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Gape limitation and piscine prey size-selection by yellow perch in the extreme southern area of Lake Michigan, with emphasis on two exotic prey items

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The trophic linkage between yellow perch *Perca flavescens* and two exotic prey items, alewife *Alosa pseudoharengus* and round goby *Neogobius melanostomus*, was investigated in the extreme southern area of Lake Michigan during the summer of 2002. Yellow perch ≥100 mm total length, L_T ($n = 1293$) exhibited size selective feeding, with 148 fish containing round gobies and 120 fish containing alewives. The mean round goby L_T, preyed on by yellow perch, was 23% of the predator L_T, with a range of 7 to 47%, and mean alewife L_T was 32% of yellow perch L_T, with a range of 18 to 46%. Although the selection of prey size by yellow perch increased proportionally with yellow perch L_T, prey consumed appeared smaller than theoretically possible based on gape size.

Key words: Lake Michigan; prey; size selectivity; yellow perch.

INTRODUCTION

Historically, yellow perch *Perca flavescens* (Mitchell) have been an important sport and commercial fish in southern Lake Michigan, but their recent abundance has fluctuated greatly (Shroyer & McComish, 1998). Many studies have attributed declines in yellow perch to the negative interactions with the non-indigenous alewife *Alosa pseudoharengus* (Wilson) (Jude & Tesar, 1985; Shroyer & McComish, 2000), established in Lake Michigan in 1949 (Miller, 1957). In the past decade, yellow perch abundance has been at a historic low (P.J. Allen, T.E. Lauer & T.S. McComish, unpubl. data). This decline resulted in the closing of the Indiana commercial fishery in the mid 1990s, and restricted daily sport bag limits in an effort by management agencies to protect the yellow perch stock. Many of the changes in the near-shore community assemblage of the Great Lakes were found to be a result of fluctuation in the benthos and other trophically linked organisms (Crowder, 1980; Trometer & Busch, 1999).

Although several studies have examined the food eaten by yellow perch in the extreme southern area of Lake Michigan (Webb, 1973; Bergh, 1977; Gallinat,

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1987), understanding yellow perch diets is necessary to help explain population fluctuations, and in formulating a management strategy for the species in southern Lake Michigan. No comprehensive yellow perch feeding studies for the extreme southern portion of the lake have been conducted since the introduction of the round goby *Neogobius melanostomus* (Pallas) in the 1990s (Marsden & Jude, 1995). Thus, understanding the trophic relationships among yellow perch, alewife and round goby is essential if current and future management strategies for the yellow perch population are to be successful.

The non-indigenous round goby is one of the more recent invaders of the Great Lakes, and was first found in the St Clair River in 1990 (Jude *et al.*, 1992). It has since spread throughout the Great Lakes, establishing populations in south-western Lake Michigan near Calument Harbor in 1991 (Marsden & Jude, 1995), moving east to Gary and Michigan City in 1998 (P.J. Allen, T.E. Lauer & T.S. McComish, unpubl. data). The aggressive behaviour of round goby towards competitors, wide environmental tolerance and high recruitment potential have increased its range (Dubs & Corkum, 1996). The presence of round goby has nearly extirpated the mottled sculpin *Cottus bairdii* Girard (Janssen & Jude, 2001; Lauer *et al.*, 2004) and johnny darter *Etheostoma nigrum* Rafinesque (Lauer *et al.*, 2004), and could negatively affect other native species including the yellow perch.

Gape size can determine the relationship between predator and prey (Werner, 1974; Persson *et al.*, 1996; Brooking *et al.*, 1998; Dorner & Wagner, 2003; Scharf *et al.*, 2003). Feeding in larval bluegill *Lepomis machrochirus* Rafinesque and yellow perch, has been shown to be dependent on gape size (Schael *et al.*, 1991; Bremigan & Stein, 1994), as has been shown in perch *Perca fluviatilis* L., bluegill, pike *Esox lucius* L., walleye *Sander vitreus* (Mitchell) and largemouth bass *Micropterus salmoides* (Lacepède) (Werner & Hall, 1974; Guma'a, 1978; Nilsson & Bronmark, 2000; Huskey & Turingan, 2001; Dorner & Wagner, 2003; Kahilainen & Lehtonen, 2003). There is only limited information on the importance of gape size on feeding in adult yellow perch (Knight *et al.*, 1984) and this study failed to include recent changes in the fish fauna of the Laurentian Great Lakes. Although Juanes (1994) provided a comparative summary of prey size selectivity by piscivorous fishes, this was misleading as prey-specific morphological characteristics, not simply size, can influence predator-prey interactions (Webb, 1986; Hoyle & Keast, 1987; Scharf *et al.*, 2003). Thus, when food selection by yellow perch varies temporally as found in southern Lake Michigan (Gallinat, 1987; Nalepa *et al.*, 1998), species and size specific information is necessary to determine predator-prey interactions.

