Food web alterations that promote native species: the recovery of cisco (*Coregonus artedi*) populations through management of native piscivores

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Abstract: We evaluated the effects of fisheries management on food webs in three northern Wisconsin lakes with exotic rainbow smelt (*Osmerus mordax*). In two of the lakes, restrictions on fishing reduced mortality rates on adult walleye (*Sander vitreus*) during the study period. In these lakes, walleye populations increased concurrently with a decline in rainbow smelt populations. As rainbow smelt populations declined in both lakes, native cisco (*Coregonus artedi*) populations increased. Our analysis of walleye diets illustrated that walleye fed selectively on rainbow smelt but did not feed on cisco during the summer months. When entered into bioenergetics simulations, this information demonstrates that walleye predation alone was enough to cause the observed rainbow smelt declines in our study lakes. Our results indicate that increased walleye density allows for a parallel increase in cisco density. Based on our results, fishery regulations to restore walleye to high densities in lakes invaded by rainbow smelt may restore native planktivores that have co-evolved traits.

Résumé : Nous avons examiné les effets de la gestion des pêches sur les réseaux alimentaires dans trois lacs du nord du Wisconsin contenant des éperlans arc-en-ciel (*Osmerus mordax*) exotiques. Dans deux des lacs, la restriction de la pêche a entraîné une réduction des taux de mortalité chez les dorés (*Sander vitreus*) adultes durant la période d'étude. Dans ces lacs, les populations de dorés se sont accrues parallèlement à un déclin des populations d'éperlans arc-en-ciel. Au fur et à mesure que les populations d'éperlans arc-en-ciel ont diminué dans les deux lacs, les populations indigènes de ciscos de lac (*Coregonus artedi*) ont augmenté. Notre analyse du régime alimentaire des dorés montre que durant les mois d'été les dorés se nourrissent préférentiellement d'éperlans arc-en-ciel, mais non de ciscos de lac. Cette information, incorporée aux simulations bioénergétiques, démontre que la seule prédation par les dorés ne suffit pas à expliquer le déclin des populations d'éperlans arc-en-ciel observé dans nos lacs d'étude. Nos résultats indiquent que la densité accrue de dorés permet un accroissement en parallèle de la densité des ciscos de lac. D'après ces résultats, les règlements de pêche qui visent la restauration des fortes densités de dorés dans les lacs envahis par l'éperlan arc-en-ciel peuvent rétablir les planctonophages indigènes qui possèdent des caractéristiques coévoluées.

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Introduction

Food web manipulation offers a mechanism to manage aquatic ecosystems that have been invaded by exotic species. Within this context, predation by piscivores represents an agent that may prove useful for controlling unwanted prey fish species. However, commercial or sport fishing interests often exploit predator populations, decreasing their abundance and effects on prey species. In fact, many of the world's fisheries are overexploited (Myers and Worm 2003), and decreased predator populations have caused substantial changes in food web characteristics (Cox et al. 2002).

In some cases, decreased predator densities caused by fishing may allow less desirable fish species to dominate. For example, exotic forage fish, such as rainbow smelt (*Osmerus mordax*) and alewife (*Alosa pseudoharengus*), dominated the Lake Michigan food web after piscivore populations declined (Kitchell and Crowder 1986). This may have caused the decline of one or more commercially important native species (Crowder 1980).

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Exotic rainbow smelt are rapidly colonizing small lakes in the upper midwest and western reservoirs (Jones et al. 1994; Johnson and Goettl 1999). In many ecosystems in which rainbow smelt became established, similar patterns of negative effects were observed (Franzin et al. 1994; Hrabik et al. 1998; Hrabik and Magnuson 1999). Native coregonid species, such as cisco (*Coregonus artedi*) and lake whitefish (*Coregonus clupeaformis*), show particularly rapid declines following rainbow smelt establishment in many small northern temperate lakes (Loftus and Hulsman 1986; Evans and Loftus 1987; Hrabik et al. 1998). Therefore the future status of native coregonine populations in the upper midwest will likely be related to the range expansion and success of rainbow smelt.

Restoring or recovering native piscivore populations may provide a mechanism to control harmful exotic fish species and promote the recovery of native planktivores. In the Laurentian Great Lakes, decreases in predator abundance in response to commercial exploitation and sea lamprey predation led to increases in exotic alewife and rainbow smelt populations (Smith 1968; Wilberg et al. 2002). However, an intensive predator stocking program increased consumption of exotic prey fishes, which eventually led to decreased rainbow smelt and alewife abundance in Lake Michigan (Kitchell and Crowder 1986). Furthermore, recent changes in the fish community of Lake Superior suggest that increased predation by lake trout is associated with rainbow smelt population declines and may have facilitated reciprocal increases in native coregonine species (Hansen 1994).

Five lakes in the Northern Highland Lakes District of Wisconsin offer the opportunity to examine the influence of predator density on exotic rainbow smelt populations. Two lakes support walleye (*Sander vitreus*) populations that have increased as a result of more stringent fishing regulations and extensive stocking. A third lake contains rainbow smelt but few predators, and represents a control system that allows us to assess a rainbow smelt population in a predator depauperate environment. Data from this control lake also demonstrate the negative effect of rainbow smelt on native planktivores. In the lakes with walleye, the smelt populations declined concurrently with reciprocal increases in native cisco populations. However, the two rainbow smelt populations declined at different rates. The fourth and fifth lakes contain native piscivores and native cisco populations and allow us to determine whether cisco populations recently increased owing to changes in local climate. Our objective was to determine the cause of the observed changes in the rainbow smelt and cisco populations that occurred concomitantly with increased predator abundance in the lakes in which fishing regulations changed. The different rates of decline in rainbow smelt population sizes and subsequent increases in cisco population sizes offer insight into the influence of predators on rainbow smelt and cisco interactions. Long-term changes in prey biomass due to changes in predation rates measure the influence of a predator on a prey community (Beisner et al. 2003). We therefore hypothesized that selective predation by walleye reduced rainbow smelt abundance and led to compensatory increases in cisco populations. To evaluate this hypothesis, we used data from field studies to describe fish distribution and abundance in the five lakes from 1981 to 2002. We analyzed walleye diets and modeled fish consumption to estimate the interaction strength among walleye, cisco, and rainbow smelt in two of the lakes. We also compiled information on fishery management within the study lakes because harvest has a strong influence on predator mortality (Cox and Walters 2002; Post et al. 2002). We sought to determine whether walleye fishery restrictions led to increased walleye predation on rainbow smelt and allowed for cisco recovery. Therefore we examined the following: (*i*) correlations among population characteristics of walleye, cisco, and rainbow smelt; (*ii*) walleye diet composition throughout the open-water season to identify whether walleye preyed selectively on rainbow smelt; and (*iii*) walleye consumption rates on rainbow smelt estimated using bioenergetics models.

Materials and methods

Study sites

We studied five lakes in the Northern Highland Lakes District in Vilas County, Wisconsin (Fig. 1) from 1981 to 2002. Fence and Crawling Stone lakes are under the jurisdiction of the Lac Du Flambeau Band of the Lake Superior Chippewa Natural Resource Department, while Crystal, Trout, and Big Muskellunge lakes are under the jurisdiction of the Wisconsin Department of Natural Resources (WDNR; see Table 1 for the physical characteristics of study lakes). Trout, Big Muskellunge, Fence, and Crawling Stone lakes support popular sport fisheries and sustain relatively high densities of walleye that are augmented by annual stocking. Crystal Lake contains few piscivorous fish and is not regularly stocked.

