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ARTICLE

Influence of Predation Mortality on Survival of Chinook Salmon Parr in a Lake Michigan Tributary

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Abstract
Predation mortality among Chinook salmon *Oncorhynchus tshawytscha* parr can act at small spatiotemporal scales and cause variability in parr survival and potential recruitment. We analyzed predator diets and multiplied per capita consumption rates by predator population estimates to evaluate the relative effect of predation by stocked sport fishes on the variability in survival of Chinook salmon parr in the Muskegon River, Michigan, from 2004 to 2007. Brown trout *Salmo trutta* were a major predator of Chinook salmon parr, consuming from 15% to 34% of the total number available, while walleyes *Sander vitreus* consumed from 0.2% to 15%. Walleyes also consumed large quantities of brown trout and rainbow trout *O. mykiss*. Brown trout predation on Chinook salmon parr was largely dependent on parr size, while walleye predation was buffered by the availability of rainbow trout and brown trout. Predation mortality appeared to be responsible for a more than three-fold difference in the survival of Chinook salmon parr in the Muskegon River. The vulnerability of Chinook salmon parr to predation appeared to be controlled by parr growth rates, brown trout stocking dates, and the number of brown trout stocked. Fishery regulations to manipulate piscivore abundance may lead to higher survival and lower variability in the survival of Chinook salmon parr.

The survival of the early life history stages of Pacific salmon *Oncorhynchus* spp. is influenced by many factors that can operate over relatively confined (i.e., local) spatial and short temporal scales (Pyper et al. 2005). Of these factors, predation on salmonid parr has been extensively studied in freshwater habitats along the Pacific coast, as it can influence parr survival (Tabor et al. 1993; Fayram and Sibley 2000; Emmett et al. 2006) and potential recruitment (Maynard et al. 2004; Melnychuk et al. 2007; Wertheimer and Thrower 2007). However, little is known about the degree to which predation influences naturalized Pacific salmon populations in the Laurentian Great Lakes, most notably Chinook salmon *O. tshawytscha*.

The Muskegon River contains one of the most productive nursery areas for naturally produced Chinook salmon parr in the Great Lakes basin (Carl 1982; Connerton et al. 2009). The average annual production of naturally produced Chinook salmon

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parr in the river nursery area is estimated to be about 350,000 individuals, and production may range from 70,000 to 700,000 individuals (Edward Rutherford, unpublished data, 2010). The number of parr entering Lake Michigan is unknown, however. Combined with funding cuts, the large number of naturally produced Chinook salmon parr prompted fishery managers to discontinue stocking hatchery-produced Chinook salmon smolts in the Muskegon River after 2005. Hence, the numbers of naturally produced Chinook salmon parr from the Muskegon River and other Lake Michigan tributaries remain highly variable and unpredictable (e.g., Clapp et al. 1998). While the relative magnitude of natural reproduction is generally known, there is uncertainty regarding the factors that control the production of Chinook salmon parr and the number that actually enter Lake Michigan.

The survival of juvenile Chinook salmon is not well understood in river nursery habitats or during the spring out-migration from Lake Michigan tributaries. The life history of Chinook salmon in Lake Michigan is similar to that of its oceanic source population from the Green River, Washington (Carl 1982); spawning occurs from mid-September to early November, eggs hatch in late March, and parr leave the river from May through June. In large West Coast rivers, hydroelectric dams are responsible for parr mortality rates of 10–45% per dam and predators may consume an additional 15% of the salmonids that enter the associated reservoirs (Beamesderfer et al. 1990; Rieman and Beamesderfer 1990; Shively et al. 1996). Predation may regulate the number of Chinook salmon parr emerging from the Muskegon River to Lake Michigan (e.g., Shively et al. 1996; Johnson et al. 2007), although temperature, photoperiod, and river flow are also important determinants of out-migration timing and smoltification (Carl 1982, 1984; Seelbach 1985).

The Michigan Department of Natural Resources and Environment (MDNRE) continues to stock other important sport fishes that may be predators of young Chinook salmon. Walleyes *Sander vitreus*, brown trout *Salmo trutta*, and rainbow trout *O. mykiss* (both steelhead and resident strains) are stocked into Muskegon River nursery habitats to create a recreational fishery. During this time, walleyes may consume large numbers of Chinook salmon parr (e.g., Johnson et al. 2007). Walleye predation on emigrating parr also may depend on the abundance of alternative prey, including hatchery brown and rainbow trout and alewives *Alosa pseudoharengus*. Thus, fishery management activities, especially stocking in the Muskegon River and Muskegon Lake, are likely to have direct effects on species interactions and the survival of wild Chinook salmon.

Although natural variability in biotic (number and/or size of spawning adults) and abiotic factors (temperature, flow) can influence salmonid reproductive success in any tributary system, we hypothesized that predation mortality is an important source of variability in Chinook salmon survival in the Muskegon River. We further postulated that the parr growth rate may impact the survival and potential production (and/or recruitment) of Chinook salmon parr in the river. Food web effects resulting from management actions have the ability to control the survival of Chinook salmon parr through manipulation of piscivore populations (e.g., Beamesderfer et al. 1996; Krueger and Hrabik 2005). Thus, our objectives were to (1) estimate the relative abundance of piscivores, (2) determine the abundance, growth, and mortality of wild Chinook salmon parr, and (3) quantify prey consumption by piscivores in the Muskegon River. We addressed these objectives using empirical data collected from 2004 to 2007. While other sources of mortality on Chinook salmon parr may be as important as or more important than predation (e.g., Welch et al. 2008), we focused on predation mortality because the stocking of potential predators is a management activity that can be directly controlled.

STUDY SITE

The Muskegon River estuary system (MRES) is a drowned river mouth tributary system to Lake Michigan that is located in western Michigan (Figure 1). The MRES is composed of the Muskegon River, its associated wetlands, Muskegon Lake, and the channel connecting Muskegon Lake to Lake Michigan. The Muskegon River extends 352 km from Houghton Lake in north-central Michigan to the city of Muskegon, where it discharges into Lake Michigan. We focused our sampling on river kilometers (rkm) 47–72 of the Muskegon River, which is just downstream of the impassible Croton Dam, the lowermost dam on the river (Figure 1). Chinook salmon spawn within this section of the river, which has moderate gradient (0.6–1.9 m/km) with predominately cobble and gravel substrate (O'Neal 1997). Subsequent references to the upper MRES allude only to this stretch of the river; references to the lower MRES allude to rkm 7–47 (Figure 1). Muskegon Lake is a 1,680-ha lake that connects to southeastern Lake Michigan via a navigation channel (Muskegon Channel). Muskegon Lake is relatively shallow and mesotrophic, with an average depth of 7.1 m (maximum, 21 m; Carter et al. 2006).

METHODS

Environmental Variables

Mean daily water temperature and river discharge measurements for the upper MRES were acquired from U.S. Geological Survey station 04121970 in Croton, Michigan. Water temperature is an important determinant of parr growth and piscivore consumption rates. River discharge may influence feeding success, the location of parr in the river, and the timing of parr emigration to Lake Michigan (Carl 1982; Seelbach 1985; Edward Rutherford, unpublished data).

Fish Abundance

Chinook salmon parr.—The relative abundance of Chinook salmon parr was estimated using traps and electrofishing surveys in the Muskegon River from 2004 to 2007 and seines in Muskegon Lake in 2006. In 2004, we deployed a 2.4-m-diameter auger trap (EG Solutions, Inc.) near the downstream

