Foraging ecology of walleye and brown trout in a Great Lakes tributary

Damon M. Krueger [a,*], Edward S. Rutherford [b], Doran M. Mason [b], YoonKyung Cha [c]

[a] University of Michigan, School of Natural Resources and Environment, 440 Church St., Ann Arbor, MI 48109, USA
[b] NOAA Great Lakes Environmental Research Laboratory, 4840 South State Road Ann Arbor, MI 48108-9719, USA
[c] University of Seoul, School of Environmental Engineering, Seoulsiripdae-ro 163, Dongdaemun-gu, Seoul 02504, Korea

ARTICLE INFO

ABSTRACT

The role of alternative prey on predator diet selection and survival of juvenile (parr) Chinook salmon (*Oncorhynchus tshawytscha*) is not well understood in the Laurentian Great Lakes. Therefore, measures of predator foraging ecology (prey species and size selection), prey densities, and functional response relationships were determined for adult walleye (*Sander vitreus*) and brown trout (*Salmo trutta*) (hatchery-reared) feeding on parr and alternate prey in the Muskegon River, a tributary of Lake Michigan, USA, from 2004 to 2007. Walleye selected for smaller than average brown trout and rainbow trout (hatchery-reared) but walleye prey size (with-in-prey) was independent of predator size. In general, walleye showed neutral selection for all prey species but, in some years, showed positive selection for rainbow trout and negative selection for parr. Hatchery-reared brown trout selected the smallest parr in the environment although prey size was independent of predator size. Parr were positively selected by brown trout only in April. Functional response curves were fit to describe the consumption of parr and other prey types by walleye (type II) and brown trout (type I). Interactions among rainbow trout, walleye, and brown trout favored parr survival, i.e. the presence of alternate prey (rainbow trout) significantly influenced walleye predation on parr, while brown trout appeared to become quickly limited by size or escape ability of parr. Our results should enhance understanding of food web dynamics in Great Lakes tributary habitats.

© 2015 International Association for Great Lakes Research. Published by Elsevier B.V. All rights reserved.

Introduction

Foraging ecology of predatory fishes can have consequences for the distribution, abundance, and growth of prey fish populations (Lundvall et al., 1999). Predation, in general, can affect the structure of biological communities in many ways (e.g., Payne, 1969). Piscivory, more specifically, has been shown to structure fish community composition (Caley, 1993), influence short and long-term population dynamics of prey fishes (Dörner et al., 2007; Krueger et al., 2011, 2013), stabilize interactions among forage species by controlling population abundances (Pimm and Hyman, 1987), and control food webs via a top-down trophic cascade (e.g., Hairston et al., 1960). For example, Krueger and Hrabik (2005) showed that a native predator (walleye, *Sander vitreus*) was responsible for recovery of a native planktivore (lake herring, *Coregonus artedi*) through suppression of an exotic predator/competitor (rainbow smelt, *Osmerus mordax*). Observing and analyzing the foraging ecology of top predators in an ecosystem can allow for enhanced understanding of trophic structure and interspecific relations via knowledge of a predator's overall impact.

The evidence is not so strong, however, where predators actively consume multiple prey types. In [more] natural systems, multiple prey species are often present and may directly or indirectly interact with one another (Chesson, 1989; Gotceitas and Brown, 1993). Hence, alternate prey can confound and/or direct predator foraging as they tend to buffer consumption of other prey (Czesny et al., 2001; Gilinsky, 1984; Kean-Howie et al., 1988). Because prey size and species-specific vulnerability are important attributes in prey selection by predators (Bannon and Ringler, 1986; Juanes, 1994), we expect that presence of alternate prey would buffer size-structured predation mortality (e.g., Czesny et al., 2001; Hyvärinen and Huusko, 2006).

In the Muskegon River, a tributary to Lake Michigan, USA, the food web [for our purposes] is fairly simple and consists of walleye, Chinook salmon (*Oncorhynchus tshawytscha*) parr, brown trout (*Salmo trutta*), and rainbow trout (*Oncorhynchus mykiss*). The former species is the apex predator in the Muskegon River, while the latter three species are prey of walleyes. Foraging by trout and walleyes in rivers has been analyzed to some extent, but further investigation is critical for understanding food web dynamics and ecological ramifications. Krueger et al. (2011) found that survival of Chinook salmon parr (henceforth referred to as "parr") is heavily influenced by predation from walleyes and brown trout. Walleyes were found to consume some parr though they consumed far greater quantities of hatchery-reared brown trout and rainbow trout. Further results indicate that hatchery brown trout, despite their smaller size, consumed more parr as a group than the much larger walleyes. The authors concluded that survival of parr was

* Corresponding author.
E-mail address: damonkr@umich.edu (D.M. Krueger).

likely controlled by parr growth, alternate prey abundance, and stocking practices for brown trout.

In the present study, we build upon those previous efforts in the Muskegon River to better understand the interactions between and among multiple predator and prey species and the associated ecological consequences. Whereas Krueger et al. (2011) focused on quantifying predation mortality by walleyes and hatchery trout on Chinook salmon parr only; in this paper we analyze prey species and size selection by walleye and brown trout relative to population biomass of all prey combined over a 3 month time period. This approach differs from many other studies of walleye and brown trout forage ecology (e.g., Elliott and Hurley, 2000; Forney, 1974; Porath and Peters, 1997; Ringler, 1979; Rudstam et al., 2015; Swenson and Smith, 1973) that were performed in controlled laboratory settings using only one prey type, or used empirical data on predator consumption of single prey species and ignored biomass and consumption of other available prey.

Methods

Study site

The Muskegon River extends 365 km from Houghton Lake in north-central Michigan to Muskegon, Michigan, USA, where it empties into Lake Michigan. The focus of this study was on the (ca.) 22.5 km salmonid nursery section of the Muskegon River, between Croton and Newaygo (Fig. 1; also see Godby et al., 2007). This section of river experiences mean discharge rates of approximately 85 $m^3 s^{-1}$ (range 61 – 261 $m^3 s^{-1}$) from April to June and the substrate is predominantly cobble and gravel, which provides excellent spawning habitat for Chinook salmon and other important sport fishes such as walleye and migratory rainbow trout (Auer and Auer, 1990; Merz et al., 2004; Quinn, 2005).

