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PERTURBATION AND RESILIENCE: A LONG-TERM, WHOLE-LAKE STUDY OF PREDATOR EXTINCTION AND REINTRODUCTION¹

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Abstract. This paper presents the results of a long-term study of changing predator densities and cascading effects in a Michigan lake in which the top carnivore, the largemouth bass (*Micropterus salmoides*), was eliminated in 1978 and then reintroduced in 1986. The elimination of the bass was followed by a dramatic increase in the density of planktivorous fish, the disappearance of large zooplankton (e.g., two species of *Daphnia* that had historically dominated the zooplankton community), and the appearance of a suite of small-bodied cladoceran (zooplankton) species. The system remained in this state until bass were reintroduced. As the bass population increased, the system showed a steady and predictable return to its previous state; planktivore numbers declined by two orders of magnitude, large-bodied *Daphnia* reappeared and again dominated the zooplankton, and the suite of small-bodied cladocerans disappeared. Within each cladoceran species there was a steady increase in mean adult body size as planktivore numbers declined. Total zooplankton biomass increased ≈ 10 -fold following the return of large-bodied *Daphnia*, and water clarity increased significantly with increases in *Daphnia* biomass and total cladoceran biomass. These changes in community structure and trophic-level biomasses demonstrate the strong impact of removing a single, keystone species, and the capacity of the community to return to its previous state after the species is reintroduced.

Key words: cascading effects; food-chain; keystone predator; Michigan; *Micropterus*; predation; species interactions; trophic level; W. K. Kellogg Biological Station; zooplankton.

INTRODUCTION

Predicting the effects of biotic and abiotic perturbations in natural communities is the litmus test of any theory professing to explain how communities function. As ecologists we would like to be able to predict, for example, what happens to a community when a species is added or removed. The ability to make such predictions would demonstrate a working knowledge of the processes structuring communities, and it would help guide efforts to conserve native species and forecast the impacts of biological invaders. However, this straightforward goal is often difficult to achieve due to the complexity of natural systems. Most ecological communities consist of a diverse array of species whose interactions are often poorly known, and a multitude of biotic and abiotic processes may potentially influence the dynamics of each species and its life stages. Therefore, predicting the consequences of species extinctions or invasions seems a daunting task.

One way to deal with complex communities is to focus on the interaction strengths between species and to try to identify specific subsets of interactions that govern the primary dynamics of a community (e.g., MacArthur 1972, Paine 1992). The most dramatic examples of strong interactors are “keystone species,” whose removal leads to a striking change in community structure (Paine 1969, 1980, Estes and Palmisano 1974, Brown and Heske 1990, and others). However, as Mills et al. (1993) note, we do not know how commonly keystone species are present in natural communities, nor are there many studies that address both the short- and long-term effects of species removals.

Recent studies in freshwater communities have provided some of the clearest demonstrations of strong impacts of top predators on lower trophic levels (e.g., Henrikson et al. 1980, Power et al. 1985, Carpenter et al. 1987, Kerfoot and Sih 1987, Benndorf 1990, Turner and Mittelbach 1990, Bronmark et al. 1992, Martin et al. 1992, Carpenter and Kitchell 1993). However, in most of these experimental studies, the time-frame is short, the spatial-scale small, and the fish “populations” static. Even in manipulations of whole lakes (e.g., Henrikson et al. 1980, Carpenter et al. 1987, Elser and Carpenter 1988, Reinertsen et al. 1990, Carpenter

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and Kitchell 1993), the temporal scale is typically abbreviated (often on the order of 2–3 yr per manipulation), and the dynamics of the fish are largely limited to behavioral responses and within-generation dynamics. Further, most studies have followed a trophic-level manipulation in only one direction (i.e., a species is either added or removed) and there are few data on the capacity of freshwater communities to return to their previous state once a perturbation has ended (but see Carpenter and Kitchell 1993, Persson et al. 1993). Studies that follow a system through a “full cycle of change” (e.g., species removal followed by species addition) allow one to ask not only if the system responds to a perturbation in the direction and magnitude predicted, but also whether (and how quickly) the system returns to its original state after the perturbation is removed (the system’s resilience, *sensu* Holling 1973).

Here we present the results of a long-term study of the cascading effects associated with changing piscivore densities in a small, Michigan lake in which the dominant piscivore, the largemouth bass (*Micropterus salmoides*), was eliminated by a natural event in 1978 and then intentionally reintroduced in 1986. Using data from our own studies and the studies of Threlkeld (1979), Hall and Ehlinger (1989), and Johannes (1990), we show that the response of fish and zooplankton to the elimination of the bass was dramatic and in the direction predicted by cascading trophic interactions (Carpenter et al. 1985) and size-selective predation. Moreover, we show that reintroduction of bass was followed by a steady and predictable return of the system to its previous state. The effects of these perturbations, observed over 15 yr and a full cycle of change, illustrate that the species composition and biomass of a complex community may be driven by the interactions among a few, key species.

METHODS

Site description and recent history

Wintergreen Lake is a small (15 ha), shallow (6.3 m maximum depth, 2.5 m mean depth), hardwater lake located on the W. K. Kellogg Biological Station (KBS) in southwestern Michigan. Because it is part of the Kellogg Bird Sanctuary, Wintergreen receives substantial nutrient input from both resident and migratory waterfowl (Fetterolf 1952, Manny et al. 1975), has an annual mean pelagic productivity $>1200 \text{ mg C} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ (Manny 1971, Manny et al. 1975), and is classified as hypereutrophic by Wetzel (1983). The number of ducks and geese using Wintergreen Lake has remained relatively constant for the past 20 yr (W. C. Johnson, resident manager, *personal communication*) and limnological data from a variety of sources show no major changes in nutrients or water chemistry during this time (see *Discussion*). The phytoplankton of Wintergreen Lake tends to be dominated by cryptomonads, *Chlamydomonas*, and other small flagellated algae in spring;

by midsummer the phytoplankton shifts to large blue-green algae (e.g., *Anabaena*, *Aphanizomenon*, and *Microcystis*). The lake thermally stratifies at 2–3 m depth and deoxygenation of the hypolimnion occurs rapidly after stratification. Because Wintergreen Lake is relatively shallow and very eutrophic, it is subject to low oxygen concentrations during winters with long ice cover and heavy snowfall, which limit photosynthesis (Hall and Ehlinger 1989).

Fish surveys conducted sporadically from 1930 to 1965 document that Wintergreen had a typical warmwater fish community. Sunfishes (Centrarchidae) dominated the community biomass; the largemouth bass was the most abundant predator and the bluegill sunfish (*Lepomis macrochirus*) was the overall numerical and biomass dominant (Cooper 1935, Funk 1942, Fetterolf 1952; W. C. Johnson, *personal communication*). During 1976–1978, back-to-back winters of dense snow and extended ice cover resulted in severe oxygen depletion and complete elimination of bluegill and bass from the lake (Hall and Ehlinger 1989). More tolerant species [e.g., pumpkinseed (*L. gibbosus*), golden shiner (*Notemigonus crysoleucas*), yellow perch (*Perca flavescens*), grass pickerel (*Esox americanus vermiculatus*), bowfin (*Amia calva*), and yellow bullhead (*Ictalurus natalis*)] persisted. The only outlet (there is no stream inlet) to the lake does not allow fish migration, so no natural recolonization has occurred since the winterkill.