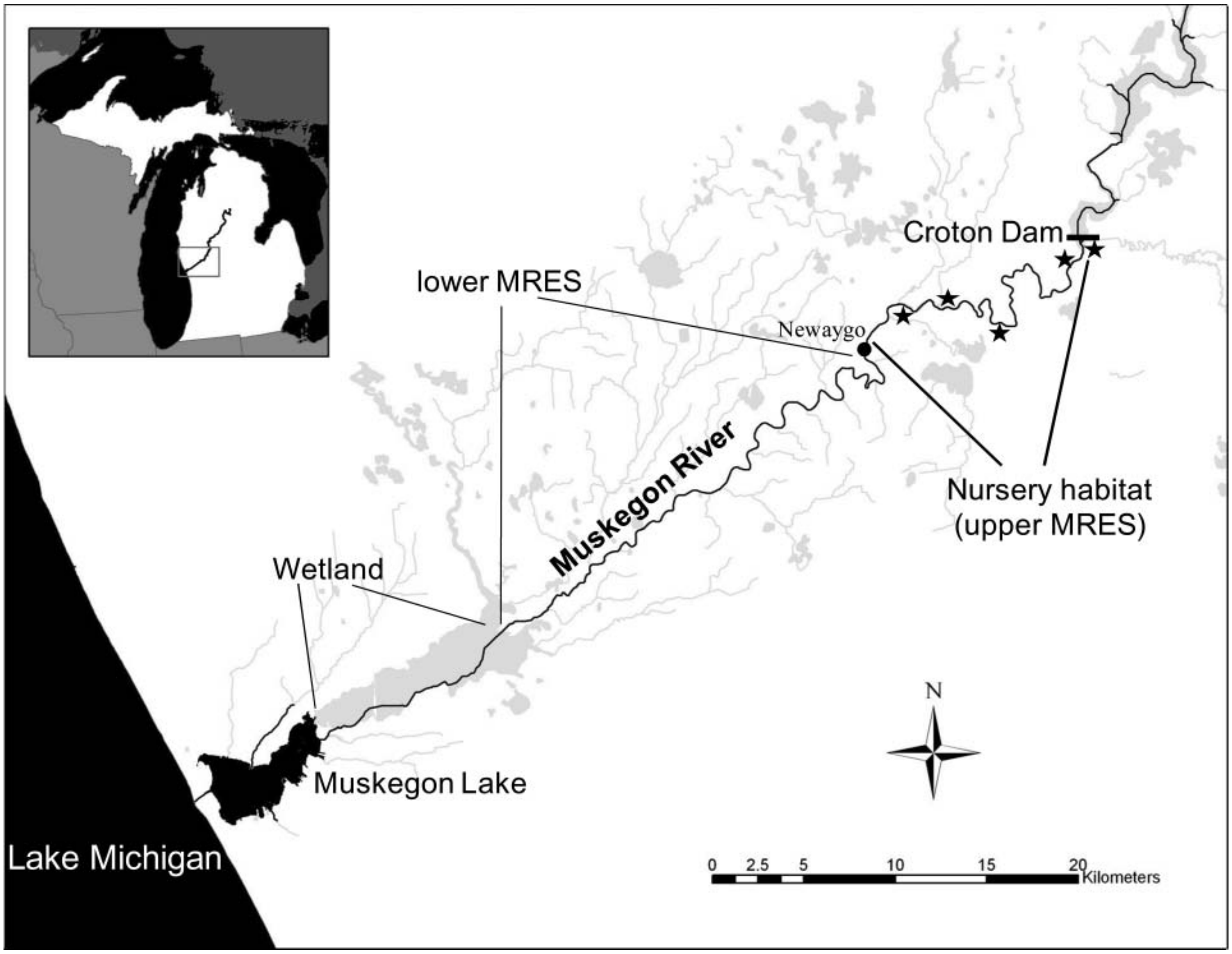

FIGURE 1. Map of the Muskegon River estuary system (MRES). Stars indicate the barge electrofishing reference sites used to estimate the population abundance of Chinook salmon parr.

end of the upper MRES from May 6 to June 29 to collect Chinook salmon parr during the historic peak of their emigration from the Muskegon River. The trap fished continually night and day and was checked each morning for parr. Each day, parr were identified, counted, weighed (nearest 0.1 g), and measured (mm total length [TL]). We estimated trap efficiency by marking migrating Chinook salmon parr that were captured in the trap, releasing them approximately 0.5 km upstream of the trap, and then capturing and counting marked and unmarked individuals. Because debris occasionally halted operations for several days (May 9–12, 14, 16–18, 22–26), we linearly interpolated parr abundance from the observed catches on surrounding dates. Using a capture efficiency estimate of 2% (Edward Rutherford, unpublished data), we extrapolated from the catches of parr ($\geq$50 mm TL) in the auger trap to total abundance ($\pm$error; all error estimates are reported as 95% confidence intervals). At 50 mm TL, Chinook salmon parr begin to emigrate from the Muskegon River and approach the average size at which small potential piscivores, such as hatchery-raised brown and rainbow trout, become gape limited (e.g., Bannon and Ringler 1986; Damsgård 1995).

During the periods May 6–7, 2004, April 19–June 15, 2005, April 20–June 7, 2006, and May 8–June 6, 2007, we employed a barge-style electrofishing unit (3 A, 240 V) to sample Chinook salmon parr along 100-m shoreline transects at five established reference sites (Carl 1982; Figure 1). We used a three-pass depletion protocol to estimate parr density (number of parr/m of shoreline; e.g., Zippin 1956, 1958). We sampled each reference site twice monthly and most sites five times in a given field season (2005–2007 only). For each electrofishing transect, we measured and weighed a subsample of 30 Chinook salmon parr, while the remaining individuals were counted and batch-weighed. We then extrapolated from these parr density estimates to the abundance in the entire nursery area from Croton Dam to Newaygo (as defined by Godby et al. 2007; Figure 1) by multiplying the mean parr density (number/100 m) of the five reference sites by the length of the total nursery shoreline from Croton Dam to Newaygo (22.5 km $\times$ 2 sides $=$ 45 km).

We estimated the initial abundance of Chinook salmon parr by developing a linear relationship between parr length and abundance over time; the linear model best described the relationship between length and abundance. We assumed that parr abundance at 37 mm TL (length at emergence; Beacham and Murray 1990) was the initial abundance. We also calculated the peak abundance of Chinook salmon parr larger than 50 mm for each sampling season to determine an index of potential emigration from the Muskegon River to Lake Michigan (e.g., Carl 1984). From mid-May to mid-June of 2006, we used beach seines to sample Chinook salmon parr along the shores of Muskegon Lake and Lake Michigan to determine the presence or absence of Chinook salmon in Muskegon Lake and to provide a rough estimate of out-migration timing.

Predators.—The relative abundance of walleyes, hatchery brown trout, and hatchery rainbow trout was determined using a barge electrofisher and a 20-ft (6.1-m) Smith-Root boom-style AC electrofishing boat. Electrical current ranged from 4 to 6 A, and voltage was set to 240 V in all electrofishing transects. Spring (April to June) electrofishing transects in the Muskegon River were performed biweekly (at minimum), were run downstream for approximately 10 min, and were always performed in daylight. Upon capture, fish were placed in a 284-L recirculating live well for the duration of the transect. The relative abundances of piscivores were not determined for Muskegon Lake.

The index of relative walleye abundance (catch per unit effort [CPUE; number/h) was based on the electrofishing transects and scaled to the estimated abundance of spawning walleyes in the Muskegon River (approximately 38,000 individuals) in 2002 (Hanchin et al. 2007). Changes in CPUE across time were scaled to fish abundance, with the maximum CPUE being scaled to the initial (i.e., maximum) abundance. The maximum abundance of spawning walleyes was assumed to be 38,000, with walleye numbers declining as the fish returned to the lake. Hatchery brown and rainbow trout loss rates were calculated in the same way, but initial abundance indices were based on stocking numbers (Table 1) for a given year.

Piscivore Diet and Consumption

Piscivore collection.—The diets of piscivorous fishes from 2004 to 2007 were determined from samples collected in the Muskegon River and Muskegon Lake using electrofishing, gill nets, and angling. In the Muskegon River, fish were captured using the electrofishing methods described above. In Muskegon Lake, all three methods were used. Electrofishing was conducted with a 20-ft Smith-Root boom-style electrofishing boat; the transects were approximately 1 km in length (~10 min) and conducted in shallow water (depth, ≤2 m) at night. Upon capture, fish were placed in a recirculating live well. Horizontal gill nets (3 × 30 m, 89- and 127-mm stretch mesh) were set weekly

TABLE 1. Stocking dates for hatchery trout into the Muskegon River (upper MRES). The rainbow trout were entirely Eagle Lake strain, and the steelhead were Michigan strain. The brown trout were all Wild Rose strain except for those stocked on June 8, 2004 (Gilchrist Creek strain).

Date	Brown trout	Rainbow trout	Steelhead
2004			
Mar 16	10,000	0	0
Apr 4	0	25,000	0
Apr 13	13,350	61,726	0
Apr 14	23,732	30,000	0
Apr 15	0	9,361	0
Apr 16	0	0	55,004
May 13	11,250	0	0
Jun 8	20,359	0	0
Total	78,691	126,087	55,004
2005			
Apr 11	0	50,000	0
Apr 12	0	55,000	0
Apr 13	40,000	5,000	0
Apr 14	25,000	0	0
Apr 15	10,000	0	55,000
Apr 20	0	9,583	0
Apr 26	0	9,008	0
Apr 27	0	0	5,000
Apr 9	9,600	0	0
Apr 11	0	16,704	0
Total	84,600	145,295	60,000
2006			
Mar 30	20,000	0	0
Apr 14	0	30,000	30,000
Apr 17	10,000	0	25,522
Apr 18	0	16,900	0
Apr 19	0	36,000	0
Apr 21	20,000	0	0
Apr 27	10,000	0	0
May 1	15,000	0	0
May 2	9,600	0	0
May 4	0	44,000	0
May 9	0	0	5,500
Total	84,600	126,900	61,022
2007			
Apr 9	0	0	29,000
Apr 11	0	27,500	0
Apr 13	0	27,500	0
Apr 16	0	30,000	0
Apr 18	0	30,400	0
Apr 20	0	0	26,500
Apr 30	35,600	0	0
May 8	0	9,943	0
Total	35,600	125,343	55,500

in May and June of 2005–2007. Gill nets were set near shore (depth, 2–5 m) for 3 h at night to minimize the digestion of stomach contents and to maximize the number of fish caught. Lastly, anglers' creels were sampled at Muskegon Lake boat ramps from angling that occurred at dusk or after dark. Predators collected from Muskegon Lake were utilized only in diet analyses.