Fish abundance, biomass and size

Methods to estimate the abundance and size of parr, minnows (Cyprinidae), walleyes, brown trout and rainbow trout in the Muskegon River from 2004 – 2007 were previously reported by Krueger et al. (2011). A brief description of those methods follows. In 2004, a 2.4 m diameter auger-style smolt trap was used to capture out-migrating Chinook salmon parr from May 6 to June 29. Fish were identified, counted, weighed (nearest 0.1 g) and measured (TL mm) daily. Densities of Chinook salmon parr and cyprinids were estimated for the remaining years (April 19 – June 15, 2005; April 20 – June 7, 2006; May 8 – June 6, 2007) using a barge-style electrofishing unit (3 Amps, 240 V) along daytime 100 m transects, run upstream, at five established reference sites (Carl, 1982). A pass depletion protocol (e.g. Zippin, 1958) was used to estimate parr abundance because they were generally too small (<50 mm) for effective mark and recapture estimates. We sampled each reference site twice a month and sampled most sites five times in a given field season. We weighed and measured a sub-sample of 30 Chinook salmon parr from each electrofishing transect and counted and batch weighed the remaining individuals. Abundances and biomass of Chinook salmon parr and Cyprinidae were estimated for the whole river by multiplying the mean density ($\# \cdot m^{-1}$) of fish at the five reference sites by the mean fish weight (g) on each sampling date, times the total nursery shoreline (22.5 km x 2 sides = 45 km).

Walleyes, hatchery brown trout, and hatchery rainbow trout were collected by barge electrofisher using the aforementioned methods and reference stations in addition to collections with a Smith Root boom-style AC electrofishing boat (3 Amps, 240 V). Boom-electrofishing transects were run in a downstream fashion and were always performed during the day. Upon capture, fish were placed in a 189-liter recirculating live well and counted at the end of each transect. Population abundances of these three species were estimated using data from boom electrofishing transects. Date-specific indices of abundance for brown trout and
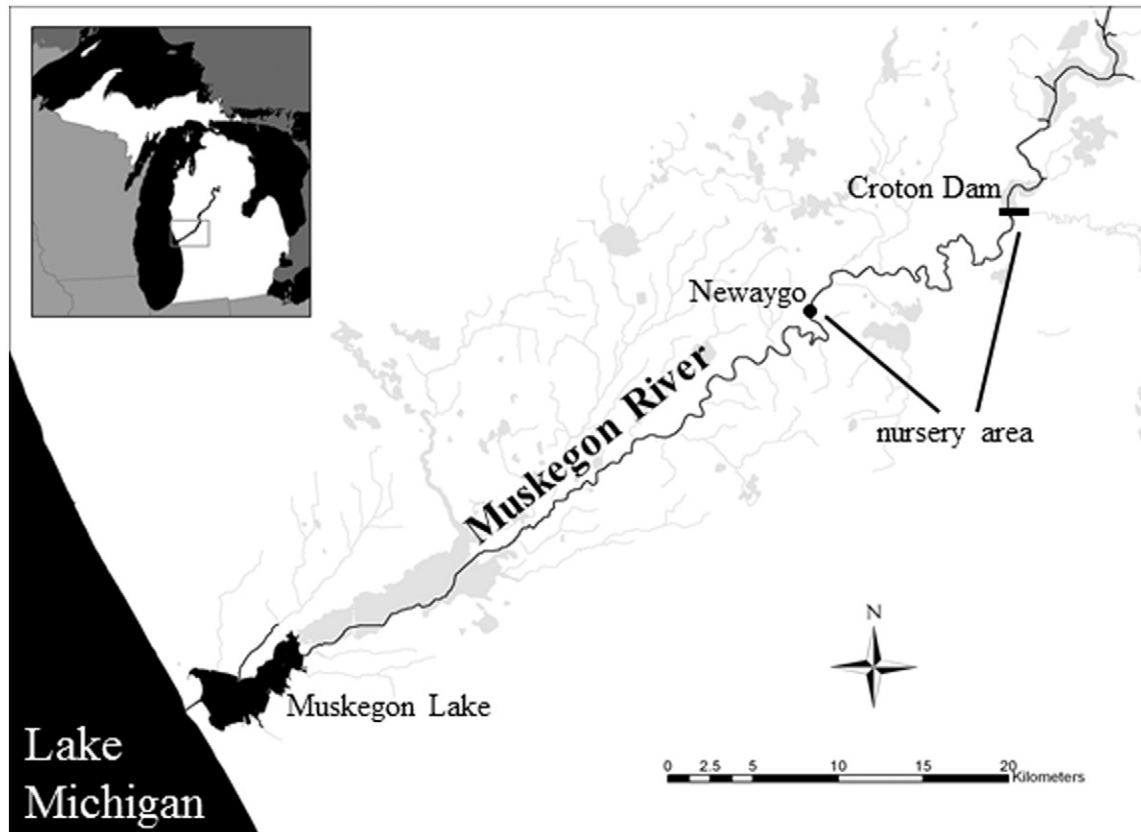

Fig. 1. Location of the Chinook salmon parr nursery area within the Muskegon River, Michigan, USA.

rainbow trout were estimated by scaling catch per unit effort (catch per unit effort [CPUE]; number/hr) in electrofishing transects to the number of trout stocked. Maximum CPUE was scaled to the initial (i.e., maximum) abundance at stocking. The decline in CPUE and abundance of stocked hatchery trout was assumed to result from harvest, predation and emigration from the river. We used linear interpolation to determine fish abundances for dates in between sampling efforts. Walleye abundance was calculated in the same way, but initial abundances were based on estimates of spawning walleye abundance in the Muskegon River (approximately 38,000 individuals) in 2002 (Hanchin et al., 2007). Individual fish were also weighed (g) to obtain estimates of relative biomass for each species.

Predator diet and ration

The methods used to determine predator diet composition are reported in detail in Krueger et al. (2011). Here, an abbreviated version is provided. At the completion of each electrofishing transect, predators were measured (mm L_T) and weighed (0.01 kg) and their stomach contents were flushed using a garden sprayer (Seaburg, 1957). Diet items were qualitatively identified and recorded (when possible) in the field and then preserved in 95% ethanol or 10% formalin (invertebrates only). In the laboratory, undigested stomach contents were measured (mm L_T) and weighed (0.1 g wet weight), and identified. Fish prey items were identified to species when possible, while invertebrate prey items were identified to order. Partially digested prey fish were identified based on diagnostic structures (i.e., vertebral count) and compared with weight-at-length data for prey fish from the Muskegon River (Krueger et al., 2011). The "meal-turnover" method described by Vigg et al. (1991) was used to quantify the daily rations of walleye and brown trout in the Muskegon River.

Predator feeding behavior

Feeding behavior of predators was addressed by evaluating prey size and species selection. Size-selective predation was determined by comparing mean length of ingested prey (L_I) to mean prey length in the environment (L_E; e.g., Shively et al., 1996; Wankowski, 1979). Monthly mean residuals were calculated for lengths of each prey type ($L_I − L_E$). Piscivores were considered size-selective if the mean length of ingested prey was significantly greater or less than the environmental mean (based on 95% confidence intervals). In addition, prey lengths were regressed on piscivore lengths to determine whether prey size consumed was correlated with piscivore size. The slopes of these relationships were tested for significance using a student t-test. Maximum prey/predator ratios (as % of L_T) were estimated for piscivorous walleye and brown trout based on the largest prey/predator ratio observed for each predator species.

