Interactions between Young-of-the-Year Exotic Rainbow Smelt and Native Yellow Perch in a Northern Temperate Lake

THOMAS R. HRABIK, MICHAEL P. CAREY, AND MICHAEL S. WEBSTER

Center for Limnology, University of Wisconsin–Madison, 680 North Park Street, Madison, Wisconsin 53706, USA

Abstract.—Yellow perch Perca flavescens recruitment in Crystal Lake, Vilas County, Wisconsin, has declined since the exotic rainbow smelt Osmerus mordax increased in abundance. The yellow perch population is in decline because of low juvenile survival. However, diet analyses indicate that predation by adult smelt does not appear to be the cause. We investigated interactions between age-0 yellow perch and age-0 rainbow smelt by comparing changes in abundance and distributions, maximum mouth gaps, and the amount and type of prey eaten. During 1995 and 1996, age-0 smelt and perch hatched at similar times, had similar spatial distributions, and preferred similar prey. Diet overlap exceeded 45% on all sampling dates during the spring and summer of 1995 and 1996 and exceeded 60% on all but the first and last sampling dates in 1996. Two species of Diaptomus were the preferred prey of both smelt and perch, although smelt ate more of the larger size-classes than did perch throughout 1996. Consumption by smelt may have led to a decline in Diaptomus during the early summer of 1996. Estimates of temperature, hatch date, and growth derived from a long-term data set were used as input for bioenergetic simulations that estimated the proportion of maximum attainable consumption realized by the average age-0 perch in each year, when they occurred, between 1981 and 1996. During 1995 and 1996, years where age-0 smelt and perch were documented together, the proportion of maximum attainable consumption was significantly below that of any successful year-class observed during the long-term record. Age-0 perch did not survive in measurable numbers through the entire summer in either 1995 or 1996. Exploitation competition between age-0 perch and smelt may reduce the likelihood of strong year-classes of yellow perch when year-classes of rainbow smelt occur.

Introductions of rainbow smelt Osmerus mordax have occurred widely throughout the upper Laurentian Great Lakes, upper Mississippi River, and Hudson Bay watersheds (Crossman 1991; Franzin et al. 1994). Each year we find new inland lakes containing rainbow smelt, and it is clear that expansion will continue into the near future (Franzin et al. 1994; Hrabik and Magnuson 1999). Rainbow smelt often negatively influence native species; interactions between adult rainbow smelt and native species have been the focus of many studies (e.g., Crowder 1980; Brandt and Madon 1986; Evans and Waring, 1987; Evans et al. 1988). Adult rainbow smelt can negatively affect native fishes through predation (e.g., Loftus and Hulsemann 1986; Evans and Loftus 1987) and competition (e.g., Hrabik et al. 1998). Adult rainbow smelt are usually distributed in cool, metalimnetic, and hypolimnetic areas (Nellbrin 1989), and interaction strength may be related to the extent of spatial overlap between them and native fishes (Hrabik et al. 1998). Age-0 rainbow smelt may interact with different fishes than do the adults because the young live in warm epilimnetic waters and use different resources. However, there are few studies addressing interactions between age-0 rainbow smelt and native fishes, despite the recent range expansions of rainbow smelt.

In temperate climates, many freshwater fishes spawn concurrently and early life stages exist in the same warm epilimnetic areas (Becker 1983). Larval fishes often are extremely abundant, and have high relative consumption and metabolic rates (Post 1990). This is particularly true after feeding commences and growth occurs at a high rate. Thus, the presence of adequate food resources is critical at this time; a reduction in available food may result in poor survival of age-0 fishes and potentially recruitment failure (May 1974; Miller et al. 1988). Age-0 fishes that hatch at similar times and use similar resources may influence prey abundance and experience the effects of competitive interactions (DeVries et al. 1991; Garvey and Stein...
Furthermore, competitive interactions may occur between species that show only moderate overlap in resource use (Olson et al. 1995). Densities of age-0 fish may reach high levels when cohorts begin feeding and growing rapidly. Thus, the potential for competitive interactions between age-0 rainbow smelt and native fishes may be high during the few weeks following hatching and first feeding.

