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EFFECTS OF FOOD WEB COMPENSATION AFTER MANIPULATION OF RAINBOW TROUT IN AN OLIGOTROPHIC LAKE[1]

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Abstract. Stocking of the dominant planktivore of Castle Lake (rainbow trout) was discontinued to examine the impact of food web interactions on zooplankton communities and inter- and intra-annual dynamics of ecosystem properties (light penetration, primary productivity). Dynamics of zooplankton and ecosystem processes were examined for 3 yr following the manipulation and compared to 2–3 yr of premanipulation data. Sampling of vertebrate and invertebrate planktivores documented shifts in other members of the zooplanktivore guild as rainbow trout declined. Reduction of rainbow trout densities led to compensatory responses in other components of the Castle Lake fish assemblage as brook trout and golden shiners increased in abundance. This compensation resulted in increased rates of vertebrate planktivory on daphnids within 2 yr after trout stocking was discontinued. Zooplankton shifts in response to discontinuance of trout stocking were more rapid, particularly an immediate increase in a previously rare invertebrate predator (*Diacyclops thomasi*). Other limnological parameters also responded rapidly following the manipulation: water transparency declined and primary productivity (PPr) increased. In addition, intra-annual patterns (i.e., seasonal development) and the vertical distribution (shallow vs. deep) of PPr appeared to be affected by the food web manipulation. Our results indicate that complexities of real food webs complicate the prediction of the outcome of food web perturbations. Reduction of the previously dominant planktivore (rainbow trout) led to increases in other zooplanktivores (*Diacyclops,* golden shiners, brook trout) that resulted in enhanced predation pressure on zooplankton herbivores. Our results also indicate that alterations in water quality parameters (transparency, PPr) in response to food web alterations need not necessarily be mediated through changes in the abundance of *Daphnia,* as strong limnological responses preceded reductions in *Daphnia* by a year. We hypothesize an alternative mechanism for food-web-induced changes in lake ecosystem dynamics: changes in water clarity and productivity can result when cyclopoid predation strongly affects micrograzers.

Key words: cascading trophic interactions; ecosystem variability; food web compensation; lake food webs; primary productivity.

INTRODUCTION

The idea of "Cascading Trophic Interactions" (or CTI; Carpenter et al. 1985) has provided a conceptual framework for understanding the impact of higher trophic levels on ecosystem dynamics. Since the publication of that paper, a rapidly expanding number of studies has demonstrated that fish, through their effect on zooplankton, affect various aspects of ecosystem function (Leibold 1989, Carpenter and Kitchell 1993, Hairston and Hairston 1993). Tests of these ideas have also been extended to terrestrial ecosystems (Spiller and Schoener 1990, 1994). The CTI hypothesis, as originally formulated, placed the many components of complex pelagic food webs into dominant trophic levels consisting of piscivores, zooplanktivores, large and small zooplankton, and phytoplankton. While the compression of pelagic food webs into distinct trophic levels has considerable heuristic value, ecologists recognize that the components of real food webs are not readily categorized into distinct trophic levels (Cousins 1987). It remains an open question whether natural food webs function as predicted by CTI, especially when food webs are altered (Kerfoot and DeAngelis 1989).

One critical issue regarding whether changes in top predators propagate to cause substantial changes at the primary producer level involves the extent to which predators at the top of the food web segregate functionally into strong trophic interactors (sensu Paine

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1980) or whether compensatory shifts among multiple predator–prey species attenuate changes in predator abundance (Power 1992, Strong 1992, Hairston and Hairston 1993). Several conceptual approaches have been developed to analyze this type of trophic complexity. Kerfoot and DeMott (1984) refer to "dependent chains" and "vaulting" in food webs, in which multiple predator species interact both through their shared resources but also when one predator is able to exploit other predator taxa. Polis (1991) and Polis and Meyers (1989) have developed a similar concept ("intraguild predation," or IGP), describing predators that use similar resources and thus are potential competitors but also prey on each other. Work reviewed by Polis and co-workers indicates that intraguild predation is a nearly ubiquitous component of real food webs; they concluded that food webs in nature are unlikely to conform to the simple configurations originally postulated in the CTI hypothesis. Polis and Holt (1992) suggest that the occurrence of IGP makes the outcome of food web changes considerably less predictable than is suggested by the initial formulations of the CTI hypothesis. Community shifts could compensate for decreases in the abundance of one species, such that the overall intensity of predation on the shared food resources of multiple predator species would be largely unaffected. Few studies at the ecosystem scale have documented how trophic complexity potentially alters the outcome of changes in food web structure on ecosystem processes such as primary productivity.

We investigated the effects and mechanisms of food web alteration on ecosystem processes by manipulating the trophic structure of Castle Lake, California. Recent analyses of the 30-yr data set for Castle Lake have contributed to the accumulating evidence for the role of fish in influencing lake ecosystems (Jassby et al. 1990). Using multivariate techniques for analysis of time series, Jassby et al. isolated two independent components of the spatial (vertical) and seasonal variability in primary productivity (PPr) in this lake. The first and dominant mode of variability involved PPr early in the ice-free season deep in the water column (15–25 m layer); interannual variability in this component was correlated only with climatic variables such as winter precipitation and time of ice-out. The second mode of variability reflected dynamics of PPr in the upper 10 m late in the summer; interannual variation in this mode correlated only with food-web related variables, such as the biomass of the herbivore *Daphnia* (a negative correlation) or the relative abundance of rainbow trout (a positive correlation). To test for the mechanisms underlying these correlations, we initiated a food web manipulation by discontinuing stocking of rainbow trout. Herein we report the dynamics of zooplankton, water transparency, and PPr over a 3-yr period (1989–1991) following stocking manipulation. Dynamics are compared to 3 yr of monitoring before manipulation (1986–1988). We also monitored the dynamics and diets of other potentially planktivorous fish in Castle Lake (brook trout and golden shiners) following the manipulation to evaluate whether compensatory responses among these species influenced the impact of reduced rainbow trout abundance on lower trophic levels.

METHODS

Study site and experimental food web manipulation

Castle Lake (mean depth: 11.4 m, maximum depth: 35 m, surface area: 0.21 km^2) is located at an elevation of 1657 m in the Siskiyou mountains of northern California (41°13′ N, 122°22′ W). The lake has been under nearly continuous limnological monitoring since 1959, with an emphasis on nutrient dynamics and primary productivity (Goldman and DeAmezaga 1984). Previous studies have indicated that nitrogen (N) is the nutrient primarily limiting to phytoplankton growth in Castle Lake (Axler et al. 1981, Goldman and DeAmezaga 1984) and so we focus on N dynamics here. The crustacean zooplankton community has generally been dominated by the cladoceran *Daphnia rosea* and the calanoid copepod *Diaptomus novamexicanus,* with *Bosmina longirostris* and *Holopedium gibberum* occurring as subdominants (Janik 1988, Elser 1992). During the period preceding our study, invertebrate predators (e.g., cyclopoid copepods, dipteran larvae) were absent or rare.

As described by Jassby et al. (1990), rainbow trout (*Oncorhyncus mykiss*) and brook trout (*Salvelinus fontinalis*) have dominated the fish community of Castle Lake throughout the 30-yr period of study. Small numbers of golden shiners have been observed since the early 1980s. Brook trout reproduce naturally in Castle Lake (Wurtsbaugh et al. 1975). Rainbow trout do not reproduce in the lake or watershed and are maintained by stocking by the California Department of Fish and Game. Based on prior diet and behavior studies (Swift 1970, Paulson 1977), our own analyses of rainbow trout diets, and the relatively heavy stocking rates, the predominant source of predation pressure on zooplankton in Castle Lake has likely been planktivory by rainbow trout. Creel surveys also indicate that heavy angling pressure removes rainbow trout before they reach sizes at which they would be capable of extensive piscivory (300 mm standard length; Beauchamp 1990). Further support for the suggestion that rainbow trout have functioned predominantly as planktivores in Castle Lake comes from the correlative analyses of Jassby et al. (1990): the secondary mode of PPr variability associated with food web components varied negatively with *Daphnia* biomass but positively with rainbow trout abundance, as gauged by angler catch-per-unit-effort. If rainbow trout exerted their indirect influence on PPr primarily as piscivores (indirectly enhancing *Daphnia*), then this mode of variability should have varied negatively with rainbow trout abundance. It did not. An alternative explanation for the correlation between productivity variation and trout abundance is that excretion of nutrients by rainbow trout feeding extensively on littoral zone prey items directly affected phytoplankton productivity. Based on previous studies, this possibility appears unlikely. Paulson (1977) compared the nitrogen demand of phytoplankton productivity to estimates of rates of nitrogen excretion by rainbow trout during years of relatively heavy trout stocking (1975–1976). N excretion by rainbow trout only accounted for an average of 3.6% of the growing season N demand, with a maximum summer value of 13%. Thus, it is unlikely that direct effects of trout N excretion were associated with past correlations of PPr variation and trout abundance or with the changes in PPr following stocking manipulation documented in the following.

From 1958 until our experimental manipulations, a nearly constant annual stocking rate of 10 000 underyearling rainbow trout (7–10 cm) had been maintained. These fish were generally added in late summer or early fall. As a result of this external maintenance, rainbow trout have dominated the fishing harvest from the lake, consisting of 75% of the total catch during 1960–1971 and >90% in years of more sporadic creel census in the 1970s and 1980s (Jassby et al. 1990). At our request, California Fish and Game did not stock the lake with rainbow trout in fall 1988; stocking was also withheld during 1989–1990 (stocking was resumed in fall 1991). Thus, the first postmanipulation year for our study was 1989. We monitored limnological dynamics during 1989–1991 and compared these dynamics to the 2- or 3-yr period preceding the manipulation. We also monitored abundance, growth, and diets of fish populations during 1989–1991 to document the decline of rainbow trout due to angling and other mortality and to determine the potential response of naturally reproducing fish planktivores following the reduction of the externally maintained planktivore.

