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AN EVALUATION OF CAUSES FOR THE DECLINE OF THE LAKE TANEYCOMO TROPHY RAINBOW TROUT FISHERY

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the Faculty of the Graduate School
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Master of Science

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by
MARK A. WEILAND

Dr. Robert S. Hayward Thesis Supervisor

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The undersigned, appointed by the Dean of the Graduate Faculty, have examined the thesis entitled

AN EVALUATION OF CAUSES FOR THE DECLINE OF THE LAKE TANEYCOMO TROPHY RAINBOW TROUT FISHERY

presented by Mark A. Weiland
a candidate for the degree of MASTER OF SCIENCE and hereby certify in their opinion it is worthy of acceptance

Dr. Robert Hayward ______________________

Dr. Douglas Noltie Doug Noltie

Dr. James Carrel James E Carrel

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ABSTRACT

Causes for the loss of a previous capacity for stocked rainbow trout (Oncorhynchus mykiss) to grow to large sizes in Lake Taneycomo, a cold-water impoundment, were studied. Monthly in situ estimates of daily food consumption by rainbow trout in 1991 and 1992 indicated these fish now consume less than maintenance ration on most days of the year. Food consumption rates were poorest for larger rainbow trout (> 26 cm total length). Presently high stocking rates in response to annually increasing fishing pressure, have resulted in high standing densities of rainbow trout in months when fishing intensity is lower. These higher densities of fish exceed the growth support capacity of the prey base. In summer months when many rainbow trout were removed by angling, small rainbow trout consumed sufficient food biomass to grow. Little diet separation occurred between small and larger rainbow trout, with larger fish being most negatively affected by intraspecific trophic competition. Diets of rainbow trout sampled in this study were substantially different from rainbow trout diets described in a comparable study done in the early 1970s in this same system. These long-term diet shifts indicate a eutrophication-related effect on the prey community, and suggest the prey base has become less suitable for sustaining high densities of rainbow trout. Evaluations of residence times of stocked rainbow trout also indicated that fish now remain in the system for shorter time periods than occurred historically when fish grew to large sizes. Monthly residence times were inversely related to monthly fishing pressure.

Despite a generally reduced capacity for rainbow trout growth due to an apparent change in trophic status of the system, it is concluded that re-establishment of large rainbow trout through in situ growth can still be achieved. This would require reducing standing densities of rainbow trout while also increasing their residence times. Establishment of a larger prey component suitable for large rainbow trout is recommended to allow diet separation between small and large fish. Also, the data suggested that rainbow trout in residence for longer periods (>100 d) became more effective feeders in the system, consuming up to twice the food biomasses eaten by shorter-residence counterparts. Therefore, in addition to reducing standing densities of rainbow trout, lengthening of residence times should improve presently poor feeding and growth rates.

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INTRODUCTION

Many sport fisheries involving rainbow trout (Oncorhynchus mykiss) and other salmonids are sustained by the regular stocking of these fish into the cold-water tailraces of impoundments (Swink 1983). Since their establishments, many of these fisheries have experienced increases in both angling pressure and fish stocking rates, as well as changes in the tailrace environment (Axon 1974; Johnson et al. 1987). Paralleling these changes are reports of shifts from "put-grow-take" to "put-take" fisheries (Axon 1974). Described herein are findings of an intensive, three-year field study of causes for the loss of large, "trophy-size" rainbow trout in Lake Taneycomo, Missouri, a cold-water tailrace system into which rainbow trout are regularly stocked at a size of about 26 cm total length. While the conditions found to underlie this loss of large fish may be more extreme than in many comparable systems, this study should contribute to a fuller appreciation of the ecological energetics of salmonid fishery resource populations in cold-water tailraces.

Lake Taneycomo is a cold-water impoundment in southern Missouri that supports a popular rainbow trout fishery. Rainbow trout are stocked continuously to sustain the population against annually high, but seasonably variable, fishing pressure. Historically, stocked rainbow trout grew at an average rate of 1.8 cm/month (Turner 1977), and many reached trophy size (≥ 40.6 cm total length). During the past 15-20 years, however, numbers of trophy-size rainbow trout in the system have declined to negligible levels (Figure 1), with parallel evidence of a decline in relative weight (Figure 2). At present, the mean size of rainbow trout in catches does not exceed the sizes stocked (Goddard et al. 1988).