Age-0 fishes are often size-selective predators (Siefert 1972; Schael et al. 1991; Bremigan and Stein 1994; DeVries et al. 1998), and ontogeny may influence competitive interactions among young fish (Houde 1989; Olson et al. 1995). As young develop, their mouth gape increases rapidly, thereby influencing prey selectivity (Werner 1986; and resource availability (Rothschild 1986; DeVries et al. 1998). The quality of food resources influences growth and survival of larval fishes (Sissenwine 1984; Rothschild 1986; Houde 1989), and understanding interactions between early life stages of exotic and native fish may be important in predicting the impacts of expanding exotic species.

Our objectives were to assess the potential influence of age-0 exotic rainbow smelt on age-0 yellow perch Perca flavescens by measuring spatial and temporal overlap in hatch date, spatial distribution, and food resource use in Crystal Lake, Vilas County, Wisconsin. Sanderson et al. (1999) showed that intraspecific interactions caused a consistent cyclic population dynamic in yellow perch before 1993. In this population, year-classes occurred in 1981–82, 1986–87, and 1991–92; cannibalism by juvenile perch and the lack of mature adults may have led to an absence of age-0 perch in some years (Sanderson et al. 1999). Because of a consistent 4–5-year cycle in year-classes of yellow perch, we expected year-classes to occur between 1995 and 1997 and conducted field surveys during these years. We focused on the early life stages of both species because of the lack of spatial overlap between adult rainbow smelt and young yellow perch (Hrabik et al. 1998). Also, the absence of age-0 fish from the diets of adult smelt collected shortly after smelt and perch hatched during 1995 and 1996 (Hrabik unpublished data) indicated that predation by adult smelt was not a significant factor in the decline of perch. We documented changes in mouth gape and prey selectivity of perch and smelt through their first summer of life during 1995 and 1996, and we used long-term data to estimate age-0 abundance. In addition, consumption rates for age-0 perch and smelt were estimated using the Wisconsin bioenergetics model (Hanson et al. 1997) to determine whether significant impacts on feeding success of age-0 perch were attributable to smelt year-classes.

**Methods**

**Study site.**—Crystal Lake is an oligotrophic lake that has been a primary study lake of the North Temperate Lakes-Long Term Ecological Research (NTL-LTER) project (see Magnuson et al. 1994 and http://limnology.wisc.edu) that has supported measurement of physico-chemical and biological characteristics, including fishes, on a suite of north-temperate lakes since 1981. The lake has an area of 46 ha and a maximum depth of 20 m; approximately 15% of its volume is less than 2 m in depth (NTL-LTER database). The lake is circular and has a shoreline development factor of approximately 1.0; the littoral zone is homogeneous and predominated by sand. Macrophytes and woody debris are scarce. This seepage lake receives little groundwater flow, and is exceptionally clear (average Secchi depth of approximately 9 m). Historically, a population of slow-growing yellow perch has dominated the fish community. In 1985 rainbow smelt were detected during yearly NTL-LTER fish surveys; they became the most numerous fish in the lake in 1993, and yellow perch have since declined (Figure 1).

**Seasonal fish sampling.**—Pelagic areas were sampled for age-0 fishes during the day and night from late May through mid-July during 1995 and 1996; littoral areas were sampled concurrent with pelagic sampling in 1996. We sampled biweekly in 1995 and weekly in 1996. The density of age-0 fishes in the pelagic zone was estimated with replicate hauls (4–6/d) with a 1-mm-mesh purse seine (approximately 100 × 6 m). In 1996, the littoral zone was also sampled with three consecutive 33-m-long hauls with two types of beach seines on each sample date. At two sites, a beach seine 4 m long with 1-mm mesh was used; at the third site a beach seine 12.2 m long with 4-mm mesh was used. Two types of seines were used to ensure that we caught all size ranges of age-0 fishes in the littoral zone. All age-0 kept for stomach analysis were anesthetized in iced club soda to prevent regurgitation of stomach contents and then preserved in 95% ethanol.

In August of each year from 1981 to 1996, the NTL-LTER fish survey sampled a minimum of 12 sites, 33 m long, within the littoral zone at night using the 12.2-m-long, 4-mm-mesh beach seine. In this study, we consider "successful" year-classes of yellow perch or rainbow smelt to be those
that occurred in years in which the total number caught exceeded five individuals in the beach seine samples collected by the NTL-LTER project in August.