Prior to 1989, the Lac Du Flambeau tribal council maintained liberal fishing regulations on Fence and Crawling Stone lakes. Both lakes had no minimum length limit, and non-tribal anglers were allowed to harvest five walleye per day. In 1990, the WDNR implemented a statewide 15-in (1 inch = 2.5 cm) minimum length limit on walleye. Regulations on Fence and Crawling Stone lakes became more conservative in 1997 when tribal fishery managers imposed an 18-in minimum length limit and a bag limit of three walleye per day. In addition to sport fishing, Fence and Crawling Stone lakes experienced unregulated spear fishing on walleye prior to 1997. From 1986 to 1997, spear fishers removed thousands of adult walleye each year (L. Wawronowicz, P.O. Box 67, Lac Du Flambeau, WI 54538, USA, personal communication). In 1997, the Lac Du Flambeau tribal council banned spear fishing (with the exception of tribal youth spearing in 2002) to allow the walleye populations in each lake to recover and to support egg collections for local hatchery operations.

Population density and dynamics

Fish collection

We collected walleye, cisco, and rainbow smelt using a variety of methods in Fence and Crawling Stone lakes. In the spring of 2002, we set 1.5 m square mouth, 5 mm mesh fyke nets to capture walleye during the spawning period at known spawning shoals and reefs. We removed walleye from the nets daily for 15 consecutive days on each lake. Nets were not moved during the spawning period. After spawning activity ended, we used a boom-style AC electrofishing boat to collect walleye at night from near-shore areas of both

Fig. 1. Map of northern Wisconsin, USA, showing the locations of (*a*) Crawling Stone Lake (89°53′4″ W, 45°56′25″ N); (*b*) Fence Lake (89°50′22″ W, 45°56′56″ N); (*c*) Crystal Lake (89°36′43″ W, 46°0′5″ N); (*d*) Big Muskellunge Lake (89°37′22″ W, 46°0′9″ N); and (*e*) Trout Lake (89°40′9″ W, 46°1′9″ N).
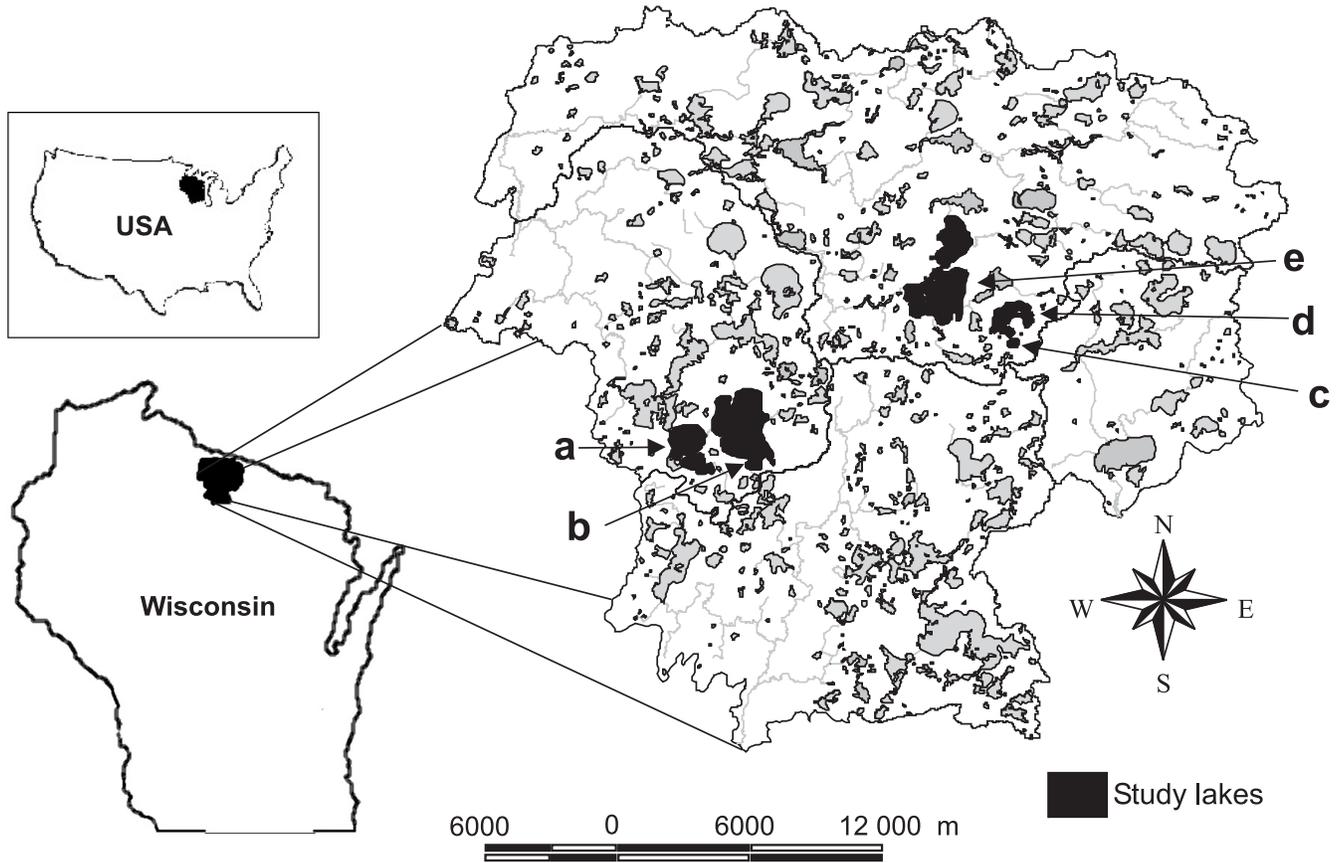

Table 1. Physical characteristics of the five study lakes likely to influence smelt colonization and viability.

Lake	Lake type	Lake area (ha)	Maximum depth (m)	Area > 6 m (%)
Fence	Drainage	1438	31	0.7
Crawling Stone	Drainage	593	24	0.6
Crystal	Seepage	46	20.5	0.6
Trout	Drainage	1544	38	0.76
Big Muskellunge	Seepage	376	21	0.56

Note: Thermocline depth was 6 m in Fence, Crawling Stone, and Crystal lakes in 2002.

lakes and to quantify the littoral zone prey fish community. We fished two 1-km transects weekly on Fence and Crawling Stone lakes from 21 May through 27 June 2002. We rotated among five sites on each lake. Following thermal stratification, we used 30 m × 3 m vertical gillnets with mesh size measuring 19, 25, 32, 38, 54, 69, 89, and 127 mm to capture pelagic fishes in Fence and Crawling Stone lakes. Nets were set monthly and biweekly throughout the summers of 2001 and 2002, respectively, to measure the abundances and sizes of pelagic forage fishes and to recover walleye diets. We set gillnets at night for less than 6 h to minimize digestion of walleye stomach contents and to maximize the number of fish caught. Using gillnet catch data, we quantified the thermal overlap among fish species (e.g., see Schoener 1970; Hrabik et al. 1998). The Long-Term

Ecological Research – North Temperate Lakes (LTER–NTL) project sampled fish in Crystal Lake annually (see Magnuson et al. 1984, 1994) using fyke nets, trammel nets, and a size spectrum of vertical gillnets ranging from 19 to 89 mm stretch mesh.