Diet composition.—Fish were measured (mm TL) and weighed (0.01 kg), and their stomach contents were removed. The stomach contents of live fish were flushed using a garden sprayer (e.g., Seaburg 1957) and the fish were released; whole stomachs were excised from deceased fish (i.e., those captured with gill nets). 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 separated, measured (mm TL), weighed (0.1 mg 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 forage fish from the Muskegon River.

Piscivore consumption.—The "meal-turnover" method, as described by Vigg et al. (1991; see also Fresh et al. 2003), was used to quantify the daily, monthly, and total consumption of Chinook salmon parr by walleyes and newly stocked brown trout in the Muskegon River. In addition, we determined the potential impact of walleye predation on the abundance of stocked brown and rainbow trout to see whether walleye predation on alternative prey was beneficial to the survival of Chinook salmon parr. The meal-turnover approach involved identification of piscivore stomach contents, back-calculation of original prey weights, estimation of the state of prey digestion (based on the difference in prey weight and back-calculated prey weight at ingestion), and prediction of the time (h) to 90% evacuation of a meal for walleyes. The back-calculated lengths of digested prey were estimated from a regression of total length on the length from the nape to the base of the tail for three common prey fish in the Muskegon River. The weights of prey were estimated from lengths using weight–length regressions. The equations to predict the time to 90% evacuation (h in hours) for walleyes (equations 1–3; Swenson and Smith 1973; Wahl and Nielsen 1985) and brown trout (equation 4; He and Wurtsbaugh 1993) were as follows:

$$\text{prey} < 1.1\text{ g}: h = (-7.450 + 0.178D + 0.088R) / 0.0283T^{1.1899} \quad (1)$$

$$\text{prey } 1.1 - 2.5\text{ g}: h = (-4.476 + 0.208D + 0.031R) / 0.0415T^{1.1899} \quad (2)$$

$$\text{prey} > 2.5\text{ g}: h = (-0.065 + 0.231D + 0.047R) / 0.0415T^{1.1899} \quad (3)$$

$$R_e = 0.053e^{0.073T} \quad (4)$$

where D is percent of prey weight digested, R is prey meal ration (g/g), T is temperature (°C), and R_e is the instantaneous rate of evacuation (per hour) in brown trout. The number of prey consumed per predator per day was computed as the daily consumption (g/d) of each prey type divided by the mean mass of the prey type. A meal was defined as all diet items whose state of digestion did not vary by more than 20% (Swenson and Smith 1973). Daily consumption rates were then extrapolated to the entire piscivore (walleye and brown trout) population by multiplying daily consumption by estimates of daily abundance (e.g., Rieman et al. 1991; Vigg et al. 1991; Beamesderfer and Rieman 1991) to determine the daily, monthly, and seasonal loss of Chinook salmon parr from predation and any losses of stocked trout from walleye predation.

Chinook Salmon Growth

Growth rates of Chinook salmon parr were estimated from barge electrofishing collections at the five reference sites in the Muskegon River. These rates were estimated as the changes in average parr length over time observed in bimonthly sampling. In addition, the date at which 50% of Chinook salmon parr measured at least 50 mm TL was recorded. The approximate time needed for parr to grow from emergence (at 37 mm) (Beacham and Murray 1990) to 50 mm was used to determine the amount of time that parr were vulnerable to small, gape-limited predators (e.g., Damsgård 1995; Quinn 2005). It was assumed that Chinook salmon eggs were deposited on October 1 based on MDNRE creel data from 2000 to 2005 (Tracey Kolb, MDNRE, personal communication), and the mean daily temperature was used to estimate the incubation time and emergence date for each year based on 1,000 accumulated thermal units (ATUs) and empirical relationships between the number of ATUs and temperature (McMichael et al. 2005). The total time that Chinook salmon parr spent in the river (i.e., from swim-up to the mean emigration date) also was estimated to determine the temporal overlap with other piscivores that are not gape-limited by Chinook salmon parr (e.g., walleyes, basses *Micropterus* spp., etc).

Fish Mortality and Loss Rate

Instantaneous daily total loss rates (Z_{total}) for Chinook salmon parr from 2005 to 2007 were estimated from the slope of a linear regression of $\log_e$ transformed parr density estimates against time. The parr density estimates were the average of densities at all sites within a 2-d period. Since reference sites were sampled only once in 2004 (Edward Rutherford, unpublished data), the total loss rate in 2004 was assumed to equal the mean total loss rate from 2005 to 2007. The total daily loss rate incorporates predation mortality (Z_{pred}) and emigration from the river (Z_{emig}, which includes other unknown sources of mortality, e.g., Ricker 1975). Seasonal consumption estimates of predation by walleyes and brown trout were summed to estimate the percentage of the Chinook salmon parr population consumed by predators (A) and then transformed to instantaneous daily predation mortality

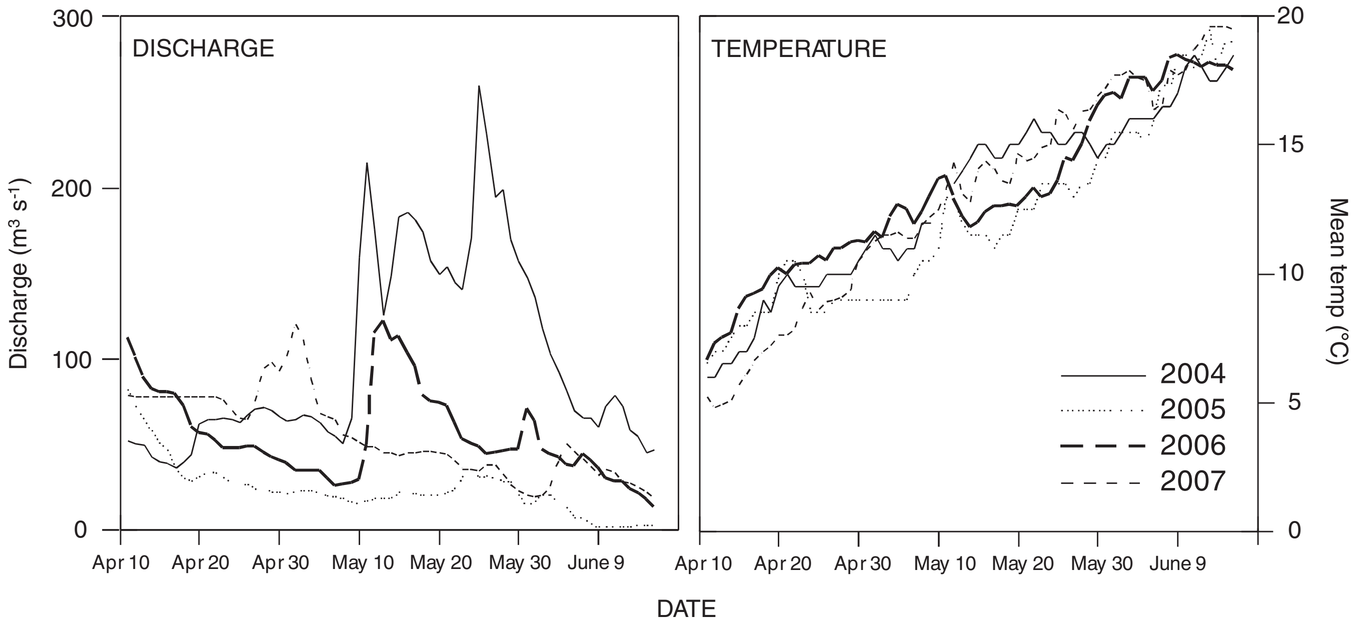

FIGURE 2. Intra- and interannual variation in river discharge and temperature in the upper MRES from 2004 to 2007. Data are only shown for the approximate duration of the Chinook salmon nursery period (emergence to out-migration). The data were recorded at U.S. Geological Survey station 04121970 in Croton, Michigan.

rates (Ricker 1975) by means of the equation

$$Z_{\text{pred}} = -\log_e(1 - A)/t, \tag{5}$$

where t is the number of days that Chinook salmon parr overlapped spatially with brown trout and walleyes, that is, the window of vulnerability to predation. Instantaneous daily loss rates due to emigration (Z_{emig}) were estimated as the difference between Z_{total} and Z_{pred}.

RESULTS

Environmental Variables

The trends in water temperature in the Muskegon River were similar among years. In each year, temperature rose steadily from about 6°C in early April to about 20°C in mid-June, although in 2007 there was a brief warm period in early April (Figure 2). The water temperature from April to June was approximately 11.4 ± 0.9°C in 2004, 2006, and 2007 but only 10.4 ± 0.9°C in 2005. River discharge, however, differed between years. In 2004, the Muskegon River experienced anomalous flood conditions throughout the month of May, and river discharge while Chinook salmon parr occupied the nursery habitat (late March–June) was the highest (118.6 ± 11.6 m^3/s) of all four years. In 2005, river discharge was low throughout the spring and summer (66.4 ± 9.5 m^3/s). Discharge was intermediate in 2006 and 2007 (88.2 ± 7 m^3/s; Figure 2).

