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Seasonal effects of variable recruitment of a dominant piscivore on pelagic food web structure

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Abstract

Piscivorous fish play an important role in regulating lake food web structure. However, most ultimately piscivorous fish pass through a period of planktivory before becoming piscivorous. In 1993 and 1994, two large cohorts of young-of-the-year largemouth bass (*Micropterus salmoides*) were recorded in Paul Lake, Michigan. The 1993 and 1994 cohorts were the largest recorded in data extending back to 1984 and occurred during a period in which adult and juvenile bass biomass was low. In 1993, consumption of large-bodied zooplankton by the young-of-the-year cohort eliminated large-bodied cladocerans by the middle of August. As large cladocerans declined, small cladocerans, especially *Bosmina longirostris*, increased. By early September the biomass of *B. longirostris* was similar to that of the entire cladoceran community in previous years. Coincident with the shifts in the cladoceran community were increases in epilimnetic Chl *a* concentrations <35 μm . However, total epilimnetic Chl *a* did not increase. In contrast, the 1994 cohort had no discernible effect on pelagic food web structure because production of large-bodied zooplankton rapidly exceeded predation. Our results show the potential for large cohorts of piscivorous fish to affect food web structure, at a seasonal scale, through intense planktivory.

The effects of piscivorous fish on food web structure are central to biomanipulation efforts to improve water quality (Shapiro et al. 1975; Benndorf 1990; Jeppesen et al. 1990; Kitchell 1992). Piscivorous fish are important to lake food webs because they may depress planktivorous fish populations, thereby allowing large-bodied zooplankton to flourish, which results in relatively low phytoplankton biomass. Yet, the strength of this cascading interaction in unmanipulated systems remains a topic of continued debate (Crowder et al. 1988; McQueen et al. 1989; DeMelo et al. 1992).

The effect of fish populations on food web dynamics is mediated by recruitment (Carpenter 1988; Rudstam et al. 1993), an inherently variable process (LeCren 1962; Fogarty et al. 1991). Previous studies have demonstrated seasonal food web effects of a large year class of young-of-the-year (YOY) planktivorous fish (Mills et al. 1987; Carpenter and Leavitt 1991; Helminen 1994) and long-term food web ef-

fects of a large cohort of long-lived obligate planktivorous fish (Rudstam et al. 1993). No study has yet shown the impact of a large year class of a long-lived and ultimately piscivorous fish on food web dynamics.

Largemouth bass (*Micropterus salmoides*) exhibit highly variable recruitment (Summerfelt 1975) and as adults may control food web structure through intense predation on planktivorous fishes (Carpenter and Kitchell 1993; Mittelbach et al. 1996). As a cohort matures, bass grow through periods of zooplanktivory and benthivory before becoming piscivorous. This trophic ontogeny (sensu Werner and Gilliam 1984) interacts with prey populations such that a large cohort may differentially affect food web dynamics at multiple temporal scales (Carpenter et al. 1985; Carpenter and Kitchell 1987). In theory, a large cohort may initially increase zooplanktivory, shifting the zooplankton community toward smaller bodied zooplankton species and increased edible phytoplankton (Carpenter and Kitchell 1987). This period of zooplanktivory is expected to be short-lived (Keast and Eadie 1985; Olson 1996). As members of the cohort grow, they select progressively larger prey, become piscivorous, and their impact on food web structure reverses (Carpenter and Kitchell 1987). Based on the theories of trophic ontogeny and cascading trophic interaction, Carpenter and Kitchell (1987) and Carpenter (1988) predicted that trophic cascades derive in unmanipulated systems as a consequence of fish recruitment dynamics.

Our study site, Paul Lake, has served as the unmanipulated reference system for a number of previous studies (e.g. Carpenter and Kitchell 1993; Carpenter et al. 1996). As a reference system, the lake demonstrates the inherent background variability of an unmanipulated lake. Here we present evidence for the effects of two large year classes of large-

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mouth bass on food web dynamics of Paul Lake. These natural experiments offer evidence of the magnitude and timing of food web effects by piscivorous fishes.

Methods

Study site—Paul Lake is a small (1.7 ha, max. depth 15 m), oligotrophic lake located at the University of Notre Dame Environmental Research Center (Gogebic County, Michigan). Paul Lake has served as the reference basin for a series of whole-lake manipulations and has been consistently sampled since 1984. The Paul Lake largemouth bass population has been unmanipulated and unexploited since 1976. The lake and its history are fully described in Leavitt et al. (1989) and Carpenter and Kitchell (1993).

Fish population estimates—Population estimates for juvenile and adult largemouth bass were conducted during May and August of each year using Petersen or Schnabel mark-recapture methods (Krebs 1989). To minimize recapture bias, marks and recaptures were conducted by using a combination of angling and electroshocking. Biomass was estimated by multiplying the average mass of juveniles and adults by the population estimate of each respective age group. Annual biomass was calculated as the average of May and August biomass estimates. Population estimates for YOY largemouth bass were made in August using Petersen mark-recapture methods. Standard error estimates for YOY populations were estimated according to Krebs (1989). Because angling was not possible for YOY, all marks and recaptures were made by electroshocking. When mark-recapture population estimates were not available, the abundance of YOY largemouth bass was estimated from the relationship between catch per unit effort and mark-recapture estimates from other years (population estimate = $8.3 \times$ number caught $- 156.7$; $N = 6$, $R^2 = 0.94$). For the standard error of these population estimates, we used the standard error estimate for predicted values around the fitted regression (Draper and Smith 1981). The abundance of YOY largemouth bass at hatching was estimated from the number of successful nests observed (11 in 1993 and 22 in 1994; in situ observations) and an estimate of the number of fish produced from each nest (3,000; Scott and Crossman [1973] and Becker [1983]).