Hall and Ehlinger (1989) documented many of the changes that occurred in the fish and zooplankton communities in the years immediately following the winterkills of 1977 and 1978. Most notably, after the elimination of bass and bluegill, the fish community became dominated by zooplanktivorous fish, particularly the golden shiner, a large minnow that is an extremely efficient planktivore (Ehlinger 1989). Coincident with this change in the fish community was a shift in the zooplankton assemblage from a community dominated by large-bodied *Daphnia* (*D. pulicaria* and *D. galeata mendotae*) (Threlkeld 1979) to a community composed primarily of small-bodied cladocerans (e.g., *Bosmina*, *Ceriodaphnia*, and *Diaphanosoma*) (Hall and Ehlinger 1989).

Piscivore reintroduction

Hall and Ehlinger (1989) showed experimentally that predation by planktivorous fish was the main factor preventing large *Daphnia* from occupying Wintergreen Lake after the winterkill, and they predicted that “if piscivorous fish are restocked in Wintergreen Lake, the current fish–zooplankton assemblage will probably revert to its prewinterkill structure” (Hall and Ehlinger 1989:2209). We tested this prediction by reintroducing largemouth bass to Wintergreen Lake. In the fall of 1986, ≈ 700 young-of-year (YOY) bass (60 mm average standard length [SL]) were collected from the KBS experimental pond facility and introduced to Wintergreen Lake as a cohort. We followed the dynamics

of this bass population, as well as the dynamics of the other common fish species and the zooplankton, over the next 7 yr.

Fish sampling

We assessed fish abundances via mark-recapture techniques, as did previous studies conducted by other researchers in 1951 and 1987, 1988. Fetterolf (1952) conducted the first quantitative survey in 1951, capturing fish by hoop nets, a Great Lakes trap net, and by angling. Small fish (<120 mm SL) were not included in Fetterolf's estimates, apparently because of the large (3.75–6.25 cm) mesh size of the nets. Johannes (1990) sampled the lake in late summer of 1987 and 1988 using multiple census mark-recapture techniques (Schnabel 1938, Ricker 1975). Johannes (1990) marked fish by clipping their caudal fin and recaptured them during a 2-wk period using purse seines (31 × 9.8 m, 1-mm mesh) and beach seines (31 × 1.8 m, 5-mm mesh); >5% of the estimated populations of the most common species were marked. Largemouth bass were too rare in 1987 and 1988 to estimate via mark-recapture and their abundances were instead estimated via proportional catches (as compared to yellow perch and pumpkinseed). We conducted a similar mark-recapture in collaboration with Johannes in late-summer 1989, and our own mark-recaptures in mid- to late-summer 1991 and 1993. The 1991 and 1993 mark-recaptures relied primarily on beach seining as the collection technique, using two seine sizes (23 × 1.8 m, 3.2-mm mesh, and 61 × 2.5 m, 6.4-mm mesh). In 1991 we marked >2800 fish collected from 51 seine hauls and in 1993 we marked >550 fish collected from 36 seine hauls. On average, 9% of the population of each of the four most common fish species (i.e., largemouth bass, pumpkinseed, yellow perch, and golden shiner) were marked in 1991; 5% of the bass, pumpkinseeds and yellow perch were marked in 1993 (golden shiners were essentially absent).

Zooplankton sampling

From 1984 to 1993, zooplankton were sampled by taking three vertical net tows through the entire water column (6–6.5 m depth) with a 30 cm diameter 153- μ m mesh plankton net from a single station at the deepest part of the lake. In most years, sampling began in April or May, and samples were collected approximately once every 2 wk until October. The number of sampling dates processed for any given year included at least one per month, generally more. Samples were collected during the day and preserved in a 4% solution of cold sugar formalin. Water temperature, dissolved oxygen, and secchi depth were also recorded. Zooplankton were counted and measured under a dissecting scope. Two (or more) aliquots were taken from each sample and all zooplankton in an aliquot were counted. Counts were then converted to numbers per litre (assuming a net efficiency of 100%). Cladocera were iden-

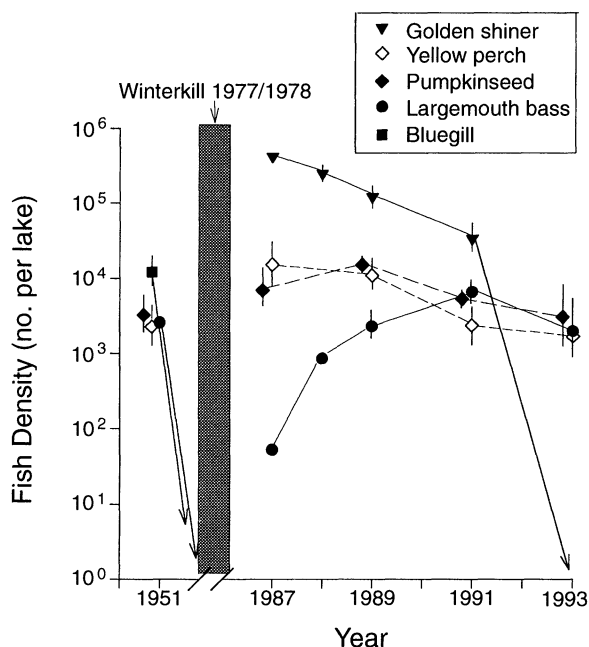


FIG. 1. Mark-recapture estimates of population size for the five most common fish species in Wintergreen Lake (note the y axis is a log scale). Vertical bars denote 95% CIs; CIs are sometimes contained within the symbols and are not available for largemouth bass in 1987, 1988. Arrows pointing towards the x axis for the bluegill and largemouth bass populations indicate that these species were eliminated from the lake by severe winterkills in 1977 and 1978. Golden shiners were present in 1951, but were not captured by the large-mesh trap nets used. Estimates of golden shiner densities prior to 1977/1978 indicate that they were less abundant than either bluegill, pumpkinseed, bass, or yellow perch (Cooper 1935, Fetterolf 1952, Hall and Ehlinger 1989). Bass were reintroduced as young-of-year in 1986. The arrow pointing towards the x axis for the golden shiner population in 1993 indicates that the only shiners captured were 30 young-of-year fish.

tified to species, copepods to suborder (i.e., calanoids and cyclopoids). From each sample, ≈ 50 randomly chosen individuals of each taxon were measured for total body length (exclusive of tail spines), and lengths were converted to biomasses using previously determined, taxon-specific length-mass regressions. We also report zooplankton data collected in 1976 by Threlkeld (1979) and in 1982 by Hall and Ehlinger (1989); zooplankton were sampled via vertical net tows (145- μ m mesh net) and 4-L Van Dorn samples in Threlkeld's study and via vertical net tows (156- μ m mesh net) in the study by Hall and Ehlinger.