Fish Abundance

The abundance of Chinook salmon parr at emergence averaged 491,504 ± 27,864 individuals across all sampling years and ranged from 459,717 to 511,712 (Figure 3). Chinook salmon parr at least 50 mm long were present by the first week of May in all years, although in 2006 they occurred as early as April 20. By the end of May, over 50% of the parr captured were at least 50 mm long in all sampling years. The abundance of Chinook salmon parr at least 50 mm long for all years was 325,018 ± 47,330 individuals (Figure 4A). The mean time required for parr to reach 50 mm (i.e., the period of vulnerability to predation by brown trout) was 40 d; the period of vulnerability ranged from 36 to 47 d (Figure 4B).

The daily growth rates of Chinook salmon parr were highest in 2007 (0.39 ± 0.07 mm/d), slightly lower in 2006 (0.36 ± 0.09 mm/d) and 2004 (0.35 ± 0.64 mm/d), and lowest in 2005 (0.30 ± 0.07 mm/d). Growth rates were significantly different between 2005 and 2007 (t = 2.495, P = 0.025, df = 8) but not between any other years. Chinook salmon parr successfully migrating out of the Muskegon River were caught in shallow, sandy areas of Muskegon Lake from late May to early June, but capture success was too low (n = 11) to quantify their abundance. The mean length of out-migrant Chinook salmon parr was 60 mm; length ranged from 49 to 77 mm. In 2006, 59,409 hatchery-raised Chinook salmon parr were stocked in the Muskegon Lake outlet, but these individuals were much larger (average TL = 100 mm) and were therefore unlikely to have contributed to our seine catches.

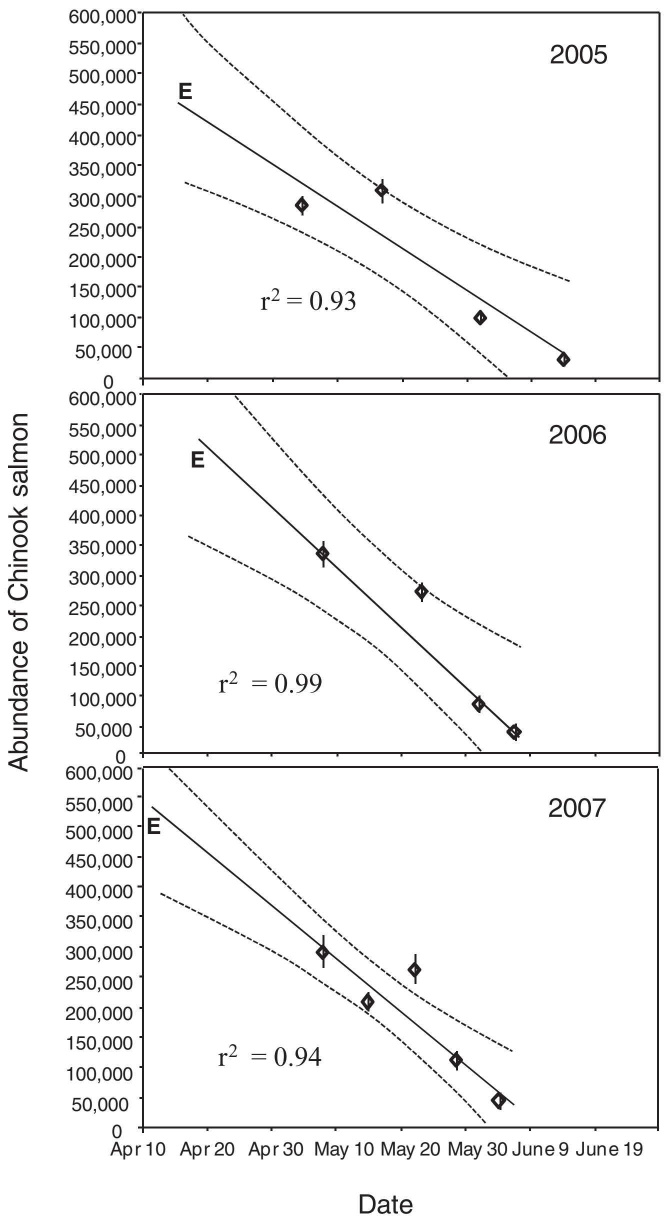

FIGURE 3. Intra- and interannual variation in the population abundance of wild Chinook salmon at emergence (E) and during their parr phase (diamonds; error bars indicate the 95% confidence intervals). Ninety-five percent confidence intervals are also shown for the regression (dashed lines). The abundance of Chinook salmon parr could not be estimated using barge electrofishing techniques in 2004.

The spawning population of Muskegon River walleyes (TL = 533 ± 25.4 mm; range = 314–810 mm) was assumed to be 38,000 for all years and to range in age from 2 to 18 years (Hanchin et al. 2007). The CPUE data indicate that most walleyes departed the Muskegon River immediately after spawning (by approximately April 1), but an estimated 2,000–3,000 adults remained through June in all years (Figure 5). In Muskegon Lake, walleye CPUE data also showed a decreasing trend postspawning, indicating either the avoidance of shallow water or migration into Lake Michigan. Walleyes were captured predominantly in shallow, sandy areas of Muskegon Lake in late May and early June, coincident with the location of Chinook salmon parr captured in beach seines.

The numbers of hatchery trout stocked from 2004 to 2007 were high, averaging 259,660 (Table 1). There was no relationship between the total length of stocked trout and stocking date. Rainbow trout (TL = 174 ± 11.1 mm) were stocked consistently (189,000 ± 11,483) over periods of several weeks in all study years (Table 1). Brown trout stocking was nearly 85,000 ± 3,860 from 2004 to 2006 but dropped by about 60% in 2007. Brown trout (TL = 164 ± 10 mm) also were stocked over several weeks in the first 3 years but in 2007 were stocked in a single day (April 30; Table 1). In all years, the abundance of brown trout declined rapidly after stocking and by mid-June, they were nearly gone (Figure 5). This decreasing trend was less pronounced in rainbow trout, which appeared to be relatively abundant throughout the sampling season (Figure 5).

Piscivore Diet Composition and Consumption

We analyzed the diets of 2,158 piscivores (Table 2) collected from 2004 to 2007 in the MRES. Equations to back-calculate the lengths of partially digested prey are reported for three common species in the Muskegon River (Table 3), as are weight–length regressions for five prey groups (Table 4). Of the walleyes examined that contained food items, 95% were piscivorous and consumed mainly hatchery brown and rainbow trout (85–90% of total prey biomass), especially in April and May (Figure 6). Chinook salmon parr, on the other hand, only comprised about 0.1–15% of the biomass of walleyes' seasonal diet (Figure 6). There was no relationship between walleye size and the type or size of prey consumed in the upper MRES. In the lower MRES, walleyes consumed primarily Cyprinidae, but the proportion of Chinook salmon parr in walleye diets increased in June. In Muskegon Lake, walleye diets were dominated by alewife and gizzard shad *Dorosoma cepedianum* (Table 5). We found no evidence of walleyes consuming Chinook salmon parr in Muskegon Lake.

Walleye consumption rates by number were higher for Chinook salmon parr than for brown or rainbow trout. In May, the mean daily consumption rate by walleyes (number of prey · predator $^{-1}$ · d $^{-1}$) of Chinook salmon parr was highest (2.45 parr) in the upper MRES and zero in the lower river. In June, walleyes' consumption of Chinook salmon parr declined slightly in the upper MRES (to 2.17 parr) and increased in the lower MRES (to 1.67 parr). Walleyes consumption of brown trout was highest in May (0.31), although consumption of rainbow trout was always higher than that of brown trout, especially in April (0.57 versus 0.22). In all years, rainbow trout appeared to be the favored forage item for walleyes (Table 6).

Approximately 40% of the stocked brown trout examined contained fish prey, and most preyed on Chinook salmon parr from 2005 to 2007. The percentage of brown trout containing food items that consumed Chinook salmon parr was highest in

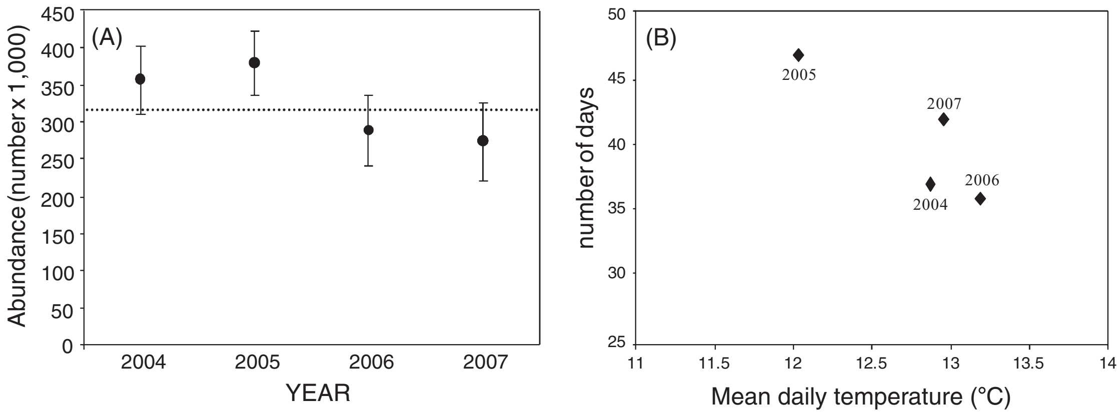

FIGURE 4. Panel **(A)** shows the peak abundance of Chinook salmon parr 50 mm or more in total length, by year; the error bars represent 95% confidence intervals, and the dashed line indicates the overall mean of 325,018. Panel **(B)** shows the approximate time after emergence required for 50% of Chinook salmon parr to reach 50 mm TL in each year; the emergence date was based on an egg deposition date of October 1, and growth was dependent on the mean temperature during the nursery period (swim-up to emigration).