Chesson's α (Chesson, 1983) was used as an index of prey species selectivity:

$$\alpha_i = \frac{r_i/p_i}{\sum_i r_i/p_i} \tag{1}$$

where r is the proportion of prey type i in the gut and p is the proportion of prey type i in the environment. Rainbow trout were predominantly insectivorous and did not feed on parr, thus were not considered in this analysis. Chesson's index was used because α does not change with food density unless consumer behavior changes. Hence, it is appropriate for detecting behavior such as "switching" (Murdoch, 1969). Alpha values were calculated for individual piscivores and averaged for April, May and June for each year.

Predator functional response

Using empirical field data, functional response models were fit to observed consumption rates for walleyes ≥ 400 mm TL and brown trout to quantify predator feeding rates in the presence of preferred and alternate prey. Estimates of walleye consumption rates ('Con', g $g^{-1}day^{-1}$) were averaged for 41 survey dates when prey biomass was estimated (PD, kg ha^{-1}). A type II functional response curve was fit to the data using the nonlinear curve fitting routine in JMP 10.0.1:

$$Con = \frac{Cmax * PD}{Khalf + PD} \tag{2}$$

where 'C_{max}' is the empirically determined maximum consumption rate, and Khalf is the prey biomass at half C_{max}. For brown trout, a type I functional response (linear model) was fit to biomass of parr. Bioenergetics model calculations of C_{max} for brown trout and walleye were conducted using the Wisconsin Bioenergetics Model framework (Version 3.0, Hanson et al., 1997), with parameter values for walleye from Kitchell et al. (1977) and for brown trout from Dieterman et al. (2004). The Type II model-predicted estimates of consumption were correlated with observed consumption for all species combined.

Results

Prey fish biomass

Fish relative abundance and biomass, size and predator diet composition were reported in Krueger et al. (2011). Estimates of prey fish biomass are provided below. Parr ranging in length from 37-50 mm were always captured in shallow water near the bank of the river with peak average biomass of 3 ± 0.2 kg ha^{-1} (mean ± 95% C.I.) and ranged from 2.8 – 3.1 kg ha^{-1} amongst years. Parr length did not differ significantly across years ($F_{2,15} = 1.584$, P-value = > 0.05) although sampling date ($F_{1,15} = 19.789$, P-value = 0.001) and water temperature ($F_{1,15} = 28.293$, P-value = 0.001) were significant sources of inter-annual variation in parr length. Rainbow trout (mean L_T ± 95% C.I., 174 ± 3.7 mm; mean wt ± 95% C.I., 61 ± 3 g) average biomass was similar across all years (56 ± 3.3 kg ha^{-1}, mean ± 95% C.I). Brown trout (mean L_T ± 95% C.I., 164 ± 3.2 mm; mean wt ± 95% C.I., 66 ± 11 g) biomass declined by approximately 60% from 26.4 kg ha^{-1} in 2004 – 2006 to approximately 11 kg ha^{-1} in 2007 due to a reduction in stocking. Cyprinid biomass averaged 0.61 ± 0.08 kg ha-1 and increased from 0.27 ± 0.26 kg ha^{-1} in April to 0.50 ± 0.53 kg ha^{-1} in May and 0.86 ± 0.52 kg ha-1 in June.

Predator feeding behavior

Prey-predator ratios differed between walleye and brown trout. Of 1,014 walleye stomachs examined, 455 individuals contained prey items. The maximum length of prey found in walleye stomachs was 47% of walleye total length and most prey fell well under this maximum. The lengths of ingested brown trout and rainbow trout by walleye averaged 30% of walleye length. Cyprinidae averaged 22% and parr averaged 10% of walleye length (Fig. 3). However, within a prey group, there were no effects of walleye size and the size of prey consumed (all P values > 0.05), indicating that relative prey size, within species, was independent of walleye size. Of 283 Brown Trout examined for diet content, 197 individuals contained prey items. Brown trout consumed parr that averaged 21% of their total length and nearly all prey fish were much smaller than the estimated maximum prey-predator length ratio of 30%. As with walleye, relative parr size was independent of brown trout size (Fig. 2).

Walleyes were size-selective predators for individual hatchery rainbow trout and brown trout as ingested prey sizes (L_I) were generally smaller than mean prey size available in the environment (L_E; Fig. 3).
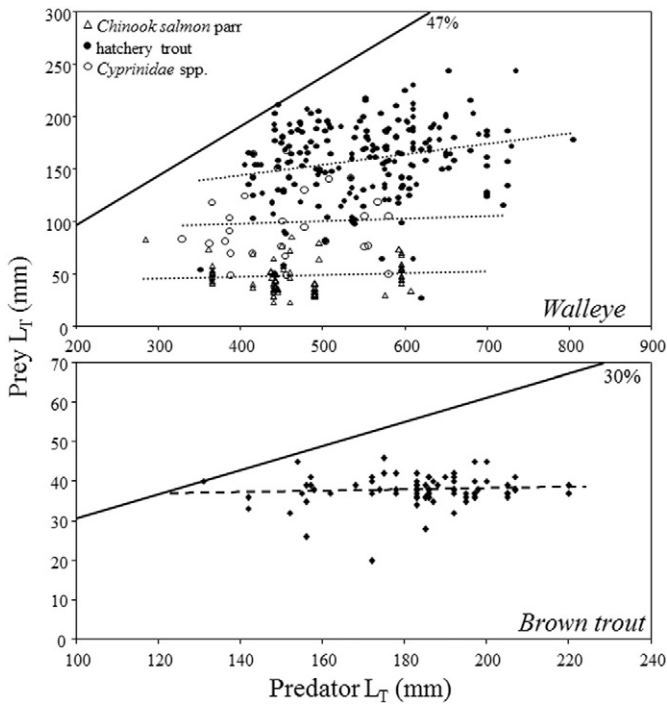
Fig. 2. Individual walleye and brown trout total length (L_T) are plotted against individual prey L_T. The solid line indicates the maximum prey/predator ratio observed for Muskegon River walleyes (47% L_T) and brown trout (30% L_T). The dashed lines in the upper panel represent the regressions for each prey type; the mean prey/predator ratio for brown trout and rainbow trout ("hatchery trout"; upper) was 30% of walleye L_T, Cyprinidae (middle) was 22% and Chinook parr (lower) was only 10% of walleye L_T. The dashed line in the lower panel represents mean parr size, which was on average ~21% of predator L_T. None of the species-specific regressions has a slope significantly different from zero (t-test, P-value = 0.05). L_T data for brown trout prey were not available for 2004 or 2005.

Mean size of parr ingested by brown trout also was significantly smaller than the mean size of parr in the environment (Fig. 3).

Walleyes exhibited neutral selection for individual prey types as a general trend although they did strongly select rainbow trout in 2005 and 2007. Conversely, walleyes selected against parr in 2004 (June), 2006, and 2007 (Fig. 4). Brown trout also exhibited species-selective feeding behavior and consumed parr in April (2006), parr and invertebrates in May, and invertebrates in June (Fig. 5). Brown trout were also

size-selective predators as they consumed parr that were smaller than the environmental mean (Fig. 3).