RESULTS

Fish dynamics

The stocking of bass in 1986 was followed by a rapid increase in bass density and a subsequent decline in the density of other fishes (Fig. 1). By 1993, the bass population had reached ≈ 2000 fish/lake (a 40-fold increase in biomass), and this estimate is similar to the

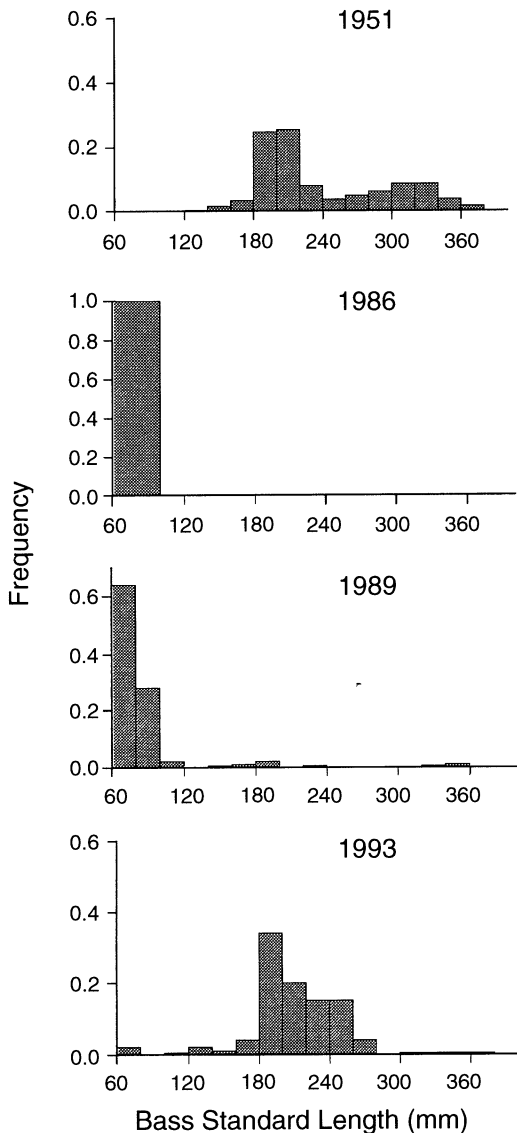


FIG. 2. Size-frequency distributions of largemouth bass collected from Wintergreen Lake; $n = >200$ fish for each panel except 1986, which shows the introduced bass cohort.

historical estimate of Fetterolf (1952) (Fig. 1). The current size structure of the bass population also approaches that observed by Fetterolf in 1951 (Fig. 2). Golden shiners are very vulnerable to bass predation (Johannes et al. 1989, Carpenter and Kitchell 1993), and their numbers declined steadily following the reintroduction of bass (Fig. 1). In 1987, shiner numbers were estimated at over 400 000 fish/lake. Shiners declined to ≈ 34 000 fish/lake by 1991 (Fig. 1), and by July 1993 we failed to catch a single adult golden shiner in over 60 beach seine and trap-net collections conducted over a 2-wk mark-recapture period (≈ 30 young-of-year golden shiners were collected).

The demise of golden shiners in Wintergreen was matched by a similar, though less dramatic decline in

the abundance of other potentially planktivorous fishes (Fig. 1). Yellow perch decreased from ≈ 15 000 fish/lake in 1987 to 1700 fish/lake in 1993. Pumpkinseeds, which may be planktivorous in the absence of bluegill (Robinson et al. 1993; G. G. Mittelbach et al., *personal observation*), also declined from ≈ 7000 fish/lake in 1987 to 3100 fish/lake in 1993. The magnitude of population decline in these fishes mirrors their relative vulnerability to bass, i.e., golden shiner $>$ yellow perch $>$ pumpkinseed (Lawrence 1957, Webb 1986, Hoyle and Keast 1987, Hambright 1991, Hambright et al. 1991).

The intensity of planktivory in Wintergreen Lake has therefore undergone a complete cycle of change over the past 20 yr; planktivory was low to moderate prior to the 1976–1978 winterkills, increased dramatically after bass were eliminated, and then declined to low levels with the reintroduction of bass and the continued absence of bluegill. This cycle of change in planktivore density is clearly reflected in the abundance, species composition, and size structure of the zooplankton community.

Zooplankton dynamics

Prior to the 1976–1978 winterkills, the Wintergreen zooplankton community was dominated by two large daphnids, *Daphnia pulicaria* and *D. galeata mendotae* (Fig. 3) (Haney and Hall 1975, Threlkeld 1979, Hall and Ehlinger 1989). Other cladocerans were rare and Threlkeld notes that small cladocerans were essentially absent during the period of his study, summer 1976 (S. T. Threlkeld, *personal communication*). Following winterkill and the dramatic increase in golden shiner numbers, large *Daphnia* disappeared from the lake (Fig. 3) (Hall and Ehlinger 1989). Replacing these large *Daphnia* was a suite of smaller cladocerans—*Bosmina longirostris*, *Ceriodaphnia reticulata*, *Diaphanosoma brachyurum*, *D. parvula*, and *D. ambigua* (Figs. 3 and 4). Although *D. parvula* was also present in 1976, it was restricted to the early spring before *D. pulicaria* and *D. galeata mendotae* became abundant (Fig. 3).

As golden shiner numbers decreased following the 1986 reintroduction of bass, the zooplankton community showed a steady return to its former state. *Bosmina*, the smallest cladoceran present, was numerically dominant throughout most of the summer in 1982 and 1984 (reaching densities >100 individuals/L) (Fig. 4). However, by 1989 and 1990, *Bosmina* was common only in early spring, and after 1991 it was rarely seen (Fig. 4). Two medium-size cladocerans, *Ceriodaphnia* and *D. parvula*, dominated the Wintergreen zooplankton community from 1989 to 1991 (Figs. 3 and 4). Then, in fall 1991, *Daphnia pulicaria* reappeared in Wintergreen Lake after more than a 10-yr absence (Fig. 3). Hall and Ehlinger (1989) document that the absence of *D. pulicaria* (and *D. galeata mendotae*) during this time period was not due to a lack of colonists, as they introduced thousands of *Daphnia* when they emptied