Morphological limitations can affect the efficiency of feeding by predators (Einfalt & Wahl, 1997; Gill, 2003). In addition, optimal foraging theory predicts that foraging behaviour maximizes fitness, through such variables as foraging time, diet selection and handling time (Werner & Hall, 1974; Krebs, 1980; Mittelbach, 1981). This would include the ontogenic shift to piscivory, as it appears to be more energetically profitable (Elliott & Hurley, 2000).

The objective of this study was to determine whether yellow perch were selecting fish species in their diet based on size and availability, and whether this could be related to theoretical maximum prey size limitations.

MATERIALS AND METHODS

SAMPLING LOCATION

Lake Michigan is one of the five Laurentian Great Lakes. It covers an area of 57 850 km^2, and has a length of 494 km, which is nearly three times longer than its width of 109 km. The maximum depth of the lake is 265 m with a mean depth of 99 m. Sampling for this study took place near the cities of Michigan City and Gary, and was entirely within waters of the Indiana jurisdiction (Fig. 1). These sites have been historical reference locations used to evaluate the fish community in the extreme southern basin, focusing on yellow perch (Shroyer & McComish, 1998, 2000). The lake is divided politically among the four border states, but there is strong reason to believe yellow perch in the south half of the lake (southern basin) compose a single population, based on movement (Marsden *et al.*, 1993), genetic (Miller, 2003) and abundance (Francis *et al.*, 1996) studies.

SAMPLING OF FISHES

Night-time bottom trawl and gillnet sampling for yellow perch was conducted at three depths (5, 10 and 15 m) at three sites (Fig. 1) from 6 June to 21 August 2002. An additional sample was collected at night on 21 May 2002 to obtain yellow perch for gape size measurements, round goby head measurements, and determine a formalin shrinkage correction factor for preserved round goby and alewife total length, L_T, measurements.

Gillnet (passive) and trawl (active) sampling was conducted to reduce gear bias for quantity and food type consumed by yellow perch (Hayward *et al.*, 1989). Trawl sampling began at sunset each night using a standard 4·9 m headrope, 5·8 m foot rope, semi-balloon bottom otter trawl with a 38·1 mm stretch-mesh and a 12·7 mm stretch-mesh codend. Each site was sampled at 5 m depth for 1 h of effort (six 10 min tows) once every first and second half of each month during the sample period, for a total of 6 h effort per site. Multi-filament nylon gillnets with dimensions of 1·6 × 137 m containing nine repeating panels of 51, 64 and 76 mm stretch-mesh were set parallel to the shore at 10 and 15 m depth. Gillnets were deployed *c.* 0·5 to 1·0 h prior to sunset and retrieved the next morning between 0600 and 0700 hours, for a total sampling effort of 12–13 h. Gillnets were set twice per month at each site for a total of 12 net-nights per year. Detailed descriptions of sampling methods and sites are provided in Shroyer & McComish (1998) and Lauer *et al.* (2004).

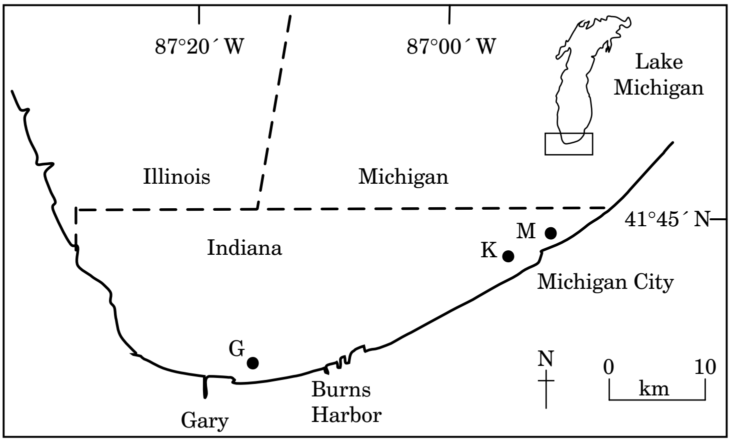

FIG. 1. Map showing the sample sites (G, K and M) in the extreme southern area of Lake Michigan.