Predator functional response

A Type II functional response relationship provided a significant fit to data on average daily walleye consumption rates and prey biomass (r = 0.36, n = 40, P < 0.05) (Fig. 6). A clear outlier identified in Fig. 6 was excluded from the analysis. The maximum estimated ration predicted by the Type II functional response relationship was 0.5 ± 0.1 percent body weight per day for walleye consumption of all prey types combined (Fig. 6). The prey biomass at which walleyes achieved half their maximum ration was estimated at 11.57 ± 10.83 kg. The average observed daily ration for all walleye was 0. 37 ± 0.07 percent body weight per day, and maximum ration was 2.3 percent body weight per day. The average maximum daily ration estimated using the bioenergetics model was 4.0 percent body weight per day, or approximately 8-fold higher than the prediction from the Type II model, and 1.7-fold higher than the estimated average daily ration.

The type I functional response relationship fit to brown trout consumption of parr biomass (kg ha^{-1}) also was statistically significant (N_e [kg ha^{-1}] = 0.0009X – 0.113; r^2 = 0.49; $F_{1,11}$ = 10.723; P-value = 0.05; Fig. 7). Bioenergetic model simulations of maximum daily consumption (C_{max}) indicated a maximum average daily ration for brown trout of 3.2 g day^{-1}, or approximately 3-fold higher than the observed daily ration.

Discussion

Walleyes are apex predators in the Muskegon River and fed selectively on prey fish with the highest biomass available while still consuming less abundant fishes. Diana (2006) found that diets of Muskegon River walleye were dominated by brown trout and rainbow trout (by mass) in 2004 and 2005 and that trend continued within and among all study years in this expanded analysis of Muskegon River predators. Although larger prey species are typically less abundant than smaller prey in most systems (Rasmussen, 1993), brown trout and rainbow trout were stocked at high levels in the Muskegon River, and their total biomass was, on average, 50 times greater than Chinook salmon parr biomass (Krueger et al., 2011). The size (65-76 g) of individual brown trout and rainbow trout prey also was much greater than the size of alternate prey (0.5-2 g), potentially further minimizing the relative importance of prey abundance and/or biomass (Kerr, 1971).
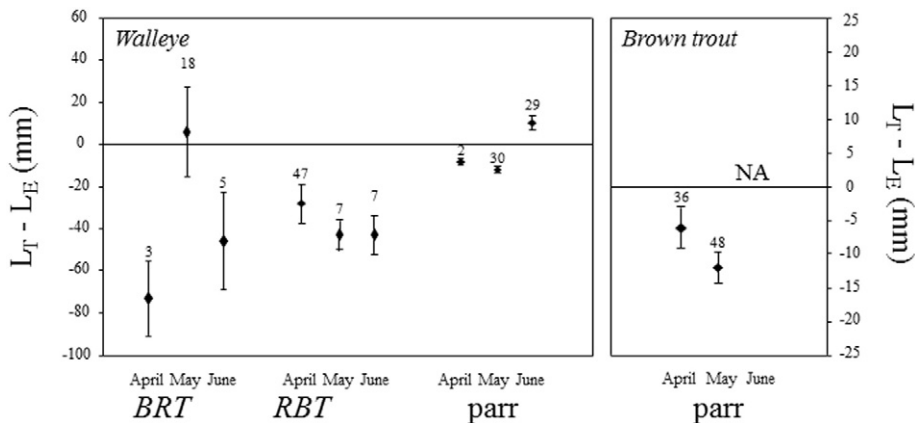
Fig. 3. Total length (L_T) of prey fish species (rainbow trout 'RBT', Chinook salmon parr 'parr', brown trout 'BRT') consumed by walleye and brown trout was compared to L_E of prey fish species in the environment in 2005 – 2007. The horizontal line at "0" represents the mean standardized size of parr in the environment. Sample sizes are listed above error bars, which represent 95% confidence intervals. A significantly positive difference in size of prey consumed relative to size of prey available (L_T–L_E) indicates walleye or brown trout are selecting fish that are bigger than those occurring in the environment. A significant negative difference indicates selection for smaller prey than occur in the environment. Only the following prey species were considered: rainbow trout, Chinook ("parr"), and brown trout. L_T data for walleye and brown trout prey items were unavailable for 2004 and insufficient for analysis in 2005 (brown trout only). In June 2006, parr were not present in brown trout diets. Brown trout were not stocked in April of 2007.
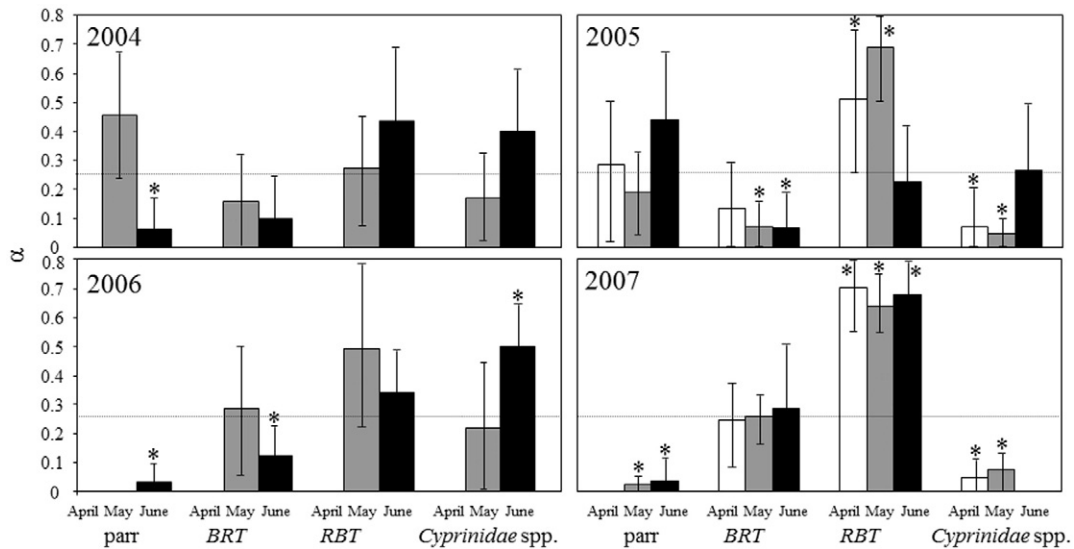
Fig. 4. Chesson's (1983) index of prey selection (α) for Muskegon River walleye from 2004 – 2007 for the following prey species: Chinook salmon parr ('parr'), brown trout ('BRT'), rainbow trout ('RBT'), and Cyprinidae spp. Error bars represent 95% confidence intervals and the dotted horizontal line in each box represents neutral selection for individual prey. Asterisks represent prey for which walleye show positive or negative selection in a given month.