Bass diets and predation rates—YOY largemouth bass diets were quantified for use with bioenergetics models to estimate predation rates on zooplankton. Fish were collected by dip net or electroshocking and preserved in 95% ethanol. The entire digestive tract was dissected and the contents were enumerated. At least 12 individuals were analyzed on eight dates from late June to late August 1993 and on nine dates from early June to late August 1994. Diets were analyzed as percent composition by mass (wet weight) using standardized weights for each prey item (Hodgson et al. 1993).

We estimated predation on zooplankton by YOY largemouth bass using the bioenergetics approach of Kitchell et al. (1977). Largemouth bass parameters were from Rice et al. (1983) and Trebitz (1991), and simulations were run with

the generalized fish bioenergetics software developed by Hewett and Johnson (1992). Water temperatures for this model were from weekly temperature measurements taken from May through September at a depth of 1 m. Prey energy densities were taken from Hewett and Johnson (1992). Energy densities of YOY largemouth bass were modeled as an increasing function of fish weight.

For the 1993 and 1994 cohorts we modeled predation by each nest school by modeling fish growth from 6.6 mg (9 mm) to the observed weights in late August. By late August 1993, fish hatched before 24 June averaged 1.7 g and fish hatched after 24 June averaged 0.85 g. In 1994, fish hatched before 3 June averaged 2.9 g and fish hatched after 3 June averaged 1.5 g. The swim-up date (date at which YOY emerge from the nest and become free-swimming) for each nest school was estimated from direct underwater observations. Underwater observations were made from late May through the dispersal of all nest schools. The entire lake was surveyed once every 2 d. Hatching occurred between 14 June and 4 July 1993 and between 24 May and 13 June 1994 (Post 1996). Mortality rates from swim-up to late August were estimated (as an exponential decay function) to be $4.2\% \text{ d}^{-1}$ in 1993 and $4.6\% \text{ d}^{-1}$ in 1994.

Chaoborus and zooplankton—*Chaoborus* and zooplankton sampling and enumeration techniques are described fully in Elser et al. (1987) and Elser et al. (1986). Zooplankton biomass was estimated using length-weight regressions from Downing and Rigler (1984), and *Chaoborus* biomass was estimated from length-weight regressions in Soranno et al. (1993b).

Daphnia production—Production of *Daphnia rosea* and *Daphnia pulex* (hereafter referred to collectively as *Daphnia*) was estimated by using weekly biomass estimates and previously published production to biomass ($P:B$) ratios for Paul Lake (Stross et al. 1961). Stross et al. (1961) reported an average daily biomass of 1.51 g m^{-2} and seasonal production of 7.2 g m^{-2} (for the period 1 May through 1 October [153 d]), resulting in an average daily $P:B$ ratio of 0.031. The current zooplankton and phytoplankton community are similar to those of the late 1950s (Stross et al. 1961; Leavitt et al. 1989; Carpenter and Kitchell 1993). We compared estimates of predation by YOY largemouth bass to production of *Daphnia* based on a daily $P:B$ ratio of 0.03. Estimates of YOY bass predation and *Daphnia* production in 1993 and 1994 were from Post and Kitchell (1997).

Phytoplankton biomass—We used Chl *a* as an indicator of phytoplankton biomass. Samples were filtered on Whatman GF/F filters and analyzed by using a calibrated fluorometer (Marker et al. 1980). Chl *a* values are the mean of Chl *a* concentrations from samples collected at depths representing 100, 50, and 25% of surface irradiance and therefore represent epilimnetic Chl *a* concentrations only. Chl *a* concentrations $< 35 \mu\text{m}$ were determined from samples pre-filtered through $35\text{-}\mu\text{m}$ mesh. A previous analysis noted no significant changes in chlorophyll vertically integrated above 5% surface irradiance (Carpenter et al. 1996). This paper presents epilimnetic concentrations that have not previously

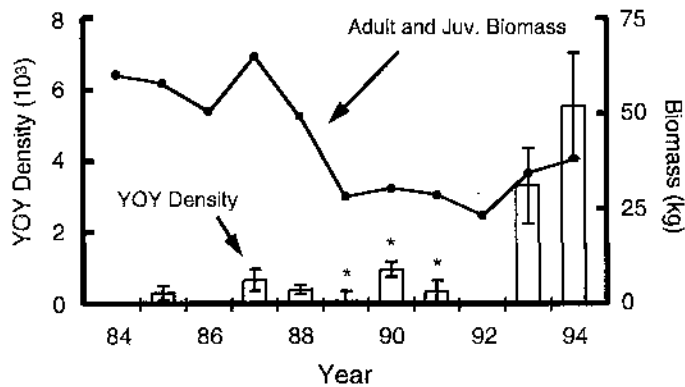


Fig. 1. Average summer biomass (kg) of juvenile and adult bass and August abundance estimates (\pm SE) of young-of-the-year bass for 1984 through 1994. Estimates in some years (*) derive from the relationship between catch per unit effort and population estimates for young-of-the-year in other years.

been published and that responded significantly to zooplankton changes.