Throughout the summer of 2002, length and weight information was continually collected on all fishes, and scales were collected from a subsample of each species for age estimation. Each subsample was composed of two fish for every 5-mm increment in total length. We removed at least three scales from behind the left pectoral fin in all instances.

We collected supplemental catch data for cisco and walleye in two additional LTER–NTL lakes, Trout Lake and Big Muskellunge Lake. Both lakes support sport fisheries for large piscivores, although neither supports rainbow smelt.

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Data from these lakes allowed us to track indices of cisco biomass in the absence of rainbow smelt predation but with a potential risk of predation. We also hoped to assess whether regional processes were responsible for the observed trends in cisco abundance in Fence and Crawling Stone lakes. Data were collected online via the University of Wisconsin, Center for Limnology LTER–NTL fish database.

Mark and recapture

We tagged and released walleye to obtain mark–recapture population estimates in Fence and Crawling Stone lakes using Chapman's modification of Schnabel's method (Ricker 1975). Fish were captured via electrofishing and fyke nets along the near shore areas of Fence and Crawling Stone lakes in early spring. After we marked individual walleye with T-bar floy tags, they were released in random locations, which were generally in the pelagic area of the lake. We marked 340 walleye averaging 530-mm total length from Fence Lake, and 202 walleye averaging 513-mm total length from Crawling Stone Lake.

Hydroacoustic sampling

Hydroacoustic transects were performed following lake stratification to obtain estimates of fish size, depth distribution, and density in each study lake. The LTER–NTL program used a Simrad EY-M 70 kHz single-beam ecosounder to run yearly hydroacoustic transects on Crystal Lake (three transects) from 1981 to 1994 and on Fence and Crawling Stone lakes (six and five transects, respectively) in 1993. HADAS postprocessing software was used to analyze these transects (Rudstam et al. 1993; Sanderson et al. 1999). We used a 120-kHz BioSonics DT6000 split-beam echosounder to collect hydroacoustic data in 2001 and 2002 on Fence, Crawling Stone, and Crystal lakes. We ran five transects on Fence and Crawling Stone lakes in 2001 and 2002 and three on Crystal in 2002. We used Echoview (v.3.0) software to analyze acoustic data for two nights in 2001 and four nights in 2002 on Fence and Crawling Stone lakes and one night in 2002 on Crystal Lake. Hydroacoustic estimates of smelt population density in Crystal Lake were proportional to gillnet catch rates (population estimate = 67.6 × gillnet catch per unit effort (CPUE), $r^2 = 0.95$, $p < 0.001$). We used this relationship between gillnet catch rates and hydroacoustic estimates to approximate population sizes and biomass when no acoustic data were available (1995–2000). Hydroacoustic data for Fence and Crawling Stone lakes were not available for years prior to 1993. We assumed that population densities of pelagic species were proportional to gillnet catch, as in Crystal Lake. We used 1993 gillnet catch and 1993 population estimates for Fence and Crawling Stone lakes to estimate the proportional relationships and population sizes for 1982 in Fence Lake and 1986 in both lakes.

Simrad and BioSonics echosounders were calibrated bimonthly with standard tungsten carbide spheres of known target strength. We corrected 1993 fish density estimates for bias owing to differences in target strength distributions between single and split-beam echosounders (e.g., Rudstam et al. 1999). We used fish species composition, depth distribution, and size data from vertical gillnets to categorize individual hydroacoustic targets by species. We then estimated total lake population sizes by multiplying the density of each species within 1-m depth strata with the volume of water within each stratum as in Rudstam et al. (1993) and Sanderson et al. (1999).

Analyses of body condition and fish size

Estimation of body condition

We developed lake-specific length–weight regressions to estimate variability in rainbow smelt body condition in Fence Lake (where rainbow smelt declined) and Crystal Lake (where rainbow smelt increased) between periods of high and low rainbow smelt abundance. Rainbow smelt body condition is associated with variability in their population density and offers a useful index of feeding success (Hrabik et al. 1998). We applied a linear model to log-transformed body mass and total length data pooled across years within each lake (Hrabik et al. 1998). A single regression fit to all length and weight observations across all years for a lake was used to estimate a lake-specific length–weight relationship. We grouped the residuals for individual fish by year and used the mean residual in each year as an index of the body condition of rainbow smelt in each lake. We did so to examine whether trends in smelt body condition in Fence Lake corresponded to decreases in their abundance, or whether smelt performance in Fence Lake may have been influenced by an alternative environmental variable. In addition, we sought to identify whether smelt in Crystal Lake, where predators were rare, exhibited indications of density dependence. Body condition was not calculated for Crawling Stone Lake because no rainbow smelt were captured after 1993.

Analyses of fish size

Variability in the sizes of rainbow smelt and walleye were examined to identify any changes in size that coincided with changes in abundance and mortality rates in each population. We examined the mean length of rainbow smelt in Crystal and Fence lakes and of walleye in Fence Lake through time; data points represent periods with marked differences in the abundance and mortality of each species in each lake. We expected that smelt sizes would decrease in response to increases in predation pressure by walleye in Fence Lake, and that the size of walleye would increase with decreases in their mortality.

Diet composition

We analyzed 220 walleye stomachs collected via electroshocking, gillnets, and angling in Fence and Crawling Stone lakes. Following capture, stomach contents were flushed from live fish (Seaburg 1957) and whole stomachs were excised from deceased fish caught in gillnets. We preserved stomach contents of all walleye in 95% ethanol and later separated and dried contents to obtain biomass proportions for input into bioenergetics modeling scenarios. We used numerical proportions of the common prey items to estimate prey selection using Chesson's (1983) alpha. Alpha values were calculated for individual walleye and averaged for May, June, July, and August.

Bioenergetics modeling

Fish growth

We examined scales to determine growth rates for 85 and 81 walleye from Fence and Crawling Stone lakes, respectively. We then used the proportional method (DeVries and