Muskegon River walleyes consumed rainbow trout and brown trout that were smaller than the average length of either species in the environment; individual trout prey were approximately 30% of walleye total length. Similarly, in Wisconsin lakes and in Lake Erie, walleyes selected prey that had similar prey/predator length ratios found in this study (range 0.2 to 0.3; Campbell, 1998; Parsons, 1971). Forney (1974) also showed that walleyes preferred small prey (<20% prey/predator length), although this may have been caused by low abundance of larger prey species.

In the present study, walleyes positively selected for rainbow trout in multiple months but selected against brown trout, despite the species' similar size and morphology. Negative selection for brown trout always occurred in June when brown trout abundance was very low. One explanation is that piscivorous brown trout were found in very shallow water more frequently than rainbow trout, perhaps

searching for parr (D. Krueger., unpubl. data). Rainbow trout, on the other hand, were found in the middle of the river or in plunge pools more frequently than brown trout, feeding on invertebrates in the drift. Walleye also were captured in deeper, faster moving water, similar to rainbow trout. The opposing foraging strategies of brown trout and rainbow trout may therefore have led to higher spatial overlap between walleye and rainbow trout and may explain the asymmetric predation rates observed in walleye. Another explanation is that brown trout may have better predator detection capabilities, thereby improving their ability to flee from potential predators (e.g., Ydenberg and Dill, 1986).

Spatial overlap between walleyes and parr also must have been very low due to the extremely shallow water in which parr were found (Krueger et al., 2011). Hence, walleye consumption of parr was relatively low compared to brown trout piscivory; walleye actually selected
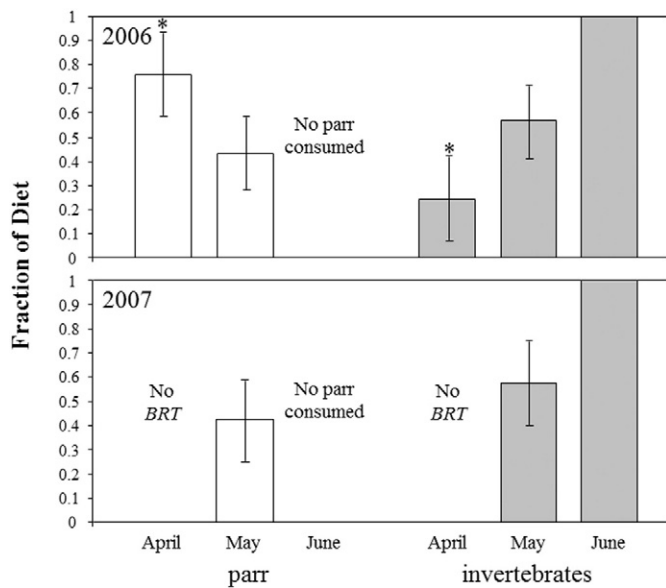

Fig. 5. Relative proportions (by biomass) of Chinook salmon parr (clear bars) and macro-invertebrates (grey bars) in stomachs of brown trout (BRT) in April, May and June of 2006 and 2007 in the Muskegon River, Michigan.
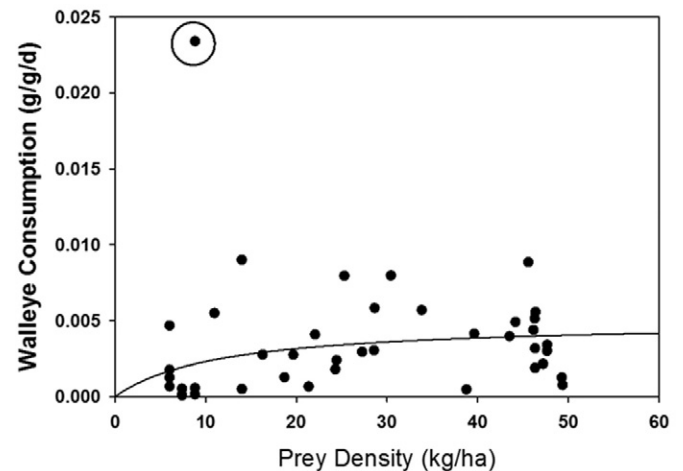

Fig. 6. Functional response of walleye to combined biomass densities of prey species (Chinook salmon parr, Cyprinidae, brown trout, rainbow trout) in the Muskegon River. Each data point represents the daily mean consumption rate by walleye for biomass of all prey species combined. The solid line represents the type II functional response curve fitted to the empirical data. The circle identifies an outlier datum that was not included in the functional response analysis.
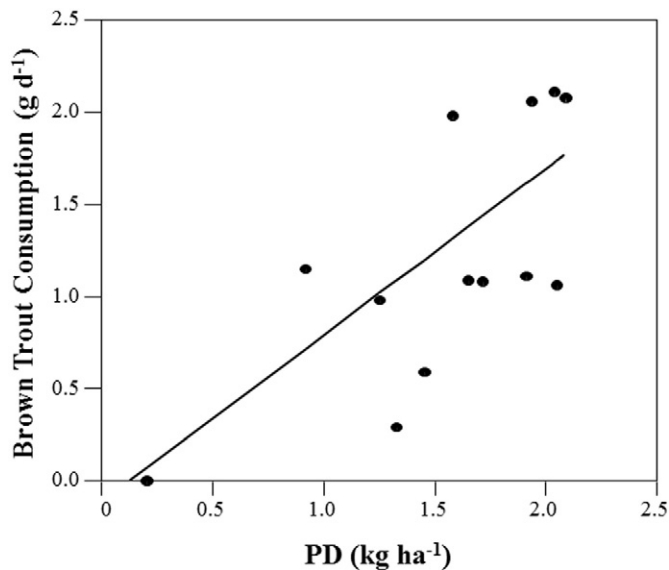
Fig. 7. Type I functional response of brown trout to variable abundance of Chinook salmon parr (PD = prey density) in the Muskegon River. Each data point represents the daily mean consumption rate by brown trout upon Chinook parr. The solid line represents the type I functional response curve fitted to the empirical data.

against parr in three of four study years. In addition, no relationship was found between walleye size and size of consumed parr. Very few walleyes (of any size) consumed parr in any given year. Walleye feeding behavior was similar in Lake Huron, where they preferred larger alewife *Alosa pseudoharengus* prey over smaller Chinook smolts (Johnson et al., 2007). Further, the very small size of parr may have reduced the perceptual volume of walleye (through a reduced detection distance due to small size), thereby leading to lower encounter rates relative to rainbow trout and brown trout (Gerritsen and Strickler, 1977). The few walleyes that consumed large numbers of parr may have responded to transient dense patches of prey (e.g., Petersen and DeAngelis, 2000). Had we excluded these few walleyes that had likely encountered rare opportunities to feed on parr, mean consumption of parr by walleyes would have been considerably lower.