Results

Largemouth bass population—The annual average biomass of adult and juvenile bass fluctuated almost threefold between 1984 and 1994, reaching a minimum from 1989 through 1994 (Fig. 1). The density of adult bass (not shown) generally tracked biomass. The 1993 (estimate of 3,303; 95% C.I. = 1,789–6,167) and 1994 YOY cohorts (estimate of 5,551; 95% C.I. = 3,587–9,757) were 3.5 and 6 times

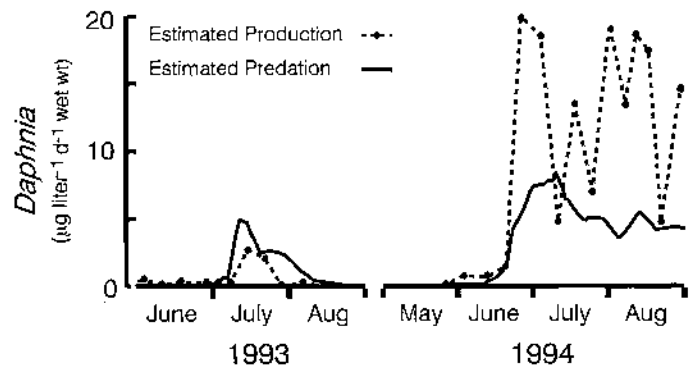


Fig. 2. Estimated daily predation on *Daphnia* by the 1993 and 1994 largemouth bass cohorts and estimated daily production ($\mu\text{g liter}^{-1} \text{ day}^{-1}$ wet wt) of *Daphnia* assuming a $P:B$ of 0.03.

more abundant than any previously recorded year class (Fig. 1), and both cohorts reached a maximum biomass near the end of August (4.6 kg in 1993, 10.6 kg in 1994).

YOY diets and predation rates—In 1993, YOY largemouth bass initially preyed on copepod nauplii and small cladocerans (*Bosmina longirostris* and *Polyphemus pediculus*), but quickly switched to feeding on *Daphnia* (Table 1). *Daphnia* was then replaced in diets by *Holopedium gibberum*, *B. longirostris*, and adult copepods toward the end of August. Predation on *Daphnia* peaked around mid-July (Fig. 2) and then declined as the proportion of *Daphnia* in the diets of YOY largemouth bass declined. In 1994, YOY bass diets were initially similar to those observed in 1993, how-

Table 1. Diet composition of young-of-the year largemouth bass in Paul Lake during the summers of 1993 and 1994. Results are presented as percent composition by mass.

Date	Zooplankton as percentage of total diet	Percent composition of zooplankton component of total diet				
		<i>Daphnia</i> spp.	<i>Holopedium gibberum</i>	Small cladocerans*	Adult copepods	Copepod nauplii
1993						
28 June	100	0	0	1	0	99
2 July	100	22	0	76	2	1
6 July	90	14	0	86	0	0
10 July	100	99	0	1	0	0
14 July	98	95	0	0	5	0
19 July	43	94	0	0	6	0
9 August	2	5	49	26	20	0
20 August	2	1	38	39	22	0
1994						
8 June	100	34	0	62	4	0
15 June	100	83	0	2	15	0
22 June	100	84	0	6	10	0
29 June	89	99	0	0	1	0
6 July	15	100	0	0	0	0
13 July	10	100	0	0	0	0
27 July	20	97	0	0	2	0
5 August	29	100	0	0	0	0
22 August	31	100	0	0	0	0

* Small cladocerans include *Bosmina longirostris*, *Diaphanosoma birgei*, *Polyphemus pediculus*, and several species of Chydoridae.

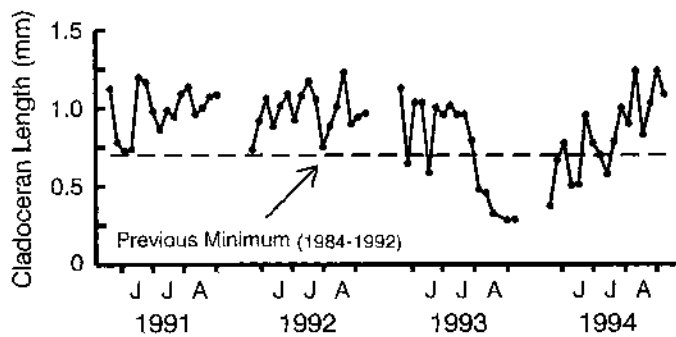


Fig. 3. Mean cladoceran length (mm) for 1991 through 1994. The line labeled "previous minimum" represents the lowest mean cladoceran length recorded for any date between 1984 and 1992.

ever *Daphnia* remained an important diet item through the summer (Table 1). Furthermore, YOY bass did not prey on *H. gibberum* in 1994 and they did not switch back to small cladocerans and adult copepods at the end of the summer. Predation on *Daphnia* peaked in early July, declined slightly, and then remained relatively stable for the remainder of the summer as YOY bass continued to prey on *Daphnia* (Fig. 2).

Chaoborus—*Chaoborus* biomass estimates have been relatively similar since 1984 (Soranno et al. 1993b). The average summer *Chaoborus* biomass was 0.264 g m^{-2} (SE = 0.037; or $7.1 \mu\text{g liter}^{-1}$) in 1992, 0.207 g m^{-2} (SE = 0.034; or $5.54 \mu\text{g liter}^{-1}$) in 1993, and 0.324 g m^{-2} (SE = 0.079; or $8.7 \mu\text{g liter}^{-1}$) in 1994. In each year *Chaoborus* biomass declined toward the end of the summer as a result of pupation and the recruitment of newly hatched larvae.

Zooplankton—The average mean cladoceran length in the lake was 1.0 mm from 1984 to 1992. Prior to 1993 mean weekly cladoceran length had never been <0.7 mm. In 1993, mean cladoceran length started to decline after mid-July, falling below 0.3 mm by the end of August (Fig. 3).

This decline in cladoceran length reflected a change in the species composition of the cladoceran community. From 1984 through 1992 the cladoceran community of the lake was dominated by the large-bodied species, *H. gibberum*, *D. pulex*, and *D. rosea*. In the summer of 1993, however, these large cladocerans declined and were replaced by a succession of smaller cladoceran species (Fig. 4). By the end of the summer, the cladoceran community had become a near monoculture of *B. longirostris*, with a biomass similar to that reached by the entire cladoceran community earlier in the summer (Fig. 4).