2007 (38% of the total), was lower in 2005 (33%), and was lowest in 2006 (30%). Brown trout ate Chinook salmon parr in April immediately after the brown trout were stocked, but their consumption of Chinook salmon parr ceased around May 24 in each year. The diet composition (by biomass) of brown trout was approximately 40% Chinook salmon parr in April and May from 2005 to 2007 (Figure 6). The consumption of Chinook salmon parr by brown trout from 2005 to 2007 was

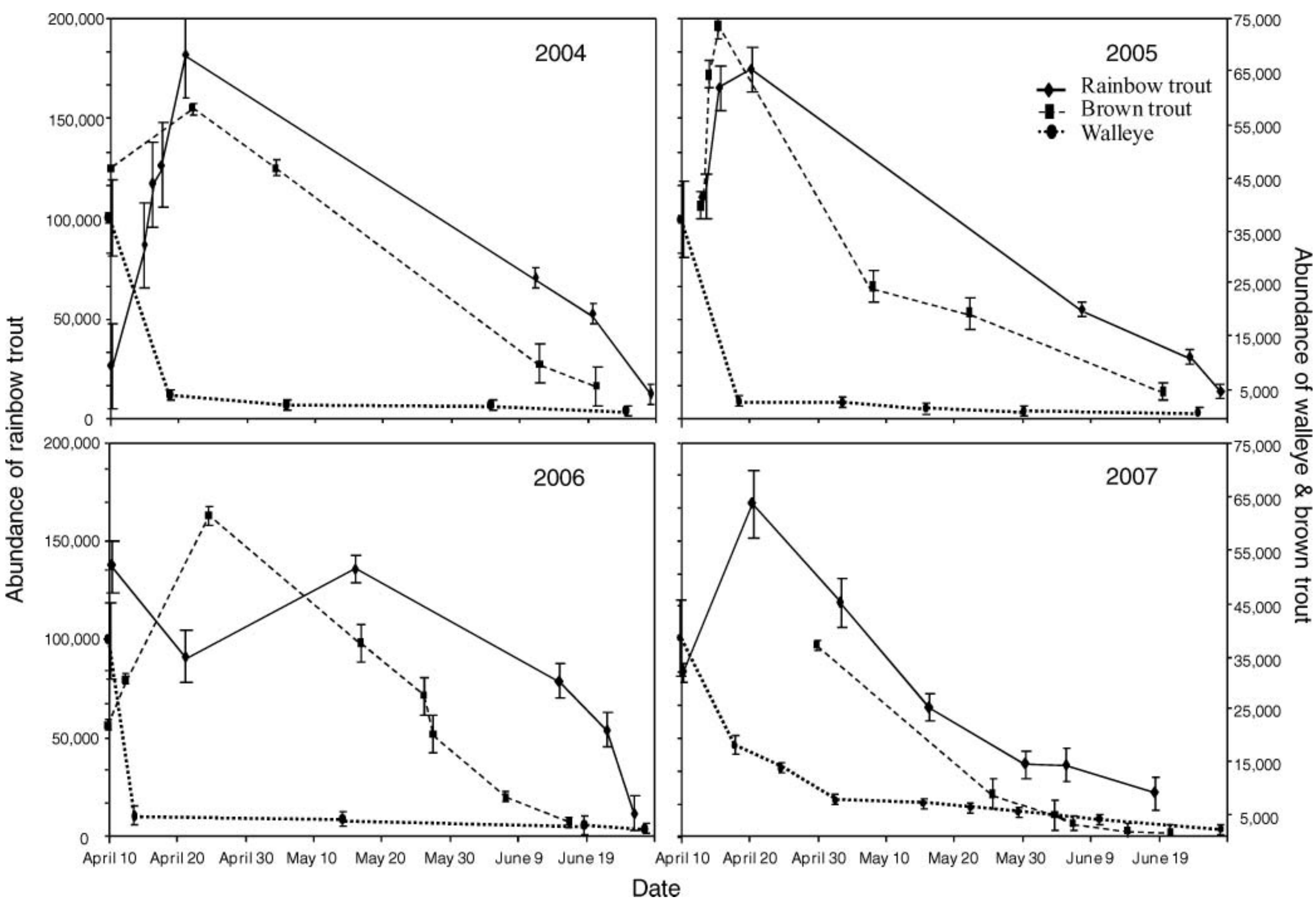

FIGURE 5. Intra- and interannual variation in the population abundances of brown trout, rainbow trout, and walleyes.

TABLE 2. Number of stomachs analyzed for each piscivore species examined, proportion of empty stomachs, and number of Chinook salmon parr (CHS) consumed per predator. The "other" category includes bowfin *Amia calva*, northern pike *Esox lucius*, largemouth bass *Micropterus salmoides*, and burbot *Lota lota*. The values for CHS/predator are 95% confidence intervals; the values in parentheses are the number of individual predators that consumed Chinook salmon parr in a given year.

Year and variable	Walleye	Brown trout	Rainbow trout	Smallmouth bass	Other
2004	238	0	0	25	16
Stomachs examined					
Proportion empty	0.57			0	0.5
CHS/predator	13.5 ± 10.5 (11)				
2005	371	33	52	22	12
Stomachs examined					
Proportion empty	0.71	0.11	0.04	0.11	0.08
CHS/predator	6.86 ± 2.3 (35)	1.6 ± 0.8 (10)		1.0 (5)	1.67 ± 0.8 (3)
2006	155	184	180	127	68
Stomachs examined					
Proportion empty	0.37	0.29	0.26	0.17	0.19
CHS/predator	1.5 ± 1.4 (2)	2.06 ± 0.6 (40)	2.8 ± 1.8 (5)	1.0 (4)	2.0 (2)
2007	250	66	238	97	17
Stomachs examined					
Proportion empty	0.41	0.44	0.19	0.16	0.24
CHS/predator	2.5 ± 1.3 (20)	2.54 ± 1.3 (14)	1.75 ± 0.56 (4)	1.0 (3)	6.0 (1)
Total	1,014 (68)	283 (64)	470 (9)	271 (12)	113 (6)

higher than that by walleyes in April and May but lower than that by walleyes in June (Figure 7). The mean daily consumption of Chinook salmon parr by brown trout was highest in April at approximately 1.42 · predator $^{-1}$ · d^{-1}, decreased by 38% in May, and declined to zero in June, when all brown trout were insectivorous (Table 6).

The average annual consumption of Chinook salmon parr by walleyes over all years was lower (46,809 parr) than that by brown trout (127,632 parr). Walleyes consumed approximately 91,288 ± 39,783 and 71,191 ± 25,350 Chinook salmon parr in the spring of 2004 and 2005, respectively (Figure 7). In 2007, however, walleyes only consumed 24,824 ± 11,473 Chinook salmon parr, and in 2006 their consumption was 934 ± 441. In comparison, brown trout consumed nearly twice as many Chinook salmon parr each year (an estimated 157,169 ± 32,778 and 131,100 ± 39,316 in 2005 and 2006, respectively) but only 77,516 ± 27,110 in 2007 (Figure 7).

Predation on Chinook salmon parr by other fish species was negligible. Only a small proportion (average = 2%) of rainbow trout consumed Chinook salmon parr (Table 2); nearly all rainbow trout diets were composed exclusively of invertebrates (mainly *Trichoptera* and *Ephemeroptera* spp.). We collected diet samples from other piscivorous species as well, though in most cases the species were rare or only a small proportion of the sampled individuals contained Chinook salmon parr. Although numerous, smallmouth bass *Micropterus dolomieu* of all sizes consumed mainly crayfish *Orconectes* spp. prey. Large brown trout (>220 mm TL) were rare compared with hatchery-raised brown trout (6–12%), and only a small proportion of those individuals consumed Chinook salmon parr (0–11%). Hence, only walleyes and hatchery brown trout were included in subsequent analyses.

Mortality/Loss Rates

Predation mortality was probably a large component of the total loss rates for Chinook salmon parr. Total instantaneous daily loss rates for Chinook salmon parr averaged 0.049 and ranged from 0.045 to 0.052 (Table 7). Instantaneous daily predation mortality was highest in 2005 (0.0141) and lowest in 2006 (0.0082). Peak annual predation mortality on Chinook salmon

TABLE 3. Linear regression model ($Y = a + bX$) statistics for total length (Y) as a function of length from nape to base of tail (X) for three common prey species in the upper MRES.