FOOD HABIT EVALUATION

Fishes were placed on ice immediately after removal from the nets to prevent regurgitation and to slow digestion (Doxtater, 1963; Bowen, 1996). Field processing and standard data collections from individual fishes of all species took place within 15 h of trawl or gillnet capture. Visual observations from stomach analysis suggested that during this time, between collection and processing, prey fishes in the stomach did not deteriorate, probably because of their relative large size. In addition, the size structure and identification of fishes did not appear to be compromised. A digital micrometer was used to measure yellow perch maximum vertical and horizontal gape to the nearest 0·1 mm at the mouth entrance (Brooking *et al*., 1998). Alewife maximum body depth was measured with digital calipers to the nearest 0·1 mm from the anterior of the dorsal fin to body depth at that location. Round goby heads were measured at the operculum to the nearest 0·1 mm for maximum body width and height measurements. After counting, tagging, weighing, sexing and measuring whole fish, the gastrointestinal tract anterior to the pyloric caecum for each yellow perch was dissected and preserved individually in 10% formalin following Johnson *et al*. (1992).

Only stomachs from yellow perch $\geq$100 mm L_T were used in this diet analysis, following that of Bergh (1977) and Gallinat (1987). Yellow perch $<$100 mm L_T were collected, but were found not to consume alewives or round gobies, and hence, were not used in this diet analysis. Additionally, since yellow perch often shift from a primarily zooplankton and macroinvertebrate diet to piscivory between 150 and 200 mm L_T (Schneider, 1973; Clady, 1974), using only fish $\geq$100 mm L_T was a conservative approach that probably included all piscivorous yellow perch. Yellow perch stomachs were pooled by month of capture (June, July and August), and then randomly sub-sampled by 10 mm L_T classes in an effort to obtain at least 10 stomachs per 10 mm L_T class from 100 to 360 mm that contained fishes, when available in each month. If stomachs were visually 'empty' (containing few to no food items) or contained prey other than alewife and round goby (Truemper, 2003), they were not included in this study.

Contents of individual stomachs were flushed into a Petri dish, and prey items identified to appropriate taxonomic level, enumerated and measured. Prey items found in stomachs were corrected for L_T based on a shrinkage correction factor (2·2%) resulting from formalin and alcohol preservation. This factor was determined from analysis of fish ($n = 111$) collected in May, and evaluated over a 45 day period, approximating the period from fish collection to laboratory analysis. In addition, a relationship between L_T and standard length (L_S) was established, as the caudal fin was often partially digested (Table I). Therefore, prey fishes found in the stomachs were measured to L_T when possible, or L_S if the caudal fin was missing or damaged. Since multiple prey items found in individual yellow perch stomachs were not considered statistically independent,

TABLE I. Coefficients for the relationships between standard length and total length and volume for fishes collected from sample sites in southern Lake Michigan from 21 May to 21 August 2002. Fishes were preserved in 10% buffered formalin for at least 45 days and corrected for shrinkage before being measured

	L_S and L_T[1]				L_S and volume[2]				
Species	a	b	n	r^2	a	b	n	r^2	Size range L_T (mm)
Alewife	1·17	5·98	79	0·95	2·86	−4·61	228	0·99	28–189
Round goby	0·86	−2·28	123	0·99	3·13	−4·91	120	0·99	21–170
Yellow perch	1·15	1·66	67	0·99	3·00	−4·81	66	0·97	29–69

[1] L_T (mm) $= aL_S$ (mm) $+ b$.

[2] Log_{10}volume (ml) $= a\log_{10}L_S$ (mm) $+ b$.

a mean prey size for both alewife and round goby was used in analyses rather than raw data to eliminate statistical pseudoreplication.

STATISTICAL TREATMENTS

The relationship between yellow perch gape and L_T was examined using regression analysis (Minitab™ statistical software, v. 13). Male and female yellow perch gapes were measured separately, and subsequently compared using ANCOVA with control for body size to detect sexual differences in gape size. Alewife body depth and round goby head measurements were regressed against L_T to evaluate whether a relationship existed between these two measurements. A χ^2 test of homogeneity was used to test for frequency variation in both alewife and round goby consumed using 25 mm yellow perch L_T classes from June to August, and also to determine differences between alewife and round goby L_T frequencies captured with the trawl (available) and alewife and round goby L_T frequency consumed. Prey morphological measurements were completed using 10 mm L_T classes, but the low sample size for some length groups prevented χ^2 analysis. Thus, alewives and round gobies were grouped into 25 mm L_T classes to facilitate statistical testing. For each χ^2 test that rejected the null hypothesis, a subset χ^2 analysis was performed to detect differences between size classes (Sokal & Rohlf, 1995).