Monitoring

Fish.—Rainbow trout, brook trout, and adult golden shiners were captured in bottom-set gill nets set monthly from June to September in 1989–1991. A stratified random design was used to place one net randomly within each of four areas within the lake each night. Each net was 30 m long, 2 m high, and composed of five mesh sizes (19, 25, 32, 39, and 45 mm bar). Nets were set at night from dusk until dawn; each netting period lasted between two and five nights. All fish were removed from gill nets, measured (total length to the nearest millimetre), weighed (wet mass to the nearest 0.1 g) and sexed. Stomachs of up to 50 individuals of each species were removed and preserved in a 10% formalin solution. Scales of selected rainbow trout and golden shiners were also collected for age determination.

In addition to bottom-set gill nets, a series of vertical gill nets was set at monthly intervals beginning in July 1990. Five nets (3 m wide × 30 m deep, each either 19, 25, 32, 39, or 45 mm mesh) were set at a central lake station for 3–5 d and harvested twice daily at dawn and dusk. The depth of each fish capture was recorded and size and stomach contents were determined.

Stomach contents from gill-netted fish were removed and examined under a dissecting microscope. Prey were assigned to the following categories: daphnids, cyclopoid copepods, calanoid copepods, other zooplankton, crayfish, golden shiners, other fish, aquatic insects, and terrestrial insects. A visual estimate of the volumetric proportion of each group present was made from each stomach. For selected stomachs, the volume of individual prey taxa was measured with a graduated cylinder. The volumetric proportion of prey taxa estimated visually was compared to measured volumetric proportion for these selected stomach contents.

In 1989 only small numbers of age-0 golden shiners were observed in shallow regions of the lake. However, in response to the potential recruitment of golden shiners to the pelagic zone, in 1990 we began small-fish sampling using modified acoustic surveys and purse seines. Juvenile golden shiners were collected in the pelagic zone with a small purse seine (34 m long × 9 m deep, 3.2 mm mesh). The purse seine was set at 4–6 locations during the day (1200–1600) and night (2200–0100) in the pelagic region on several dates in July and August of each year. The net sampled a volume of $\approx$380 m^3 and fished efficiently from the surface to a depth of 5 m. Golden shiners were the only fish species captured. Each individual was measured (total length ± 0.1 mm), weighed (wet mass ± 0.01 g), and preserved in 70% EtOH for examination of stomach contents. Each item was identified as daphnid, cyclopoid copepod, calanoid copepod, copepod nauplii, aquatic insect, or terrestrial insect and measured to the nearest 0.03 mm with a dissecting microscope.

A series of hydroacoustic surveys was conducted in early September of each year to assess the abundance and spatial distribution of fish. One survey consisted of six cross-lake transects covering a distance of 3.2 km. Preliminary surveys indicated that fish densities were highest from midday until dusk; therefore we focused our acoustic sampling on this period. Each survey was repeated twice during the day (1300–1500) and twice during dusk periods (beginning 1 h after sundown). Acoustic surveys were then repeated the next day providing four estimates during the day and four estimates from the dusk period. Acoustic studies were made with a BioSonics model 105 echosounder equipped with a 420-kHz dual beam (6 × 15°) transducer (BioSonics, Seattle, Washington, USA) that permitted estimates of fish size. We sampled at a rate of 2 pings/s traveling at a boat speed of 2–4 m/s. Data were recorded directly into computer files as digitized echoes and were also digitized and recorded on Betamax videotape.

Along with the moving acoustic surveys, beginning in 1990 we also collected acoustic data from a stationary platform near the middle of the lake to estimate abundances of golden shiners that primarily occupied surface layers poorly sampled by moving acoustic surveys. For these stationary surveys we submerged the transducer to a depth of 2 m and pointed the acoustic beam sideways so that a large volume of epilimnetic water within 90 m of the transducer was being sampled. These stationary surveys were conducted just before nighttime purse seine collections. Each survey consisted of four 15-min periods of data collection with the transducer set from a different side of the platform.

Acoustic data were analyzed by counting echoes with dual beam information processed with a BioSonics ESP Dual Beam Processor (Model 281) and software (BioSonics, Seattle, Washington, USA). Only single fish targets within 4° of the acoustic beam axis were used to calculate fish target strength and to obtain fish density estimates. Stationary surveys were assumed to primarily sample golden shiners while roving surveys were assumed to sample trout populations (after correction for small targets). We used single fish targets with dual beam target strengths ranging from -59 to -35 decibels (db), representing fish of $\approx$1–40 cm total length (TL) (Love 1971). Fish targets between -52 to -35 correspond to salmonids greater than 1 year of age or to adult golden shiners (5–40 cm). Fish targets between -59 and -52 db correspond to young-of-year golden shiners or brook trout of 1–5 cm TL. Only echoes that met the single-target shape criteria used by the analysis software were selected to calculate densities and target strengths. The bottom window region where fish targets were indistinguishable from the bottom was set at 1.0 m.

Limnological parameters.—Most of the methods for monitoring of physical, chemical, and biological characteristics of Castle Lake have been held constant throughout the 30 yr that the lake has been studied. Details can be found in previous publications (Goldman and DeAmezaga 1984, Goldman et al. 1989, Jassby et al. 1990). The lake was sampled at a single station in the deepest part of the lake at 5-d (1986–1988) or 7-d (1989–1991) intervals during the summer (June–September). In other months, sampling frequency was similar (for example, the periods following ice-out in 1990–1991) or less frequent (2–3 wk intervals in fall and spring, monthly intervals in winter, depending on the condition of the ice cover). On each date, vertical profiles of temperature (at 1-m intervals using a thermistor), dissolved chemical nutrients (NO_3-N and NH_4-N; 3–5 m depth intervals), and primary productivity (PPr; 1–3 m intervals) were determined. Water transparency was quantified by measuring the vertical profile of light penetration (photosynthetically active radiation) from 0 to 30 m using a submersible quantum sensor and by using a 20-cm white Secchi disk. Water chemistry analyses were usually performed on fresh filtered samples. NO_3-N was determined using the hydrazine reduction method (Kamphake et al. 1967) and NH_4-N by the phenol-hypochlorite method (Solorzano 1969). Concentrations of soluble reactive phosphorus were also determined but concentrations were extremely low and erratic and will not be presented. PPr was determined using the ^{14}C method (Goldman 1968) with 4-h incubations performed in situ during the midday. Concentrations of dissolved inorganic carbon were determined using an infrared analyzer. After incubation in the presence of 74–185 kBq of $NaH^{14}CO_3$, phytoplankton were filtered onto Millipore type HA membrane filters (0.45-μm pore size), dried, and assayed for radioactivity using a thin-window Geiger-Mueller counter. Further details regarding methods for PPr estimates may be found in Goldman (1968) and Goldman and DeAmezaga (1984).

Because the mode of variability most strongly correlated with food web dynamics in the analyses of Jassby et al. (1990) occurs in the surface waters, we decided to streamline zooplankton collections by obtaining composite samples from the epilimnion (generally 0.5, 3, and 5 m) rather than discrete samples from multiple depths throughout the water column. This approach was initiated in 1987 and therefore we present no zooplankton data for 1986. Zooplankton samples were collected using a 12-L clear Schindler sampler. Because zooplankton in Castle Lake engage in pronounced diel vertical migration (Redfield and Goldman 1978), we sampled both during the day (1100–1300 Pacific Standard Time [PST]) and at night (2000–0000 PST) so that on each date two epilimnetic composite samples were obtained. During our study period, two mesh sizes (64 μm, 1987–1989; and 85-μm, 1990–1991) were used in collection nets in the Schindler sampler. Examination of samples collected with both meshes indicated that samples obtained with 85-μm mesh considerably underestimated rotifers and nauplii. As we have been unable to establish a reliable correction factor for this effect, we report results for crustacean zooplankton taxa only (excluding nauplii).

Zooplankton samples from 1987 to 1988 were preserved in $\approx$5% sucrose-formalin; samples from 1989–1991 were preserved with Lugol's solution buffered with sucrose. Samples were examined under a dissecting microscope and enumerated according to species. Biomasses of crustacean zooplankton were estimated using standard length-mass regressions (Downing and Rigler 1986) or relationships developed specifically for certain Castle Lake taxa (Redfield 1980), allowing us to estimate total zooplankton biomass on each sampling date as well as the biomass contributed by the major crustacean species.

Data analyses

Fish consumption dynamics.—We used a bioenergetics analysis of fish growth processes (Hewett and

Johnson 1987) to estimate the seasonal and annual consumption dynamics of fish populations in Castle Lake from 1989 to 1991. These energy simulations allow estimation of consumption of different prey types by the average individual of a fish cohort given information on growth rate, diet proportions, and thermal history of individual fish of that cohort. The simulation model operates by iteratively fitting an average consumption rate (*P* value) such that the observed growth of the mean individual fish of a cohort is realized. The *P* value is expressed as a proportion of the maximum consumption possible for a fish of a given size and species, at the prescribed temperature. These estimates of individual consumption were then multiplied by the abundance of fish in each cohort to determine the consumption dynamics of each fish population. We used Hewett and Johnson's (1987) generalized salmonid parameters for analysis of rainbow trout and brook trout, and their generalized cyprinid parameters for golden shiner. This approach allowed us to examine the effects of concurrent changes in abundances of planktivorous fish species and their diet compositions on overall rates of vertebrate predation on zooplankton populations (Luecke et al. 1990*a*, 1992, Stewart and Iberra 1991). We stress interannual changes in consumption of *Daphnia* as this prey item was the most frequently eaten zooplankton species taken by all three fish species. We also emphasize that, while aquatic and terrestrial insects comprised a substantial proportion of the diets of all three species, the relevant parameter from our perspective was primarily whether rates of vertebrate planktivory on *Daphnia* were important for *Daphnia* dynamics rather than whether *Daphnia* was the dominant food source for the fish.

