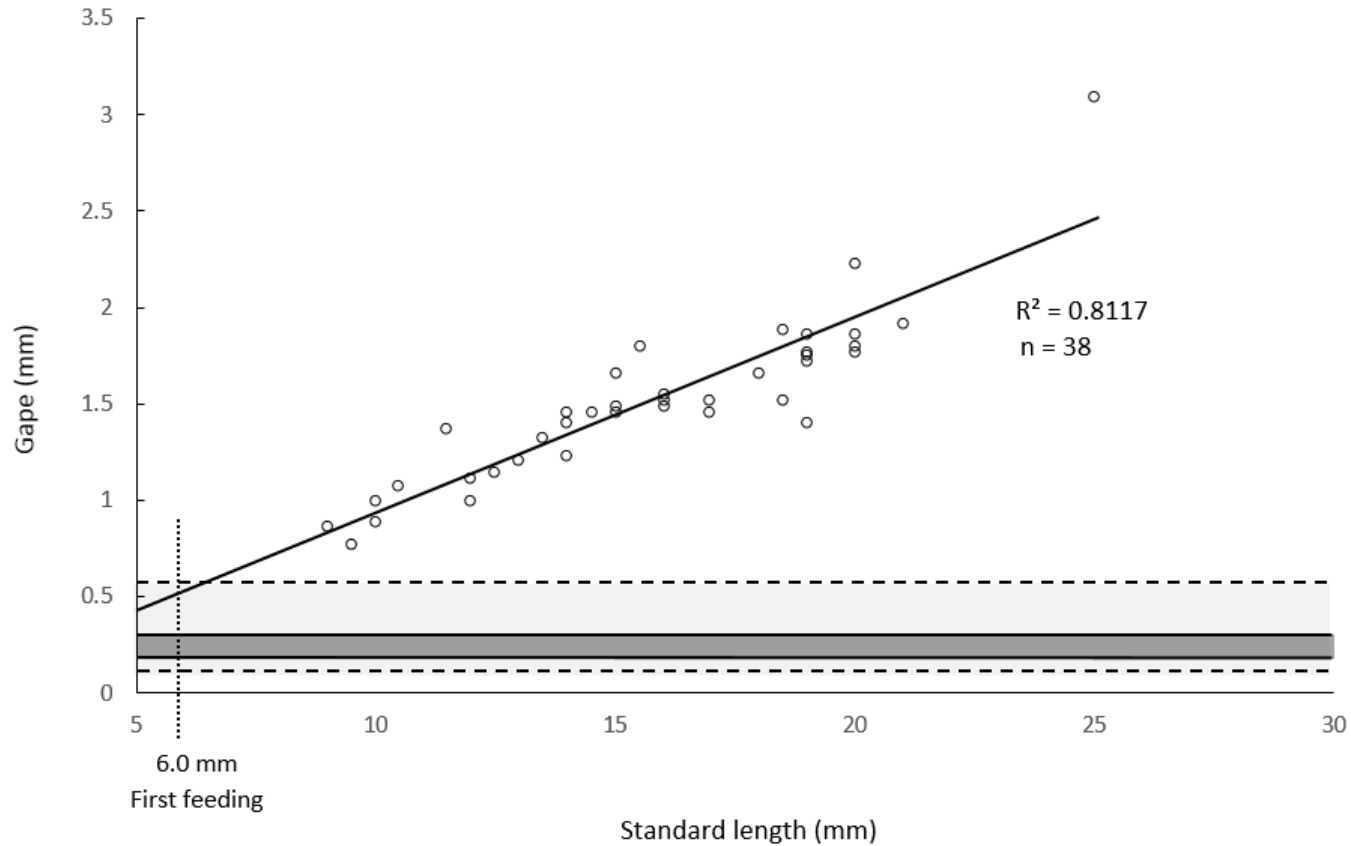


Figure 2. Linear regression of SL and gape for round goby fry in a size range of 9 – 25 mm SL. The range of widths of ingested prey is provided for comparison. Widths of chydorids ($n = 28$, white) and harpacticoid copepods ($n = 9$, black) recovered from stomach contents of round goby fry ranged from 156–300 μm (mean: 237 μm) and 100–220 μm (mean: 120 μm), respectively. Size at first feeding (6.0–6.2 mm, Logachev and Mordinov 1979) is marked by a dotted line.