Descriptive models of prey vulnerability to yellow perch were created by regressing the maximum prey size ingested with yellow perch L_T. The model for round goby that could be consumed by yellow perch was based upon head and gape sizes, respectively. The model for alewife was based on maximum body depth measurements.

RESULTS

Yellow perch (total $n = 2212$) were captured in June ($n = 474$), July ($n = 866$) and August ($n = 872$) trawl and gillnet samples. From these fish, stomachs ($n = 1293$) were randomly sub-sampled from this population in 10 mm length classes for each month. Of the 1293 sub-sampled yellow perch stomachs examined, 268 contained alewife or round goby and were used for subsequent diet analysis.

Round gobies ($n = 1290$) sampled from Lake Michigan were collected mostly by trawl ($n = 1283$), with few ($n = 7$) by gillnetting. The number of round gobies caught in trawl samples differed by month and size, decreasing from a high abundance in June ($n = 595$) to a lower abundance in August ($n = 228$) (Fig. 2). The round goby L_T frequency varied by month (Table II), with mean size decreasing from June to August using 25 mm L_T size groups between 0 to 199 mm (Fig. 2).

Alewives ($n = 2242$) were mostly present in trawl samples, although 14 were captured in gillnets. Monthly and L_T based differences occurred (Table II) for each 25 mm L_T class between 125 and 225 mm (Fig. 2). Total abundance of alewives decreased throughout the sample period from 1357 fish in June to 447 fish in August.

Yellow perch vertical and horizontal gape ($n = 284$) was measured to determine morphological feeding limitations. Male yellow perch ($n = 56$) had a larger horizontal gape (Table III, equation 1) than vertical gape (Table III, equation 2) at each L_T. Female yellow perch ($n = 228$) followed a similar trend with a larger horizontal gape (Table III, equation 3) in comparison to vertical gape (Table III, equation 4). Since the smaller of the two gape measurements would limit feeding abilities, vertical gape was used for analyses of both female and male yellow perch

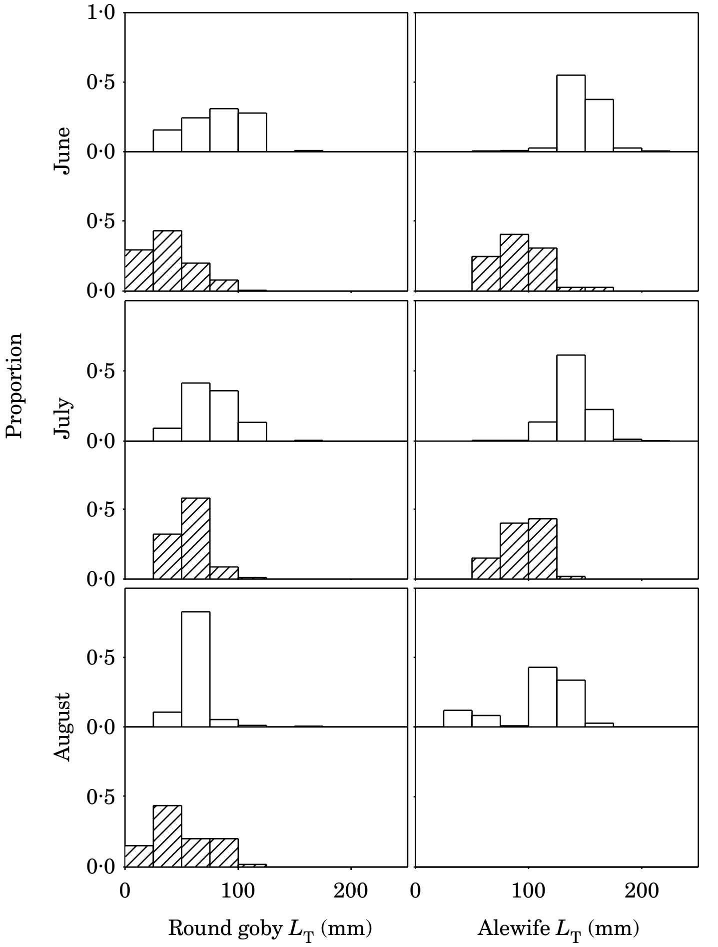

FIG. 2. The proportion of total alewife and round goby by total length L_T available (□) and consumed (▨) by yellow perch in the extreme southern area of Lake Michigan during June, July and August 2002.

in determining maximum prey sizes that could be ingested. Males and females did not differ by gape size (ANCOVA, d.f. = 1, $P > 0·05$), and were combined.