Muskegon River walleyes appeared to respond quickly to changes in prey densities. Although walleye did not eat for the first few weeks in the river (i.e., March – early April) when they were actively spawning, they began feeding by mid-April – after spawning – when trout were first stocked. Brown trout and rainbow trout were stocked at boat launches and were patchily distributed thereabout throughout the early spring (April – May). Walleyes that consumed brown trout and rainbow trout were generally found aggregated near these boat launches. Walleyes that consumed other prey items were more isolated (i.e., walleyes were captured one at a time; D. Krueger, unpubl. data). Once walleyes began to feed, they preferred to consume rainbow trout and the artificially high densities of stocked trout likely elicited this observed walleye feeding response (e.g., Baldwin et al., 2003; Lyons, 1987; Petersen and DeAngelis, 1992). Then, walleye diet composition changed late in the sampling season. Following the departures of preferred (rainbow trout) and alternate (parr) prey species, walleye predation on Cyprinidae increased in three of four study years coincident with seasonal increases in cyprinid biomass. Further, walleyes that remained in the river continued to prey upon cyprinids into July and August (D. Krueger, unpubl. data).

Typically, brown trout are piscivorous at sizes of 300 mm L_T or greater (Hyvärinen and Huusko, 2006; Keeley and Grant, 2001), but high rates of piscivory in much smaller individuals have been found when prey are small and abundant (e.g., Vik et al., 2001; Kahilainen and Lehtonen, 2002), including the present study. This result is perhaps not surprising given the high abundance of very small parr in the Muskegon River. It

appeared that brown trout selected the smallest available parr and avoided larger prey, similar to results from Hyvärinen and Huusko (2006). Brown trout exhibited especially high rates of piscivory and positive selection for parr early in the sampling season when parr were very small. As parr grew larger throughout the spring, consumption by brown trout tapered and mean size of ingested parr was always significantly less than size of parr in the environment. By June, mean size of parr in the environment was still < 40% of the theoretical gape limit of the average brown trout (Damsgård, 1995), yet brown trout did not prey upon parr. Hence, maximum prey size was likely dictated by the increase in handling time and ability to escape that a larger prey item represented. Therefore, the maximum prey/predator ratio found in this study is probably more realistic for North American conditions than that provided in Damsgård (1995).

Given the relatively small gape of brown trout, parr growth may be a useful predictor of parr survival and associated changes in relative abundance. Parr inhabit the nursery area of the Muskegon River for approximately 60 days post-emergence, and because they can reach 50 mm within 40 days (Krueger et al., 2011), it appears they can attain a size refuge from brown trout well before out-migration. Rapid growth would therefore reduce parr vulnerability to predation throughout the latter portion of the nursery-dependent life stage (Krueger et al., 2011). Hence, hatchery brown trout may impose high predation rates on parr only in the early spring when parr are less than 40 mm L_T and appear to be most vulnerable.

Brown trout preyed explicitly upon parr during the short temporal overlap with parr smaller than 50 mm in length. Still, in May and June, invertebrate prey became an increasingly large component of brown trout diets. Some invertebrate taxa (Ephemeroptera, in particular) may have experienced large emergence events during this time although sufficient data were not available to detect changes in invertebrate biomass over time. Hence, brown trout predation on parr may have decreased due to increased availability of invertebrates throughout the spring as invertebrates became more prevalent and vulnerable to predation in the drift.

Functional Response

The functional response observed for walleye in the Muskegon River was similar to predatory responses observed in other field and laboratory studies of walleye (Forney, 1977; Rudstam et al., 2015; Swenson, 1977) and other piscivorous fishes (Fresh and Schroder, 1987; Ruggerone and Rogers, 1984). Because our functional response model was fit to average observed consumption points rather than maximum observed consumption points, values for walleyes were much lower than the expected maximum daily ration estimated with bioenergetics. Regardless, daily average consumption rates for all prey species suggest that the assumption of a type II functional response is reasonable for walleye foraging. Fresh and Schroder (1987) reported that the foraging behavior of stream salmonids on variable abundances of juvenile chum salmon *O. keta* also fit a type II pattern. Further, salmonid predators responded rapidly (<48 hours) to variable abundances of released chum salmon in small stretches of natural (1.5 – 2.3 km) and artificial (33 m) streams.

The type I functional response by brown trout to variable prey abundance in the Muskegon River nursery indicates that this predator may not be satiated by the observed abundances of parr. According to the functional response model for brown trout, this level of consumption would occur at a parr density approximately double that of the typical initial (i.e., maximum) abundance of parr in the Muskegon River. It seems brown trout are therefore capable of consuming an even larger number of available parr compared to what was observed, if provided sufficiently small prey. Hence, while brown trout may provide an indirect benefit to parr by buffering predation mortality from walleye, we suggest this benefit is outweighed by their direct predatory effect on parr survival.

Many studies have described foraging ecology of walleye and brown trout (e.g., Elliott and Hurley, 2000; Forney, 1974; Porath and Peters, 1997; Ringler, 1979; Rudstam et al., 2015; Swenson and Smith, 1973), though several of the studies were performed in controlled laboratory settings using only one prey type. The functional response models presented in this study used empirically derived data to describe the consumption of predators in response to varying densities of multiple prey types.

Several factors may have contributed to the variability in walleye consumption rates. First, prey fish abundances were estimated for a large study area (22.5 km) whereas consumption rates were estimated for walleyes collected at sites and may represent only the site density of prey. Our study area was larger than in other studies of walleye foraging (33 m to 2.3 km; Fresh and Schroder, 1987; Ruggerone and Rogers, 1984) which may have affected our ability to collect sufficient diet data. Second, we observed predator fish foraging ecology over a three–month period while most studies only observed foraging ecology for several hours or days. Predation rates are highly variable for fish in natural habitats (Fresh and Schroder, 1987; Peterman and Gatto, 1978). Third, some studies have averaged walleye consumption rates over time and ignored other species in the diets. Swenson (1977) reported a functional response between walleye consumption rates of juvenile yellow perch and perch prey densities for two Minnesota Lakes and Lake Superior. The plotted values, however, were compiled for all three lakes, represented monthly average consumption rates and ignored consumption of other prey items which may have dampened the variability in predation rates that we observed in migratory fishes in the Muskegon River.

Although our empirical estimates of predator consumption were variable, the reasonable fits of the functional response models to those data indicate the models may be broadly applicable in other Great Lakes tributaries where these species are common. However, detailed knowledge of walleye and brown trout foraging ecology in lacustrine, estuarine, and riverine habitats will be critical towards understanding future Great Lakes food web dynamics and associated management implications, because adult Chinook salmon abundance in the Great Lakes has recently decreased and walleye have regained their status as a top predator in the system. Our work portrays feeding behavior of walleyes in a spawning tributary at a time when parr are smaller-than-optimal prey size for walleye, are growing rapidly, and are migrating to Lake Michigan. The predator/prey dynamics we observed may be quite different when alternate buffering prey (e.g., alewife, *Alosa pseudoharengus* or round goby, *Neogobius melanostomus*) are encountered farther downstream near the tributary mouth.

Acknowledgements

References

Auer, M.T., Auer, N.A., 1990. Chemical suitability of substrate for walleye egg development in the Lower Fox River Wisconsin. Trans. Am. Fish. Soc. 119, 871–876. http://dx.doi.org/10.1577/1548-8659(1990)119<0871:CSOSFW>2.3.CO;2.