Information on growth rate and diet proportion came from fish captured in gill nets and purse seines. Thermal history was derived from the location of salmonids in vertical gill nets, the depth of hydroacoustic targets, and weekly vertical temperature profiles. Abundance estimates of salmonids were derived from acoustic sampling of fish targets proportioned into species and cohorts based on gill net catches. Golden shiner abundances were estimated from hydroacoustic surveys and purse seine catches.

A repeated-measures ANOVA was used to test for interannual differences in gill net catches; catch-per-unit-effort in each summer month was the repeated variable. The statistical significance of interannual differences in fish density determined by hydroacoustics was determined by ANOVA.

Limnological parameters.—To characterize the seasonal development of water column stratification, we calculated Schmidt stability (S; Schmidt 1928) based on the lake's hypsographic curve and the temperature profile. S is an integrated measure of the amount of work that would be required to completely homogenize the water column of the lake given its temperature (density) distribution on a given date. S provides an index of the interannual and intra-annual dynamics of physical variation due to changes in insolation, wind, and air temperature. Water density was calculated as a function of temperature and depth using the International Equation of State (Millero and Poisson 1981).

Many of our analyses focused on the dynamics of parameters in the epilimnion as variability in the seasonal development of primary productivity in the epilimnion correlated most strongly with food web parameters in the study of Jassby et al. (1990). We calculated mean concentrations of NO_3-N and NH_4-N in the surface waters (usually 0, 3, and 5 m) to evaluate changes in the availability of nitrogen during the study period. We also segregated our analyses of the PPr data into considerations of: (1) whole water column data; (2) data confined to the upper 10 m to specifically examine changes in productivity in the layer identified by Jassby et al. (1990) as most correlated with food web variables; and (3) data confined to the 15–25 m layer identified by Jassby et al. (1990) as correlated with climatic variables. We were also interested in examining changes in the seasonality of various parameters, especially in the abundance and composition of the zooplankton and in phytoplankton productivity. To do this, we generally aggregated data within 2-wk intervals for the summer period (June–September) and examined intra-annual dynamics in different years. By aggregating data within 2-wk intervals and using only the means within those intervals in our analyses, potential effects of differential sampling intensity during different years or months were minimized.

Approaches to the interpretation of the results of whole-ecosystem perturbations have been the subject of considerable debate (Hurlbert 1984, Stewart-Oaten et al. 1986, Carpenter 1990). The results reported here examine temporal dynamics during 3-yr intervals before and after a deliberate perturbation of a single system. Thus, we cannot employ the BACI approach described by Stewart-Oaten et al. (1986) or Randomized Intervention Analysis (RIA) for paired experimental-reference systems as developed by Carpenter et al. (1989), as these approaches require simultaneous sampling of a paired reference system. In this paper we apply a hybrid approach. First, we follow the recommendations of Hurlbert (1984) and present graphical summaries of responses, along with response variability, permitting a direct evaluation of the magnitude of imputed changes in various variables. Our interpretations are enhanced by our access to a long record of monitoring for this ecosystem and thus we can better evaluate whether conditions following manipulation are anomalous. Second, we were interested in examining whether response variables changed both on interannual and intra-annual (i.e., seasonal) time scales following stocking manipulations. To do so, we employed repeated-measures (RM) ANOVA (Gurevitch and Chester 1986) comparing premanipulation (1986–1988) and postmanipulation (1989–1991) periods using data segregated into 2-wk intervals, testing for significant "period" (i.e., pre- vs. postmanipulation) × sampling interval (i.e., seasonal development) interaction terms. This analysis also permits conservative univariate tests of "main effect" differences between pre- and postmanipulation periods while compensating for sequential correlation for observations made within years. Because RM ANOVA does not compensate for potential sequential correlation of observations between different years within the pre- and postmanipulation periods we also tested for differences between pre- and postmanipulation periods using Randomized Intervention Analysis, with correction for lag-1 autocorrelation (Carpenter et al. 1989). Results for RM ANOVA and RIA regarding statistical significance of pre- and postmanipulation changes were generally consistent and so we do not present RIA results here. It is important to note that significant differences between pre- and postmanipulation periods, whether detected by RM ANOVA or RIA, do not necessarily demonstrate a causal relationship between the manipulation and the response variable. As discussed by Carpenter (1990), conclusions regarding causality ultimately rest on the soundness of the biological reasoning that accompanies the analysis.

RESULTS

Physical–chemical conditions

Castle Lake experienced an irregularly variable climatic regime during the 6-yr study period, resulting in some degree of interannual variability in water column stability (Fig. 1A) and the timing of physical events such as ice break-up. Ice break-up occurred as early as day 93 of the year (early April) in 1990 and as late as days 139–142 (mid-May) in 1988 and 1991. In contrast to the 49-d difference for the time of ice-out, the date on which maximum water column stability occurred varied by only 21 d. This narrow range in the timing of peak stability indicates that water column conditions late in the stratified season are relatively insensitive to the fine-scale details of climate that determine the timing of ice-out and initial thermal stratification. Therefore, comparison of summer limnological dynamics on a calendar-year basis, as done by Jassby et al. (1990), is valid. No substantial differences between pre- and postmanipulation years were observed for S that might obscure evaluation of the impacts of food web manipulations on this system (Fig. 1A; RM ANOVA: $F_{1,4} = 3.76$, $P = 0.13$).

NO_3-N and NH_4-N were highly variable during the study period, both within and between years (Fig. 1B, C). High concentrations of nutrients accumulated under the ice and were rapidly depleted following ice-out. NH_4-N was particularly variable and no seasonal or manipulation period differences were observed. NO_3-N varied seasonally (RM ANOVA: $F_{7,28} = 7.26$, $P < 0.001$). NO_3-N seasonality differed between pre- and postmanipulation periods (RM ANOVA: $F_{7,28} = 5.57$, $P < 0.001$), reflecting a tendency in postmanipulation years (especially 1990 and 1991) for NO_3-N concentrations to be relatively low and constant for all four summer months while in premanipulation years NO_3-N in June was relatively high. Most importantly for interpretation of increases in PPr and decreases in water clarity following the manipulation, these data indicate that major abiotically driven differences in nutrient loading coincident with the food web manipulation did not occur.

Fish sampling

Rainbow trout catches in standardized horizontal gill nets decreased from 1989 to 1991 (Fig. 2). Rainbow trout CPE (catch per effort) was significantly different among years (RM ANOVA: $F_{2,6} = 105.6$, $P < 0.001$). A Bonferroni multiple comparison of means indicated that catch rates declined significantly each year of the study. During this period, brook trout catches increased (Fig. 2; RM ANOVA: $F_{2,6} = 53.9$, $P < 0.001$). Based on a Bonferroni comparison of means, brook trout catches were lower in 1989 than in 1990 and 1991.

The abundance of golden shiners also increased from 1989 to 1991. In 1989 a few adult golden shiners were captured in horizontal gill nets, but no young-of-the-year (YOY) golden shiners were observed in the main basin of the lake. In June 1990 a small number of golden shiners were again captured in gill nets, and numerous YOY golden shiners were observed in the pelagic regions of the lake. Purse seine catches and stationary epilimnetic hydroacoustic sampling indicated that the golden shiner population produced two very strong year classes in 1990 and 1991 (Table 1).

Brook trout and golden shiner populations appeared to compensate for reduced rainbow trout abundance, as hydroacoustic estimates of total pelagic fish abundance were similar among years (Fig. 3; ANOVA of density of fish targets larger than −52 db (5 cm TL): $F_{2,10} = 0.122$, $P = 0.74$). Gill net catches indicated that the reduction in rainbow trout numbers was primarily compensated for by increases in brook trout.

In addition to changes in the abundance of fish species in Castle Lake, the size distributions of these populations also changed between 1989 and 1991. The majority of rainbow trout sampled during this study resulted from fish stocked in fall 1987 and spring 1988, as there was no indication of natural reproduction in the lake. Mean length of rainbow trout captured in gill nets increased from 244 mm in 1989 to 281 mm in 1991 as this 1988 cohort grew in size. The mean length of brook trout captured in gill nets decreased as this species produced relatively stronger year classes after stocking of rainbow trout ceased. The two very strong year classes of golden shiners produced in 1990 and 1991 resulted in a decrease in the mean length of shiners collected in gill nets from 135 mm in 1989 to 86