Zooplankton sampling.—Zooplankton were sampled with a 2-m long (45 L) Schindler–Patalas plankton trap with a 53-μm mesh in the pelagic (single vertical hauls from 2 m to the surface and from 2 to 4 m) and littoral (trap moved horizontally 2 m forward near the beach seine sites) zones. Samples were preserved in Lugol’s solution (Wetzel and Likens 1979) and processed later using a dissecting microscope. Zooplankton were identified to species using the key of Balcer et al. (1984). Using an ocular micrometer, we measured the length and maximum width of 10 individuals of each species caught at each depth. Zooplankton were measured using the methods of Downing and Rigler (1984) and Culver et al. (1985). Also, epilimnetic standing stock of the prey items preferred by yellow perch and rainbow smelt was calculated by multiplying the volumetric biomass estimate (μg/L) by the number of liters in each strata in which the fish were collected (littoral zone, 0–2
m, and 2–4 m). The strata estimates were subsequently summed to achieve a standing stock estimate. Plankton data collected by the NTL-LTER project were used to show the average abundance of positively selected prey found in Crystal Lake in June, July, and August of each year from 1981 to 1997.

Gape measurements.—A predictive relationship between gape and total length for each species was developed and used to estimate gape for each individual age-0 rainbow smelt and yellow perch caught during our study. Using a digital gape micrometer (Arts and Evans 1987), mouth gape was measured on a subsample of each species each year. To do this, a precisely machined cone of a known angle was inserted into the mouth of the fish until the mandible and maxilla were fully extended, and the distance from the end of the cone to the corner formed by the fish’s maxilla and mandible was measured using a micrometer. The measured distance on the cone corresponded to a diameter, which provided an estimate of gape for each fish measured. A relationship between gape and total length facilitated estimating gapes for all individual fish.

Diet analyses.—We analyzed stomach contents from 915 age-0 rainbow smelt and 275 age-0 yellow perch caught in Crystal Lake between 24 May and 15 July in 1995 and between 31 May and 1 August, 1996. Total lengths of the smelt ranged 8.9–37.5 mm in 1995 (N = 157) and 8.7–42.5 mm in 1996 (N = 758); the perch ranged 5.9–14.7 mm in 1995 (N = 65) and 5.6–22.7 mm in 1996 (N = 210). Stomach contents were identified with a dissecting microscope and enumerated. Zooplankton prey were identified to species (key in Balcer et al. 1984), and for each stomach, lengths of the first 10 individuals of each prey taxon, when present, were measured. By combining stomach content information with the zooplankton abundance information, we estimated the prey selectivity with Chesson’s electivity index (Chesson 1978) for several size categories of each prey taxon consumed by perch and smelt. Electivity was computed for each individual, and the mean and 95% confidence interval for the electivity index was then computed for each size-class of smelt and perch. Diet overlap in 1995 and 1996 was estimated with stomach content information for both species and Schoener’s (1970) proportional overlap.

Bioenergetics modeling.—We estimated hatching dates of rainbow smelt and yellow perch from 1981 to 1994 by assuming spawning temperature and development periods for each species from values reported in the literature and based on the long-term temperature record compiled by the NTL-LTER program. We estimated daily water temperature in Crystal Lake each year by linear interpolation between water temperature measurement dates in each year. Rainbow smelt commence spawning at approximately 4.4°C, and their eggs may take approximately 25 d to hatch (Becker 1983; Scott and Crossman 1973). Yellow perch commence spawning at about 9.0°C and hatching occurs after 10 d (Becker 1983). We assumed spawning commenced on the date that the respective spawning temperatures were exceeded and that hatching occurred after the reported development increment. The assumed hatch dates of perch and smelt were also compared to our observed hatch dates in 1995 and 1996. In 1995, smelt hatched before our sampling was begun, but in 1996, when smelt hatched during our sampling, we found that length increased linearly with the number of days posthatching throughout the summer (R^2 = 0.864, P < 0.000). We estimated this relationship using linear regression: length = (day number)(0.47 + 5.79) and then used this relationship to solve for the date of hatching for smelt in 1995, based on their length on our first sample date.