Baldwin, C.M., McLellan, J.G., Polacek, M.C., Underwood, K., 2003. Walleye predation on hatchery releases of Kokanees and rainbow trout in Lake Roosevelt Washington. N. Am. J. Fish Manag. 23, 660–676. http://dx.doi.org/10.1577/M02-021.

Bannon, E., Ringler, N.H., 1986. Optimal prey size for stream resident brown trout (Salmo trutta): tests of predictive models. Can. J. Zool. 64, 704–713. http://dx.doi.org/10.1139/z86-104.

Caley, M.J., 1993. Predation, recruitment and the dynamics of communities of coral-reef fishes. Mar. Biol. 117, 33–44.

Campbell, E.A., 1998. Predation by small walleyes on yellow perch: Effects of prey size distribution. Trans. Am. Fish. Soc. 127, 588–597. http://dx.doi.org/10.1577/1548-8659(1998)127<0588:PBSWOY>2.0.CO;2.

Carl, L.M., 1982. Natural reproduction of Coho salmon and Chinook salmon in some Michigan streams. N. Am. J. Fish Manag. 2 (4), 375–380.

Chesson, J., 1983. The estimation and analysis of preference and its relationship to foraging models. Ecology 64, 1297–1304.

Chesson, J., 1989. The effect of alternate prey on the functional response on Notonecta hoffmani. Ecology 70, 1227–1235.

Czesny, S., Dabrowski, K., Frankewicz, P., 2001. Foraging patterns of juvenile walleye (Stizostedion vitreum) in a system consisting of a single predator and two prey species: testing model predictions. Can. J. Zool. 79, 1394–1400. http://dx.doi.org/10.1139/z01-087.

Damsgård, B., 1995. Arctic charr, Salvelinus alpinus (L.), as prey for piscivorous fish – a model to predict prey vulnerabilities and prey size refuges. Nord. J. Freshw. Res. 71, 190–196.

Diana, C.M., 2006. (MS Thesis) Prey utilization and somatic growth of walleye Sander vitreus in the Muskegon River and Muskegon Lake. University of Michigan, Ann Arbor, Michigan.

Dieterman, D.J., Thorn, W.C., Anderson, C.S., 2004. Application of a bioenergetics model for brown trout to evaluate growth in southeast Minnesota streams Minn. Dept. Nat. Resour. Invest. Rep. 513.

Dörner, H., Hülsman, S., Hölker, F., Skov, C., Wagner, A., 2007. Size-dependent predator-prey relationships between pikeperch and their prey fish. Ecol. Freshw. Fish 16, 307–314.

Elliot, J.M., Hurley, M.A., 2000. Optimum energy intake and gross efficiency of energy conversion for brown trout, Salmo trutta, feeding on invertebrates or fish. Freshw. Biol. 44, 605–615.

Forney, J.L., 1974. Interactions between yellow perch abundance, walleye predation, and survival of alternate prey in Oneida Lake, New York. Trans. Am. Fish. Soc. 103, 15–24. http://dx.doi.org/10.1577/1548-8659(1974)103<15:IBYPAW>2.0.CO;2.

Forney, J.L., 1977. Reconstruction of yellow perch (Perca flavescens) cohorts from examination of walleye (Stizostedion vitreum vitreum) stomachs. J. Fish. Res. Board Can. 34, 925–932.

Fresh, K.L., Schroder, S.L., 1987. Influence of the abundance, size, and yolk reserves of juvenile chum salmon (Oncorhynchus keta) on predation by freshwater fishes in a small coastal stream. Can. J. Fish. Aquat. Sci. 44, 236–242. http://dx.doi.org/10.1139/f87-033.

Gerritsen, J., Strickler, J.R., 1977. Encounter probabilities and community structure in zooplankton: a mathematical model. J. Fish. Res. Board Can. 34, 73–82. http://dx.doi.org/10.1139/f77-008.

Gilinsky, E., 1984. The role of fish predation and spatial heterogeneity in determining benthic community structure. Ecology 65, 455–468.

Godby, N.A., Rutherford, E.S., Mason, D.M., 2007. Diet, feeding rate, growth, mortality, and production of juvenile steelhead in a Lake Michigan tributary. N. Am. J. Fish Manag. 27, 578–592. http://dx.doi.org/10.1577/M06-077.1.

Gotceitas, V., Brown, J.A., 1993. Risk of predation to fish larvae in the presence of alternate prey: effects of prey size and number. Mar. Ecol. Prog. Ser. 98, 215–222.

Hairston, N.G., Smith, F.E., Slobodkin, L.B., 1960. Community structure, population control and competition. Am. Nat. 94, 421–425.

Hanchin, P.A., O'Neal, R.P., Clark, R.D., Lockwood, R.N., 2007. The walleye population and fishery of the Muskegon Lake System, Muskegon and Newaygo counties, Michigan in 2002. Michigan Department of Natural Resources, Fisheries Special Report 40, Ann Arbor, Michigan.

Hanson, P.C., Johnson, T.B., Schindler, D.E., Kitchell, J.F., 1997. Fish Bioenergetics 3.0 for Windows. Wisconsin Sea Grant, Madison, WI.

Hyvärinen, P., Huusko, A., 2006. Diet of brown trout in relation to variation in abundance and size of pelagic fish prey. J. Fish Biol. 68, 87–98. http://dx.doi.org/10.1111/j.0022-1112.2006.00879.x.

Johnson, J.E., DeWitt, S.P., Clevenger, J.A., 2007. Investigations into causes of variable survival of Chinook stocked into Lake Huron. Michigan Department of Natural Resources, Fisheries Research Report 2086, Ann Arbor, Michigan.

Juanes, F., 1994. What determines prey size selectivity in piscivorous fishes? In: Stouder, D., Fresh, K., Feller, R. (Eds.), Theory and Application of Fish Feeding Ecology. University of South Carolina Press, Columbia, South Carolina, pp. 79–100

Kahilainen, K., Lehtonen, H., 2002. Brown trout (Salmo trutta L.) and arctic charr (Salvelinus alpinus (L.)) as predators on three sympatric whitefish (Coregonus lavaretus(L.)) forms in the subarctic Lake Muddusjärvi. Ecol. Freshw. Fish 11, 158–167.

Kean-Howie, J.C., Sifford Jr., P., Lloyd, M.D., 1988. Experimental predation by sticklebacks on larval mackerels and protection of fish larvae by zooplankton alternative prey. J. Exp. Mar. Biol. Ecol. 124, 239–259.

Keeley, E.R., Grant, J.W.A., 2001. Prey size of salmonid fishes in streams, lakes, and oceans. Can. J. Fish. Aquat. Sci. 58, 1122–1132. http://dx.doi.org/10.1139/f01-060.

Kerr, S.R., 1971. Prediction of fish growth efficiency in nature. J. Fish. Res. Board Can. 28, 815–819. http://dx.doi.org/10.1139/f71-122.