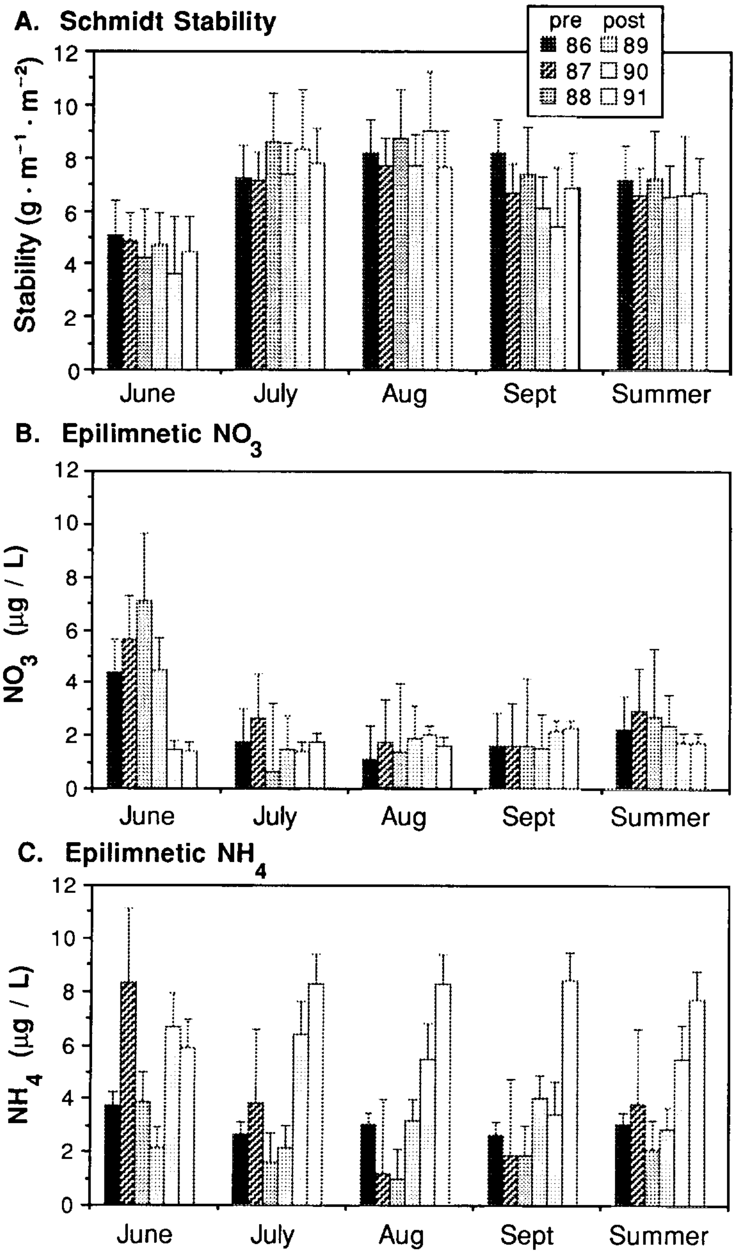

FIG. 1. Dynamics of monthly mean and summer mean values of: (A) water column stability, (B) epilimnetic NO_3-N, and (C) epilimnetic NH_4-N, in Castle Lake during during 1986–1991. Monitoring data were first segregated into two intervals per month and the mean of all observations within that interval was calculated. Error bars indicate 1 SD calculated for those duplicate values per month or for the eight observations for the summer season.

mm in 1991. Shiners captured in purse seines in August of 1990 and 1991 averaged 36 and 43 mm, respectively.

These changes in abundances and size distributions of fish populations resulted in changes in total and relative species biomass in the fish assemblage of Castle Lake (Fig. 4). Total fish biomass was lowest in 1990 but increased to the highest levels in 1991 due mainly to increases in age-2 brook trout.

Diet analyses of the three species of planktivorous fish indicated that *Daphnia* comprised a higher proportion of stomach contents of golden shiners than of rainbow or brook trout (Fig. 5). A substantial proportion of the diets of the salmonids consisted of terrestrial and aquatic insects. Daphnids comprised a higher proportion of the diet of rainbow and brook trout in late summer compared to other seasons as high surface water temperatures likely precluded salmonids from rising to the surface to consume terrestrial insects. During

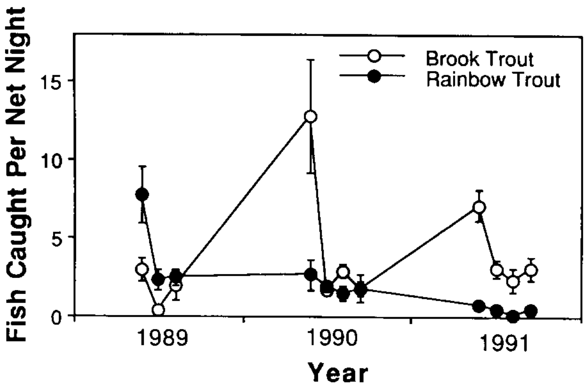

FIG. 2. Catch-per-unit-effort of rainbow and brook trout in 1989–1991. Data represent means (± 1 SE) of number of fish caught in four nets set per night (2–5 consecutive nights of sampling per sampling event). Nets were set in June, July, and August of 1989 and in June, July, August, and September of 1990 and 1991.

late summer, ≈25% of salmonids and 65% of golden shiner diets were composed of daphnids (Fig. 5). In 1991, however, the few remaining, relatively large rainbow trout (mean length 321 mm) did not consume zooplankton. Few other zooplankton taxa were present in fish stomachs.

Consumption dynamics of fish

Bioenergetics simulations were conducted to estimate how changes in the fish assemblage affected rates of fish consumption of zooplankton species among years. Inputs to the energy simulations are presented in Table 2 and Fig. 5. Changes in masses of each cohort of fish (Table 2) were low compared to other populations (Tabor and Wurtsbaugh 1991). Abundance estimates for each cohort were estimated from August acoustic and purse seine sampling (Table 2). We assumed that these abundances were representative of midsummer conditions. Results of energy simulations indicated that consumption of daphnids was greatest in mid- to late summer of each year (Fig. 6). In 1989 rainbow trout consumed the greatest mass of daphnids, followed by brook trout and golden shiners. Rainbow trout consumption of daphnids declined during the 3-yr period as abundance of this fish dwindled and the remaining larger rainbow trout consumed fewer daphnids. However, late summer consumption of daphnids by the total fish assemblage was three times as great in 1991 compared to 1989. This increase occurred mostly because of greater numbers of brook trout and golden shiners that consumed higher proportions of daphnids than rainbow trout (Fig. 5). The higher mass-specific consumption demand of the smaller brook trout and golden shiners also contributed to increased estimates of total predation on daphnids.

Zooplankton

The first and most pronounced change in the zooplankton community following cessation of rainbow trout stocking in fall 1988 was a dramatic increase in early 1989 in the abundance of the planktivorous cyclopoid copepod *Diacyclops thomasi* (Fig. 7A). This species was present only at background densities during 1987 and 1988, as well as during nearly 20 yr for which zooplankton data are available, but reached densities of 10 animals/L (average of day and night samples) early in 1989 and increased more in 1990 and 1991, peaking at 25 animals/L in midsummer 1990. The absence of appreciable densities of *D. thomasi* from nearly 20 yr of zooplankton collections in Castle Lake argues strongly that the increase observed in 1989 was highly unusual. Although potentially superfluous for such a dramatic event, statistical tests of differences in densities of *D. thomasi* in years before and after the manipulation were significant (RM ANOVA $F_{1,3}$ = 26.6, P = 0.014). Accompanying this increase in *D. thomasi* in 1989 was a decline in the biomass of the herbivorous calanoid copepod *Diaptomus novamexicanus* that began in midsummer 1989 (Fig. 7B). The decline in *D. novamexicanus* following manipulation was marginally significant (RM ANOVA: $F_{1,3}$ = 6.12, P = 0.089).

The epilimnetic biomass of *Daphnia rosea* in 1989 was similar to 1987 and 1988 (Fig. 7C); however, *Daphnia* biomass decreased substantially in 1990 and 1991. These declines were particularly pronounced late in the summer, as *Daphnia* declined precipitously during these months in postmanipulation years but remained high during this period in the previous 3 yr. Reflecting the apparently delayed response of *Daphnia* to trout manipulation, *Daphnia* biomass in pre- and postmanipulation periods did not differ significantly (RM ANOVA: $F_{1,3}$ = 0.70, P = 0.46). However, there was a significant seasonal trend in *Daphnia* biomass (RM ANOVA: $F_{5,15}$ = 3.96, P = 0.017) and a signif-

TABLE 1. Density (numbers per 1000 m^3) and lake-wide abundance of golden shiners in the epilimnion during late August of 1990 and 1991. Mean (± 1 SE) of density of small fish targets (−59 to −52 db) in four side scanning hydroacoustic samples, and mean (± 1 SE) of eight purse seine estimates are presented. Estimates were based on nighttime assessments only; densities of fish estimated from nighttime purse seine and acoustic surveys were 10 and 4 times higher, respectively, than daytime estimates. Abundances were calculated assuming these densities included only the top 5 m of the lake. Due to low abundances, no efforts were made to quantify golden shiner densities in 1989.

	1990	1991
Acoustic density ($\bar{X}$ ± 1 SE)	6.98 ± 1.29	9.72 ± 2.47
Purse seine density ($\bar{X}$ ± 1 SE)	7.46 ± 2.88	6.13 ± 3.45
Acoustic abundance	7540	10 500

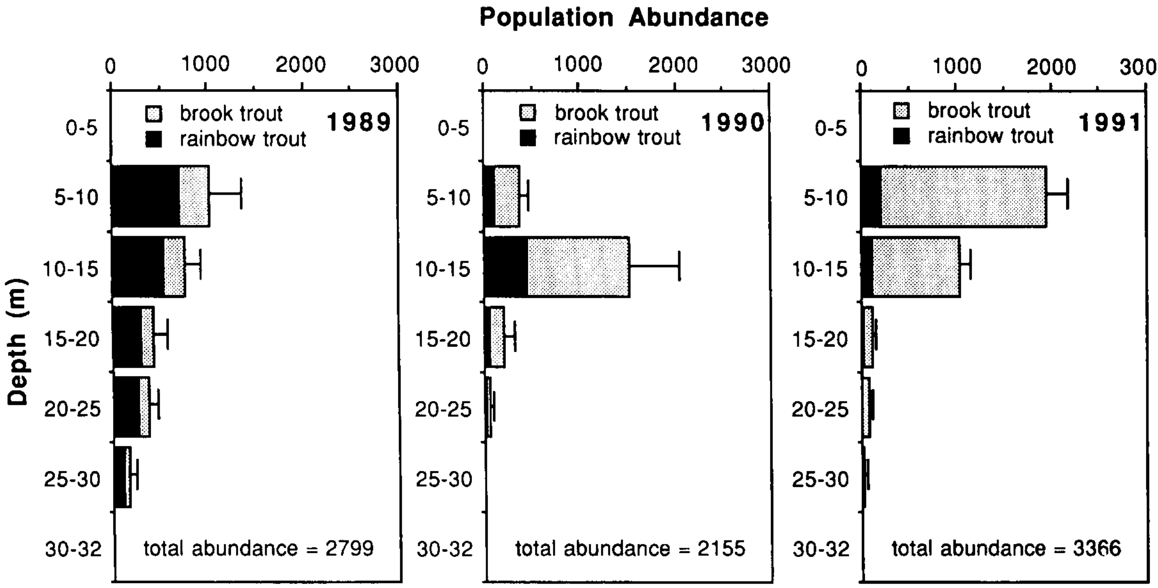

FIG. 3. Hydroacoustic estimates of pelagic fish abundance in 1989–1991. Mean estimates (and 1 SE) of fish abundance stratified by depth from four surveys collected on two nights in late August or early September of each year are depicted. Abundances were calculated from the product of densities and volume of water in each depth strata. Hydroacoustic targets were partitioned into rainbow (black) and brook trout (stippled) based on relative catch in gill nets. Lake-wide estimates of fish populations are indicated.

icant change in this seasonality before and after the manipulation (RM ANOVA: $F_{5,15} = 3.63$, $P = 0.024$), reflecting the tendency for *Daphnia* biomass to increase during summer months before the manipulation but to decrease during summer following the manipulation (Fig. 7C).