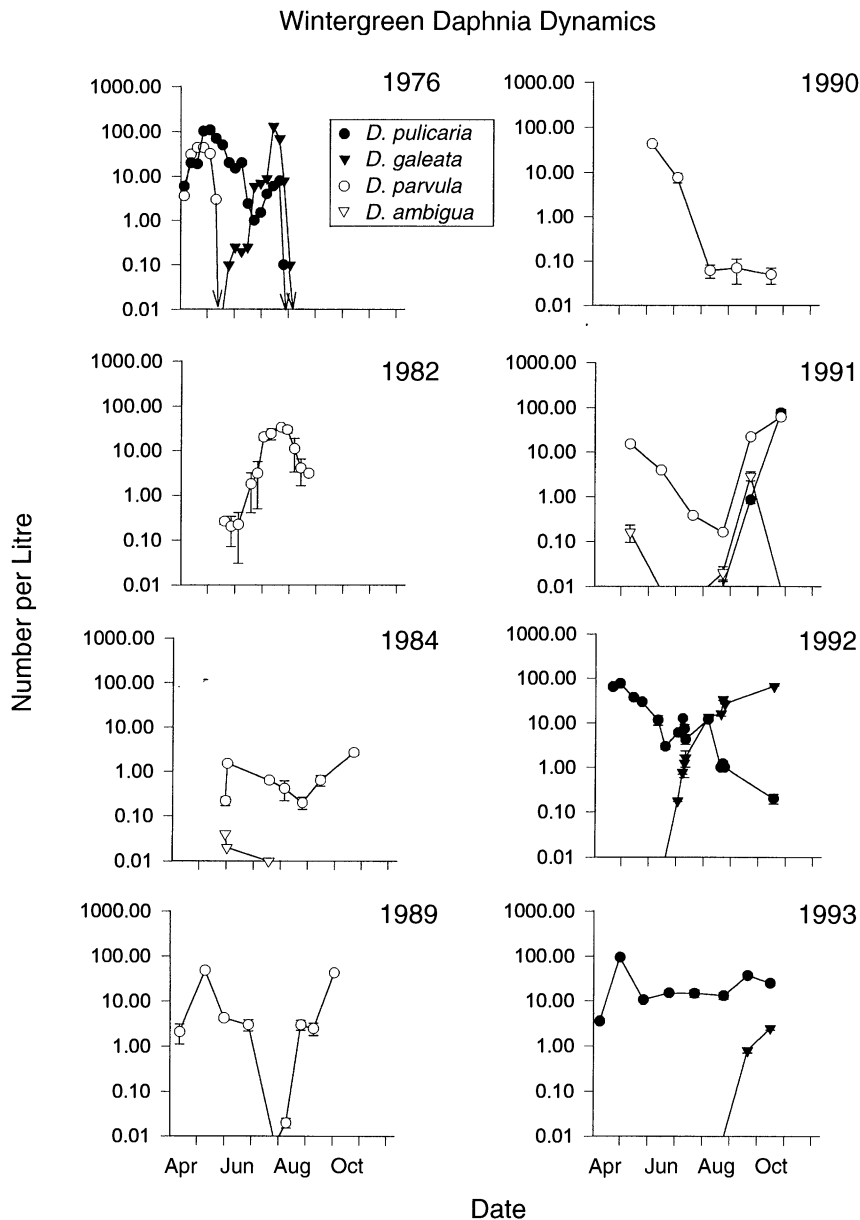


FIG. 3. *Daphnia* dynamics in Wintergreen Lake from 1976 to 1993 (mean densities ± 1 SE). Shaded symbols are for *D. pulicaria* and *D. galeata mendotae*, two large-bodied species, and open symbols are for *D. parvula* and *D. ambigua*, two small-bodied species. In 1993 the *D. pulicaria* population was a mixture of *D. pulicaria* and asexual *D. pulex* (see Results: Zooplankton dynamics for details). Arrows pointing toward the x axis in 1976 indicate that a species was absent after a given sampling date.

their experimental enclosures. The reappearance of *D. pulicaria* was followed by the return of the second, historically dominant species, *D. galeata mendotae*, in July 1992. The dynamics and composition of the zooplankton community in 1992 were very similar to the pre-winterkill pattern documented by Threlkeld (1979). *D. pulicaria* and *D. galeata mendotae* were again the two dominant cladocerans in the plankton (Figs. 3 and 4). *D. pulicaria* was most abundant in early spring and then declined over the summer, while *D. galeata men-*

dotae appeared after the peak in *D. pulicaria* density and increased in June and July. Unlike 1976, however, the two *Daphnia* species remained extant in the lake throughout the summer and fall of 1992.

By 1993, planktivory in Wintergreen Lake had arguably reached the lowest levels in recent history: adult golden shiners were essentially absent, bluegill were absent, and yellow perch densities were only 11% of what they were in 1987 (74% of their 1951 densities). During 1993, small cladocerans were extremely rare in