Consumption by the average age-0 yellow perch in year-classes between 1981 and 1996 was estimated with the bioenergetics model developed by Kitchell et al. (1977), the software developed by Hanson et al. (1997), and parameter estimates from Post (1990) for juvenile yellow perch. Input data included the estimated hatching date in each year, average weight in late summer, and epilimnetic temperature on each sample day. Yearly (1981–1994) consumption rates of perch in year-classes were simulated beginning with the average weight at first feeding and ending with the mean weight of individuals caught in the beach seine sampling late in the summer. We assumed weight at hatching for perch was consistent across years and used measurements from the first sampling date in 1996 as representative of the weight at first feeding for the population (5.6 mm; 0.0024 g). In 1995 and 1996, we estimated consumption throughout the sampling season using the same methods used to estimate consumption during the long-term record. Consumption potential is directly related to body size and metabolic rate; as such, the proportion of maximum attainable consumption estimated from bioenergetics simulations (P) is based on temperature dependent functions (Δt) for respiration, egestion, excretion, and
caught in June, July, and August of each year. We then performed a stepwise multiple regression using the mean P-value of age-0 perch in each year as a response variable and using the biomass of each potential prey taxon, the abundance of the predatory zooplankton Chaoborus and Leptodora, and the number of degree days as independent variables. The maximum alpha levels were 0.05 for inclusion into the stepwise model and 0.15 for exclusion after entry.

**Results**

All size classes of yellow perch in Crystal Lake, particularly juveniles older than age 1, have decreased in abundance since 1992. The magnitude of yellow perch year-classes have declined with the increase in rainbow smelt abundance in Crystal Lake. Smelt year-classes occurred in every year since 1990, whereas in 1995 and 1996, when year-classes of smelt occurred, perch year-classes failed before summer’s end (Figure 1).

**Timing of Hatch**

Under the environmental conditions in Crystal Lake, perch generally hatch in the presence of rainbow smelt, although smelt may hatch earlier than perch more often than not. The mean hatching date estimated from the long-term temperature record was May 4 (95% confidence interval [CI] = 23 April–18 May) for rainbow smelt and May 11 (21 April–31 May) for perch. Based on temperature records, the estimated first hatching date for yellow perch was 25 May in 1995 and 30 May in 1996. For rainbow smelt, the estimated first hatch date from temperature records was approximately 9 May in 1995 and 30 May in 1996. In 1995, we began sampling on 24 May and found age-0 fish of both species, indicating the swim-up fry stage had already occurred by this date. We observed perch with residual yolk sacs on 24 May suggesting that swim-up had just begun. We saw no evidence of yolk sacs on smelt captured on the same date, and smelt contained food in their stomachs, indicating that their swim-up stage began earlier than perch in that year. Using length of age-0 smelt measured on our first sampling date in 1995, which was larger than those initially captured in 1996, coupled with a linear length–day relationship found in 1996, we estimated that smelt swim-up began 11 May 1995. In 1996, a year when the water warmed relatively quickly after a cold period in the spring, swim-up for the two species began on approximately the same date, 31 May. Estimated mean hatch dates in 1996 were 2 June for perch and 30 May for smelt. Hatch dates estimated from temperature records in each year were consistent with those observed in the lake in both 1995 and 1996 and appeared accurate to within a few days.

**Seasonal Abundance and Location**

Age-0 rainbow smelt and yellow perch in 1995 and 1996 had similar patterns of abundance and habitat occupation during the spring and summer (Figure 2). In both years, smelt and perch abundance increased rapidly during early June. Both species remained at higher abundance for approximately 4 weeks, declining thereafter. In mid-June of 1996, both species migrated into the shallows on a similar date. In 1995 a similar pattern of onshore smelt migration was indicated by the presence of age-0 smelt in the NTL-LTER beach seine sampling and concurrent absence of any age-0 fishes in the purse seine catch. The abundance of age-0 smelt was much lower in 1995 than in 1996. The abundance of smelt in 1995 was similar to the abundance of age-0 perch in either year.

**Ontogenetic Changes in Gape, Diet, and Prey Preferences**

A significant relationship between gape and length (L) was found for both yellow perch and rainbow smelt. For perch, gape equaled L-0.071 (r² = 0.98, N = 38). For smelt, two linear regression lines provided a better fit than a single line or a nonlinear model; we estimated values that minimized the total sums of squares for both regressions. For rainbow smelt shorter than 17 mm, gape equaled L-0.042 (r² = 0.99, N = 28) and for those longer than 17 mm, gape equaled L-0.124–1.58 (r² = 0.95, N = 73). In 1995, smelt had a larger gape than perch on three of the four sampling dates when both were captured (Figure 3; Table 1). In 1996 we found no consistent significant difference between perch and smelt mouth gape across the sampling dates; perch had a larger gape on three dates and smelt had a larger gape on one.