In 1994, mean cladoceran length gradually increased and by the end of the summer was similar to those observed in 1991 and 1992 (Fig. 3). *H. gibberum* and *B. longirostris* were initially abundant, but *B. longirostris* densities declined rapidly as large-bodied cladocerans regained dominance. By the end of the summer of 1994, the cladoceran community was similar to that observed in 1991 and 1992.

Phytoplankton—The average concentration of $<35\text{-}\mu\text{m}$ Chl *a* for 1991 through mid-1993 fluctuated around the long-term mean of $2.0 \mu\text{g liter}^{-1}$ (1991–1992, Fig. 5). By the end

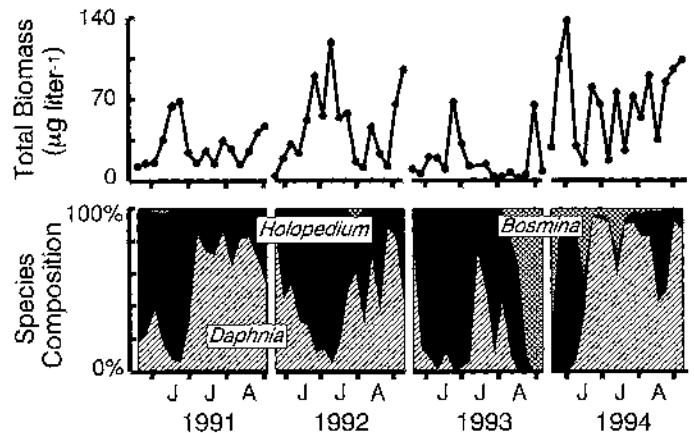


Fig. 4. Total cladoceran biomass (1991–1994; $\mu\text{g liter}^{-1}$ dry wt) and species composition of the cladoceran community. Cladoceran species that represented $\leq 1\%$ of the total biomass were excluded from the species composition panel. Species composition in 1993 and 1994 were previously reported in Post and Kitchell (1997).

of the summer of 1993, $<35\text{-}\mu\text{m}$ Chl *a* had reached levels more than twice those previously observed (Fig. 5). Average $<35\text{-}\mu\text{m}$ Chl *a* in August of 1993 ($4.4 \pm 1.9 \mu\text{g liter}^{-1}$) was significantly higher than that for August of previous years ($1.77 \pm 0.62 \mu\text{g liter}^{-1}$; two-tailed *t*-test, $T = -3.1$, $P = 0.03$). There was, however, no significant increase in total Chl *a* ($P = 0.99$, Fig. 5). In 1994, total and $<35\text{-}\mu\text{m}$ Chl *a* were at levels similar to those observed before 1993 (Fig. 5).

Discussion

For nearly 10 years predation by adult and juvenile large-mouth bass in Paul Lake had effectively minimized populations of zooplanktivorous fish, large cladocerans dominated the zooplankton community, and phytoplankton $<35 \mu\text{m}$ were suppressed by intense grazing (Carpenter and Kitchell

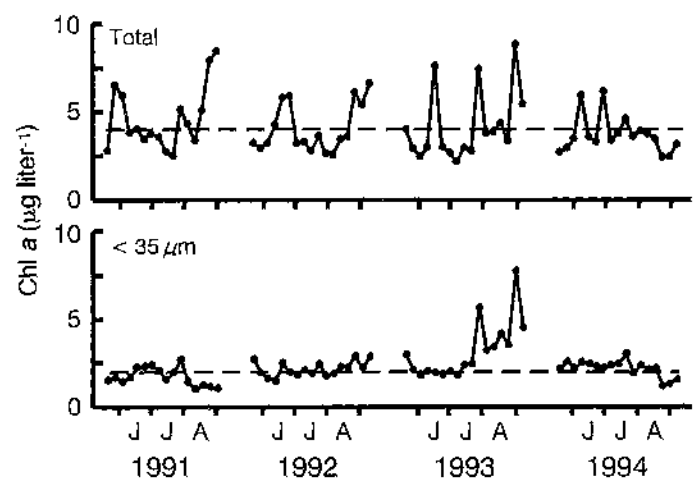


Fig. 5. Total and $<35 \mu\text{m}$ epilimnetic Chl *a* concentrations (1991–1994; $\mu\text{g liter}^{-1}$). The dotted lines indicate long-term mean concentrations of total (1984–1992) and $<35 \mu\text{m}$ (1991–1992) epilimnetic Chl *a*.

1993). In 1993, however, the food web structure of this unmanipulated system was disrupted for a short period by one of the largest cohorts of largemouth bass recorded since 1984. This large recruitment event, the consequence of natural population fluctuations, increased zooplanktivory, eliminated large-bodied cladocerans, and allowed $<35\text{-}\mu\text{m}$ Chl *a* to increase. In contrast to our previous whole-lake experimental studies (e.g. Carpenter and Kitchell 1993; Carpenter et al. 1996), these results illustrate the inherent background variability of an unmanipulated reference system.

Fish-zooplankton interactions—In 1993, predation on *Daphnia* equaled or exceeded production (Fig. 2), indicating that the decline of *Daphnia* resulted from predation by the 1993 cohort of largemouth bass. In contrast, predation by the 1994 cohort had little effect on *Daphnia* populations. The different effects of these two large cohorts demonstrate the importance of interactions between predation rates and *Daphnia* biomass and production. The strong effects observed in 1993 were the result of high YOY bass densities and low *Daphnia* biomass. In 1993, predation by YOY largemouth bass increased and peaked while *Daphnia* biomass was low. In 1994, *Daphnia* biomass increased before predation was able to limit growth of the *Daphnia* population. Once high *Daphnia* biomass was well established, predation by the 1994 cohort was not sufficient to control *Daphnia* populations.