Dynamics of subdominant taxa (*Holopedium, Bosmina*) were somewhat erratic and more difficult to interpret. *Bosmina* and *Holopedium* biomass generally appeared to increase following manipulation (Fig. 7E, F); however, these changes were not statistically significant (RM ANOVA: $F_{1,3} < 4.02$, $P > 0.13$).

Total herbivorous crustacean biomass (excludes *D. thomasi*) appeared to decline during the postmanipulation period (Fig. 7F). During 1990 and 1991, average September herbivore biomass was 58 and 43% of its levels, respectively, in 1987–1988. Average summer herbivore biomass was relatively unchanged in 1989 compared to 1987–1988 but was reduced in 1990 to 67% and in 1991 to 36% of premanipulation levels. Despite the sizable reductions in 1990 and 1991, pre- and postmanipulation periods did not differ statistically in total herbivore biomass (RM ANOVA: $F_{1,3} = 0.48$, $P = 0.54$), likely the result of both the delay in the *Daphnia* reduction following the manipulation as well as partially compensating reciprocal responses in *Bosmina* and *Holopedium* (Fig. 7D, E).

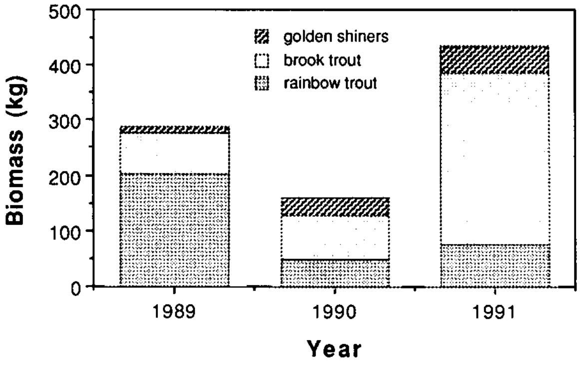

FIG. 4. Biomass of fish species in 1989–1991 estimated from abundances of fish sampled with mobile and side-scan acoustic surveys multiplied by the mean mass of individuals collected in gill net and purse seine samples from each year.

Productivity and water clarity

Phytoplankton-related ecosystem responses to the changing food web were examined by considering two main parameters: primary productivity and water transparency. We considered two aspects of PPr: whole water column values and the amount of PPr in the 0–10 m layer (shallow) vs. in the 15–25 m layer (deep). We examined three measures of water transparency: Secchi depth (which in Castle Lake characterizes light penetration through both the epilimnion and much of the metalimnion), the depth of 1% light penetration (euphotic zone depth), and the vertical attenuation coefficient (k per metre) for photosynthetically active radiation in the 0–10 and 15–25 m water layers. In Castle Lake, as in most unstained lakes, water transparency and light penetration are determined primarily by the

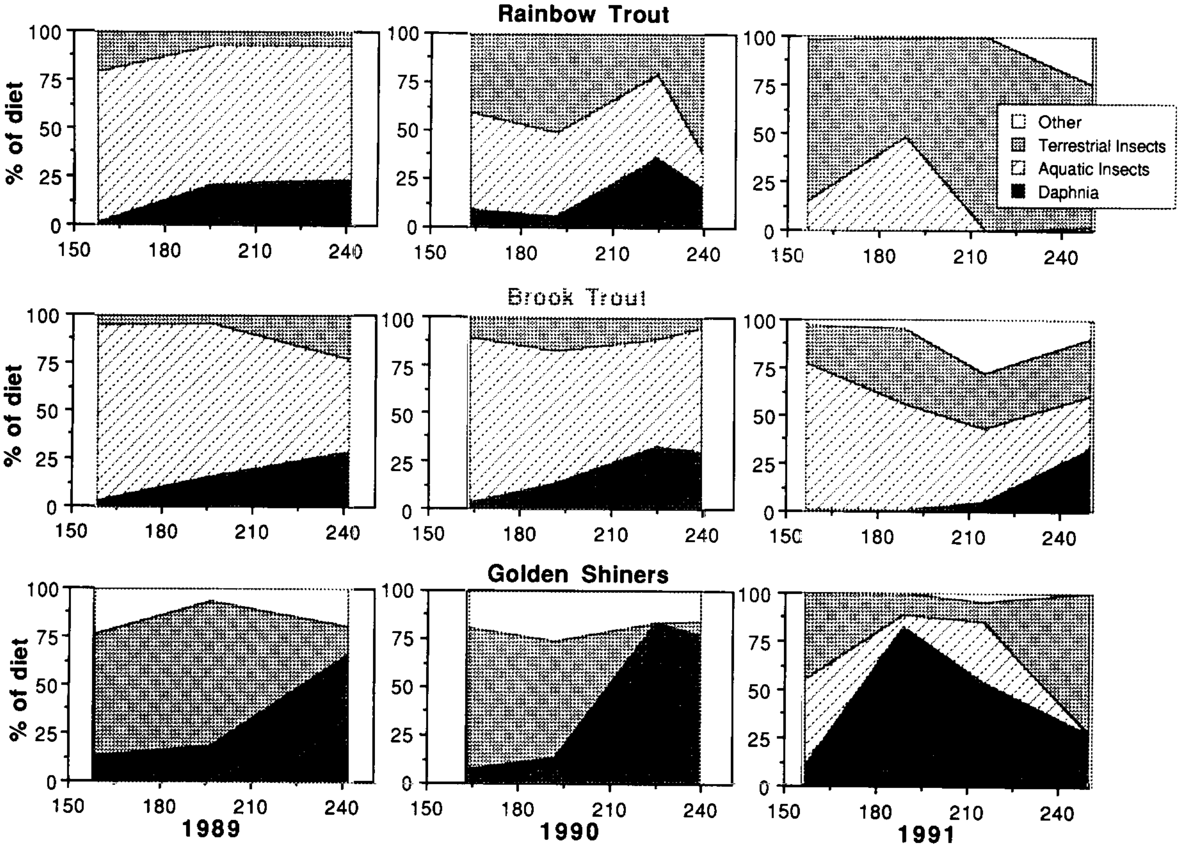

FIG. 5. Percent composition of diet of rainbow trout, brook trout, and golden shiners as determined volumetrically from stomach samples taken from fish collected in gill nets during summers of 1989–1991. "Other" prey include nondaphnid zooplankton, chydorids, and molluscs.

total concentration of phytoplankton and detritus (Priscu 1983, Elser 1988). A secondary but substantial influence is associated with the size distribution of phytoplankton cells, as small cells are more efficient in absorbing and scattering light for a fixed total biomass (Elser 1988, Mazumder et al. 1990). Thus, the decreases in water clarity that we report here potentially reflect increases in both the abundance of suspended particles and in the relative contribution of small phytoplankton taxa.

Secchi transparency declined rapidly in 1989 compared to premanipulation levels, with decreases in water transparency observed as early as July of that year (Fig. 8A; RM ANOVA: $F_{1,4} = 76.2$, $P < 0.001$). Reductions in water clarity appeared to be strongest in late summer (August/September). The unusual nature of the decline in late summer Secchi transparency from ≈12–13 m in 1986–1988 to 9–10.5 m in 1989–1991 can be better appreciated by considering the long-term dynamics of this parameter in Castle Lake (Fig. 9). Late summer Secchi transparency values as low as those seen during each of the 3 yr between 1989 and 1991 have been observed on only one occasion (1981) in the 17-yr data record, with 1984 transparency being nearly as low. No sustained (≥3-yr) period in the data record of water transparency was observed as low as that in the 3 yr following food web manipulation.

Responses of light penetration parameters were similar to those observed for Secchi transparency. Euphotic zone depth declined in the postmanipulation period from average summer values of ≈23–25 m in 1986–1988 to ≈19–20 m in 1989–1991 (Fig. 8B; RM ANOVA: $F_{1,4} = 28.2$, $P = 0.006$). Effects of manipulation on euphotic zone depth appeared to occur even more rapidly than for Secchi depth, with reductions in euphotic zone depth apparent in June 1989. Decreases in water clarity occurred throughout the water column, as light extinction in both shallow (0–10 m) and deep (15–25 m) layers increased (RM ANOVA: $F_{1,4} > 13.2$, $P < 0.03$).

While changes in water transparency following food web manipulation were immediate and strong, changes in ecosystem productivity patterns were more subtle (Fig. 10). Pre- and postmanipulation levels of water column and layer-specific PPr were more variable than water transparency parameters, including relatively high PPr values in 1988 and relatively low values in 1991. As a result, only marginally significant differ-

TABLE 2. Abundance, beginning and ending masses, mortality, and the proportion of maximum consumption (*P* value) of each cohort of fish used in bioenergetics simulations. Abundance estimates were calculated from hydroacoustic surveys partitioned to species based on gill net or purse seine catches. Beginning and ending masses were from early June and early September for salmonids and early July and late August for golden shiners. Daily mortality rates were estimated from annual losses of a cohort. RBT = rainbow trout, BT = brook trout, GS = golden shiner. "2^+" refers to the age-2 cohort.