Prey morphological measurements were taken to relate to prey L_T and determine feeding limitations based on size for yellow perch. Round goby maximum head width and height measurements ($n = 156$) showed width (Table III, equation 5) was only slightly larger than height (Table III, equation 6) for any given L_T. The feature of maximum size of the alewife was the body depth measurement, which increased with increasing L_T (Table III, equation 7). Thus, the head width measurement for round goby and body depth for alewife was predicted to be the limiting morphological component for the predatory yellow perch, and was used for the descriptive model equation.

Models were created to relate theoretical maximum ingestible food items based on size of prey consumed by yellow perch (Table III and Fig. 3). This

TABLE II. The results of testing differences in length-frequencies of available prey and prey consumed by yellow perch in southern Lake Michigan during 2002 using χ^2 tests. Available prey was based on trawl catches. All comparisons were made by length-frequency categories based on 25 mm total length groups

	χ^2	d.f.	P
Round goby			
(a) Available compared among months	386·7	10	<0·001
(b) Consumed compared among months	203·3	10	<0·001
Available *v*. consumed within months			
(c) June	326·1	5	<0·01
(d) July	64·9	3	<0·01
(e) August	103·2	3	<0·01
Alewife			
(f) Available compared among months	84·8	6	<0·001
Available *v*. consumed within months			
(g) June	117·2	7	<0·001
(h) July	124·7	7	<0·001
(i) August	–	–	–
Round goby and alewife			
(j) Consumed compared among size classes	50·8	6	<0·001

–, insufficient data.

study focused on the relationship between yellow perch, round goby and alewife although other prey items were found in the stomachs of yellow perch, including three other fishes: spottail shiner *Notropis hudsonius* (Clinton) (1·8% by volume), rainbow smelt *Osmerus mordax* (Mitchill) (trace amounts) and yellow perch (3·6% by volume). Truemper (2003) described the remaining composition of the stomachs including invertebrates (<2·0% by volume), plants (4·0% by volume), and sand and gravel (9·0% by volume). Maximum food items ingested

TABLE III. Descriptive models of prey vulnerability to yellow perch gape. The model for round goby that could be consumed by yellow perch was based upon head and gape sizes, respectively, while the model for alewife was based on maximum body depth measurements

Linear equations used to relate yellow perch vertical (V) and horizontal (H) gape measurements (G, mm) to L_T for males (M) and females (F)

(1) $G_{HM} = 0{\cdot}167L_T - 2{\cdot}010$, where $n = 56$ and $r^2 = 0{\cdot}98$
(2) $G_{VM} = 0{\cdot}136L_T + 0{\cdot}157$, where $n = 56$ and $r^2 = 0{\cdot}96$
(3) $G_{HF} = 0{\cdot}159L_T - 0{\cdot}344$, where $n = 228$ and $r^2 = 0{\cdot}98$
(4) $G_{VF} = 0{\cdot}124L_T + 2{\cdot}300$, where $n = 228$ and $r^2 = 0{\cdot}97$

Linear equations used to relate round goby width (W) and height (H) head measurements (R) to L_T and to relate alewife body depth (D) to L_T

(5) $R_W = 0{\cdot}177L_T - 2{\cdot}233$, where $n = 156$ and $r^2 = 0{\cdot}96$
(6) $R_H = 0{\cdot}176L_T - 2{\cdot}623$, where $n = 156$ and $r^2 = 0{\cdot}95$
(7) $D = 0{\cdot}205L_T - 0{\cdot}011$, where $n = 154$ and $r^2 = 0{\cdot}89$