These results are consistent with the view that the magnitude and timing of predation, relative to prey biomass and production, are important to fish-zooplankton interactions (Luecke et al. 1990; Johnson 1995; Post and Kitchell 1997). For example, had *Daphnia* biomass increased a few weeks later in 1994, predation by the 1994 YOY cohort should have been sufficient to keep *Daphnia* at low densities through the summer. However, because *Daphnia* biomass increased before predation by the 1994 cohort, even the large 1994 cohort was unable to regulate *Daphnia* densities. The potential for a YOY largemouth bass cohort to suppress and hold *Daphnia* at low densities is therefore a function of *Daphnia* biomass, YOY biomass, and the timing of peak predation (Post and Kitchell 1997).

Zooplankton length, especially mean cladoceran length (Soranno et al. 1993a), provides a robust indicator of zooplanktivory by fishes (Hrbáček et al. 1961; Brooks and Dodson 1965) and is an important indicator of zooplankton-phytoplankton interactions (Pace 1984; Carpenter et al. 1991). The decline in mean cladoceran length observed in 1993 (almost 0.75 mm; Fig. 3) was of a magnitude similar to that reported in previous experimental manipulations (Post and McQueen 1987; Carpenter and Kitchell 1993). The observed patterns of species decline and replacement were consistent with previously reported changes in zooplankton communities responding to intensified size-selective predation by fish (Hrbáček et al. 1961; Brooks and Dodson 1965; Mills et al. 1987; Carpenter and Kitchell 1993; He et al. 1994).

The patterns of species replacement were also consistent with evidence from the paleolimnological record of Paul Lake. Although large cladocerans have dominated the zooplankton community in recent history, the paleolimnological record shows strong zooplankton community shifts corre-

sponding to historic changes in the fish community. The fossil record shows the replacement of *Daphnia* by *B. longirostris* after a decline in a stocked trout population and an increase in the abundance of minnows (Leavitt et al. 1989). This replacement cycle was reversed when largemouth bass entered the lake around 1978 (Leavitt et al. 1989). Thus, large cladocerans have been replaced by small cladocerans during previous periods of high planktivory in the lake.

Holopedium gibberum generally peaks early in the summer and then declines as the summer progresses and as *Daphnia* biomass increases (Fig. 4; Stross et al. 1961; Soranno et al. 1993a). *H. gibberum* appeared to follow this pattern in 1993. Thus, the initial declines of *H. gibberum* may have been part of its seasonal cycle. Predation by the 1993 YOY bass cohort, which began consuming *H. gibberum* only after *Daphnia* had declined (Table 1), may have accelerated the decline of *H. gibberum* at the end of the summer.

In some systems, shifts in the composition of the zooplankton community have been attributed to changes in invertebrate predation (Dodson 1974; Vanni 1988; Arnott and Vanni 1993). An increase in small cladocerans may be a result of decreased invertebrate predation. The biomass of the major invertebrate predator in Paul Lake, *Chaoborus*, was not different from previous years. It is therefore unlikely that *Chaoborus* had a direct role in the zooplankton changes that occurred.

Zooplankton-phytoplankton interactions—The impact of zooplankton grazing on the phytoplankton community is more strongly related to cladoceran (or crustacean) length than to zooplankton biomass (Pace 1984; Carpenter et al. 1991; Cyr and Pace 1993; but see Sterner 1989; Cyr and Pace 1992). In 1993, total cladoceran biomass declined in midsummer as the community shifted from large-bodied to small-bodied species (Fig. 4). By the end of the summer, mean cladoceran length had declined by nearly 0.75 mm (Fig. 3), yet cladoceran biomass (predominantly *B. longirostris*) had reached levels similar to those reached earlier in the summer (Fig. 4). Following the decline in mean cladoceran length, epilimnetic $<35\text{-}\mu\text{m}$ Chl *a* nearly doubled (Fig. 5a). The increase in $<35\text{-}\mu\text{m}$ Chl *a* was consistent with the observed role of zooplankton size in the regulation of the phytoplankton community (Pace 1984; Bergquist et al. 1985; Carpenter and Kitchell 1993; Carpenter et al. 1996). *B. longirostris* may not have maintained the same grazing pressure on $<35\text{-}\mu\text{m}$ phytoplankton as did the larger cladocerans. This is likely a result of lower grazing rates (Knoechel and Holtby 1986) and narrower diets of *B. longirostris* (Burns 1969; DeMott 1989).

The shift in food web structure in 1993 produced no significant response in total Chl *a*. This result is consistent with previous studies that have shown an inverse relationship between small (e.g. $<35\text{ }\mu\text{m}$) and large algae (Bergquist et al. 1985; Carpenter and Kitchell 1993). The compensatory response of small and large algae may result from interactions between competition for nutrients and the relative vulnerability to grazing (Lehman and Sandgren 1985; Sommer et al. 1986; Sterner 1989). There was also no response of vertically integrated Chl *a* (above 5% surface irradiance), perhaps because the increase in the epilimnion was compensat-

ed by a decrease in the metalimnion (Christensen et al. 1995). Nevertheless, epilimnetic Chl *a* <35 μm was a substantial component of primary producer biomass at the end of 1993, and its increase was ecologically and statistically significant.

Long-term implications of fish-fish interactions—In Paul Lake, intense cannibalism by adult and juvenile bass (Hodgson et al. 1993) strongly regulates recruitment (Post 1996). The large 1993 and 1994 cohorts were produced while adult and juvenile biomass were near their lowest recorded levels (Fig. 1). Simulation models incorporating density-dependent regulation of recruitment suggest that large recruitment events and subsequent food web effects should occur at time scales at or near the life span of the dominant fish species (Carpenter 1988). Recruitment variability may then be transmitted from piscivores to phytoplankton through cascading trophic interactions (Carpenter 1988). This result depends on the strength of the interaction between adults and YOY bass and on patterns of adult mortality.