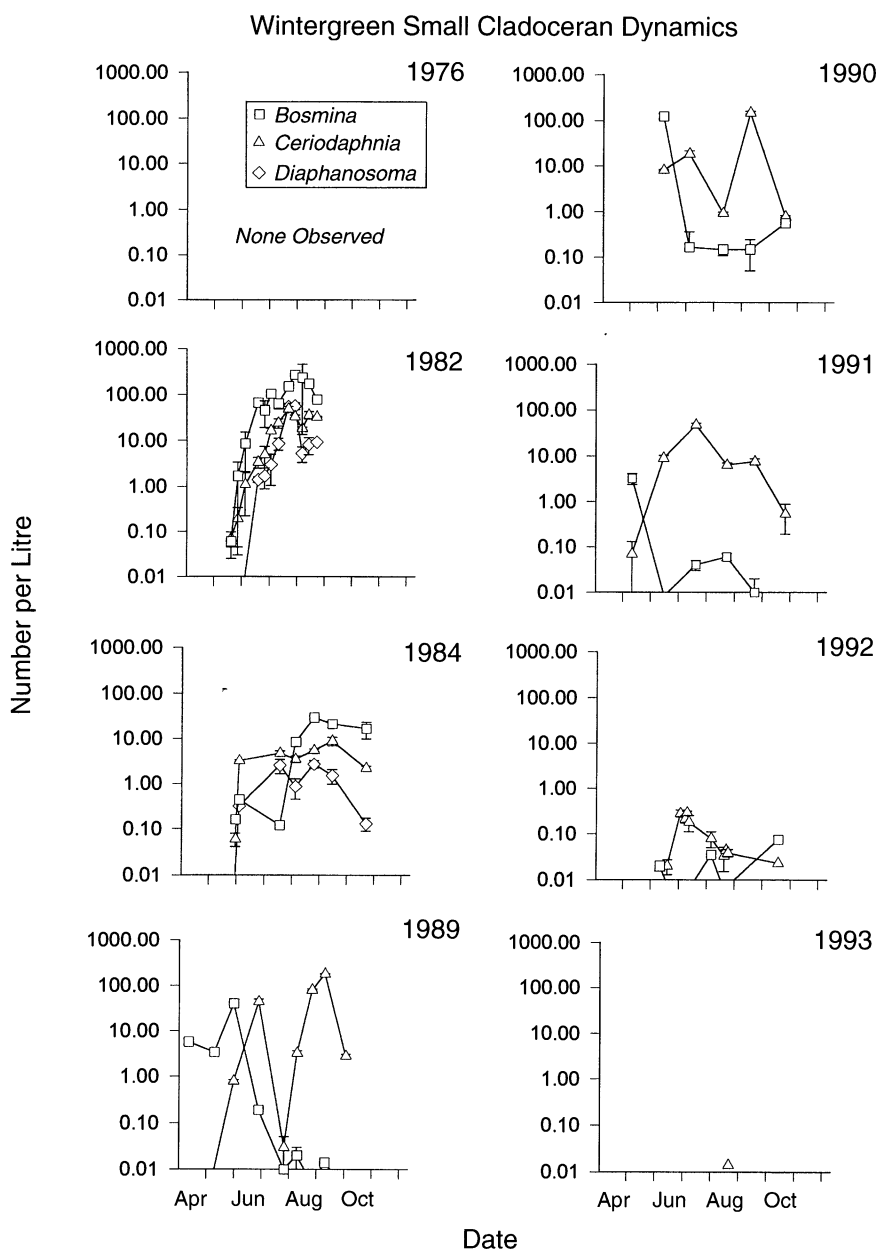


FIG. 4. Small cladoceran dynamics in Wintergreen Lake from 1976 to 1993 (mean densities ± 1 SE). Quantitative data for 1976 are not available, but qualitative observations document that small cladocerans were extremely rare (S. T. Threlkeld, *personal communication*).

the plankton (Fig. 4) and *D. galeata mendotae* occurred only in very low numbers in the fall. Instead, the plankton was dominated throughout the summer by *D. pulicaria* and a morphologically indistinguishable sibling species, asexual *D. pulex* (Hebert et al. 1993). *D. pulex* is commonly found in small ponds and fishless lakes (Hebert et al. 1993) and was not observed in Wintergreen in 1992 (results of electrophoretic studies of A. Tessier and K. Geedey, *personal communication*). Because these two groups can only be distinguished elec-

trophoretically, we did not separate them in our plankton counts.

The reintroduction of bass and the subsequent decline in planktivorous fish were followed by a 10-fold increase in total cladoceran biomass (Fig. 5) and a more than twofold increase in average cladoceran body length (Fig. 6). Copepods, on the other hand, showed no change in total biomass through time (Fig. 5) and only a slight increase (<10%) in body length (Fig. 6). The dramatic increase in cladoceran body size through

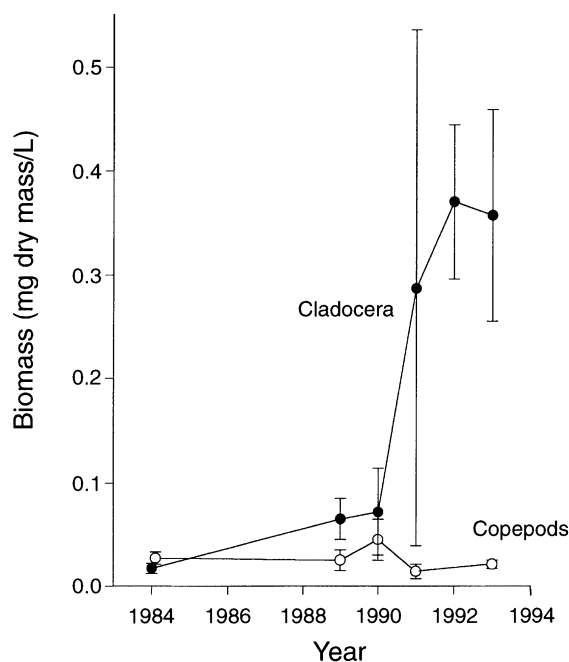


FIG. 5. Mean (± 1 SE) biomass (mg dry mass/L) of cladocerans and copepods in Wintergreen Lake from 1984 to 1993. Yearly mean biomass determined by summing the total biomass of each cladoceran (or copepod) taxon present on a given date, and then averaging across all sample dates within a year. Copepods were present in 1992 but were not counted.

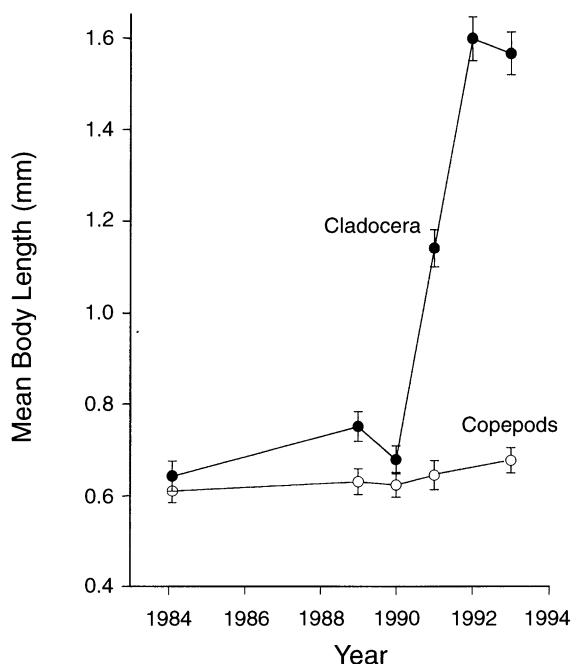


FIG. 6. Average body length ($\bar{X} \pm 1$ SE) of cladocerans and copepods in Wintergreen Lake from 1984 to 1993. Yearly means determined by calculating the average body length for each sample date and then averaging across dates; contributions of individual taxa to sample date means were weighted by taxon density.

time was due to two factors: (1) replacement of smaller species by larger species (Figs. 3 and 4), and (2) an increase in average size within a species (Fig. 7). By 1993, the average adult *Daphnia* size had reached nearly 2 mm, and the lake was dominated by the largest *Daphnia* species found in the region.

Water clarity

There were pronounced differences in water clarity (as measured by secchi depth) associated with the presence or absence of large *Daphnia* (i.e., *D. pulicaria*, *D. galeata mendotae*, and *D. pulex*) in Wintergreen Lake. Large *Daphnia* were absent from 1982 through the fall of 1991 (Fig. 3), and during this period mean monthly secchi depths averaged 1.1 ± 0.07 m ($\bar{X} \pm 1$ SE) and only once reached 2 m. In contrast, during the years when large *Daphnia* were abundant (1992 and 1993), secchi depths averaged 2.9 ± 0.3 m, and often exceeded 4 m. In 1976, prior to the winterkill, secchi depth was also >4 m in early spring when *D. pulicaria* was abundant, but declined to ≤ 1 m when *Daphnia* disappeared in late summer. There was a significant, positive relationship between cladoceran biomass and secchi depth ($r = 0.55$, $P = 0.001$, $n = 31$; Fig. 8). A virtually identical relationship is found between *Daphnia* biomass and secchi depth ($r = 0.56$, $P = 0.001$, $n = 31$), as most of the variation in cladoceran biomass among dates and years in Wintergreen Lake is driven by the abundance of *Daphnia*.