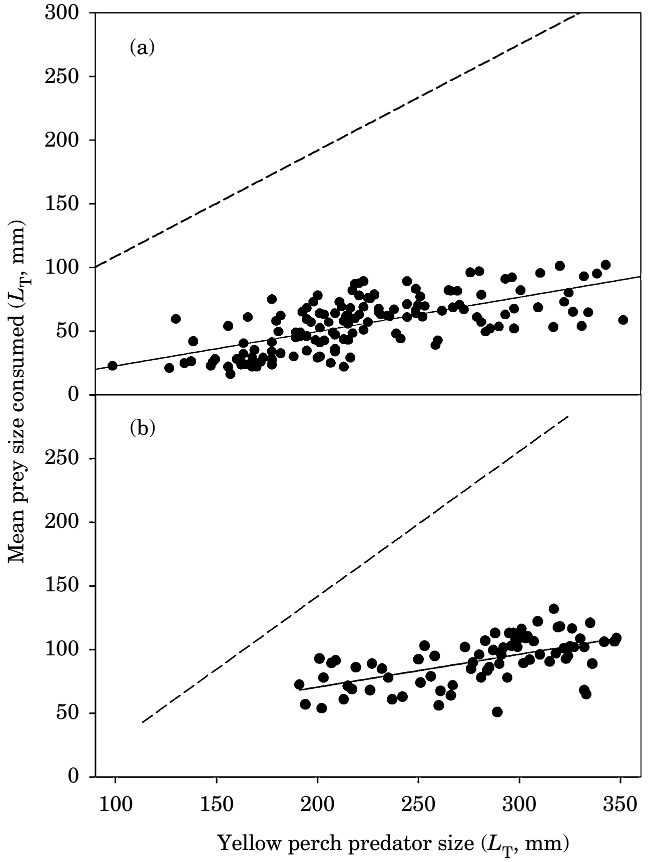

FIG. 3. (a) Round goby and (b) alewife total length eaten by yellow perch in the extreme southern area of Lake Michigan from 6 June to 21 August 2002. Each point represents either the L_T of the fish found in the yellow perch stomach when $n = 1$, or the mean L_T value when $n > 1$. The curves were fitted by: (a) $y = 0{\cdot}291x - 9{\cdot}005$ ($n = 148$, $r^2 = 0{\cdot}44$) and (b) $y = 0{\cdot}257x + 19{\cdot}140$ ($n = 120$, $r^2 = 0{\cdot}35$). ---, the theoretical maximum size prey that could be ingested by the yellow perch based upon yellow perch gape and prey maximum morphological measurements (see Table III, equations 4, 5, 7): (a) $y = 0{\cdot}899x + 10{\cdot}651$ and (b) $y = 0{\cdot}777x + 1{\cdot}627$.

were defined as those that could physically fit into the yellow perch mouth, as determined by the minimum gape (vertical) and maximum prey size (round goby head width and alewife body depth) equations. The resulting combined equations established the maximum round goby and alewife L_T that could be ingested by various L_T of yellow perch. In addition, mean prey (round goby and alewife) sizes consumed for each yellow perch were averaged and regressed with yellow perch L_T (Fig. 3).

Prey sizes consumed by yellow perch were compared to prey availability, based on trawl catches by month and size (Fig. 2). At <100 mm L_T, no round gobies were consumed by the sub-sampled yellow perch (Fig. 3). Round gobies ($n = 386$) were found in the stomachs of 148 yellow perch ≥ 100 mm L_T, occurring in 21% of the stomachs and comprising 34% of the total food items by volume (Truemper, 2003). Yellow perch consumption of round gobies occurred incidentally from 100 to 149 mm L_T. Yellow perch $\geq$150 mm L_T, however, consumed round goby as a major prey item (Fig. 3). Yellow perch consumed round gobies that were 7 to 47% of yellow perch L_T, with an average prey size of 23% of yellow perch L_T. Round gobies consumed by yellow perch ranged from 2 to 53% of the yellow perch vertical gape. Length-frequencies of round gobies consumed by yellow perch (Fig. 2) differed monthly (Table II) for each 25 mm L_T size group from 0 to 199. Within each monthly sample, length-frequencies of round goby consumed by yellow perch were significantly smaller than those available (Table II) for each 25 mm L_T class. Young-of-the-year or small round goby may have been present in the population, but were not fully recruited to the sampling gear. This was suggested by the number of round goby $<$25 mm L_T eaten by yellow perch in June and August, despite an absence of these length frequencies in the trawl catch.

Alewives ($n = 142$) were found in the stomachs of 120 yellow perch that were all $\geq$175 mm L_T, despite sampling fish as small as 100 mm L_T (Fig. 3). Alewife occurred in 17% of the stomachs with prey, comprising 45% of the volumetric diet (Truemper, 2003). Yellow perch consumed alewife ranging from 18 to 46% of their L_T, with an average of 32%. Alewives consumed were 23 to 68% of yellow perch vertical gape. Within June and July samples, frequencies of alewives consumed were different than those available (Table II) for each 25 mm L_T class. Although alewives were available in August, sub-sampled yellow perch failed to consume any alewife.