Diet overlap between the two species exceeded 45% on all sampling dates in each year (Figure 4). In 1995, overlap exceeded 60% (a level considered to be ecologically significant when prey is limiting; Wallace 1981) on both dates that feeding perch were caught. In 1996, overlap also exceeded 60% on all dates except the first and the last date when values of 50% and 46% were observed. In each year, maximum diet overlap was observed in
Figure 2.—Abundance (±SE) of age-0 rainbow smelt and yellow perch (A, B) in the pelagic area (solid line) of Crystal Lake during summer of 1995 and (C, D) in the pelagic and littoral (dashed line) areas in 1996. Note the differences in scale for the y-axis, which shows the seasonal pattern of abundance across years.

Table 1.—Results of paired t-tests (α = 0.10) of mouth gape of age-0 yellow perch and rainbow smelt caught on each sample date in Crystal Lake; P-levels are Bonferroni corrected for number of comparisons. Numbers in parentheses are the number of smelt and perch, respectively.

<table>
<thead>
<tr>
<th>Year and date collected</th>
<th>Species with largest gap size</th>
<th>t</th>
<th>P</th>
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<tr>
<td>1995</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>May 25</td>
<td>Smelt</td>
<td>34 (21, 13)</td>
<td>&lt;0.00</td>
</tr>
<tr>
<td>Jun 02</td>
<td>Smelt</td>
<td>12 (16, 3)</td>
<td>0.01</td>
</tr>
<tr>
<td>Jun 06</td>
<td>Smelt</td>
<td>100 (55, 47)</td>
<td>0.00</td>
</tr>
<tr>
<td>Jun 19</td>
<td>Smelt</td>
<td>76 (79, 6)</td>
<td>0.06</td>
</tr>
<tr>
<td>Total</td>
<td>Smelt</td>
<td>222</td>
<td></td>
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<tr>
<td>1996</td>
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<tr>
<td>May 25</td>
<td>NS</td>
<td>83 (47, 41)</td>
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</tr>
<tr>
<td>Jun 06</td>
<td>NS</td>
<td>147 (86, 41)</td>
<td>0.38</td>
</tr>
<tr>
<td>Jun 12</td>
<td>NS</td>
<td>155 (155, 30)</td>
<td>0.00</td>
</tr>
<tr>
<td>Jun 16</td>
<td>Perch</td>
<td>176 (139, 26)</td>
<td>0.02</td>
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<tr>
<td>Jun 23</td>
<td>Perch</td>
<td>164 (136, 30)</td>
<td>0.01</td>
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<tr>
<td>Jul 01</td>
<td>Smelt</td>
<td>149 (139, 10)</td>
<td>0.01</td>
</tr>
<tr>
<td>Jul 06</td>
<td>NS</td>
<td>82 (79, 2)</td>
<td>1.0</td>
</tr>
<tr>
<td>Jul 17</td>
<td>NS</td>
<td>29 (27, 2)</td>
<td>1.0</td>
</tr>
<tr>
<td>Total</td>
<td>NS</td>
<td>965</td>
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</table>

*NS = not significantly different.
June; a level of 77% occurred on 6 June 1995 and 89% on 23 June 1996.

In 1996, *Diaptomus minutus* and *Diaptomus or- gerus* (hereafter referred to as *Diaptomus*) were the most consistent prey items, by mass, found in the perch and smelt diets (Figure 5). In 1996 both species exhibited positive selection for *Diaptomus* that persisted as gape size increased (Figure 6); positive selection for other prey was not significant. However, smelt began eating a higher proportion of prey items other than *Diaptomus* after gape exceeded 1.0 mm (Figure 6). Early in their development, smelt tended to contain larger *Diaptomus* than did perch, but the proportion of larger size-classes of *Diaptomus* in the perch diet increased with gape (Figure 7). As the gape diameter of both species increased, the size of *Diaptomus* in their diets became increasingly similar. However, smelt continued to eat a higher proportion of the larger *Diaptomus* relative to perch. The largest size-class of perch (captured in July) did not exhibit positive selection for any one prey taxon (Figure 6).

### Prey Consumption and Mortality

The average yellow perch *P*-value (proportion of maximum consumption), which may be considered a measure of feeding success, in the year-classes of 1995 and 1996 was significantly lower than *P*-values for perch year-classes that occurred between 1981 and 1994. For successful year-classes of yellow perch (i.e., those that made it to the August seine sampling), the average *P*-value was 0.476 (95% CI = 0.15, range = 0.326–0.626; Figure 8). However, the average *P*-value observed in 1996 was 0.29, which was below the lowest value observed when a successful year-class was formed. Perch were not found in our beach seine samples in 1996 after mid-July. In 1995 the *P*-value for perch was 0.19 or less than half of the mean estimated for successful year-classes; age-0 perch were not found after mid-June of that year. The low consumption rates by perch in 1995 and 1996 suggest that the average daily ration was so low that survival of perch was seriously compromised, as was also reflected by the elimination of the year-classes by midsummer.