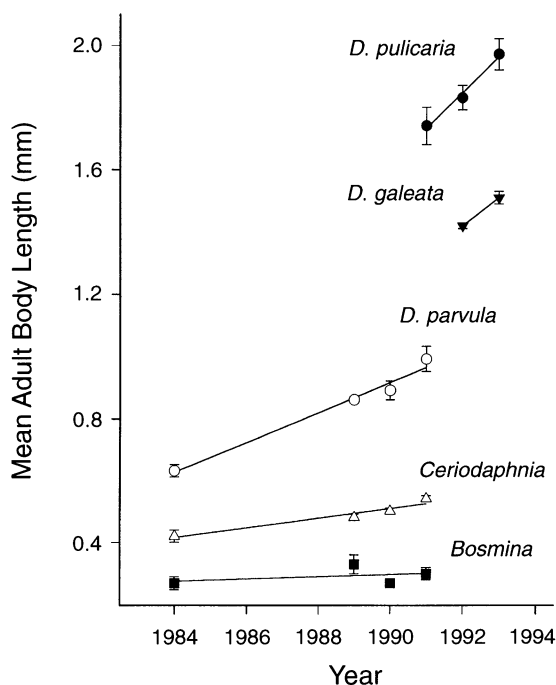


FIG. 7. Average adult body length ($\bar{X} \pm 1$ SE) for individual cladoceran species in Wintergreen Lake from 1984 to 1993. For each species, adults were defined as all individuals larger than the smallest individual observed carrying eggs.

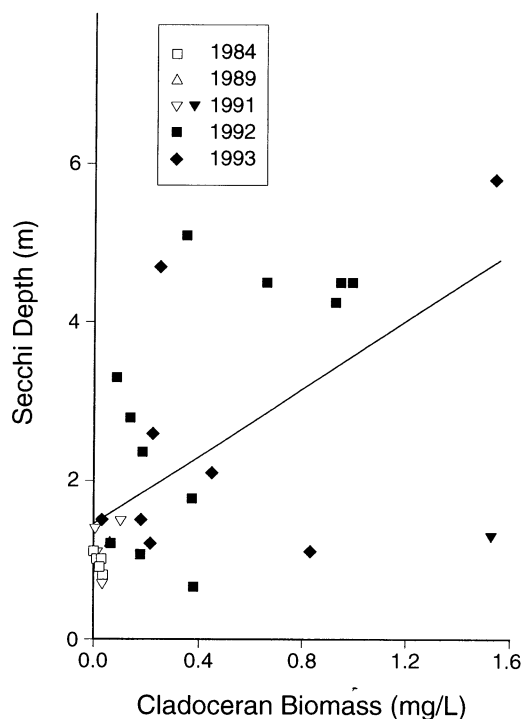


FIG. 8. Secchi depth as a function of total cladoceran biomass in Wintergreen Lake from 1984 to 1993 (cladoceran biomasses not available from 1976 and 1982). Closed symbols indicate periods when large *Daphnia* dominated the zooplankton.

While total cladoceran biomass, or *Daphnia* biomass, each explain a significant fraction of the variation in secchi depth, there is considerable scatter in these relationships (e.g., Fig. 8). At least some of this variation is related to sampling date. The residuals from these relationships are negatively correlated with sampling date ($r = -0.45$, $P = 0.01$, $n = 31$ for cladoceran biomass; $r = -0.40$, $P = 0.03$, $n = 31$ for *Daphnia* biomass), suggesting that a given biomass of cladocerans (or *Daphnia*) results in greater water clarity in spring than in late summer. This is consistent with the observation that the phytoplankton in Wintergreen (and many temperate lakes) becomes dominated by relatively inedible forms in mid to late summer (Wetzel 1983, Sommer et al. 1986, Lampert et al. 1986, Sterner 1989, Vanni and Temte 1990, Sarnelle 1993).

DISCUSSION

The elimination and reintroduction of a top predator in Wintergreen Lake dramatically changed the species composition and size structure of the fish and zooplankton communities. These changes were in the direction predicted by cascading trophic interactions and size-selective predation, and they support a growing number of aquatic studies documenting strong effects of upper trophic levels (usually fish) on the structure and biomass of pelagic and littoral zone communities

(e.g., Henrikson et al. 1980, Shapiro and Wright 1984, Power et al. 1985, Gulati et al. 1990, Vanni et al. 1990, Bronmark et al. 1992, Bronmark 1994, Carpenter and Kitchell 1993, and references therein). The response of the Wintergreen community to changes in the density of a top carnivore was unusually strong in comparison to most piscivore manipulations. Moreover, the response was played out over a number of generations and through a complete cycle of change in the abundance of the top predator. As a result, this study offers a number of insights into the effects of a keystone predator on pelagic community structure.

Interpreting the results

In any unreplicated study (such as this and most other whole-lake manipulations), there are two critical questions regarding the interpretation of results (Carpenter and Kitchell 1993): (1) did the system change following the manipulation, and (2) did the manipulation cause the change? In the case of Wintergreen Lake, there is little doubt that the fish and zooplankton communities changed following the extinction and reintroduction of the bass. For example, the two historically dominant zooplankters (*D. pulicaria* and *D. galeata mendotae*) completely disappeared from the lake for at least 10 yr following the removal of bass, and then reappeared and again became dominant after bass were reintroduced. Other species showed similarly dramatic changes, as did the size structure of the zooplankton community.

The second question, did the manipulation cause the changes, cannot be addressed statistically in any unreplicated study. Instead, resolution of this issue often rests on the ecological interpretation of the results and in demonstrating that the manipulation is the most likely cause of the change (Frost et al. 1988, Carpenter et al. 1989, Rasmussen et al. 1993). Therefore, we focus our discussion on three crucial aspects of the study: (1) well-established mechanisms of species interactions can explain the observed results, as can general models of food-chain dynamics, (2) alternative hypotheses are unable to account for the dynamics, and (3) the system's dynamics following the removal and reintroduction of the predator mirrored one another, providing a "double test" of the predictions.