Fig. 2. The estimated biomass of predator and prey species in each study lake from 1982 to 2002. (*a*) The biomass of predatory fish in Crystal Lake represented as a combined estimate of lake trout (*Salvelinus namaycush*) and walleye (*Sander vitreus*). (*b*) The biomass of rainbow smelt (*Osmerus mordax*; solid bars) and native perch (*Perca flavescens*; open bars) in Crystal Lake.(*c*) The biomass of walleye in Fence Lake. (*d*) The biomass of rainbow smelt (solid bars) and native cisco (*Coregonus artedi*; open bars) in Fence Lake. (*e*) Walleye biomass through time in Crawling Stone Lake. (*f*) The biomass of rainbow smelt (solid bars) and native cisco (open bars) in Crawling Stone Lake. Note the difference in scale for the *y* axis between predator and prey species.
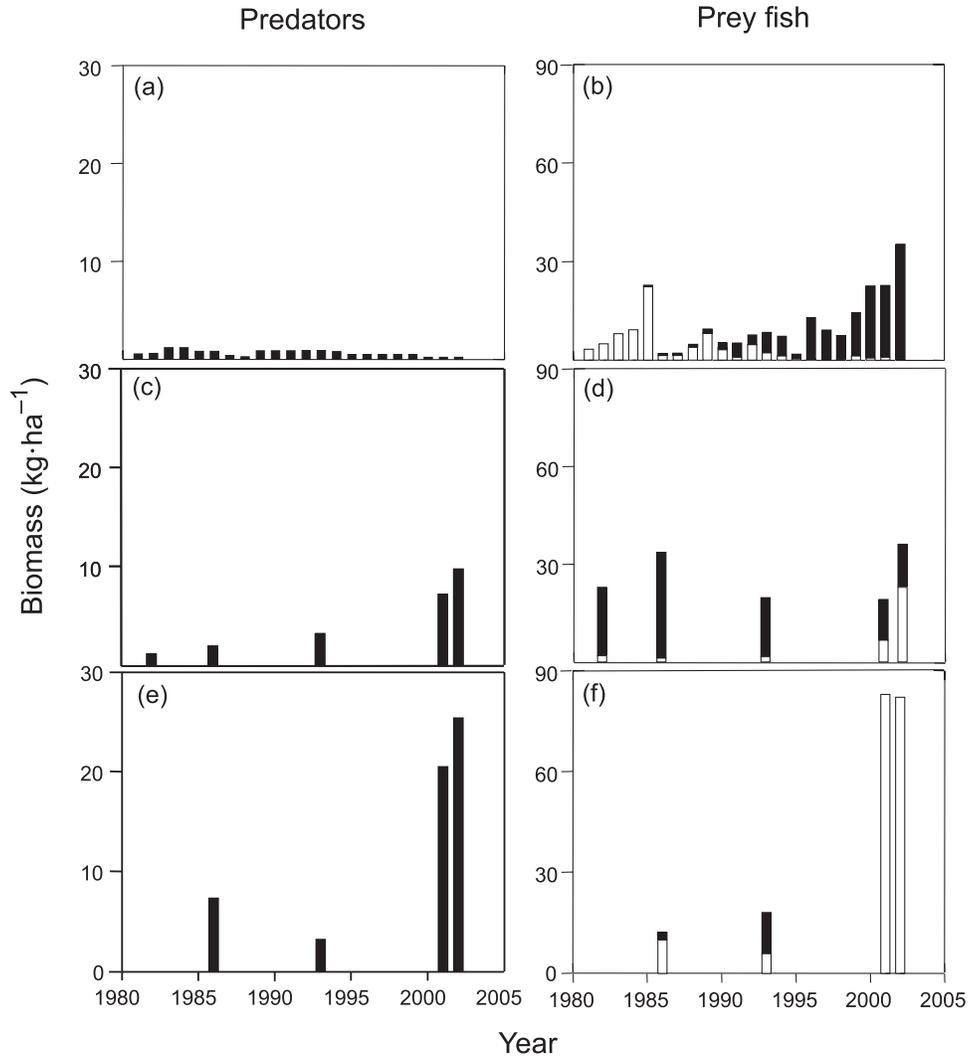
Frie 1996) to back calculate length at age for individual fish. The same method was used to estimate size at age and growth rates for rainbow smelt and cisco. Finally, we grouped individual fish into year classes according to length and averaged weights for each year class. For walleye, we also estimated the age structure of the entire population, based on the subsample of fish we aged. First, we estimated a length range for each age class. Second, we determined the proportion of sampled fish that fell into each length range. Last, we multiplied the length-at-age proportions by the acoustic population estimate to achieve a whole-lake age structure for walleye.

Temperature

We measured temperature profiles monthly during the summer of 2002 in Fence and Crawling Stone lakes. The LTER–NTL program measured temperature profiles in Crystal Lake biweekly from ice out to late November from 1981

to 2002. We estimated daily water temperature at depth in all three lakes using linear interpolation between water temperature measurement dates in each year. Temperature data were input into bioenergetics modeling scenarios.

Estimation of prey consumption

We used fish bioenergetics models to assess the potential impact of walleye predation on rainbow smelt and of rainbow smelt predation on young cisco in Fence Lake. We quantified these effects by simulating consumption by walleye and rainbow smelt with the Wisconsin bioenergetics 3.0 software (Hanson et al. 1997). In situ weight-at-age data were input as start and end points to estimate the energy budget for average individual walleye and rainbow smelt. We also input species- and depth-specific thermal data, as well as diet composition (for walleye), to estimate total annual consumption by walleye and rainbow smelt in 1982 (Fence Lake only), 1986, 1993, 2001, and 2002 in Fence and

Crawling Stone lakes. To estimate total consumption, we first found the proportion of fish in each age class using the aforementioned methods. Then, we multiplied consumption of the average individual in each age class by the acoustic population estimate for each age class to estimate total consumption in each study year. In addition, we compared rainbow smelt biomass consumed by walleye with rainbow smelt biomass available in Fence Lake to determine the proportion of the rainbow smelt population walleye consumed in each year of the study. We obtained the caloric densities of yellow perch (*Perca flavescens*), cyprinids, and rainbow smelt used in our modeling scenarios from Bryan et al. (1996), and the caloric density of walleye from Kitchell et al. (1977).

Results

Walleye population dynamics

In Fence and Crawling Stone lakes, walleye population size and mean length increased considerably from 1982 to 2002. In Fence Lake, the adult walleye (total length > 300 mm) population density increased from 3.2 kg·ha^{-1} (1.4–5 kg·ha^{-1}) in 1993 to 9.7 kg·ha^{-1} (6.2–12 kg·ha^{-1}) in 2002 (Fig. 2). Mark–recapture estimates for walleye ranged from 3 to 42 fish·ha^{-1} (3.9–54.6 kg·ha^{-1}). Mean length of walleye increased from 361 mm in 1982 to 507 mm in 2002, indicating a significant increase in size structure (Fig. 3). Stocking of fingerling walleye averaged 28 fingerlings·ha^{-1}·year^{-1} (±12 fingerlings·ha^{-1}·year^{-1}).

In Crawling Stone Lake, the biomass of walleye also increased from 1986 to 2002. Initially, walleye biomass fell from 7.2 kg·ha^{-1} in 1986 to 3.1 kg·ha^{-1} in 1993. However, walleye biomass increased to 25.4 kg·ha^{-1} (15.2–35.4 kg·ha^{-1}) by 2002 (Fig. 2). Mark–recapture population estimates averaged 6.3 walleye·ha^{-1} and ranged from 4 to 60 walleye·ha^{-1} (4.8–72 kg·ha^{-1}) owing to low recapture rates. However, these estimates are comparable to hydroacoustic estimates. Walleye mean length was 495 mm in 2002, just short of the average in Fence Lake. Stocking of walleye fingerlings in Crawling Stone Lake was higher than in Fence Lake and averaged 44 fingerlings·ha^{-1}·year^{-1} (±17 fingerlings·ha^{-1}·year^{-1}).

In Trout Lake, catch rates of adult walleye appeared to rise slightly from 1981 to 2002. However, in Big Muskellunge Lake, there was no apparent pattern in catch rates of adult walleye (Fig. 4).

Rainbow smelt population dynamics

We observed the highest density of rainbow smelt in predator-poor Crystal Lake. The biomass of rainbow smelt increased steadily since their detection in 1986, and approached 35 kg·ha^{-1} in 2002 (Fig. 2). As rainbow smelt biomass increased after 1993, their mean length distribution did not change (Fig. 5). Rainbow smelt body condition declined after 1993 and the trend was consistent with density-dependent processes associated with increases in population size (Fig. 5). Population size of yellow perch (*Perca flavescens*), once the dominant planktivore in the lake, declined and their biomass was negatively correlated to rainbow smelt biomass (Fig. 2).