The decline in numbers of large rainbow trout in Lake Taneycomo has been ascribed to numerous factors, including a decline in densities of the amphipod (_Gammarus pseudolimnaeus_) (Goddard et al. 1988), historically the most important prey in the rainbow trout diet (Pflieger 1977). Also implicated have been heavy fishing pressure, over-stocking of rainbow trout, fluctuating flow rates, and water quality changes associated with substantial development activity in the watershed (Goddard et al. 1988; Morris 1989).

After reviewing background information on this fishery, it was hypothesized that present levels of rainbow trout stocking, which have increased substantially from previous years (Figure 3), are contributing to low rainbow trout growth rates in Lake Taneycomo which underlies the decline in numbers of large fish in the system. The increase in rainbow trout stocking rates has been a response to steadily increasing fishing pressure (Figure 4). The higher standing densities of rainbow trout that have likely resulted may be

FIGURE 1. Numbers of rainbow trout ≥40.6 cm caught per hour of electrofishing effort in the upper 6 km of Lake Taneycomo in August 1979-1990. Data are from the Missouri Department of Conservation.

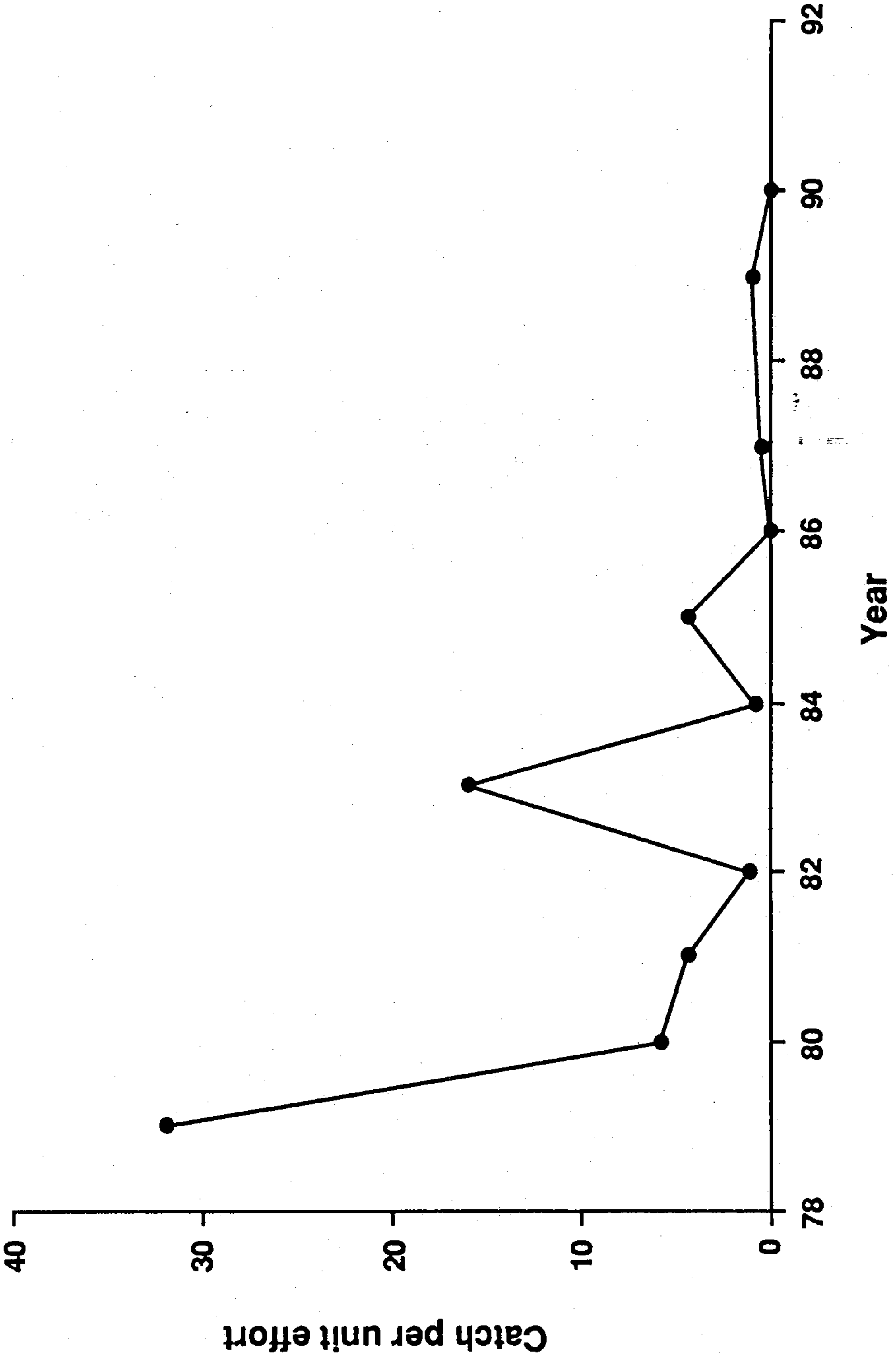

Catch per unit effort
0
10
20
30
40
78
80
82
84
86
88
90
92
Year

FIGURE 2. Mean relative weight (Wr) of rainbow trout (35.6-50.8 cm) in the upper 6 km of Lake Taneycomo from August electrofishing, 1979-1990. Data are from the Missouri Department of Conservation.

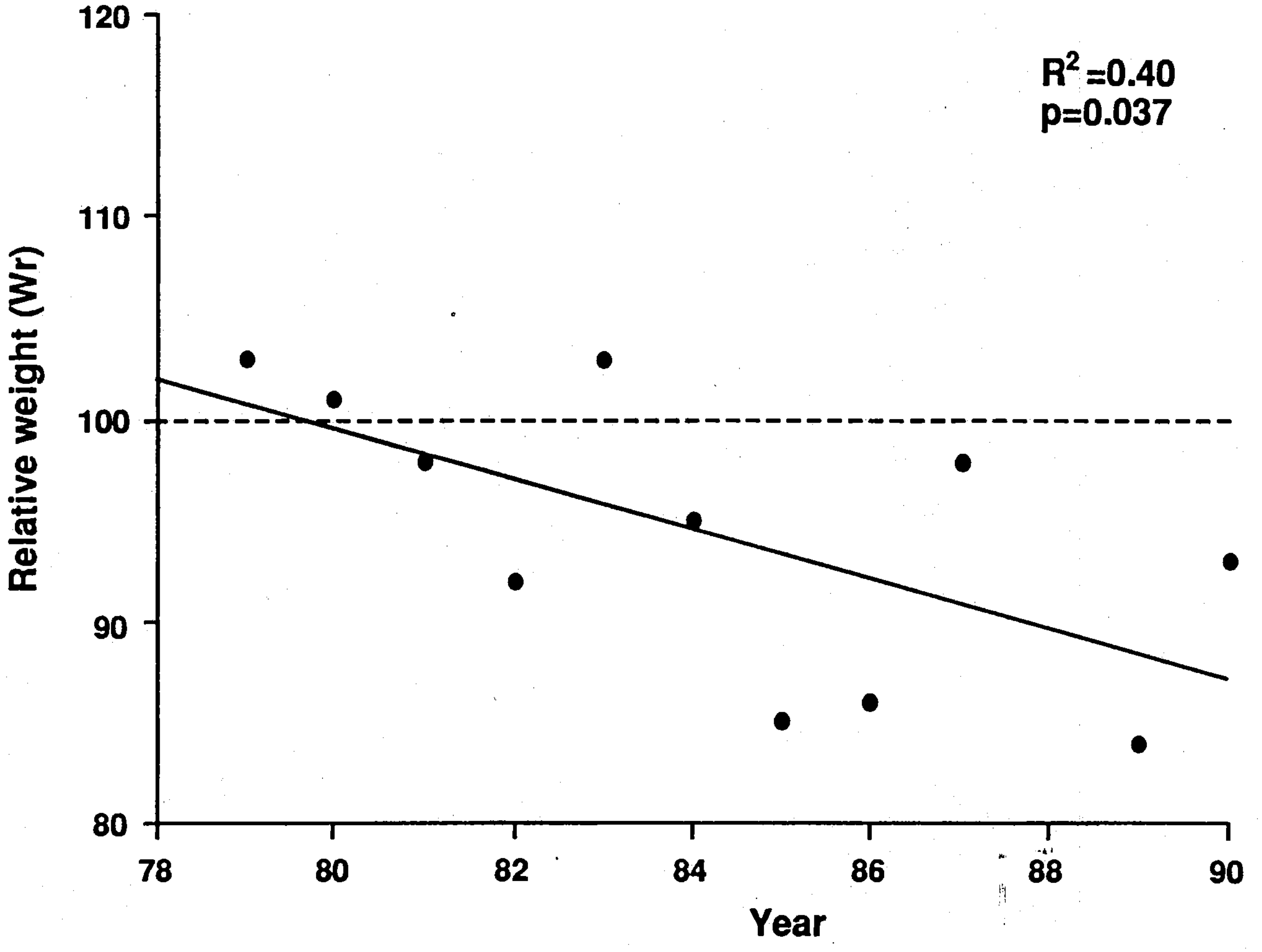

R^2=0.40
p=0.037
Relative weight (Wr)
120
110
100
90
80
78
80
82
84
86
88
90
Year

FIGURE 3. Total numbers of rainbow trout stocked annually into Lake Taneycomo between 1958 and 1990. Data points indicate 5-year median values. Data are from the Missouri Department of Conservation.