DISCUSSION

Yellow perch preferred round goby or alewife prey (79% by volume; Truemper, 2003) depending on their size. This portion of the yellow perch diet contrasts with historic fish prey items, such as mottled sculpin and johnny darter (Bergh, 1977; Gallinat, 1987). The round goby invasion and subsequent establishment probably caused this shift (Jude *et al.*, 1995; Jude, 1997; Janssen & Jude, 2001; Lauer *et al.*, 2004), and provides support that yellow perch are generalist feeders (Thorpe, 1977). This feeding strategy allowed a diet shift from mottled sculpin and johnny darter as prey items in 1972 and 1984 to a diet incorporating round goby in 2002. Due to the decline in other prey items (Nalepa *et al.*, 1998), the presence of round goby in the diets of yellow perch (150 to 250 mm L_T) has increased in importance. Since alewives were consumed only by yellow perch $>$175 mm L_T, the newly established round goby may be providing prey for smaller yellow perch. With the current abundance of various round goby cohorts (P.J. Allen, T.E. Lauer & T.S. McComish, unpubl. data), yellow perch that are too small to select for alewife have an abundant food source. The ease of this diet shift is notable, as the southern Lake Michigan benthic prey composition will probably continue to change over time with further introductions and destabilization by non-indigenous species.

Yellow perch have been considered opportunistic feeders, with prey consumption typically linked with availability (MacLean & Magnuson, 1977; Knight *et al.*, 1984). Thus, if yellow perch were randomly feeding, the prey length frequency consumed by the yellow perch might be expected to be similar to the length frequency of round goby and alewife found in the trawl samples. This was not the case, however, as the mean prey size was 23% of the yellow perch L_T for round goby and 32% for alewife (Fig. 3). Similarly, Lake Erie yellow perch consumed clupeids [alewife and gizzard shad *Dorosoma cepedianum* (Lesueur)] that were 26% of yellow perch L_T (Knight *et al.*, 1984).

Non-random size selectivity indicates a 'predation window' (Claessen *et al.*, 2002) of minimum and maximum sizes selected by the yellow perch predator. This size-dependent piscivory has also been found in *P. fluviatilis* (Mittelbach & Persson, 1998) and was thought to be based on ontogenetic increases in gape height and width (Dorner & Wagner, 2003). This predator-prey size relationship has been shown for a number of species, including the largemouth bass, Arctic charr *Salvelinus alpinus* (L.), brown trout *Salmo trutta L.*, burbot *Lota lota* (L), walleye and pike (Knight *et al.*, 1984; Hoyle & Keast, 1987; Nilsson & Bronmark, 2000; Kahilainen & Lehtonen, 2003).

Yellow perch ate alewife and round goby that were smaller than the maximum possible size suggested by their gape (Fig. 3) or availability (Fig. 2). These findings agree with Juanes (1994) evaluation of 32 piscivorous studies on size selection of prey where behaviour, not gape or availability, was limiting. Moreover, the size ingested was often in the lower range of sizes possible, based on morphometrics. Mittelbach (1981) suggested that below a threshold prey L_T : predator L_T critical value, handling time remains constant, while above this threshold, handling time increased exponentially. These findings were substantiated by Werner & Hall (1974), Hoyle & Keast (1987), Nilsson & Bronmark (2000) and Scharf *et al.* (2003). In addition, slower swimming speed for proportionally smaller prey may increase capture success (Juanes, 1994; Lundvall *et al.*, 1999), thereby favouring larger prey that may have entered a size refuge (Nilsson & Bronmark, 2000). Lastly, a number of yellow perch were caught that had more than a single fish in their stomachs. In these cases, the gape may not be the limiting factor determining prey selection, but rather stomach volume. Hence, if the stomach is partially full, then the predator may choose a smaller prey. The analysis is supported by Gill & Hart (1998) and Gill (2003) who propose that feeding motivation and satiation vary with stomach fullness.