	Abundance	Beginning mass (g)	Ending mass (g)	*P*	Mortality (d^{-1})
1989					
RBT 2^+	1230	109	134	0.341	0.001
RBT 3^+	752	154	190	0.347	0.001
BT 3^+	817	142	166	0.401	0.001
GS $\geq 2^+$	347	8.7	15	0.541	0.00175
1990					
RBT 3^+	621	179	215	0.337	0.001
BT 2^+	1023	68	119	0.374	0.001
BT 3^+	511	100	135	0.590	0.001
GS 0^+	7540	0.02	0.54	0.587	0.023
1991					
RBT 4^+	335	197	214	0.238	0.001
BT 2^+	2180	69	111	0.374	0.001
BT 3^+	851	121	144	0.312	0.001
GS 0^+	6980	0.03	0.61	0.621	0.023
GS 1^+	3620	1.32	8.40	0.695	0.0036

ences were observed between pre- and postmanipulation periods for water column PPr (RM ANOVA: $F_{1,4} = 4.88$, $P = 0.09$) and shallow PPr (RM ANOVA: $F_{1,4} = 6.12$, $P = 0.068$). The manipulation appeared to affect PPr more strongly in the surface layer (0–10 m) relative to deep water (15–25 m) (Fig. 10B, C) as RM ANOVA did not detect even marginally significant differences for deep water PPr (RM ANOVA: $F_{1,4} = 0.86$, $P = 0.41$). In contrast to small pre- and postmanipulation differences in PPr on interannual time scales, pre- and postmanipulation periods differed considerably in the intra-annual (seasonal) development of PPr (Fig. 10). PPr for both shallow and deep water layers was strongly seasonal (RM ANOVA: $F_{7,28} > 3.44$, $P < 0.01$). In the shallow layer, PPr increased during the June–September period during premanipulation years but, following the manipulation, generally remained unchanged during the summer season (Fig. 10B). This shift in seasonal development following manipulation was statistically significant (RM ANOVA: $F_{7,28} = 2.42$, $P = 0.045$). In contrast, PPr in the deep layer generally decreased during the summer prior to the manipulation but increased or was largely unchanged following the manipulation (Fig. 10C). This shift in seasonal development following manipulation was also statistically significant (RM ANOVA: $F_{7,28} = 2.89$, $P = 0.021$). Because both seasonal and pre- vs. postmanipulation shifts in PPr in shallow and deep water layers had opposite tendencies, total water column PPr (the sum of PPr in deep and shallow layers) was not strongly seasonal (Fig. 10A; RM ANOVA: $F_{7,28} = 1.26$, $P = 0.31$), but there was a significant change in seasonal patterns between pre- and postmanipulation periods (RM ANOVA: $F_{7,28} = 2.81$, $P = 0.024$).

DISCUSSION

The dynamics of fish and zooplankton populations in Castle Lake following cessation of rainbow trout populations illustrate the complex nature of real food webs where species prey on species with which they potentially compete for resources. As density of rainbow trout declined, factors governing survival of small fishes appeared to change in that golden shiners and brook trout produced strong year classes. Competition for common zooplankton resources, direct predation, and changes in perceived risk of predators can all be proposed as alternative hypotheses to explain the observed increases in golden shiners and brook trout when rainbow trout decreased in abundance. Evidence supporting the competition hypothesis comes from field enclosure experiments conducted in 1992, in which shiner growth rate was strongly and positively corre-

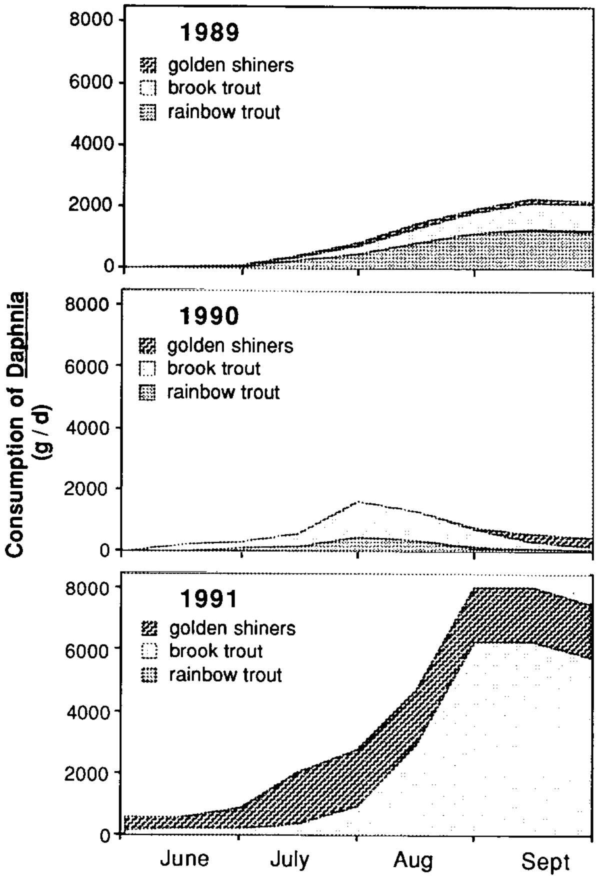

FIG. 6. Consumption of *Daphnia* estimated using bioenergetics simulations for 1989–1991. Rainbow trout were present in 1991 but diet analysis indicated that they did not consume *Daphnia*.

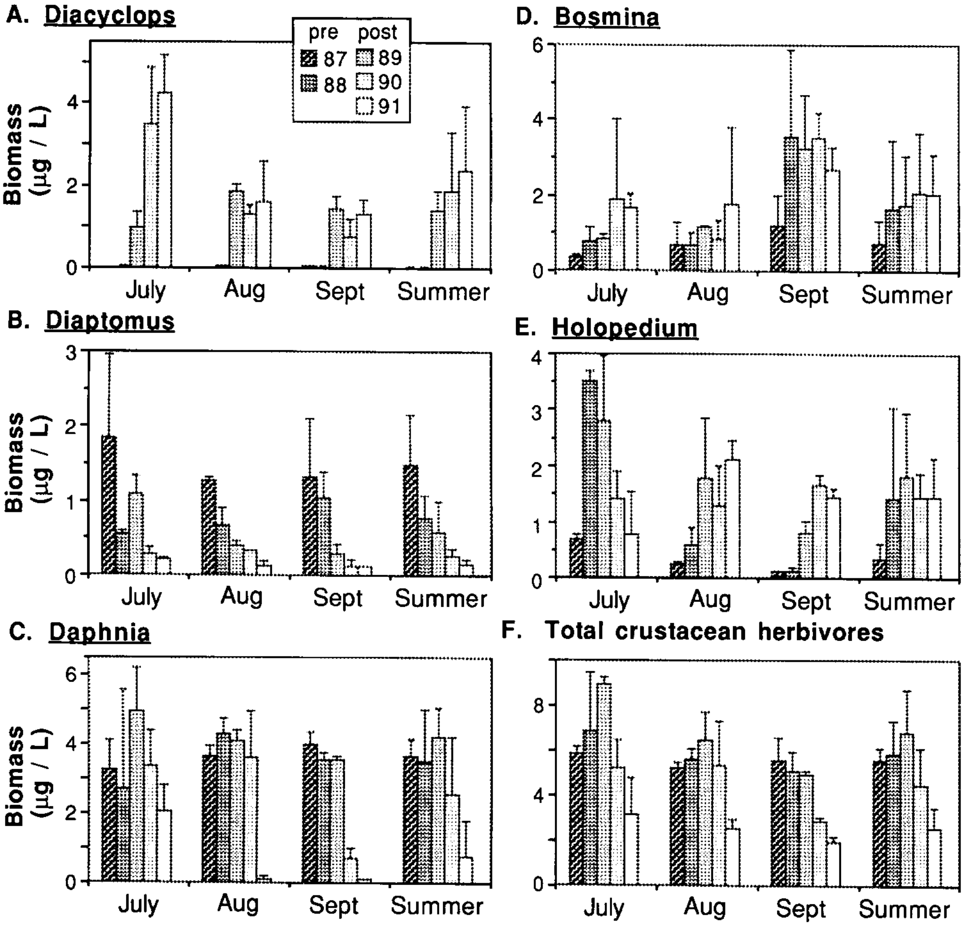

FIG. 7. As in Fig. 1, but for average day-night epilimnetic dry biomass of: (A) the cyclopoid copepod *Diacyclops thomasi*, (B) the calanoid copepod *Diaptomus novamexicanus*, (C) *Daphnia rosea*, (D) *Bosmina longirostris*, (E) *Holopedium gibberum*, (F) all crustacean herbivores (excludes *D. thomasi*). Zooplankton data were not available for 1986.

lated with *Daphnia* biomass (Brandt 1994). Although golden shiners can likely feed more efficiently on zooplankton than can rainbow trout, the consumption of *Daphnia* by this artificially maintained planktivore may still have reduced shiner growth. We have little evidence supporting the predation hypothesis. While large rainbow trout can feed on small cyprinids (Beauchamp 1990), we identified only six golden shiners in the stomach contents of over 400 rainbow trout collected from 1989 to 1992. Relevant to the predation risk hypothesis, growth of cyprinids is often reduced in the presence of piscivores (Gilliam et al. 1989, He and Kitchell 1990, Mathis and Smith 1992). In our study, golden shiners made extensive use of the food-rich pelagic regions only at night when risk of encountering piscivorous trout was low (Brandt 1994). In further support of the predation risk hypothesis, golden shiner growth rates were reduced when either visual or olfactory cues of rainbow trout were present in swimming pool experiments (C. Luecke, *unpublished data*). On the basis of this evidence we conclude that the dramatic increase in abundances of brook trout and golden shiners after rainbow trout densities declined occurred as a result of the combined effects of perceived predation risk and competition for shared zooplankton resources.