In Fence and Crawling Stone lakes, rainbow smelt biomass decreased, particularly in the latter years of our study

**Fig. 3.** Estimates of mean size of walleye caught in Fence Lake from 1982 to 2002.
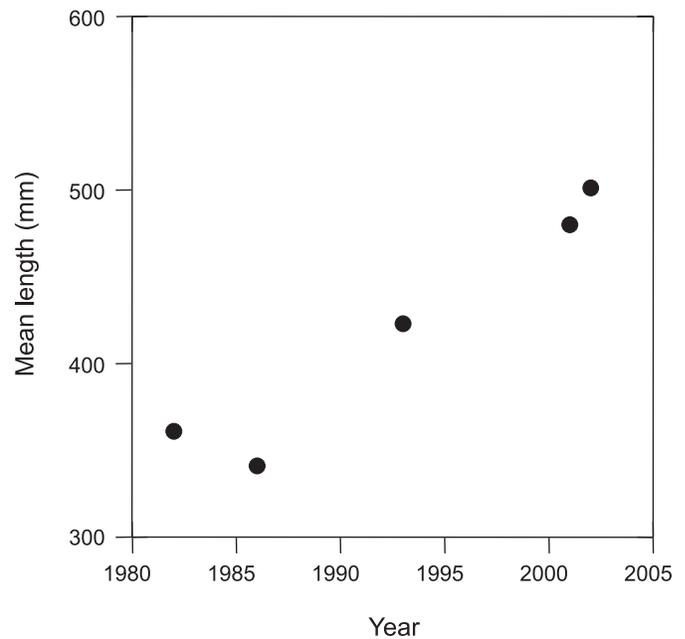
period. In Fence Lake, rainbow smelt biomass decreased from 32 kg·ha^{-1} in 1993 to approximately 13 kg·ha^{-1} in 2002 (Fig. 2). Rainbow smelt average length also decreased through time and coincided with increases in walleye biomass (Fig. 5). In contrast, the average body condition of rainbow smelt in Fence Lake increased through time (Fig. 5). According to population age frequency data, rainbow smelt total annual mortality was 59% in 2002 (e.g., Ricker 1975).

In Crawling Stone Lake, rainbow smelt population densities increased roughly sixfold from 1986 to 1993. However, rainbow smelt population biomass in Crawling Stone Lake decreased substantially after 1993. Rainbow smelt biomass declined from approximately 12 kg·ha^{-1} in 1993 to undetectable levels by 2001 (Fig. 2). Rainbow smelt were not found in Crawling Stone Lake in 2001 or 2002, which indicates a stronger decline in rainbow smelt population density than was observed in Fence Lake.

Cisco population dynamics

In Fence and Crawling Stone lakes, cisco showed tremendous increases in population size. In Fence Lake, cisco biomass increased between 1993 and 2002, and they are now the dominant pelagic planktivore in the system, both in number and by biomass. Cisco, which were common in both Fence and Crawling Stone lakes in the 1960s (S. Gilbert, Wisconsin Department of Natural Resources, 8770 Hwy J Woodruff, WI 54568, USA, personal communication), were rare in 1993 when only one individual was caught. In 1982, 1986, and 1993, no cisco younger than 4 years old were captured. Cisco abundance in Fence Lake increased substantially between 1993 and 2002. Hydroacoustic data collected in 2002 indicated that cisco biomass was approximately 23 kg·ha^{-1} in Fence Lake, a 14-fold increase from 1993 (Fig. 2). Furthermore, young fish dominated the cisco popu-

Fig. 4. Catch per unit effort (CPUE) of predator and prey species in supplemental study lakes. (*a*) CPUE of walleye (*Sander vitreus*) in Trout Lake. (*b*) CPUE of cisco (*Coregonus artedi*) in Trout Lake. (*c*) CPUE of walleye in Big Muskellunge Lake. (*d*) CPUE of cisco in Big Muskellunge Lake. Data collected by the Long-Term Ecological Research – North Temperate Lakes (LTER–NTL) program using 24-h vertical gillnet sets and three 30-min electroshocking transects (see Magnuson et al. 1984, 1994).
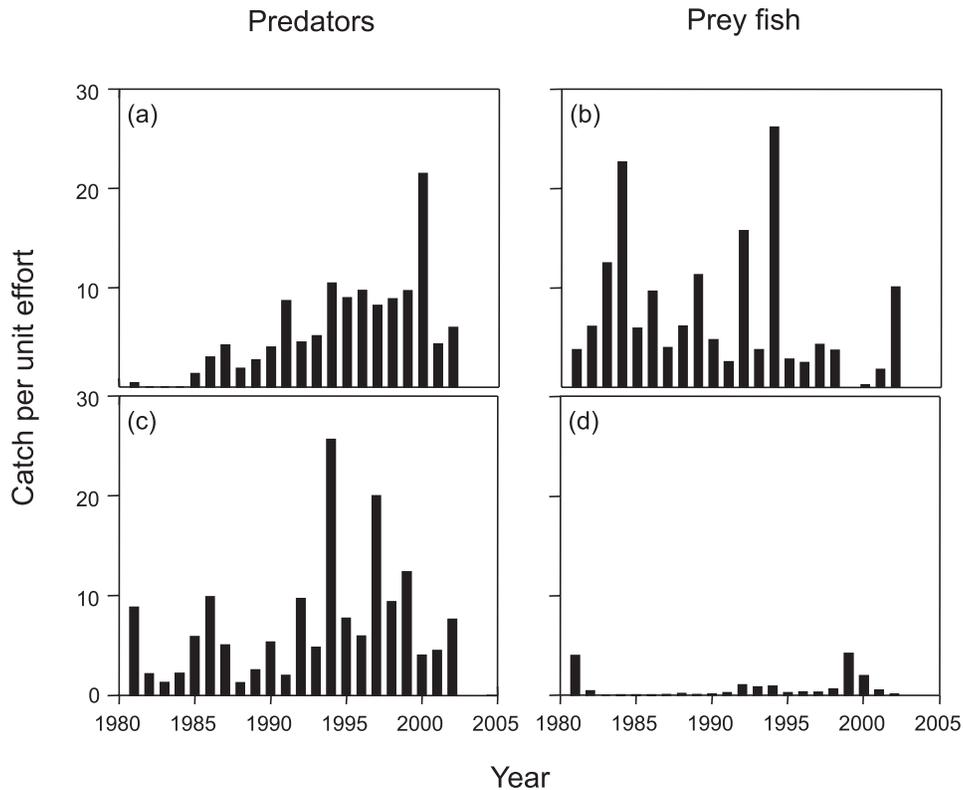
lation of Fence Lake in 2002, where most fish were younger than 2 years.

In Crawling Stone Lake, cisco biomass increased considerably from 1986 to 2002. Although cisco were abundant in Crawling Stone Lake in the 1960s and 1970s, their biomass declined to approximately 1.2 kg·ha^{-1} by 1993. By 2002, however, cisco biomass increased to approximately 82.5 kg·ha^{-1}. Cisco biomass was higher in Crawling Stone Lake than in Fence Lake, and fish of various ages were observed, including an abundant age-0 year class. Cisco in Fence and Crawling Stone lakes attained a length of 200 mm in their second year, a length exceeding the gape limitation of the average adult walleye in 2002, assuming walleye consume prey items that are <30% of their body length (Rudstam et al. 1993). In Trout and Big Muskellunge lakes, cisco catch rates did not consistently increase after 1993 (Fig. 4).