Prey species	n	Length range (mm)	a	b	r^2
Chinook salmon parr	98	37 – 77	7.1333	1.3	0.99
Rainbow trout	53	88 – 244	20.249	1.3742	0.94
Brown trout	34	64 – 200	10.004	1.1607	0.95

TABLE 4. Power regression model ($Y = aX^b$) statistics for weight (Y [g]) as a function of total length (X) for common prey species in the upper MRES. "Other fish species" consists mostly of darters *Etheostoma* spp.

Prey species	n	Length range (mm)	a	b	r^2
Chinook salmon parr	456	35–99	4.0×10^{-7}	3.7165	0.87
Rainbow trout	322	83–220	6.0×10^{-6}	3.0848	0.97
Brown trout	176	113–220	8.0×10^{-6}	3.0714	0.88
Cyprinidae	305	31–116	8.0×10^{-6}	3.0114	0.85
Other fish species	70	38–116	1.0×10^{-5}	2.9395	0.88

parr by walleyes was estimated at 18% of initial abundance (2004; Table 7). At the population level, stocked brown trout appeared to consume higher proportions of Chinook salmon parr than did walleyes, and most predation mortality was attributed to brown trout (Table 7). In 2005, annual predation mortality owing to brown trout was 34%, and total predation mortality by both species on Chinook salmon parr peaked at 49%. Based on the estimates of predation mortality (% mortality), the percentage of wild-produced Chinook salmon parr that emigrated from the Muskegon River (or experienced mortality from other sources) ranged from 27% in 2005 (124,124 ± 29,877 smolts) to 80% in 2007 (409,370 ± 50,972) (Table 7).

DISCUSSION

Interactive Effects of Abiotic Variables, Predators, and Alternative Prey

In this study, we found that the survival of Chinook salmon parr may be controlled by parr growth, the abundance of alternative prey, and stocking practices for brown trout. To a large extent, these factors are inextricably linked to abiotic factors; it is difficult to discern the relative effects of abiotic (i.e., river flow, water temperature) and biotic factors (i.e., predation and competition) in empirical studies. For example, while higher river temperatures can lead to higher growth rates of Chinook

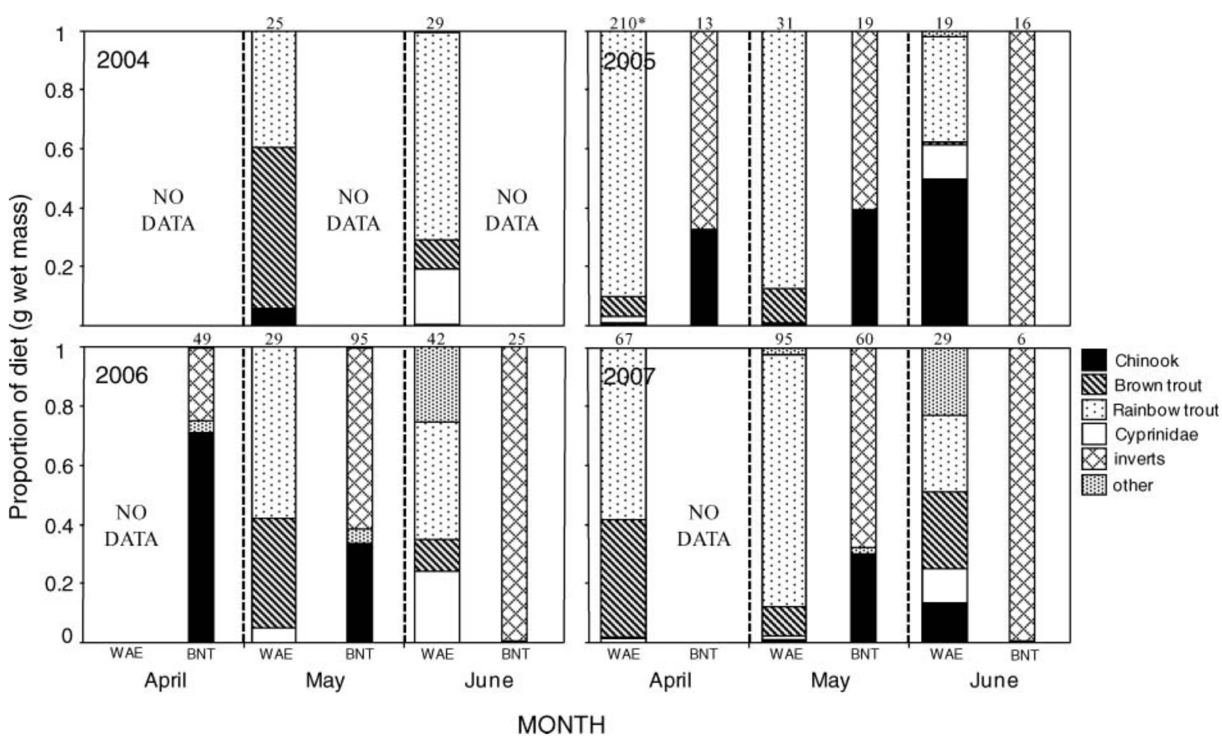

FIGURE 6. Diet composition of walleyes (WAE) and brown trout (BNT) from 2004 to 2007 in the upper MRES. The "other" category is composed mostly of northern pike (in walleye diets) and age-0 rainbow trout (in brown trout diets). Sample sizes are listed above each column. The large sample size in April 2005 was due to the capture of spawning walleyes, most of which (189) did not contain food items.

TABLE 5. Diet proportions (by wet mass) for Muskegon Lake walleyes (n = 463) during 2004–2007. The "other" category consists mostly of round goby *Neogobius melanostomus*.

Month	Chinook salmon parr	Alewife	Gizzard shad	Cyprinidae	Other
May	0	0.70	0	0.19	0.11
Jun	0	1.00	0	0	0
Jul	0	0.77	0	0.21	0.02
Aug	0	0	0.89	0.11	0

salmon parr (Connor and Burge 2003), higher temperatures also influence predator consumption rates, thereby increasing parr's vulnerability to predation (e.g., Marine and Cech 2004). The survival of Chinook salmon parr is positively correlated with river discharge (Unwin 1986; Bradford 1994; Smith et al. 2003). Early emigration of Chinook salmon parr may reduce interactions with stream predators, thereby increasing their survival in riverine habitats. In the Muskegon River in 2005, mean temperature and mean river discharge were the lowest of all sampling years and corresponded to the lowest parr emigration, lowest parr growth rate, and highest rates of predation mortality from walleyes and brown trout. In 2006 and 2007, mean water temperature and mean river discharge were significantly higher than in 2005 and corresponded to an increase in parr emigration and growth rates and a substantial reduction in predation mortality in 2007 (but not in 2006). Despite the potential influence of river temperature and discharge, it was difficult to determine how much these factors directly influenced the survival of Chinook salmon parr, since abiotic factors are highly correlated with and directly influence the behavior and spatial distribution of piscivorous fishes.

Despite the difficulty of parsing the effects of abiotic factors on the mortality of Chinook salmon parr, the predator-specific effect on Chinook salmon mortality was determined. Brown trout predation on Chinook salmon parr was consistently high and probably controlled by the growth rates of Chinook salmon parr and brown trout stocking dates. Because piscivorous hatchery brown trout may become gape limited and do not consume prey exceeding 50 mm TL (e.g., Bannon and Ringler 1985; Damsgård 1995; Montori et al. 2006), the parr growth rate will influence the duration of vulnerability to brown trout predation and therefore may be a useful predictor for survival. Our data suggest that brown trout did not consume Chinook salmon parr after (about) May 24, when parr reached a mean length of 49 mm TL and nearly 2 weeks before most Chinook salmon parr emigrated. Although Chinook salmon parr longer than 50 mm may not exceed the gape limit of all piscivorous brown trout, these larger individuals will have relatively higher burst swimming speeds than their smaller counterparts. A larger body size also represents an increase in handling time and may allow the larger individuals a greater chance to escape predation by smaller predators such as newly stocked brown trout. Further, we cannot discount the possibility that brown trout predation on Chinook salmon parr was influenced by changes in the abundance of invertebrates in May and June, when invertebrate prey became an increasingly large component of brown trout diets.

We observed mean daily growth rates of Chinook salmon parr that were similar to those reported for other Lake Michigan and Pacific Coast rivers for parr captured in nursery areas. Carl (1984) observed similar mean growth rates of Chinook salmon parr (0.28–1.01 mm/d) in Baldwin and Pine Creeks, which are tributaries to Lake Michigan. In the Columbia River, the growth of Chinook salmon parr ranged from 0.44 to 0.60 mm/d (Becker 1970; Dawley et al. 1986). The mean daily growth rates of

TABLE 6. Mean daily consumption (number of prey/predator) by walleyes and brown trout on three prey species in the upper and lower MRES from April to June 2004–2007. The letter N indicates the number of predators examined that contained particular prey; the numbers in parentheses are the numbers of stomachs containing particular diet items in each month.