As a cohort of largemouth bass matures, it feeds first on zooplankton, then invertebrates, and then fish. As it becomes progressively more piscivorous, its impact on food web structure reverses. Predation on small zooplanktivorous fish increases, reducing zooplanktivory, and allows a shift back to larger bodied zooplankton, more intense herbivory, and decreased phytoplankton. High levels of piscivory may then be sustained over the lifetime of the cohort ("predation inertia"; Stewart et al. 1981), buffering the system from additional recruitment events.

Our results support the prediction that a large cohort of ultimately piscivorous fish may cause cascading trophic interactions by increasing planktivory in their first year of life (Carpenter and Kitchell 1987; Carpenter 1988). However, the long-term impacts of a large recruitment event depend on the interaction of mortality rates and trophic ontogeny. In particular, periods of high mortality early in life may truncate the food web effects. During the winter of 1993–1994, the 1993 cohort suffered extremely high mortality (Post 1996). Mark-recapture estimates revealed that only 74 of an estimated 3,303 YOY bass survived the winter (97.8% mortality) and still fewer survived the summer of 1994. Thus, high overwinter mortality limited the ability of the 1993 cohort to have a lasting impact on food web structure.

In contrast, the 1994 cohort had no discernible effect on the pelagic food web during its first summer of life. However, a large proportion of the 1994 cohort survived the winter of 1994–1995 (Post 1996). Almost 1,500 of an estimated 5,551 YOY bass survived the winter (26% survival). In their second summer of life, members of the 1994 cohort became piscivorous and helped to eliminate rapidly the 1995 cohort (Post 1996). Although the large 1994 cohort did not affect the pelagic food web through zooplanktivory, it did affect food web structure through piscivory and may have long-term impacts on food web structure through predation on subsequent year classes.

It is clear that changes in the abundance of key fish species may impact food web structure across a wide range of aquatic ecosystems (see Northcote 1988 for a review). Yet, the potential for natural variability in fish abundance to af-

fect phytoplankton dynamics remains controversial. For example, Crowder et al. (1988) argued that many studies of top-down trophic interactions have relied on fish manipulations that were not ecologically realistic (but see Carpenter et al. 1991), and DeMelo et al. (1992) implied that cascading effects may be weak or nonexistent in unmanipulated systems. Our results stem from whole-lake observations of an unmanipulated fish population. Thus, the perturbations (natural recruitment events) and observations (at a whole-lake scale) are ecologically relevant and appropriate for understanding short-term food web perturbations induced by recruitment variability of an ultimately piscivorous fish.

The observations of recruitment variability of the unexploited Paul Lake largemouth bass population and subsequent food web effects also have implications for exploited populations. Fisheries management often aims to maintain fish populations at intermediate densities, thereby maximizing yields (Ricker 1958; Hilborn and Walters 1992). At intermediate densities recruitment variability is also maximized (Strong 1986; Fogarty et al. 1991). Thus, exploitation tends to increase variability in the recruitment of fish populations, increasing the potential for shifts in food web structure and increased ecosystem variability (Kitchell and Carpenter 1993). Therefore, our observations from an unexploited population provide a conservative indicator of the potential for short-term recruitment effects on food web structure in exploited systems.

References

- ARNOTT, S. E., AND M. J. VANNI. 1993. Zooplankton assemblages in fishless bog lakes: Influence of biotic and abiotic factors. *Ecology* **74**: 2361–2380.
- BECKER, G. C. 1983. *Fishes of Wisconsin*. Univ. Wisconsin Press.
- BENNDORF, J. 1990. Conditions for effective biomanipulation: Conclusions derived from whole-lake experiments in Europe. *Hydrobiologia* **200/201**: 187–203.
- BERGQUIST, A. M., S. R. CARPENTER, AND J. C. LATINO. 1985. Shifts in phytoplankton size structure and community composition during grazing by contrasting zooplankton assemblages. *Limnol. Oceanogr.* **30**: 1037–1045.
- BROOKS, J. L., AND S. I. DODSON. 1965. Predation, body size, and the composition of plankton. *Science* **150**: 28–35.
- BURNS, C. W. 1969. The relationship between body size of filter-feeding cladocera and the maximum size of particle ingested. *Limnol. Oceanogr.* **13**: 675–678.
- CARPENTER, S. R. 1988. Transmission of variance through lake food webs, p. 119–138. In S. R. Carpenter [ed.], *Complex interactions in lake communities*. Springer-Verlag.
- , T. M. FROST, J. F. KITCHELL, AND OTHERS. 1991. Patterns of primary production and herbivory in 25 North American lake ecosystems, p. 67–96. In J. Cole, S. Findlay, and G. Lovett [eds.], *Comparative analysis of ecosystems: Patterns, mechanisms, and theories*. Springer-Verlag.
- , AND J. F. KITCHELL. 1987. The temporal scale of variance in limnetic primary production. *Am. Nat.* **129**: 417–433.
- , AND ———. 1993. *The trophic cascade in lakes*. Cambridge Univ. Press.
- , ———, K. L. COTTINGHAM, AND OTHERS. 1996. Chlorophyll variability, phosphorus input and grazing: Evidence from whole-lake experiments. *Ecology* **77**: 725–735.
- , ———, AND J. R. HODGSON. 1985. Cascading trophic interactions and lake productivity. *BioScience* **35**: 634–639.