Walleye diet characteristics and consumption

Consumption by walleye increased throughout the study in Fence and Crawling Stone lakes, which coincided with increases in body size and population density. In 2002, Fence Lake walleye were piscivorous, and 76% of diets (*n* = 83 out of 110) contained fish prey. Walleye primarily consumed rainbow smelt, yellow perch, and cyprinids; other prey comprised less than 5% of the diet. In the early summer months, walleye fed mostly on cyprinids and perch and less so on rainbow smelt. In late summer, walleye fed selectively on rainbow smelt (Fig. 6), concomitantly with increasing spatial overlap between rainbow smelt and walleye (Fig. 7). Walleye did not feed on the abundant cisco in Fence Lake.

Consumption by walleye on fish prey increased substantially in Fence Lake from 1993 to 2002 and was related to increased walleye population density. Bioenergetics modeling indicated that the Fence Lake walleye population consumed approximately 55% of rainbow smelt biomass in 2002 (Fig. 8), which accounts for 93% of the total annual mortality experienced by rainbow smelt, based on population age frequencies (e.g., Ricker 1975).

Walleye in Crawling Stone Lake were less piscivorous than Fence Lake walleye in 2002 and a smaller proportion of diets contained food items (60%; *n* = 66 out of 110). Walleye primarily consumed ephemeropterans, yellow perch, and minnows throughout the summer. Despite the lack of rainbow smelt in gillnet samples in Crawling Stone Lake, rainbow smelt occasionally appeared in walleye diets, signifying a relict rainbow smelt population. Walleye did not feed on cisco in Crawling Stone Lake despite the relatively high abundance of the small age-0 stages of cisco.

Prey consumption by walleye in Crawling Stone Lake increased substantially from 1993 to 2002. In 2002, walleye consumed approximately 58 kg·ha^{-1}, which is roughly five times higher than the consumption rates we observed in Fence Lake (Fig. 9). We estimated that the walleye popula-

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Fig. 5. The average length of rainbow smelt (*Osmerus mordax*) in (*a*) Crystal and (*b*) Fence lakes captured in gill nets and the average body condition of smelt in (*c*) Crystal and (*d*) Fence lakes from 1985 to 2002.
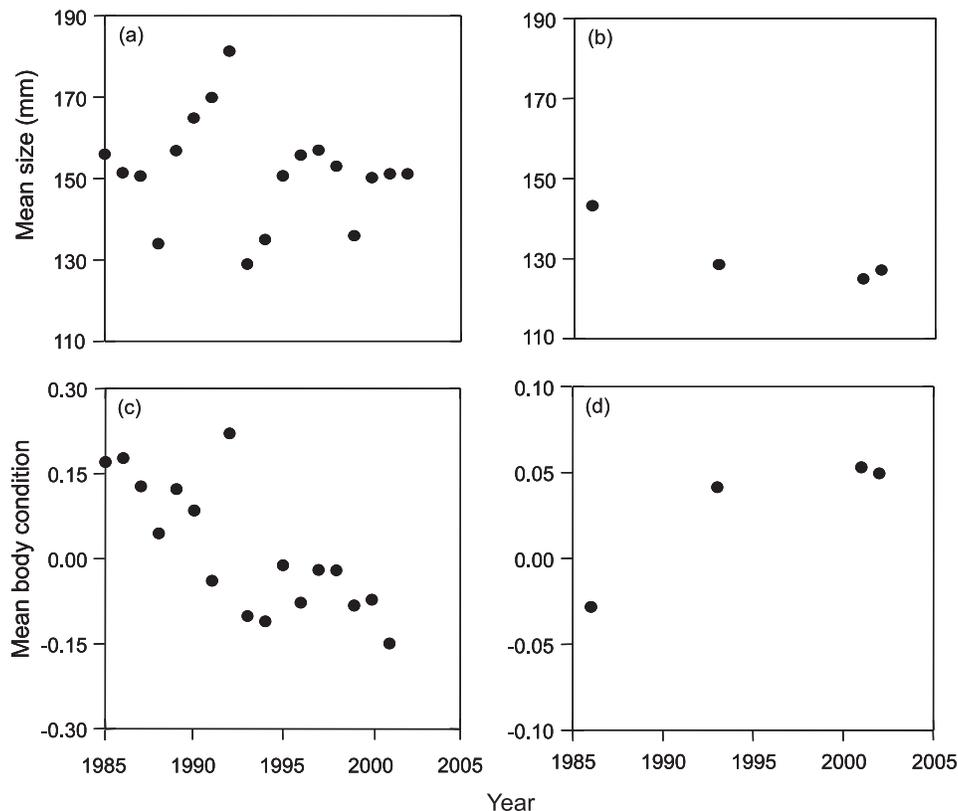
tion was capable of consuming approximately 72% of the adult rainbow smelt population in 1993, when rainbow smelt were last found in Crawling Stone Lake.

In Fence and Crawling Stone lakes, rainbow smelt population declines were concurrent with increases in prey consumption by walleye. Thus, there appeared to be a relationship between consumption rates by predators and rainbow smelt density. Consumption by rainbow smelt, the factor most likely associated with cisco declines, was negatively associated with consumption by piscivorous walleye in the study lakes (Fig. 10).

Discussion

Assessing food web structure and changes in rainbow smelt abundance

Manipulating the density of top predators in lake ecosystems represents a mechanism to generate changes in lower trophic levels through predator–prey interactions. These changes may ease competition–predation effects and facilitate recovery of a native species (Kitchell et al. 1988). Our observations in five northern temperate lake ecosystems that experienced rainbow smelt introductions indicate that manipulating predator communities yields results consistent with those observed in other lakes over the past few decades (e.g., see Kitchell and Crowder 1986; Johnson et al. 1992; Kitchell et al. 2000). In Fence and Crawling Stone lakes, where predator stocking and predator harvest regulations facilitated increases in the native predator, the food web returned to one dominated by native species. This result was

likely the effect of selective predation on exotics by native predators and species-specific characteristics.

Selective predation often alters prey community composition (Brooks and Dodson 1965; Carpenter and Kitchell 1988) and our results support this contention. Increased asymmetric predation rates in two study lakes resulted in a shift in planktivore dominance; rainbow smelt population densities declined while cisco population densities increased. Cisco biomass exceeded rainbow smelt biomass in both lakes in 2002, yet cisco were not consumed by walleye. Cisco typically represent twice the energetic benefit to a predator when compared with rainbow smelt (Bryan et al. 1996). This is counterintuitive to our finding that walleye selectively preyed upon rainbow smelt. However, our results indicate that walleye overlapped spatially with rainbow smelt more so than with cisco, particularly in late summer, and may explain the lack of cisco in walleye diets. Differences in size at age may further explain the pattern in prey preferences exhibited by walleye. All rainbow smelt were vulnerable to predation by the average-sized walleye in each lake. Cisco, however, attain a size refuge relatively quickly, making them less vulnerable to walleye predation throughout most of their lifespan. The lack of age-0 cisco in walleye diets implicates a predator avoidance behavior that may be the result of co-adaptation over longer timescales. The high consumption rates exhibited by walleye on rainbow smelt in later study years (2001 and 2002) likely allowed age-0 cisco to avoid predation by rainbow smelt with greater success than in early study years (1982–1993). Our results suggest that predation by walleye substantially reduced rainbow smelt aver-