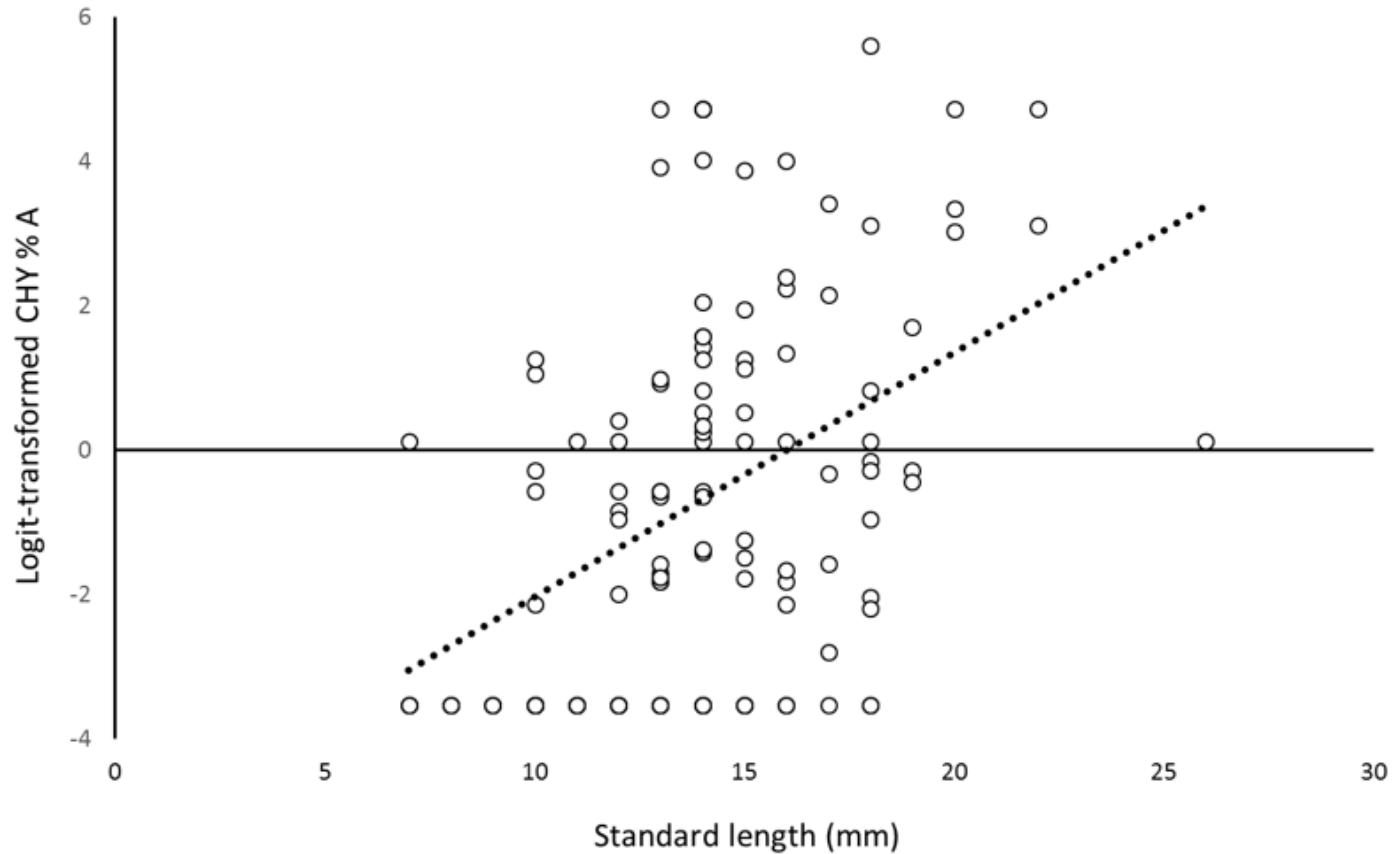


Figure 3. Linear regression between standard length (mm) and chydorid diet abundance (logit transformed) for 122 round goby fry (7 – 26 mm standard length) at six sites in western Lake Michigan and one tributary ($R^2 = 0.20$, $p = 0.00$). Either harpacticoid copepods or chydorids were the primary prey at all sites. All other prey types were excluded from this regression.