Consumption by the 1996 year-class of smelt in Crystal Lake increased dramatically during late June and July (Figure 9). *Diaptomus* was a preferred prey of both perch and smelt throughout most of the summer in 1996. In Crystal Lake during 1996, however, *Diaptomus* standing stock declined immediately after smelt consumption increased (Pearson correlation *r* = −0.67, *P* = 0.07). Further, the mean abundance of *Diaptomus* observed between the end of May and the end of August in 1995 and 1996 appeared to be lower than in the years preceding the period of smelt year-classes (1990–1997; Figure 10a).
Environmental Variables

Multiple regression analysis (mean P-value of age-0 yellow perch in each year, when present, as the response variable and mass of Diaptomus, cyclooids, Daphnia, Chydorus, Bosmina, copepod nauplii, the abundance of Chaoborus and Leptodora, and the number of degree days as independent variables) yielded a significant positive effect of Diaptomus density on P-value of age-0 perch (Table 2; also see Figure 9). No consistent change in the abundance of predatory zooplankton or in the number of degree-days coincided with the decline in age-0 perch success in Crystal Lake (Figure 10b-c, Figure 11).

Discussion

The importance of competition in shaping fish community structure has been the topic of numerous studies (e.g., Larkin 1956; Crowder 1980; Crowder, 1986; Olson et al. 1995; Hrabik et al. 1998); however, confirming or rejecting the role of competition in natural communities, particularly between age-0 fishes, is difficult. A decline in abundance of yellow perch in Crystal Lake, particularly of the juvenile stage, shows that recruitment failure occurred after the rainbow smelt invasion. This, combined with the absence of age-0 fishes in the diets of adult rainbow smelt caught in the lake during our study, suggests that indirect interactions or environmental changes caused the
observed decline. In 1995 and 1996, although substantial numbers of age-0 perch hatched, their consumption rates were lower than those for perch caught in August between 1981 and 1994, and most did not survive their first year of life. Common resource use by age-0 smelt and perch in both years indicates that exploitation competition could be disproportionately influencing growth and that presence of smelt year-classes may be decreasing the survival rate of perch year-classes.

**Timing of Hatch**

Timing of hatch can be important in determining interaction intensity. In situations where an exotic commences feeding before or simultaneous with first feeding by a native fish, the native may experience negative consequences (e.g. DeVries et al. 1991; Garvey and Stein 1998). Our estimates of hatch date from the long-term record suggest that rainbow smelt tend to hatch earlier than yellow perch, and in 1995 we observed earlier feeding by smelt. However, during 1996 we detected smelt and perch on the same date, suggesting a high degree of overlap in hatch date. In most years, it is very likely that yellow perch hatch and begin feeding in the presence of age-0 smelt in Crystal...
Lake; this may lead to increased interaction intensity between these species.

**Location and Ontogenetic Characteristics**

Similarity in ontogenetic development between rainbow smelt and yellow perch may intensify competitive interactions and lead to significant interactions when both species are present in substantial numbers. Competition may occur between age-0 fishes with moderately different life histories and very different adult stages (e.g., Olson et al. 1995; Garvey and Stein 1998); species with similar early life histories would be expected to interact more frequently than those that do not. Both yellow perch and rainbow smelt exhibit similar early life history traits because they exist in the same areas during their first summer of life, and consume similar prey. Similarity in these characteristics may lead to negative effects of smelt on perch when prey resources are limiting and spatial overlap is high.