Kitchell, J.F., Stewart, D.J., Weininger, D., 1977. Applications of a bioenergetics model to yellow perch (Perca flavescens) and walleye (Stizostedion vitreum vitreum). J. Fish. Res. Board. Can. 34, 1922–1935.

Krueger, D.M., Hrabik, T.R., 2005. Food web alterations that promote native species: the recovery of cisco (Coregonus artedi) populations through management of native piscivores. Can. J. Fish. Aquat. Sci. 62, 2177–2188.

Krueger, D.M., Rutherford, E.S., Mason, D.M., 2011. Influence of predation mortality on survival of Chinook salmon parr in a Lake Michigan tributary. Trans. Am. Fish. Soc. 140, 147–163. http://dx.doi.org/10.1080/00028487.2011.556991.

Krueger, D.M., Rutherford, E.S., Mason, D.M., 2013. Modeling the Influence of Parr Predation by Walleye and Brown Trout on the Long-Term Population Dynamics of Chinook Salmon in Lake Michigan: A Stage Matrix Approach. Trans. Am. Fish. Soc. 142, 1101–1113.

Lundvall, D., Svanbäck, R., Persson, L., Byström, P., 1999. Size-dependent predation in piscivores: interactions between predator foraging and prey avoidance abilities. Can. J. Fish. Aquat. Sci. 56, 1285–1292.

Lyons, J., 1987. Prey choice among piscivorous juvenile walleyes (Stizostedion vitreum). Can. J. Fish. Aquat. Sci. 44, 758–793. http://dx.doi.org/10.1139/f87-092.

Merz, J.E., Setka, S.D., Pasternack, G.B., Wheaton, J.M., 2004. Predicting benefits of spawning-habitat rehabilitation to salmonid (Oncorhynchus spp.) fry production in a regulated California river. Can. J. Fish. Aquat. Sci. 61, 1433–1446. http://dx.doi.org/10.1139/f04-077.

Murdoch, W.W., 1969. Switching in general predators: experiments on prey specificity and stability of prey populations. Ecol. Monogr. 39, 335–354.

Parsons, J.W., 1971. Selective food preferences of walleyes of the 1959 year class in Lake Erie. Trans. Am. Fish. Soc. 100, 474–485. http://dx.doi.org/10.1577/1548-8659(1971)100<474:SFPOWO>2.0.CO;2.

Payne, R.T., 1969. A note on trophic complexity and community stability. Am. Nat. 103, 91–93.

Peterman, R.M., Gatto, M., 1978. Estimation of functional responses of predators on juvenile salmon. J. Fish. Res. Board. Can. 35, 797–808. http://dx.doi.org/10.1139/f78-129.

Petersen, J.H., DeAngelis, D.L., 1992. Functional response and capture timing in an individual-based model: predation by northern squawfish (Ptychocheilus oregonensis) on juvenile salmonids in the Columbia River. Can. J. Fish. Aquat. Sci. 49, 2551–2565. http://dx.doi.org/10.1139/f92-282.

Petersen, J.H., DeAngelis, D.L., 2000. Dynamics of prey moving through a predator field: a model of migrating juvenile salmon. Math. Biosci. 165, 97–114.

Pimm, S.L., Hyman, J.B., 1987. Ecological stability in the context of multispecies fisheries. Can. J. Fish. Aquat. Sci. 44, 84–94.

Porath, M.T., Peters, E.J., 1997. Walleye prey selection in Lake McConaughy, Nebraska: A comparison between stomach content analysis and feeding experiments. J. Freshw. Ecol. 12, 511–520.

Quinn, T.P., 2005. The behavior and ecology of Pacific Salmon and Trout. University of Washington Press, Seattle, Washington.

Rasmussen, J.B., 1993. Patterns in the size structure of littoral zone macroinvertebrate communities. Can. J. Fish. Aquat. Sci. 50, 2192–2207. http://dx.doi.org/10.1139/f93-246.

Ringler, N.H., 1979. Selective predation by drift-feeding brown trout (Salmo trutta). J. Fish. Res. Board. Can. 36, 392–403. http://dx.doi.org/10.1139/f79-059.

Rudstam, L.G., Post, J.R., Forney, J.L., 2015. Functional response and prey population dynamics: analysis of interactions between walleye and young-of-year yellow perch in Oneida Lake. In: Rudstam, L.G., Mills, E.L., Jackson, J.R., Stewart, D.J. (Eds.), Oneida Lake: Long term dynamics of a managed ecosystem and its fishery. American Fisheries Society, Bethesda, NY (submitted).

Ruggerone, G.T., Rogers, D.E., 1984. Arctic charr predation on sockeye salmon smolts at Little Togiak River, Alaska. Fish. B-NOAA. 82 pp. 401–410.

Seaburg, K.G., 1957. A stomach sampler for live fish. Prog. Fish Cult. 19, 137–139.

Shively, R.S., Poe, T.P., Sauter, S.T., 1996. Feeding response by northern squawfish to a hatchery release of juvenile salmonids in the Clearwater River Idaho. Trans. Am. Fish. Soc. 125, 230–236. http://dx.doi.org/10.1577/1548-8659(1996)125<0230:FRBNST>2.3.CO;2.

Swenson, W.A., 1977. Food-consumption of walleye (Stizostedion vitreum vitreum) and sauger (Stizostedion canadense) in relation to food availability and physical conditions in Lake of the Woods, Minnesota, Shagawa Lake, and western Lake Superior. J. Fish. Res. Board. Can. 34, 1643–1654.

Swenson, W.A., Smith, L.L., 1973. Gastric digestion, food consumption, feeding periodicity, and food conversion efficiency in walleye (Stizostedion vitreum vitreum). J. Fish. Res. Board. Can. 30, 1327–1336. http://dx.doi.org/10.1139/f73-213.

Vigg, S., Poe, T.P., Prendergast, L.A., Hansel, H.C., 1991. Rates of consumption of juvenile salmonids and alternative prey fish by northern squawfish, walleyes, smallmouth bass, and channel catfish in John Day Reservoir, Columbia River. Trans. Am. Fish. Soc. 120, 421–438.

Vik, J.O., Borgstrom, R., Skaala, O., 2001. Cannibalism governing mortality of juvenile brown trout, Salmo trutta, in a regulated stream. Regul. Rivers 17, 583–594. http://dx.doi.org/10.1002/rrr.647.

Wankowski, J.W.J., 1979. Morphological limitations, prey size selectivity, and growth response of juvenile Atlantic salmon Salmo salar. J. Fish Biol. 14, 89–100. http://dx.doi.org/10.1111/j.1095-8649.1979.tb03498.x.

Ydenberg, R.C., Dill, L.M., 1986. The economics of fleeing from predators. Adv. Study Behav. 16, 229–249.

Zippin, C., 1958. The removal method of population estimation. J. Wildl. Manag. 22 (1), 82–90.