Fig. 6. Chesson's index of prey selection for walleye (*Sander vitreus*) caught in Fence Lake in (*a*) May, (*b*) June, (*c*) July, and (*d*) August of 2002. Error bars indicate 95% confidence intervals; the dotted horizontal line in each box represents neutral selection.
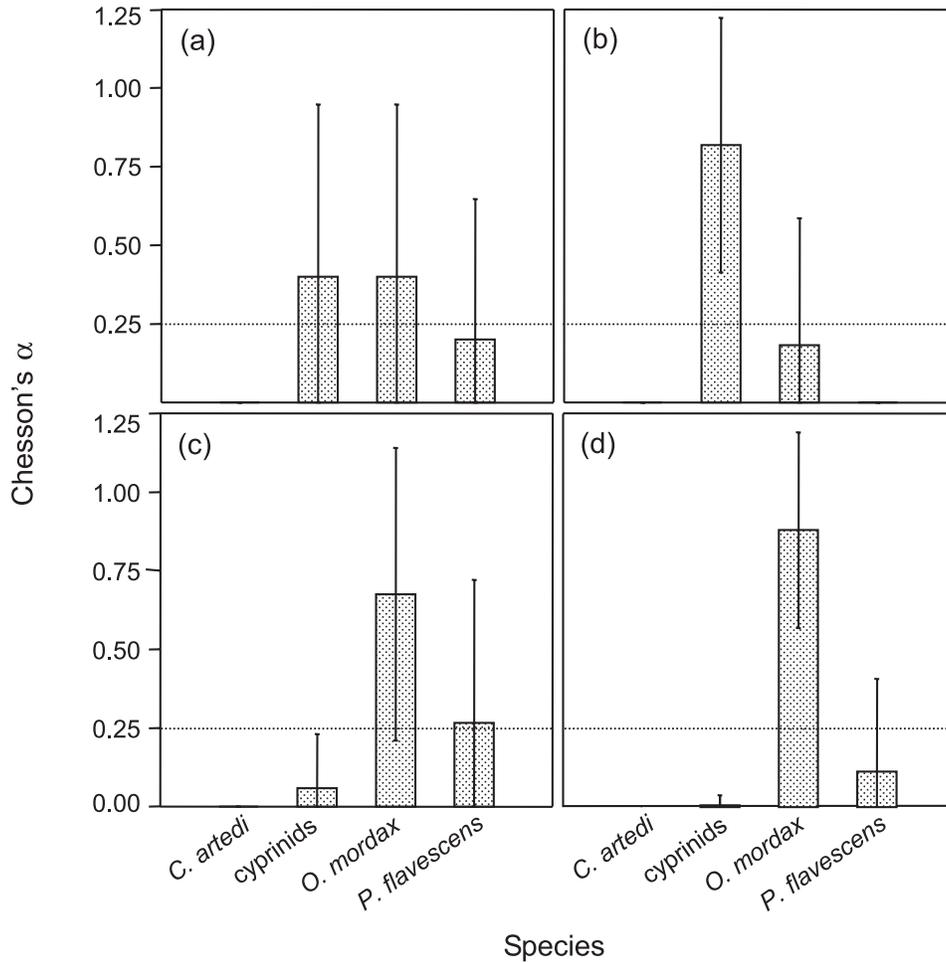

Fig. 7. Thermal overlap between walleye (*Sander vitreus*) and cisco (*Coregonus artedi*; denoted by line with solid circles) and between walleye and rainbow smelt (*Osmerus mordax*; denoted by line with ×s) as observed in vertical gillnet catch from June to August 2002 in Fence Lake.
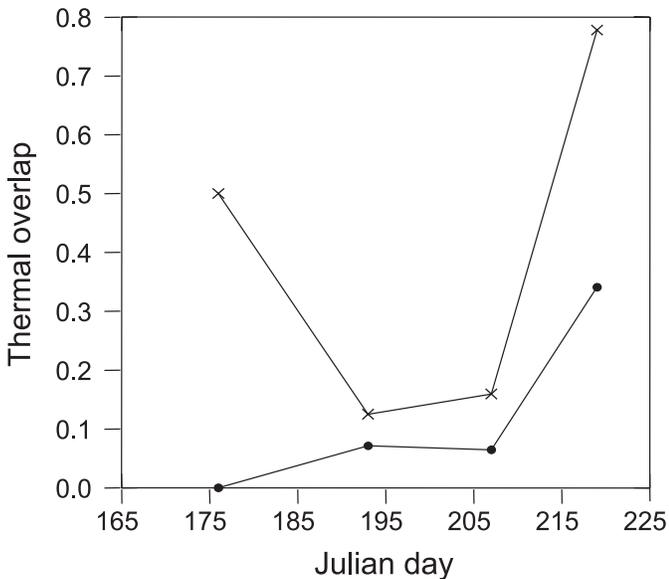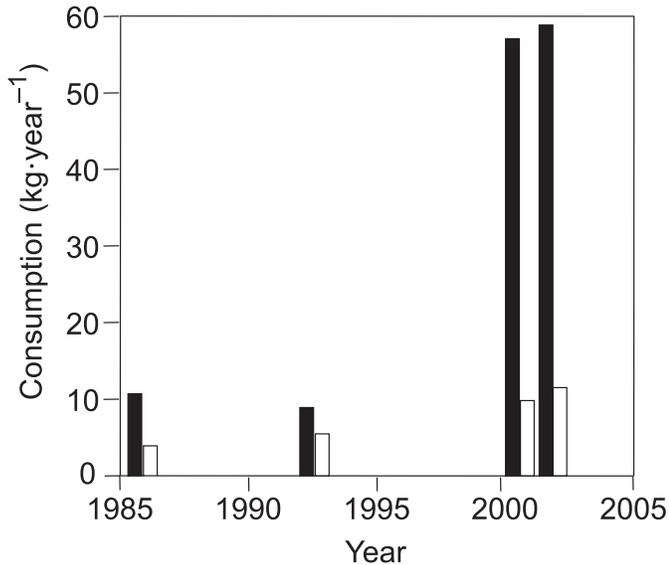

Fig. 8. Estimated consumption of smelt (*Osmerus mordax*) by walleye (*Sander vitreus*) (open bars) and estimates of smelt biomass (solid bars) in Fence Lake in each study year from 1982 to 2002.
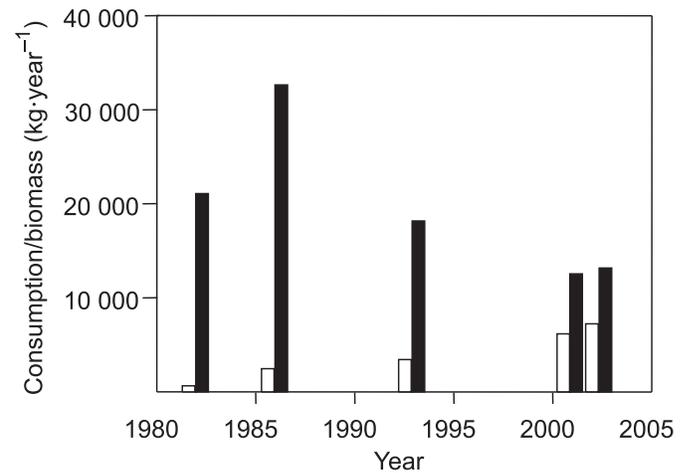
age size, rainbow smelt population density, and consumption by the rainbow smelt populations as a whole. These declines likely reduced competition and intraguild predation rates of rainbow smelt on young cisco, and thereby decreased age-0

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Fig. 9. Total consumption by walleye (*Sander vitreus*) in Fence (open bars) and Crawling Stone (solid bars) lakes from 1986 to 2002.