Yellow perch <150 mm L_T did not consume either fish prey, or apparently consumed them incidentally as in other studies that found an ontogenetic switch to piscivorous prey items for yellow perch beginning at or near 150 mm L_T (Schneider, 1973; Clady, 1974). As the size of the yellow perch increased, so did the size of the round goby and alewife prey. The shift to increased predator size may provide the yellow perch with energetic advantages provided the increased search, pursuit and handling time are maximized (Werner, 1974; Werner & Hall, 1974; Harper & Blake, 1988; Elliott & Hurley, 2000). Larger yellow perch (250–350 mm), however, ate proportionally smaller round gobies and alewives based on gape size, which is analogous to other piscivore foraging studies (Knights, 1985; Juanes, 1994; Dorner & Wagner, 2003). Because round gobies ≥ 110 mm L_T and alewives >162 mm L_T were never consumed and did not appear to be limited by size, a prey behavioural threshold may have been reached. Yellow perch ≥ 100 mm L_T could theoretically consume any round goby encountered. Round gobies ≥ 100 mm L_T, however, were never in the yellow perch stomachs when available, resulting in a size refuge for these larger round gobies. The existence of sub-optimal prey selection (*i.e.* less than the largest prey size available) could be a result of round goby behaviour rather than yellow perch morphological limitations (Bremigan & Stein, 1994). Round goby are aggressive compared to other benthic forage fishes, such as the mottled sculpin (Dubs & Corkum, 1996), which could be a deterrent for foraging yellow perch. Other handling factors may limit the size of prey consumed including, digestibility of larger prey items, visual acuity of predators (Mills *et al.*, 1994), prey availability and abundance, or other size related features (*e.g.* the cleithrum orifice size; Timmerman *et al.*, 2000).

The decline in round goby >50 mm L_T abundance over the summer was expected (Fig. 2). Natural mortality was predicted to result in declining abundance barring any new recruitment, but few round gobies >100 mm L_T were captured in the late summer. Limited studies of North American round goby populations can provide only speculation as to why larger fish are absent from collections in late summer. Spring and autumn movements of round gobies have been suggested, but are not well quantified (Jude *et al.*, 1992). Predation by other known North American round goby predators such as walleye, smallmouth bass *Micropterus dolomieu* Lacepède and lake trout *Salvelinus namaycush* (Walbaum) (Jude *et al.*, 1992; MacInnis & Corkum, 2000) is not likely because these species are only captured in low numbers at these study sites (P.J. Allen, T.E. Lauer & T.S. McComish, unpubl. data).

The failure of yellow perch to actively feed on spottail shiners contradicts the opportunistic feeding regime. Spottail shiners are similar in L_T to the round goby and alewife (Scott & Crossman, 1973; P.J. Allen, T.E. Lauer & T.S. McComish, unpubl. data), and have been a common inhabitant of warm, shallow Lake Michigan waters (Wells, 1968). Although they were the most abundant species found in the southern Lake Michigan fish community during 2002 (50·3%; P.J. Allen, T.E. Lauer & T.S. McComish, unpubl. data), their abundance in the yellow perch diet was <2%. As a comparison, alewife and round goby composed 24·0 and 12·7%, respectively, of the total trawl catch during 2002 (P.J. Allen, T.E. Lauer & T.S. McComish, unpubl. data). Unfortunately, the reasons for this apparent choice in prey selection are unknown.

Some cannibalism on YOY yellow perch occurred in August. This seasonal activity may be due to two reasons, availability and size. At the time of sampling, the year class strength of age 0 year fish was unknown, but the southern portion of Lake Michigan experienced several consecutive years of poor recruitment due to the effects of alewife (Shroyer & McComish, 2000) which have not recently abated. Moreover, yellow perch may have a small predation 'window' (Claessen *et al.*, 2002) and adults may find age 1 year and older fish not to be energetically profitable or physically too large for consumption.

Establishing a predator-prey relationship among yellow perch, round goby and alewife in southern Lake Michigan clarifies the trophic link among these three species. Because yellow perch are considered opportunistic feeders (Thorpe, 1977), the recent shift to round goby as a benthic prey species was expected. In addition, alewife consumed may also mimic availability, as alewife abundance in 2002 in southern Lake Michigan was among the highest observed in the past two decades (P.J. Allen, T.E. Lauer & T.S. McComish, unpubl. data), further supporting the choice of yellow perch prey selection. Despite this opportunistic characteristic, yellow perch did exhibit size-selective feeding in accordance with other piscivorous fishes feeding studies (Bence & Murdoch, 1986; Hambright, 1991; Juanes, 1994; Mittelbach & Persson, 1998), suggesting their choice of prey may be more complex. Although the size-related predator-prey interaction described here occurred in southern Lake Michigan, it seems plausible this relationship could be extended to all waters where these three species coexist.

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