- , AND P. R. LEAVITT. 1991. Temporal variation in a paleolimnological record arising from a trophic cascade. *Ecology* **72**: 277–285.
- CHRISTENSEN, D. L., S. R. CARPENTER, AND K. L. COTTINGHAM. 1995. Predicting chlorophyll vertical distribution in response to epilimnetic nutrient enrichment in stratified lakes. *J. Plankton Res.* **17**: 1461–1478.
- CROWDER, L. B., AND OTHERS. 1988. Food web interactions in lakes, p. 141–160. *In* S. R. Carpenter [ed.], *Complex interactions in lake communities*. Springer-Verlag.
- CYR, H., AND M. L. PACE. 1992. Grazing by zooplankton and its relationship to community structure. *Can. J. Fish. Aquat. Sci.* **49**: 1455–1465.
- , AND ———. 1993. Allometric theory: Extrapolations from individuals to communities. *Ecology* **74**: 1234–1245.
- DEMELO, R., R. FRANCE AND D. J. MCQUEEN. 1992. Biomani-pulation: Hit or myth? *Limnol. Oceanogr.* **37**: 192–207.
- DEMOTT, W. R. 1989. The role of competition in zooplankton succession, p. 195–252. *In* U. Sommer [ed.], *Plankton ecology: Succession in plankton communities*. Springer-Verlag.
- DODSON, S. I. 1974. Zooplankton competition and predation: An experimental test of the size-efficiency hypothesis. *Ecology* **55**: 605–613.
- DOWNING, J. A., AND F. H. RIGLER. 1984. *A manual on methods for the assessment of secondary productivity in fresh waters*. Blackwell Scientific Publications.
- DRAPER, N. R., AND H. SMITH, JR. 1981. *Applied regression analysis*. John Wiley & Sons.
- ELSER, J. J., M. M. ELSER, AND S. R. CARPENTER. 1986. Size fractionation of algae, chlorophyll, carbon fixation, and phosphatase activity: Relationship with species-specific size distributions and zooplankton community structure. *J. Plankton Res.* **8**: 365–383.
- ELSER, M. M., C. N. VON ENDE, P. SORANNO, AND S. R. CARPENTER. 1987. *Chaoborus* populations: Response to food web manipulation and potential effects on zooplankton communities. *Can. J. Zool.* **65**: 2846–2852.
- FOGARTY, M. J., M. P. SISENWINNE, AND E. B. COHEN. 1991. Recruitment variability and the dynamics of exploited marine populations. *Trends Ecol. Evol.* **6**: 241–246.
- HE, X., M. D. SCHEURELL, P. A. SORANNO AND R. A. WRIGHT. 1994. Recurrent response patterns of a zooplankton community to whole-lake fish manipulations. *Freshwater Biol.* **32**: 61–72.
- HELMINEN, H. 1994. Responses of lake Pyhäjärvi (SW Finland) to variable recruitment of the major planktivorous fish, vendace (*Coregonus albula*). Ph.D. Thesis, Reports from the Department of Biology, University of Turku, No. 37.
- HEWETT, S. W., AND B. J. JOHNSON. 1992. Fish bioenergetics model 2. University of Wisconsin, Sea Grant Institute. Technical Report WIS-SG-92-250, Madison.
- HILBORN, R., AND C. J. WALTERS. 1992. *Quantitative fisheries stock assessment*. Chapman and Hall.
- HODGSON, J. R., X. HE, AND J. F. KITCHELL. 1993. The fish populations, p. 43–68. *In* S. R. Carpenter and J. F. Kitchell [eds.], *The trophic cascade in lakes*. Cambridge Univ. Press.
- HRBÁČEK, J., M. DVORÁKOVÁ, V. KORINEK AND L. PROCHÁZKOVÁ. 1961. Demonstration of the effects of the fish stock on the species composition of zooplankton and the intensity of metabolism of the plankton assemblage. *Int. Ver. Theor. Angew. Limnol. Verh.* **18**: 162–170.
- JEPPESEN, E., AND OTHERS. 1990. Fish manipulation as a lake restoration tool in shallow, eutrophic, temperate lakes 2: Threshold levels, long-term stability and conclusions. *Hydrobiologia* **200/201**: 219–227.
- JOHNSON, T. B. 1995. Long-term dynamics of the zooplanktivorous fish community in Lake Mendota, Wisconsin. Ph.D. dissertation, University of Wisconsin–Madison.
- KEAST, A., AND J. M. EADIE. 1985. Growth depensation in year-0 largemouth bass: The influence of diet. *Trans. Am. Fish. Soc.* **114**: 204–213.
- KITCHELL, J. F. 1992. *Food web management: A case study of Lake Mendota*. Springer-Verlag.
- , AND S. R. CARPENTER. 1993. Synthesis and new direction, p. 43–68. *In* S. R. Carpenter and J. F. Kitchell [eds.], *The trophic cascade in lakes*. Cambridge Univ. Press.
- , D. J. STEWART, AND D. WEININGER. 1977. Applications of a bioenergetics model to yellow perch (*Perca flavescens*) and walleye (*Stizostedion vitreum vitreum*). *J. Fish. Res. Board Can.* **34**: 1922–1935.
- KNOEHEL, R., AND L. B. HOLTBY. 1986. Construction and validation of a body-length-based model for the prediction of cladoceran community filtering rates. *Limnol. Oceanogr.* **31**: 1–16.
- KREBS, C. J. 1989. *Ecological methodology*. Harper and Row.
- LEAVITT, P. R., S. R. CARPENTER, AND J. F. KITCHELL. 1989. Whole-lake experiments: The annual record of fossil pigments and zooplankton. *Limnol. Oceanogr.* **34**: 700–717.
- LECREN, E. D. 1962. The efficiency of reproduction and recruitment in freshwater fish. *Symp. Br. Ecol. Soc.* **2**: 283–296.
- LEHMAN, J. T., AND C. D. SANDGREN. 1985. Species-specific rates of growth and grazing loss among freshwater algae. *Limnol. Oceanogr.* **30**: 34–46.
- LUECKE, C., M. J. VANNI, J. J. MAGNUSON, J. F. KITCHELL, AND P. T. JACOBSON. 1990. Seasonal regulation of *Daphnia* populations by planktivorous fish: Implications for the spring clear-water phase. *Limnol. Oceanogr.* **35**: 1718–1733.
- MARKER, A. F. H., C. A. CROWTHER, AND R. J. M. GUNN. 1980. Methanol and acetone as solvents for estimating chlorophyll *a* and phaeopigments by spectrophotometry. *Arch. Hydrobiol. Ergeb. Limnol.* **14**: 52–69.
- MCQUEEN, D. J., M. R. S. JOHANNES, J. R. POST, T. J. STEWART, AND D. R. S. LEAN. 1989. Bottom-up and top-down impacts on freshwater pelagic community structure. *Ecol. Monogr.* **59**: 289–309.
- MILLS, E. L., J. FORNEY, AND K. WAGNER. 1987. Fish predation and its cascading effects on the Oneida Lake food chain, p. 118–131. *In* W. K. Kerfoot and A. Sih [eds.], *Predation: Direct and indirect impacts on aquatic communities*. Univ. Press of New England.
- MITTELBACH, G. G., A. M. TURNER, D. J. HALL, R. E. RETTIG, AND C. W. OSENBERG. 1996. Perturbation and resilience in an aquatic community: A long-term study of the extinction and reintroduction of a top predator. *Ecology* **76**: 2347–2360.
- NORTHCOTE, T. G. 1988. Fish in the structure and function of freshwater ecosystems: A “top-down” view. *Can. J. Fish. Aquat. Sci.* **45**: 361–379.
- OLSON, M. H. 1996. Ontogenetic niche shifts in largemouth bass: Variability and consequences for first-year growth. *Ecology* **77**: 179–190.
- PACE, M. L. 1984. Zooplankton community structure, but not biomass influence the phosphorus–chlorophyll *a* relationship. *Can. J. Fish. Aquat. Sci.* **41**: 1089–1096.
- POST, D. M. 1996. Recruitment variability in largemouth bass, *Micropterus salmoides*, and its role in food web dynamics. M.S. Thesis, University of Wisconsin–Madison.
- , AND J. F. KITCHELL. 1997. Trophic ontogeny and life history effects on interactions between age-0 fishes and zooplankton. *Arch. Hydrobiol. Spec. Issue Advanc. Limnol.* **49**: 1–12.
- POST, J. R., AND D. J. MCQUEEN. 1987. The impact of planktivorous fish on the structure of a plankton community. *Freshwater Biol.* **17**: 79–89.