The pronounced effect of rainbow trout on the fish assemblage of Castle Lake may reflect the artificial maintenance of rainbow trout by sustained stocking prior to 1989. These individuals, when stocked into the lake as small juveniles, are likely past the stage in their life history when recruitment is most variable (Sissenwine 1984) and recruitment success is determined (Miller et al. 1988). Populations that are artificially maintained, such as the rainbow trout of Castle Lake, have been described as donor-controlled components of the ecosystem (Vadas 1989). Donor control of certain ecosystem components can lead to greater stability and less variation in other ecosystem components. The relatively constant stocking rate of rainbow trout into Castle Lake before 1989 thus may have been responsible for the relatively small contribution of consumer effects to explanations of variation in primary production in the time series analyses of Jassby et al. (1990).

The artificial nature of the maintenance of rainbow

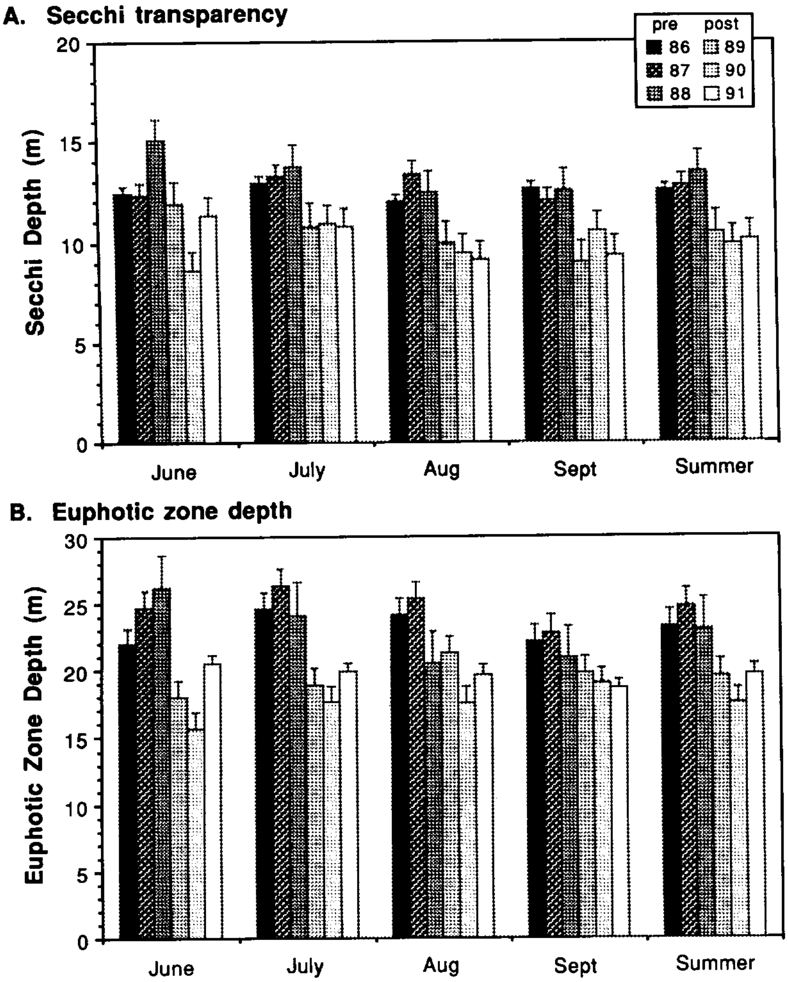

FIG. 8. As for Fig. 1, but for: (A) Secchi transparency, (B) depth of 1% light penetration (euphotic zone).

trout in Castle Lake does not detract from our inferences concerning the effect of this species on food web structure and function. Rainbow trout are representative of other species whose recruitment success is relatively constant (Cushing 1982) or species in which one strong cohort dominates the fish assemblage for many years (Carpenter et al. 1989, Rudstam et al. 1992). In these examples, the effect of the fish popu-

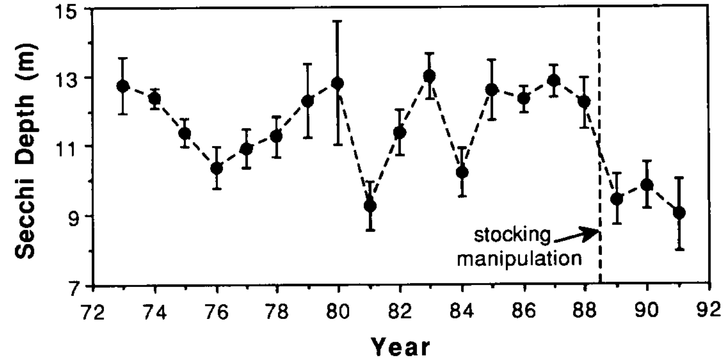

FIG. 9. Long-term dynamics of late summer Secchi transparency (mean for August–September observations) in Castle Lake, 1973–1991. Error bars indicate 95% confidence limits.

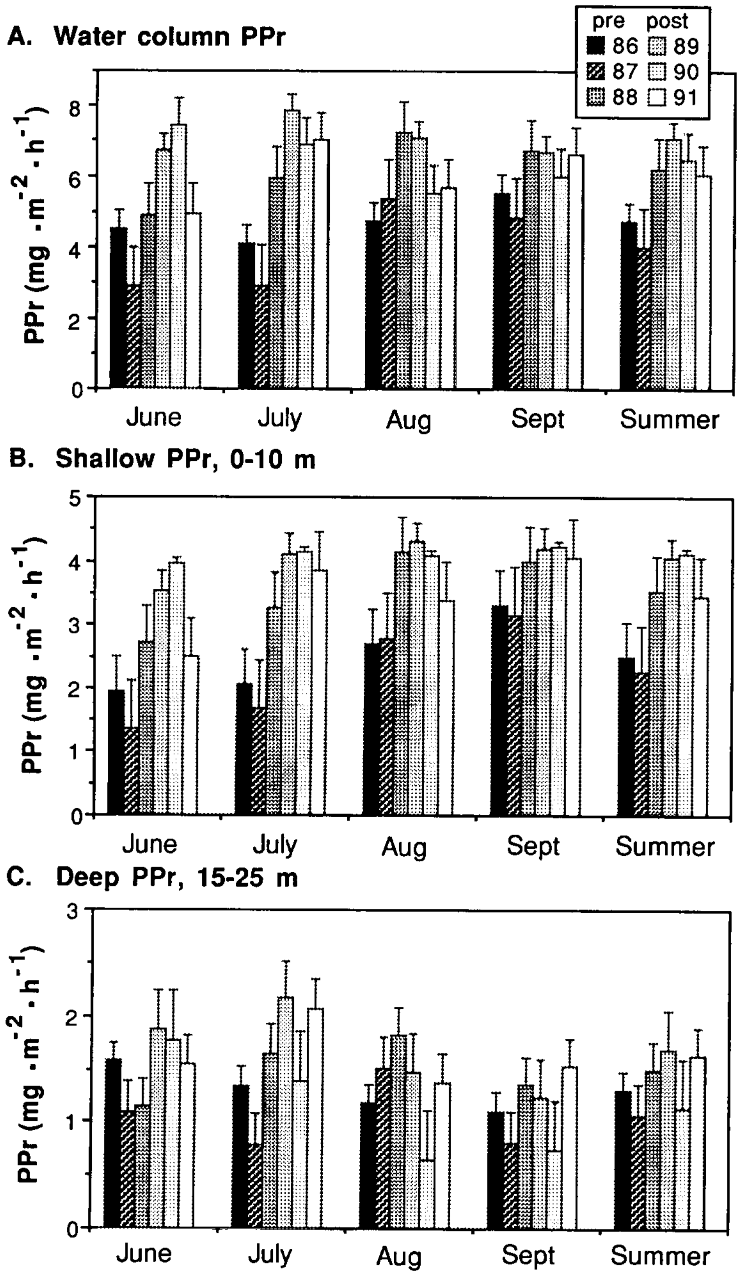

FIG. 10. As for Fig. 1, but for: (A) areal primary productivity (PPr, measured as carbon) for the entire water column, (B) areal PPr for the upper water layer (0–10 m), (C) areal PPr for the lower water layer (15–25 m).

lation is relatively constant as long as the species is present. We view the artificially maintained recruitment of rainbow trout in Castle Lake as an advantage in understanding species interactions. This relatively constant recruitment has allowed us to uncouple the dual role that climatic variation can play in food web function, that of adding variation to both fish recruitment and lake productivity (Carpenter et al. 1989). In years when rainbow trout are stocked at a constant rate, variation in lake productivity can be more easily attributed to climatic factors (Strub et al. 1985), whereas large changes in the stocking program can be followed through several years to assess top-down effects on ecosystem function (this study). Our results indicate that changes in stocking rate of rainbow trout affect a variety of ecosystem components in ways that cannot be explained by climatic variation.

A number of other instances of strong species interactions involve examples of predators that also share resources with their prey. Neill (1984) describes how recruitment of the planktivorous insect *Chaoborus* depends on the competitive interaction of early-instar *Chaoborus* and *Daphnia* in lakes in British Columbia. Luecke et al. (1990*b*) describe how recruitment of bloater chub *Coregonus hoyi* is regulated by predation and competition with alewives in Lake Michigan. The large increases in abundances of golden shiner and brook trout after rainbow trout stocking was discontinued suggest that a similar combination of predatory and competitive effects of rainbow trout on other fish planktivores was important in determining the fish assemblage in Castle Lake.