**Yellow Perch Feeding Success and Alternative Hypotheses**

Prey density is linked to feeding success, growth, and ultimately survival in age-0 fish (May 1974). Our results indicate that yellow perch food resource availability limited survival in 1995 and 1996. Aside from the presence of age-0 rainbow smelt, other factors could have caused the observed decreases in *Diaptomus* abundance observed during the period of study. For example, a predator other than age-0 rainbow smelt may have caused the decline in *Diaptomus* observed during the summer of 1996. However, in 1996 the epilimnion of Crystal Lake contained few *Chaoborus* or *Leptodora* or fish species other than smelt and perch (Hrabik and Carey unpublished data). In addition, adult rainbow smelt and yellow perch in Crystal Lake rarely eat *Diaptomus*; the proportion in the diet of adults of both species averaged less than 1% of the prey biomass in 1992, 1994, and 1996 (Hrabik, unpublished data). Although we cannot eliminate all possible explanations for the decrease in *Diaptomus* abundance (i.e., disease, reproductive failure, etc.), our estimates of consumption indicate age-0 rainbow smelt may have been eating 50–99% of epilimnetic *Diaptomus* standing stock on each day from mid-June through mid-July in 1996 (Figure 8). The reduction in prey density we observed is similar to effects of gizzard shad *Dorosoma cepedianum* on their prey resources in some Ohio reservoirs (Dettmers and Stein 1992). After the decline in *Diaptomus*, age-0 perch and smelt switched to alternative prey to some extent, but perch continued to consume *Diaptomus.*
Figure 10.—Crystal Lake sampling results from 1981 to 1997: (A) biomass of *Diaptomus*, *Daphnia*, *Bosmina*, *Diaphanosoma*, and cyclopoid copepods, where the horizontal line is the long-term average total biomass for the plankton community; (B) density of large predatory zooplankton; and (C) number of degree days relative to 0°C.

Thus, smelt consumption of *Diaptomus* may have indirectly caused the perch year-class to fail because of the decrease in their prey resources. The significant positive correlation between *Diaptomus* density and the F-value of age-0 perch, as observed from the long-term record, suggests that this prey item has been important for growth throughout that period. The recent decline in *Diaptomus* (Figure 11) is consistent with the hypothesis that age-0 smelt may decrease the abundance of this prey resource, a prey resource preferred by age-0 perch. In addition, no consistent changes in temperature or in the number of predatory plankton coincided with the decrease in age-0 perch performance.

This study offers measurements of populations under natural conditions, so we could not eliminate all alternative explanations of the patterns in the data. However, based on several lines of evidence, we concluded that exploitation competition is a significant factor in the decline of yellow perch year-classes. The evidence shows that age-0 perch

Table 2.—Results of a stepwise multiple regression using the biomass of *Diaptomus*, *Daphnia*, cyclopoids, *Bosmina*, *Chaetognatha*, copepod nauplii, all zooplankton, the predatory zooplankton *Leptodora* and *Chaoborus*, and the number of degree days as independent predictors of the proportion of maximum consumption for age-0 Crystal Lake yellow perch in each year (when they occurred) from 1981 to 1996. The $R^2$ for the relationship between *Diaptomus* abundance and the proportion of maximum consumption was 0.743.

<table>
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<td>$23.19$</td>
<td>1st</td>
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<tr>
<td>$0.016$</td>
<td>NS</td>
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and smelt prefer the same prey and live and forage in the same habitat. Furthermore, the abundance of the preferred prey is probably reduced by large year-classes of smelt, and the amount eaten by the average perch was significantly less in years with smelt year-classes than in years when successful perch year-classes were formed. We found no evidence to contradict exploitation competition as a negative influence; to the contrary, all evidence was consistent with the exploitation competition hypothesis. Our study also demonstrates that complexity associated with determining ecosystem effects of an exotic species is increased when the species has a strongly segregated life history; that is, each life stage of rainbow smelt is separated spatially and uses different prey resources, and both stages may influence native fishes and their food resources.

Invasive fishes are continuing to colonize aquatic ecosystems worldwide, as particularly due to introductions by humans. In considering the effects of an exotic fish, emphasis should focus on its life stages, especially when the species has a strongly segregated life history. The potential instability in native fish populations confronted by intentional stocking of nonindigenous species should serve as a warning against such practices (Magnunson 1976). Stocking exotic species into artificial environments has often been accepted without realistic attention to the dispersal potential of
each of its life stages and the potential regionwide effects that could be exerted on native fauna. The spread of rainbow smelt is occurring and will continue to occur throughout most of the midwestern United States and Canada even though the original intentional introductions were quite limited. The associated risk to native species from the intentional stocking or colonization of rainbow smelt is high because of the wide range of resources used by adult stages, a strongly segregated life history, and the propensity of the species to disperse quickly through rivers and streams. The results of this and other studies suggest that stocking nonindigenous species is an uncertain proposition, especially in ecosystems that contain a coevolved assemblage of fishes.

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