- RICE, J. A., J. E. BRECK, S. M. BARTELL, AND J. F. KITCHELL. 1983. Evaluating the constraints of temperature, activity and consumption on growth of largemouth bass. *Environ. Biol. Fishes* **9**: 263–275.
- RICKER, W. E. 1958. Maximum sustained yields from fluctuating environments and mixed stocks. *J. Fish. Res. Board Can.* **15**: 991–1006.
- RUDSTAM, L. G., R. C. LATHROP, AND S. R. CARPENTER. 1993. The rise and fall of a dominant planktivore: Direct and indirect effects on zooplankton. *Ecology* **74**: 303–319.
- SCOTT, W. B., AND E. J. CROSSMAN. 1973. Freshwater fishes of Canada (Bulletin of the Fisheries Research Board of Canada, No. 184). Fisheries Research Board of Canada, Ottawa.
- SHAPIRO, J., V. LAMARRA, AND M. LYNCH. 1975. Biomanipulation: An ecosystem approach to lake restoration, p. 85–96. *In* P. L. Brezonik and J. L. Fox [eds.], *Proceedings of a symposium on water quality management through biological control*. Univ. Florida.
- SOMMER, U., Z. M. GLIWICZ, W. LAMPERT, AND A. DUNCAN. 1986. The PEG-model of seasonal succession of planktonic events in fresh waters. *Arch. Hydrobiol.* **106**: 433–471.
- SORANNO, P. A., S. R. CARPENTER, AND X. HE. 1993a. Zooplankton biomass and body size, p. 172–188. *In* S. R. Carpenter and J. F. Kitchell [eds.], *The trophic cascade in lakes*. Cambridge Univ. Press.
- , ———, AND S. M. MOEGENBURG. 1993b. Dynamics of the phantom midge: Implications for zooplankton, p. 103–115. *In* S. R. Carpenter and J. F. Kitchell [eds.], *The trophic cascade in lakes*. Cambridge Univ. Press.
- STERNER, R. W. 1989. The role of grazers in phytoplankton succession, p. 107–170. *In* U. Sommer [ed.], *Plankton ecology: Succession in plankton communities*. Springer-Verlag.
- STEWART, D. J., J. F. KITCHELL, AND L. B. CROWDER. 1981. Forage fish and their salmonid predators in Lake Michigan. *Trans. Am. Fish. Soc.* **110**: 751–765.
- STRONG, D. R. 1986. Density vagueness: Abiding the variance in the demography of real populations, p. 257–268. *In* J. Diamond and T. J. Case [eds.], *Community ecology*. Harper and Row.
- STROSS, R. G., J. C. NEESS, AND A. D. HASLER. 1961. Turnover time and production of planktonic Crustacea in limed and reference portions of a bog lake. *Ecology* **42**: 237–245.
- SUMMERFELT, R. C. 1975. Relationship between weather and year-class strength of largemouth bass, p. 166–174. *In* R. Clepper [ed.], *Black bass biology and management*. Sport Fishing Institute.
- TREBITZ, A. S. 1991. Timing of spawning in largemouth bass: Implications of an individual-based model. *Ecol. Modell.* **59**: 203–227.
- VANNI, M. J. 1988. Freshwater zooplankton community structure: Introduction of large invertebrate predators and large herbivores to a small-species community. *Can. J. Fish. Aquat. Sci.* **45**: 1758–1770.
- WERNER, E. E., AND J. F. GILLIAM. 1984. The ontogenetic niche and species interactions in size-structured populations. *Annu. Rev. Ecol. Syst.* **15**: 393–425.

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