The most dramatic and immediate response of the Castle Lake zooplankton to alterations in rainbow trout stocking was the increase in the previously rare cyclopoid *D. thomasi* (Fig. 2B), which are herbivorous during juvenile stages but predatory on various zooplankton taxa as late copepodids or adults (Pennak 1989). This increase, then, is potentially the result of increased food availability for juvenile stages due to increased brook trout and golden shiner predation on crustacean herbivores potentially in competition with juvenile *Diacyclops*. This possibility seems unlikely given the observed dynamics: *D. thomasi* increased dramatically in spring 1989 following the omission of the normal fall stocking in 1988 (Fig. 7A) but increased planktivory by brook trout and shiners was not observed until 1991 (Fig. 6) and *Daphnia* did not decline appreciably until late 1990 (Fig. 7C). An alternative explanation for the sudden appearance of *Diacyclops* in early 1989 is that, prior to the manipulation, large numbers of *Diacyclops* recruited from benthic resting stages (cyclopoids overwinter as late copepodids or adults; Pennak 1989) but predation by rainbow trout fingerlings normally kept pelagic densities of *D. thomasi* at low levels prior to the manipulation. While cyclopoid copepods would not be preferred prey items for fish when present in a mixed zooplankton assemblage, upon emergence adult and late-instar *D. thomasi* would be the first relatively large zooplankters available for trout fingerlings in early spring. While previous studies have shown that the abundance of cyclopoid copepods can increase strongly following reduction in planktivorous fish populations (Hansen and Jeppesen 1992, Lathrop and Carpenter 1992), the mechanism responsible for the rapid increase in *Diacyclops* following cessation of trout stocking to Castle Lake remains uncertain. We cannot directly test the spring predation hypothesis with our current data as we do not have diet samples for underyearling trout during premanipulation years. Trout stocking has recently been resumed at Castle Lake; further sampling may resolve this issue.

Changes in Castle Lake's water clarity and primary productivity following stocking manipulation illustrate further complexities in understanding how the functioning of pelagic ecosystems responds to alterations in food web structure. Just as reciprocal changes in the abundance of alternative predator taxa provide a compensatory mechanism within the food web itself, compensatory changes within the ecosystem render certain processes conservative in response to perturbation (Schindler 1987). The effects of the manipulation on water transparency were rapid and strong (Figs. 8–9). However, changes in water column primary productivity were somewhat more ambiguous (Fig. 10). The mechanism for the conservative nature of water column PPr in this case seems clear: the manipulation increased productivity in the surface waters (Fig. 10B) but reduced light penetration to light-limited deeper waters (Fig. 8B), lowering the contribution of deep water layers to total water column productivity (Fig. 10). Thus, changes in productivity integrated over the whole water column were modest, as increases in PPr in upper water layers were compensated for by decreases in PPr in deeper layers. As a result of these compensatory changes, the food-web-induced changes in productivity were small relative to the range of variation in summertime productivity documented by the nearly 30-yr data record analyzed by Jassby et al. (1990). More extensive analyses that correct for the contributions of serial autocorrelation and climate variation will be needed for a fuller assessment of the PPr response.

Previous considerations of the effects of CTI on ecosystem productivity have primarily focused on interannual variability (Carpenter et al. 1985, Carpenter 1988). However, the apparent effects of the stocking manipulation on the depth distribution and seasonal development of PPr in Castle Lake indicated that in this case the effects of manipulation were more strongly expressed on intra-annual rather than interannual time scales. Persson et al. (1993) have also emphasized the role of food web structure in modulating seasonal variation in aquatic ecosystems. In this sense the results we present here support the correlative evidence of Goldman et al. (1989) and Jassby et al. (1990) that climatic influences strongly govern interannual variation in ecosystem productivity but food web parameters produce variation in the vertical distribution and seasonal development of productivity in this system. More specifically, the analyses of Jassby et al. (1990) indicated that food web parameters predominantly affected productivity in the surface waters late in the stratified season. Numerous aspects of our observations support this correlative evidence: highest planktivory rates by young-of-the-year fishes in late summer months (Fig. 6), significant changes in *Daphnia* seasonality before and after the manipulation, strongest reductions in Secchi transparency in August/September (Fig. 8A), strongest PPr responses in the surface waters (Fig. 10), and significant changes in PPr seasonality before and after the manipulation. Thus, although alterations in patterns of phytoplankton productivity induced by our food web manipulations occurred through a different set of mechanisms than had been operating in Castle Lake during the time interval encompassed by the analyses of Jassby et al. (1990), it appears that the nature of the productivity response was largely the same.

The dynamics of fish and zooplankton populations, along with accompanying changes in water quality parameters, in Castle Lake following food web manipulation lead us to propose an alternative mechanism for cascading effects of top predators on phytoplankton productivity and water clarity. Previous considerations of CTI have emphasized the central role of *Daphnia* in affecting water quality (Carpenter et al. 1985, Lammens et al. 1990). Our observations indicate that *Daphnia,* or other large crustacean herbivores, need not be involved in altering water quality parameters when food webs are changed: decreases in water transparency were observed early in 1989 (Fig. 8) while *Daphnia* biomass did not decline appreciably until late 1990 (Fig. 7C). We hypothesize that effects on productivity and water clarity observed in 1989 resulted from the effects of increased *D. thomasi* predation on microconsumers (rotifers, ciliates, other protozoa), reducing microconsumer grazing pressure. Studies supporting this hypothesis include a series of enclosure experiments we have performed during 1991–1993 but are too extensive to include in this paper. We summarize the conclusions here. First, experimentally enhanced densities of *D. thomasi* produced strong declines in rotifer and ciliate densities in several experiments (Brett et al. 1994, Wiackowski et al. 1994). Second, measurements of micrograzer herbivory (grazing by consumers passing a 85-μm screen) made with dilution techniques (Landry and Hassett 1982) indicated microconsumer grazing rates of ≈0.10–0.25 d^{-1} (mean: 0.13 d^{-1}) on phytoplankton biomass (Elser and Frees 1995), greater than previous grazing rate estimates made for the crustacean herbivore assemblage in Castle Lake (0.06–0.12 d^{-1}, mean: 0.076 d^{-1}; Elser 1992). These microconsumer estimates were made in 1992, after the increase in *Diacyclops* abundance in Castle Lake; thus, microconsumer grazing pressure may have been even higher in years prior to manipulation. Finally, when plankton from a nearby lake without *Diacyclops* was exposed to *Diacyclops* for 10 d, the abundance of herbivorous ciliates and microherbivory rates decreased and chlorophyll concentration and algal growth capacity increased (J. J. Elser, *unpublished data*). The evidence just summarized comes from small enclosures (≤20 L) and short-term incubations (≤ 2 wk); whether these experiments yield valid insights into observed dynamics in Castle Lake is subject to question given the known potential for misleading indications when extrapolating from small-scale, short-term studies to whole-ecosystem, long-term dynamics (Frost et al. 1988). Future observations of *Diacyclops* abundance, microconsumer dynamics, and ecosystem processes as Castle Lake responds to the resumption of trout stocking will permit us to evaluate whether the hypothesized mechanism is sound. Further experimentation by others working in nutrient-poor lakes would also be useful in establishing the generality of the unconventional multitrophic-level mechanisms we have proposed.

The results we have presented here have led us to revise our view of the functioning of the Castle Lake food web and its impacts on variation in ecosystem productivity. The correlative evidence presented by Jassby et al. (1990), in which productivity variation correlated with relative trout abundance and *Daphnia* biomass during 25 yr of relatively constant stocking intensity, initially suggested to us a simple chain of coupled predatory interactions in which rainbow trout functioned primarily as a predator on *Daphnia.* Thus, our expectation was that reduction in rainbow trout abundance would lower productivity and increase water clarity as a result of increased *Daphnia* grazing. However, the opposite effects occurred when trout were reduced, accompanied by major changes in other, previously unrecognized or unappreciated, components of the food web: *Diacyclops,* golden shiners, and brook trout. Our new view of the Castle Lake food web incorporates the trophic complexity that these unexpected responses have identified. This includes the prevalence of mixed predation–competition interactions throughout this web, especially those involving rainbow trout and three alternative planktivores (*Diacyclops,* brook trout, golden shiners). Thus, following stocking manipulation of rainbow trout in Castle Lake, food web adjustments compensated for the reduction in the historically dominant planktivore to such a degree that the overall intensity of planktivory was higher following the manipulation, resulting in increased PPr and decreases in water clarity. The complex dynamics that we have documented here suggest that compensatory mechanisms involving rare or undocumented components of lake food webs (such as invertebrate predators and microconsumers, which are not considered in many studies) may be responsible for divergent or surprising outcomes when top predators are altered. Considerable debate has occurred regarding the impact of food web processes on phytoplankton dynamics as a function of lake trophic status (McQueen et al. 1986, Benndorf 1988, Elser and Goldman 1991, Carpenter and Kitchell 1993). Power (1992) has also noted that the relationship between ecosystem productivity and the potential influence of top-down forces is crucial in discerning among several competing theoretical frameworks describing food web interactions. Castle Lake may be the most oligotrophic lake yet subjected to a deliberate whole-lake food web manipulation. In low productivity lakes, low overall food availability at most links in the food web may enhance the potential for unexpected outcomes mediated by mixed predation–competition interactions.

Our results support the arguments made by Power (1992) and Strong (1992) that the trophic complexity of food webs in nature complicates predictions of the outcome of manipulations at the top of the food web:

reductions in densities of rainbow trout intended to reduce predation pressure on herbivorous zooplankton actually increased planktivore pressure (by both vertebrate and invertebrate planktivores). Nevertheless, alterations in the planktivory regime appeared to alter various water quality parameters. Our study also suggests alternative ways by which cascading effects can reach the bottom of the food web (i.e., microconsumer grazing altered by changes in the impacts of invertebrate predators) and emphasizes that food web effects on ecosystem processes are expressed at intra-annual as well as interannual time scales.

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