	Walleyes				Brown trout			
Prey species	*N*	Apr	May	Jun	*N*	Apr	May	Jun
Upper MRES								
Chinook salmon parr	33	0.15 (4)	2.45 (17)	2.17 (12)	64	1.42 (15)	1.03 (49)	0
Brown trout	48	0.22 (10)	0.31 (27)	0.22 (11)				
Rainbow trout	152	0.57 (32)	0.48 (88)	0.39 (32)				
Lower MRES								
Chinook salmon parr	22	0	0	1.67 (22)	0	0	0	0
Brown trout	2	0	0	0.02 (2)				
Rainbow trout	7	0	0	0.09 (7)				

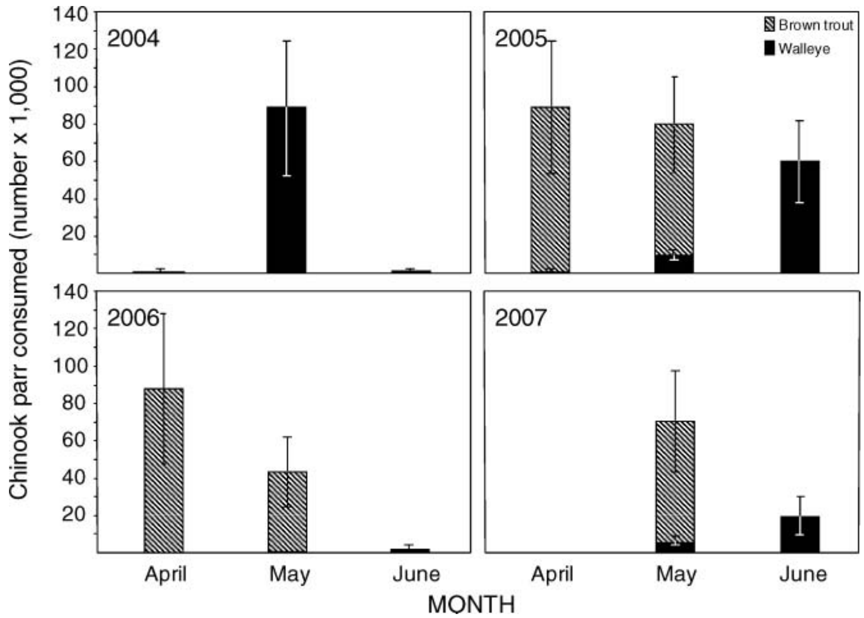

FIGURE 7. Total number of Chinook salmon parr consumed by walleyes and brown trout from 2004 to 2007 based on the empirical consumption model. Brown trout diet data were not available for 2004. The error bars indicate the 95% confidence intervals.

Chinook salmon parr were higher in river mouths or estuaries, where parr were captured at larger sizes. In the Pere Marquette and Little Manistee rivers (tributaries to Lake Michigan), the growth of Chinook salmon parr was similar to that reported by Carl (1982) (mean = 0.71 mm/d) but higher than in the Muskegon River (Seelbach 1985; Zafft 1992). The growth rates of fall Chinook salmon parr in the Nanaimo estuary and Snake River were higher yet, ranging from 1.1 to 1.32 mm/d (Healey 1980; Connor and Burge 2003).

The growth of young Chinook salmon parr is dependent on water temperature and food availability. Hence, the low growth experienced in 2005 was probably influenced by the lowest mean daily water temperatures encountered in our study. If brown trout are size-selective piscivores, low parr growth rates in 2005 may have been responsible for the highest predation mortality rates observed from 2004 to 2007. By contrast, in 2007 the mean daily water temperature was the highest in our study and predation mortality from both predators was relatively low. These conditions may have supported the highest growth rate of Chinook salmon parr in all study years. The low rate of predation mortality in 2007 was probably due to the fact that predator (i.e., brown trout) abundance was much lower than in other study years, while the initial abundance of Chinook salmon parr was the highest of all study years. Hence, during 2004–2007, the growth rates of Chinook salmon parr may have been limited primarily by water temperature and predation pressure and less influenced by density-dependent growth limitations (e.g., Chapman 1962; Mason and Chapman 1965; Unwin 1986) in the

TABLE 7. Instantaneous daily loss rates (Z/d) of Chinook salmon parr in the upper MRES from 2004 to 2007. Total loss rates (Z_{total}) were estimated as the slopes of the regressions of abundance on time; losses due to consumptive predation (Z_{pred}) were estimated from daily ration estimates; losses due to emigration (Z_{emig}) were estimated as Z_{total}—Z_{pred}. The term "predation mortality" refers to the total fraction of the initial population of Chinook salmon parr that were consumed by walleyes and brown trout; "days" is the number of days in which Chinook salmon parr overlapped spatially with walleyes and brown trout (the window of vulnerability to predation). No data were available (n.a.) on brown trout consumption of Chinook salmon parr in 2004. Ninety-five percent confidence intervals are shown for the number of emigrated parr.

		Z_{pred}					
Year	Z_{total}	Brown trout	Walleyes	Z_{emig}	Days	Predation mortality	Emigrated parr
2004	n.a.	n.a.	0.0026	n.a.	n.a.	0.18	n.a.
2005	0.045	0.011	0.0031	0.0309	38	0.49	124, 124 ± 29, 877
2006	0.050	0.0081	0.0001	0.0418	56	0.26	286, 758 ± 101, 384
2007	0.052	0.0044	0.0009	0.0467	56	0.20	409, 370 ± 50, 972

Muskegon River. This assertion is supported by the 2006 data, which suggest that intermediate water temperature and intermediate predation mortality resulted in intermediate growth rates for Chinook salmon parr.

Alternatively, the proportion of brown trout that are piscivorous, the spatiotemporal overlap between brown trout and Chinook salmon parr, and the number of brown trout stocked are factors influencing the survival and potential recruitment of Chinook salmon parr. Approximately 40% of all newly stocked brown trout (TL, ∼164 mm) sampled in the Muskegon River were piscivorous. In 2005 and 2006, brown trout were stocked early and over multiple dates, overlapped with Chinook salmon parr for a greater duration, and inflicted greater predation mortality than in 2007. Predation mortality on Chinook salmon parr by brown trout was highest in 2005, when the growth of Chinook salmon parr was lowest. Although the temporal overlap between brown trout and Chinook salmon parr was greatest in 2006 (∼60 d versus ∼45 d in 2005), brown trout were stocked in early to mid-April and in great numbers in 2005; 88% (75,000 fish) of all hatchery brown trout were stocked, while the mean length of Chinook salmon parr was 39.5 mm. In 2006, only 50% (40,000 fish) of hatchery brown trout were stocked in mid-April. In 2007, 60% (49,000 fish) fewer brown trout were stocked and on a later date (April 30) than in previous years, reducing the temporal overlap between brown trout and Chinook salmon parr by nearly 40%. This resulted in a 35% reduction in predation mortality by brown trout on Chinook salmon parr, indicating that timing and the number of brown trout stocked into the Muskegon River strongly affect the survival of Chinook salmon parr. Despite the considerable reduction in predation mortality on Chinook salmon parr in 2007, brown trout still consumed approximately 15% of the estimated initial parr abundance.

Walleyes also may impose high predation mortality rates on Chinook salmon parr before and during the latter's out-migration from the Muskegon River, though this was not observed in all study years. Unlike with brown trout, walleye predation on Chinook salmon parr was inconsistent across sampling years (although this appears to have been dependent on the presence of alternative forage). Generally, Muskegon River walleyes were opportunistic predators and consumed a low biomass of small Chinook salmon parr but a high biomass of large hatchery trout. This trend was especially obvious in May of all years when hatchery trout abundances were high; only 1.7% of pooled walleye diets were composed of Chinook salmon parr. In June, hatchery trout abundances were considerably lower, and the proportion of pooled walleye diets composed of Chinook salmon increased to 9%. Hence, the availability of alternative forage fishes (i.e., hatchery trout) may buffer walleye predation mortality on Chinook salmon parr.

In Muskegon Lake, walleyes did not appear to consume Chinook salmon parr at all but to consume alternative forage species, such as alewife and gizzard shad. Nearly all Muskegon Lake walleyes (70–100%) examined consumed the latter two species, and the rest consumed Cyprinidae. Hatchery trout, alewife, and gizzard shad abundances were ephemeral, but their availability coincided with that of emigrating Chinook salmon parr. Thus, alternative forage appeared to buffer walleye predation mortality on Chinook salmon parr throughout the MRES. Johnson et al. (2007) discovered a similar trend in tributaries to Lake Huron, where the seasonal variability of spawning alewives buffered walleye predation on hatchery salmon smolts.