Mechanisms of species interactions

Most planktivores, including the golden shiner, are size-selective predators and feed preferentially on larger zooplankton (Hall et al. 1979). Therefore, if changing golden shiner abundance was responsible for the zooplankton species replacements observed in Wintergreen Lake, there should be a concomitant change in zooplankton body size, i.e., zooplankton body size should decline when shiner numbers increase and should increase when shiner numbers fall. Further, this shift should be expressed most strongly in cladocerans, since cladocerans are the shiner's preferred prey (Hall et al. 1979, Ehlinger 1989). The data strongly support

this hypothesis. Before the winterkill, the zooplankton community was dominated by *Daphnia pulicaria* and *D. galeata mendotae*, whose adult body sizes ranged between 1.0 and 1.8 mm and 0.8 and 1.6 mm, respectively (Threlkeld 1979). After the winterkill and prior to the reintroduction of bass, these large *Daphnia* disappeared and the zooplankton community was dominated by small cladocerans (i.e., *Bosmina*, *Ceriodaphnia*, and *Diaphanosoma*) with average adult body sizes <0.5 mm. Experiments by Hall and Ehlinger (1989) in Wintergreen Lake showed that predation by golden shiners was responsible for the absence of large *Daphnia* during this period of high planktivory. When shiner numbers crashed following the reintroduction of bass, average adult body size increased for each cladoceran species (Fig. 7), with smaller bodied species eventually being replaced by larger species. On the whole, cladoceran body size increased from an average of 0.7 mm in 1984 to 1.5 mm in 1993; mean copepod body size, however, changed only slightly over this time period (0.61–0.68 mm). Therefore, the response in zooplankton size structure was consistent with the predicted impact of a rise and then fall in the intensity of size-selective planktivory.

The response of the fish community was also consistent with an increase in piscivory following the reintroduction of bass. The golden shiner showed the most dramatic response to the reintroduction of bass, declining from a density of almost a half million fish in 1987 to zero adult fish in 1993. Johannes et al. (1989) and Carpenter and Kitchell (1993) have documented that bass can inflict very high mortality on golden shiners and in nearby lakes containing bass, the golden shiner is always rare in comparison to the other species (Werner et al. 1977, Hall et al. 1979; G. G. Mittelbach et al., *personal observation*). Perch and pumpkinseeds in Wintergreen Lake declined 89 and 56%, respectively, over the same time period. These deeper bodied, spiny-rayed fishes are less vulnerable to bass predation than are narrow-bodied, soft-rayed cyprinids (minnows) such as the golden shiner (Tonn and Magnuson 1982, Hambright et al. 1991).

While the numerical response of the shiner to the return of bass was striking and occurred in <10 yr, there was also a behavioral response that occurred much more rapidly. In the early 1980s shiners were found in large numbers in the limnetic zone during the day and hundreds could be caught per hour in a single daytime gillnet (D. Hall, *personal observation*). However, within 3 yr after the bass were reintroduced, shiners became rare in the limnetic zone during the day (e.g., we caught <100 shiners total in gillnets set on eight different days from April to July 1989). Instead, shiners were found in large schools in the littoral zone during the day and migrated to the open water at dawn and dusk to feed on plankton, as they do in other lakes (Hall et al. 1979). Carpenter et al. (1987) also found a rapid, behavioral response by minnows in Peter Lake

to the presence of largemouth bass, and Johannes (1993) showed increased aggregation (schooling) by golden shiners with an increase in bass density.

The dramatic response of the fish community to the reintroduction of bass was not simply the result of reintroducing piscivores to a predator-free system. Four species of piscivorous fish survived the winterkill (i.e., bowfin, bullhead, grass pickerel, and large yellow perch) and were present in Wintergreen Lake throughout the study. These species, however, failed to control the golden shiner population. In contrast, largemouth bass, after their reintroduction, drove golden shiners to near extinction. The inability of yellow perch to control shiner numbers is especially interesting in light of work by Persson and his co-workers documenting strong effects of a morphologically similar species, the European perch (*Perca fluviatilis*), on cyprinid fishes in Scandinavian lakes (Persson 1988, Persson et al. 1991). Their work, however, also shows that European perch are less effective predators in highly productive lakes, which corresponds to the situation in Wintergreen.

The above results suggest that there are particular aspects of the bass's biology that allow it to strongly depress prey populations and to function as a keystone predator. A variety of studies from small lakes and ponds suggests that bass are more effective predators than are other piscivores (e.g., Swingle and Smith 1940, Stroud and Clepper 1975), e.g., their functional response may have a higher slope, or they may be better able to maintain high foraging rates in a variety of habitats. However, there is little specific information on what features of the bass's functional morphology, foraging behavior, or life history characteristics allow it to effectively control prey populations when other piscivorous fish cannot. Answering these types of questions, for the bass or any other species, is at the heart of understanding why some species function as keystone predators, while others do not (Mills et al. 1993, Menge et al. 1994).

Trophic cascades

There is a growing body of evidence documenting that sustained, high levels of piscivory can cascade down the food chain to produce reduced numbers of planktivores, increased zooplankton size, and often increased water clarity (see Henrikson et al. 1980, Shapiro and Wright 1984, Carpenter et al. 1987, Northcote 1987, Benndorf 1990, Carpenter and Kitchell 1993, and references therein). In Wintergreen Lake average zooplankton body length doubled and total zooplankton biomass increased by an order of magnitude following the reintroduction of largemouth bass. This increase was entirely due to the response by cladocerans (copepod biomass showed no change). During this time period (1984–1993), the pelagic zone of Wintergreen Lake went from a functionally three trophic level system (i.e., planktivores, zooplankton, phytoplankton), to a functionally four trophic level system. Food chain

theory (e.g., Oksanen et al. 1981, Carpenter et al. 1985) predicts that the addition of a fourth trophic level should lead to a decrease in the biomass of the third trophic level (planktivores), an increase in the biomass of the herbivore trophic level (zooplankton), and a decline in the primary producers (phytoplankton). Although we do not have direct measures of phytoplankton abundances in Wintergreen Lake, there is generally a good correlation between secchi depth and phytoplankton abundance when both variables are measured over a broad range within a lake (Wetzel 1983, Tilzer 1988). Therefore, the observed responses of Wintergreen Lake fish, zooplankton, and algae (as inferred by water clarity) are consistent with the predictions of food chain models. Other studies of predator manipulations have found mixed results at the planktivore and zooplankton levels. For example, Post and McQueen (1987) also found a significant negative relationship between planktivore biomass and total zooplankton biomass, while Benndorf (1987), Carpenter and Kitchell (1993), and Rudstam et al. (1993) found no relationship between planktivore density and total zooplankton biomass (although the biomass of large *Daphnia* species invariably declined).

The trophic cascade observed in Wintergreen Lake was very strong compared to other manipulations of top predators (see Benndorf 1990, Carpenter and Kitchell 1993 for reviews) and a number of factors probably contribute to this result. First, in our study the major predator was completely eliminated from the system (rather than being simply reduced in density), thereby removing any effect of a few, residual individuals (i.e., behavioral interactions, Carpenter et al. 1987). Second, no fishing is allowed in Wintergreen Lake. The lack of fishing mortality no doubt facilitated the bass population's rapid increase after reintroduction and contributed to the maintenance of a high standing stock. The importance of limiting fishing mortality on the top predator has been emphasized in a number of studies that have used piscivore introductions and/or enhancements to control planktivore densities (e.g., Benndorf 1990, Kitchell 1992). Third, Wintergreen Lake is very eutrophic (Wetzel 1983), and the strong effects associated with the extinction and reintroduction of bass may be related to the high level of primary production. Simple two-species Lotka-Volterra predator-prey models predict that the addition/removal of a top-level consumer will have a greater effect on resource abundance at high levels of productivity than at low levels (e.g., Mittelbach et al. 1988, Sarnelle 1992). Therefore, the magnitude of consumer effects on resource biomass should increase across a gradient of enrichment (Sarnelle 1992). The dramatic changes in Wintergreen Lake's fish and zooplankton communities associated with the extinction and reintroduction of a top predator, relative to more modest changes observed in other systems, are consistent with this prediction. The Wintergreen results also provide an example of a strong, tro-

phic cascade in a highly eutrophic lake, which runs counter to the expectations of McQueen et al. (1986) and Elser and Goldman (1991).