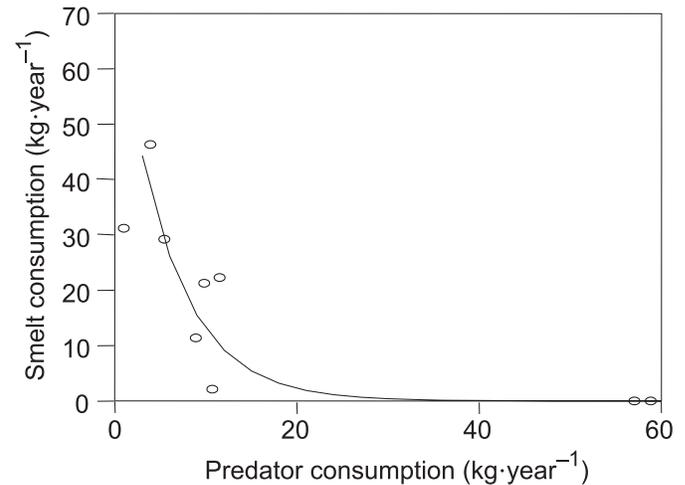**Fig. 10.** The apparent relationship between consumption by walleye (*Sander vitreus*) and consumption by smelt (*Osmerus mordax*) in Fence and Crawling Stone lakes (open circles represent observed values). The solid line represents the model SC = $70 \times e^{-0.16WC}$, where SC is consumption by smelt and WC is consumption by walleye ($p < 0.001$, $r^2 = 0.76$). The y intercept was fixed at the estimated consumption rate observed in 2002 in Crystal Lake, where smelt existed in the virtual absence of predators and where they were likely near their carrying capacity.

cisco mortality. These results provide strong evidence that restoring walleye populations in small lakes will not hinder the recovery of cisco. Instead, such management may lead to predator-mediated coexistence between cisco and rainbow smelt.

While predation by walleye may explain the observed declines in rainbow smelt in two of the study systems, alternative hypotheses for these declines include recruitment failure resulting from changes in regional climate, or a disease outbreak in both Fence and Crawling Stone lakes. We evaluated the first alternative hypothesis by examining population dynamics in Crystal Lake, which is an excellent control system since rainbow smelt experience very low predation rates and intraguild competition. Unlike the rainbow smelt populations in Fence and Crawling Stone lakes, Crystal Lake rainbow smelt biomass has continued to rise exponentially since they were detected in 1985. If regional processes had contributed to rainbow smelt recruitment failure in Fence and Crawling Stone lakes, such recruitment variability would likely only cause short-term fluctuations in rainbow smelt population densities (He and LaBar 1994) and would not explain the longer term patterns we observed. Therefore regional climate was not a likely underlying cause of the observed changes in rainbow smelt abundances in Fence and Crawling Stone lakes. Based on the cisco catch data from Trout and Big Muskellunge lakes, we also conclude that increases in cisco biomass in Fence and Crawling Stone lakes were not attributable to regional processes.

We cannot exclude the possibility that disease outbreak contributed to the decline in rainbow smelt. However, we did not observe any visible signs of disease in the Fence and Crawling Stone rainbow smelt populations in 2001 or 2002. In addition, rainbow smelt body condition was higher in 2001 and 2002 in Fence Lake than it was prior to 1994, suggesting a more healthy population. Our evidence is therefore most consistent with the hypothesis that selective predation

by walleye caused the observed declines in rainbow smelt population densities in Fence and Crawling Stone lakes.

Management implications

Managing predatory fish populations may yield several possible outcomes, including the potential control of harmful exotic species. Our study lakes represent three distinct scenarios that are defined by the level of consumption by predatory species. Predator-rich Crawling Stone Lake showed the most striking decline in rainbow smelt density. However, the extremely high density of predators in this system, coupled with the decrease in their prey, may lead to depressed growth and recruitment through density-dependent factors (Kitchell and Crowder 1986). This scenario may be acceptable if local management is focused on eliminating smelt in an effort to fully restore declining native planktivore populations. However, fishery managers may be interested in maintaining quality sport fisheries while managing for native fish populations. The intermediate walleye density represented in Fence Lake appeared to allow rainbow smelt, cisco, and walleye to coexist and maintain a diverse forage base for walleye. This situation may represent a balance between native species restoration and high predator growth rates. Jones et al. (1994) found that walleye consumed rainbow smelt almost exclusively in a Colorado reservoir, and growth increased by up to 50% in some age classes. However, the rainbow smelt population was not adversely affected by walleye predation. This was also true in Lake Champlain, where walleye and salmonid species relied heavily on rainbow smelt, but did not cause a significant decline in the rainbow smelt population (Kirn and LaBar 1996). However, in smaller oligotrophic lakes, such as Fence Lake, continued predation at current rates may further reduce rainbow smelt biomass. In Lake Michigan, rainbow smelt encountered pre-

dation rates comparable to those in Fence Lake and subsequently declined to very low levels (Kitchell and Crowder 1986). Continued monitoring of rainbow smelt populations is needed to fully examine the sustainability of rainbow smelt under current predatory conditions in Fence and Crawling Stone lakes.

In Crystal Lake, rainbow smelt appear to show an exponential population growth pattern that has nearly eliminated the native yellow perch. Because predator abundance is extremely low, rainbow smelt will likely increase until density dependence and resource limitation lead to population declines or stabilized densities.

Our study systems represent contrasting food web configurations and resultant population dynamics. We therefore propose several options for fishery managers who face declining native fish populations caused by rainbow smelt. Management objectives should incorporate predator consumption rates on prey species as a factor when formulating management prescriptions. Our findings suggest the following: (*i*) rainbow smelt populations may decline to low levels and cisco may recover when walleye consume 58 kg·ha^{-1}·year^{-1} of prey; (*ii*) walleye consumption rates at approximately 12 kg·ha^{-1}·year^{-1} may promote a diverse forage base but allow native cisco to recover; and (*iii*) unchecked rainbow smelt populations will likely grow exponentially and cause native species to decline (Hrabik et al. 2001). Our results are likely specific to situations in which walleye depend on rainbow smelt for a substantial part of their diet, and the attributes of the lakes are similar to those observed in this study. Although walleye can be significant predators on rainbow smelt and alewife (Porath et al. 2003), they may not be as effective at controlling all exotic forage fishes. Ogle et al. (1996) showed that walleye did not prey upon ruffe (*Gymnocephalus cernuus*) at high enough rates to control their abundances in the western arm of Lake Superior. Changes in the food web of Fence and Crawling Stone lakes indicate that walleye predation can indirectly allow cisco populations to recover. As a result of widespread stocking of walleye by management agencies in the upper Great Lakes region, the applicability of such strategies represents a mechanism to prevent rainbow smelt establishment and restore threatened populations of cisco in their southern ranges. Fishery managers will need to identify the food web configuration and predator consumption regime that best suits the objectives for the ecosystems within their jurisdiction.

Acknowledgements

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