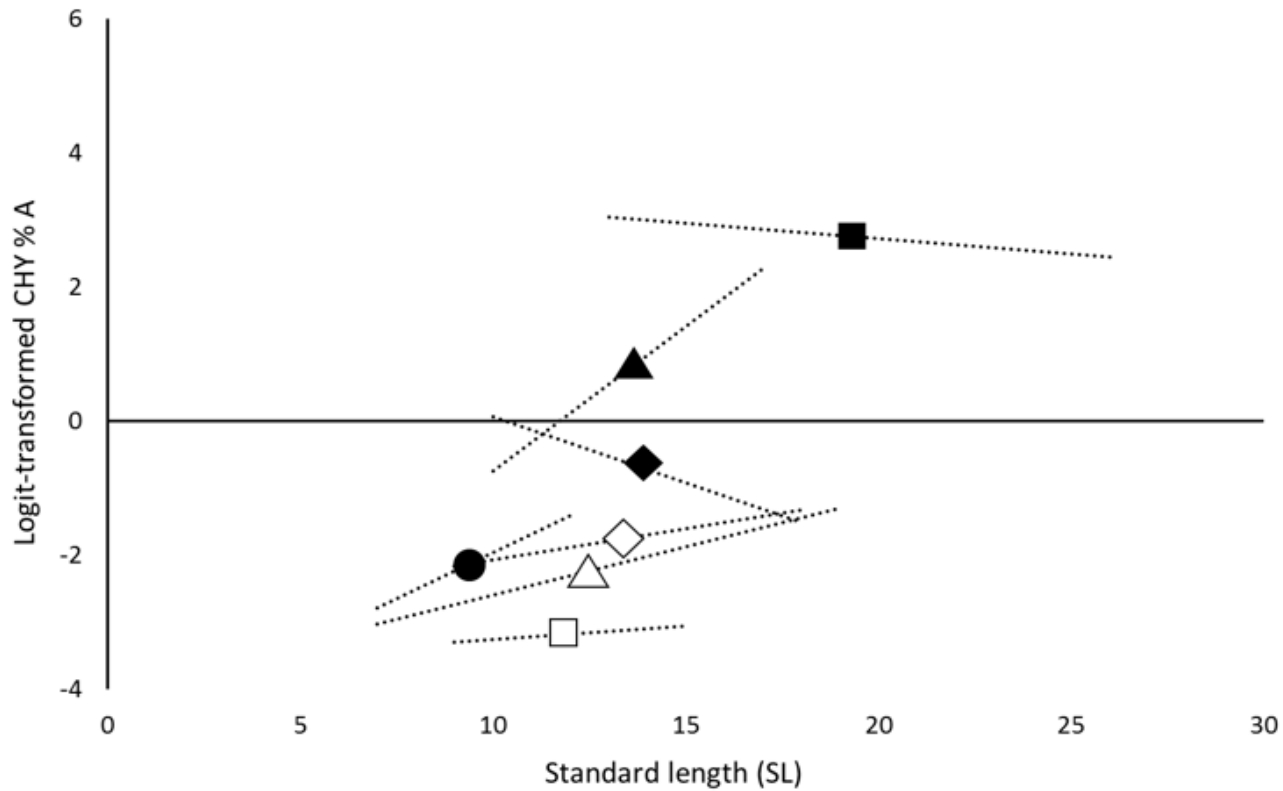


Figure 4. Linear regression between individual standard length (mm) and chydroid diet abundance (logit transformed) at six sites in western Lake Michigan and one tributary. Regressions are site specific. Either harpacticoid copepods or chydroids were the primary prey at all sites. All other prey types were excluded from this regression.