Alternate hypotheses

Three hypotheses come to mind as alternate explanations for the observed changes in the Wintergreen fish and zooplankton communities from 1976 to the present: (1) broad-scale climatic changes that affect the relative abundance of fish and zooplankton species regionally, (2) a change in the nutrient status or other abiotic conditions of Wintergreen Lake, and (3) a change in the abundance of invertebrate predators, which may impact zooplankton community structure. However, there is little empirical support for any of these hypotheses.

A number of studies conducted during the past 20 yr have examined the fish and zooplankton communities of other lakes near the Kellogg Biological Station and these studies document that the species composition and relative abundance of fish and zooplankton in these lakes have remained quite stable, at least in comparison to the whole-scale changes observed in Wintergreen Lake (see Hall and Werner 1977, Werner et al. 1977, Mittelbach 1981, 1984, Crumpton and Wetzel 1982, Osenberg et al. 1988, Werner and Hall 1988, Leibold 1989, 1991, Leibold and Tessier 1991, Tessier and Welser 1991, Mittelbach and Osenberg 1993, Olson 1993). There is also no evidence for a major change in nutrient input or other external forcing functions in Wintergreen Lake since at least the early 1970s. Data collected by R. Wetzel, A. Tessier, and L. Hedin (*personal communication*) from 1984 to 1993 show no major changes in conductivity, alkalinity, pH, NO₃, NH₄, or PO₃, from that recorded by Wetzel (1983) and others from the early to mid-1970s. There have been changes in water clarity, water temperature, and stratification (mixing depth) following the return of large *Daphnia* in 1991 (G. G. Mittelbach et al., *unpublished data*), however, these changes are consistent with Mazumder et al.'s (1990) hypothesis that reduced planktivory and increased zooplankton body size (biomass) should cause increased light penetration, greater solar heating, and deeper mixing depth. Thus, these changes in the physical environment are likely driven by the biotic interactions between species and are not themselves the agents responsible for the shifts in species composition and community structure. Finally, there is little to suggest that the dramatic changes observed in the zooplankton through time are driven by changes in invertebrate predation. *Chaoborus*, an aquatic midge larva that feeds on small-bodied zooplankton, is by far the most abundant invertebrate predator in Wintergreen Lake and can reach high densities (>1 individual/L). However, nighttime samples collected from 1989, 1992, and 1993 show that the density of the most abundant *Chaoborus* species, *C. punctipennis*, did not change significantly during the period when *Daphnia*

reinvaded the lake and small-bodied cladocerans disappeared (ANOVA test for year effects: $F_{2,6} = 2.86$, $P > 0.10$).

System predictability and resilience

Although the mechanisms underlying the changes observed in Wintergreen Lake have been well documented in other systems, as has the occurrence of trophic cascades, there remain few examples in either aquatic or terrestrial systems where a top predator has been removed and then reintroduced to a system and the community response followed for at least a generation. In fact, Connell and Sousa (1983:806–807) in their review of the evidence for community stability and persistence state, “. . . there is, to our knowledge, no evidence to show that following a disturbance any community has adjusted back to its original species composition which then resisted change beyond one complete turnover.” Although we cannot say whether our own study would satisfy the rigorous criteria set forth by Connell and Sousa, it is clear that the response by this system demonstrates a great deal of predictability and resilience (e.g., Figs. 3 and 4). This system also appears to exhibit “global stability” (sensu Lewontin 1969, Sutherland 1974) in that it returned to its original state following perturbation, rather than shifting to another configuration.

Carpenter et al. (1985) published a graphical prediction for how an open-water community should respond to the partial winterkill of a top predator and its subsequent return, and their predictions are convincingly matched by the observed dynamics in Wintergreen Lake. The Wintergreen system in fact returned to its initial state in more precise detail than Carpenter and Kitchell predicted, as the zooplankton community is not only again dominated by large-bodied cladocera, but the dominants are the same species of *Daphnia* that were present 20 yr ago. Two factors probably facilitated the return to this state. First, both *Daphnia* species produce resting egg (ephippia) that may remain viable in the sediments for many years. Second, these *Daphnia* species are the most common large daphnids found in nearby lakes. Therefore, it is very likely that they would be the first *Daphnia* species to recolonize Wintergreen Lake once conditions again became favorable for large cladocerans.

While the fish and zooplankton communities in Wintergreen Lake have in most ways returned to their previous states, there are a few notable differences that are probably related to the continued absence of bluegill from the lake. First, *Daphnia* remained abundant in Wintergreen throughout the summer in 1992 and 1993 (and based on inspection of uncounted samples, also in 1994). However, in 1976, just prior to the winterkills, both species disappeared by the end of July (Threlkeld 1979). This midsummer disappearance of *Daphnia* was due to low birth rates coupled with relatively high death rates that Threlkeld attributed to

planktivory by bluegill sunfish. One likely hypothesis for the difference in *Daphnia* midsummer dynamics is that planktivory is now lower than it was pre-winterkill. Also, the appearance in 1993 of *D. pulex*, which is more commonly found in small ponds and fishless lakes, may be another indication that planktivory has declined to below historical levels with the continued absence of bluegill.

Our planned reintroduction of bluegill to Wintergreen Lake will provide a test of these ideas as well as examine the impact of the bluegill on the fish community. Bluegill have been shown to compete with both bass and pumpkinseeds at small size classes (Mittelbach 1984, Osenberg et al. 1992, Olson et al. 1995), and we expect the reintroduction of bluegill to have significant effects. However, unlike the reintroduction of the bass, predicting either the short-term dynamics or long-term ramifications of the bluegill's return is not straightforward. The bluegill effects are mediated through stage-specific interactions that may affect a species differentially [e.g., small bass face a competitive effect while larger bass see an increased prey resource (Olson 1993, Olson et al. 1995)]. Therefore, the overall impact of the bluegill will depend on the balance among these interactions. By continuing to follow the long-term dynamics of this system, and by integrating short-term experimentation, we hope to understand the links between the mechanisms of these interactions and their long-term consequences. Indeed, such integration across time scales is crucial to the development and refinement of ecological theory.

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