Predation mortality appeared to be inversely correlated with the number of Chinook salmon parr migrating out of the Muskegon River. Predation mortality was highest in 2005 and coincided with the lowest emigration rate. By contrast, predation mortality was lowest in 2007, when total mortality and emigration rates were highest. Total instantaneous loss rates for Chinook salmon parr in the Muskegon River ranged from 2.5 to 2.91 during the nursery period in our study. In two other tributaries to Lake Michigan, the Pere Marquette and Little Manistee rivers, the total mortality rates of Chinook salmon parr were much lower and peaked at 0.38 (Zafft 1992; Seelbach 1985), though these were larger hatchery-reared fish. Achord et al. (2007) reported instantaneous mortality rates of 1.38–2.53 for Chinook salmon parr in a large river in the Pacific Northwest, although this value was due, in part, to hydroelectric dams (Beamesderfer et al. 1990) and did not incorporate emigration, as our estimate did. However, the instantaneous annual predation mortality rates of parr appeared to be much higher in the Muskegon River (range, 0.22–0.67) than for parr in the Columbia River (0.09–0.21; Rieman et al. 1991). This result suggests that predation mortality from fish can be very important in large Great Lakes tributaries, especially since the Muskegon River produces an order-of-magnitude fewer Chinook salmon parr than large West Coast rivers. Comparative data on predation mortality are lacking for other Great Lakes tributaries.

Although our methods were consistent across years, our study may have inherent biases. The density of Chinook salmon parr throughout the upper MRES nursery was assumed to be equivalent to that of the five reference sites therein. All sites were sampled in the same manner, however, so biases were consistent across sampling sites and years. Our index stations are believed to adequately represent Chinook salmon parr densities in the prime nursery area. In 2003, Edward Rutherford (unpublished data) sampled 16 additional stations in the Chinook salmon nursery area, representing nearly 5% of the potential sample area. Estimates of Chinook salmon parr density at the index sites (1.11 ± 0.37 parr/m [mean ± 2 SEs]) were not significantly different from those at all sites (1.05 ± 0.28 parr/m) in the nursery area. Further, in 2003 and 2004 transects throughout the Muskegon River system were sampled using barge electrofishing, and it was concluded that Chinook salmon parr spawn almost entirely in the nursery area described by Godby et al. (2007). There was no effective way to estimate the abundance of Chinook salmon parr in the lower MRES; they are likely to move through this section of river quickly anyway. Still, we could not quantify population consumption of Chinook salmon parr by walleyes in the lower MRES, which implies that our predation mortality estimates are conservative.

Predator migration made estimation of their abundances difficult, and we therefore assumed a linear relationship between CPUE and fish abundance. We assumed that the initial abundance for walleyes was equal in all four study years. This is not an unlikely scenario, as spawning walleye estimates made since the 1980s have typically been reported at approximately 40,000 individuals (Day 1991; Hanchin et al. 2007; R. O'Neal, MDNR, personal communication, 1998). We also used stocking values of trout species as their initial abundances and assumed no natural reproduction for any predator species. The movement of fish (trout and Chinook salmon parr) from our study sites would contribute to the loss rates (combined with natural mortality), thereby producing an underestimate of survival (especially for Chinook salmon parr). Thus, the abundance estimates for brown and rainbow trout may also be conservative. Finally, we assumed that the 1,330 predator samples containing diet items that we collected represented the diet trends of the predator populations in the MRES. In any case, our estimates of predation mortality on Chinook salmon parr provide a baseline with which the results of future studies can be compared.

Management Implications

The trophic interactions among walleyes, stocked rainbow and brown trout, Chinook salmon parr, and forage fishes have large implications for the effective management of these species in the Muskegon River. The timing, location, and strength of these interactions may determine the efficacy of fishery management in promoting the productivity of valuable sport fisheries in the MRES. Fishery managers can control predation mortality on Chinook salmon parr through stocking and harvest regulations for piscivores (e.g., Harvey and Kareiva 2005; Krueger and Hrabik 2005).

Predation mortality on juvenile stages may have a greater impact on the survival variability of wild salmon in freshwater habitats than in marine habitats (Myers 2001), though this may be seasonally dependent. We estimated seasonal predation mortality rates for Chinook salmon parr that ranged from 18% to 49% during the nursery period (April–June) in the Muskegon River. Rieman et al. (1991) estimated a predation mortality rate of approximately 30% for juvenile Chinook salmon in the Columbia River over the same time interval, though predation there may increase substantially by August, when temperatures are much higher. Chinook salmon parr leave the Muskegon River long before August, making their nursery residence period much shorter than that of fish in large Pacific coast rivers. The river systems in both regions contain important top predators that are major sources of variable mortality for emigrating Chinook salmon parr. In Lake Michigan tributaries, walleyes and brown trout are the main predators of Chinook salmon parr, while the northern pikeminnow *Ptychocheilus oregonensis* is an important predator in the Pacific Northwest (Beamesderfer et al. 1990; Friesen and Ward 1999), as it accounts for most (78%) of the predation mortality of juvenile salmonids in some large rivers (Rieman and Beamesderfer 1990; Rieman et al. 1991; Johnson et al. 2007). While smallmouth bass are an important predator of Chinook salmon parr in large Pacific coast rivers, in the Muskegon River they tended to prey on the abundant crayfish populations instead.

Manipulation of predator abundance may be helpful in assessing the relative contribution of predation to overall ecosystem structure and function (e.g., Paine 1966; Navarrete and Menge 1996; Rand and Stewart 1998). Management actions to remove northern pikeminnow have resulted in considerable reduction in salmon smolt mortality (Rieman and Beamesderfer 1990; Rieman et al. 1991). Removal of northern pikeminnow is dependent on angler participation and a sustained exploitation rate.

In the Muskegon River, the removal of piscivorous hatchery trout can be accomplished by simply curtailing stocking practices or creating effective stocking windows, thereby substantially reducing parr mortality. Unlike in larger Pacific Northwest rivers, where hydropower dams may be major determinants of salmon parr mortality (but see Welch et al. 2008), predation appears to be a significant source of mortality for Chinook salmon parr in the upper MRES. When the abundance of brown trout was significantly reduced in 2007, the survival of Chinook salmon parr increased substantially and potential emigration nearly tripled compared with that in 2005, when predation mortality peaked. The stocking of Chinook salmon parr into tributaries can also be timed to ensure that proper size and imprinting have been achieved and that alternative prey are available. Johnson et al. (2007) found that the aforementioned factors contributed strongly to higher survival rates for stocked Chinook salmon parr in Saginaw Bay (Lake Huron).

While fishery managers may direct stocking efforts to maximize hatchery efficiency and the survival of Chinook salmon parr, they must still supplement other valuable sport fish stocks. Although anglers do not specifically target walleyes in the upper or lower MRES owing to that species' short residence, angler effort was high for walleyes in Muskegon Lake and nearshore Lake Michigan (Hanchin et al. 2007). On the other hand, creel records indicate that fishing effort for brown trout was low relative to that for rainbow trout and adult Chinook salmon in all MRES habitats. Further, our empirical observations suggest that brown trout were the most significant source of variability in the survival of naturally produced Chinook salmon parr. Therefore, if the goal of fisheries managers is to improve the survival of Chinook salmon parr in the MRES, brown trout stocking should be modified. Stocking fewer brown trout, stocking them later in the spring (e.g., 2007) in the upper MRES, or stocking them entirely in another location (i.e., Muskegon Lake outlet) may help reduce the predation mortality on Chinook salmon parr and improve emigration rates into Lake Michigan. However, reducing the number of brown trout stocked into the Muskegon River could result in increased walleye predation rates on Chinook salmon parr. Although optimal foraging theory suggests that walleyes would preferentially consume the larger rainbow trout in this scenario, a more detailed analysis is required to determine the effects of competing management goals in the MRES.

The natural recruitment of Pacific salmonids in the Great Lakes has become an extremely important source of adult salmon in the past few decades. Hatchery-produced parr, combined with the increasing numbers of wild-produced parr, have led to very high adult salmon abundances that cannot be supported by the forage base (e.g., Warner et al. 2008; Murry et al. 2010). Effective management of the Lake Michigan Chinook salmon fishery depends on reliable estimates of adult salmon harvest, adult spawner returns, and Chinook salmon parr production in important tributaries. Because fishery managers now have less control over riverine Chinook salmon production, annual assessments of wild Chinook salmon survival in riverine habitats may contribute to more effective fishery management in Lake Michigan tributaries. Our study provides a template for estimating the number of naturally produced Chinook salmon parr, although additional analyses may provide further insight into long-term Chinook salmon management. Detailed analysis of piscivore feeding behavior (i.e., functional responses) in important tributaries may further elucidate predator diet trends such as those we have described. Such work could inform modeling studies attempting to investigate the complex spatial interactions involved in the migration of Chinook salmon smolts (Petersen and DeAngelis 2000), and it would allow for the evaluation of the combined effects of environmental variability and predation on the survival of Chinook salmon parr. Integrating piscivore feeding behavior, Chinook salmon habitat selection and migratory behavior (e.g., Jager et al. 1997; Railsback and Harvey 2002), and fluctuating abiotic variables in such a modeling approach may improve mechanistic understanding of the recruitment process of Chinook salmon in the Great Lakes.

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