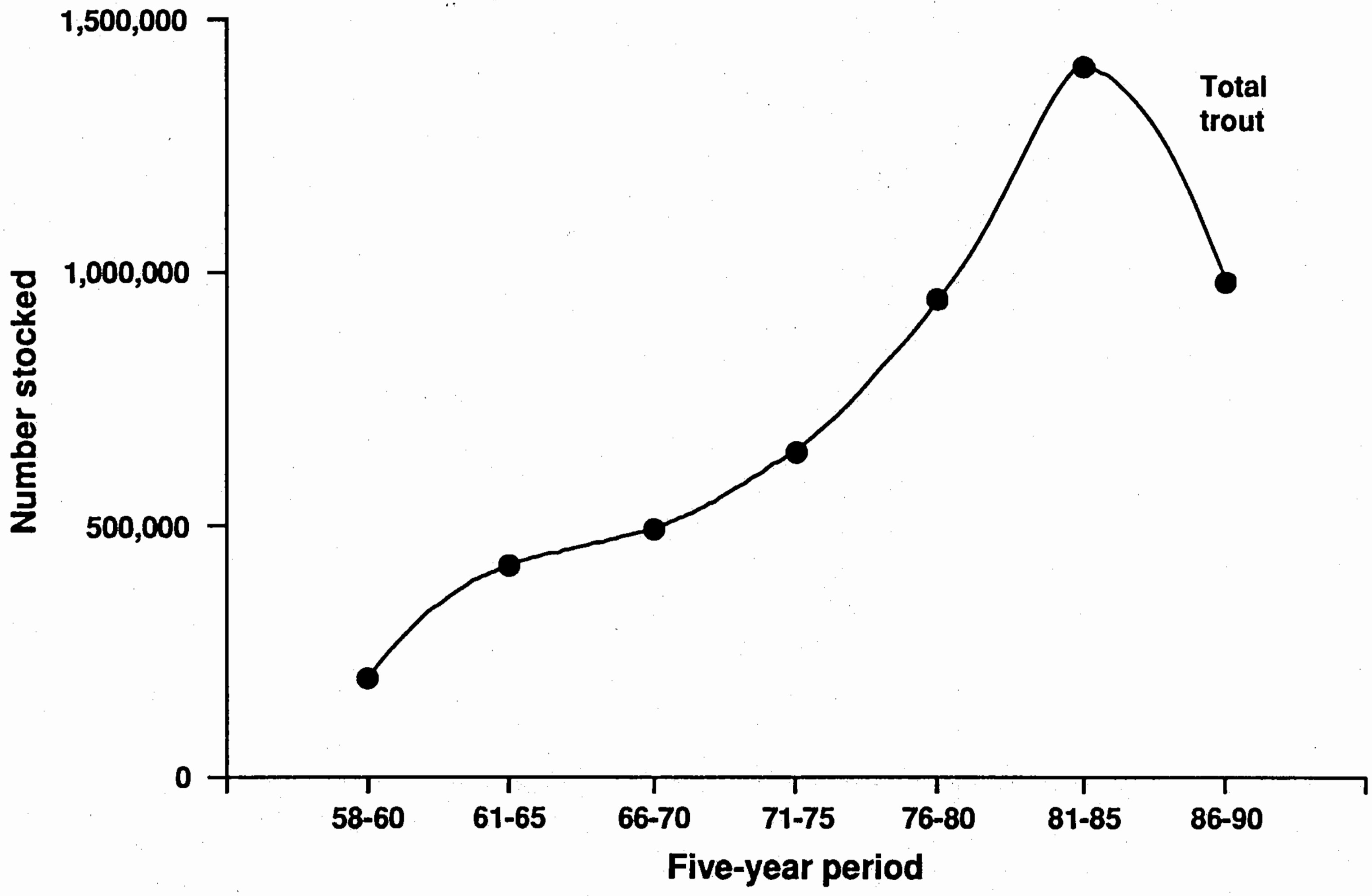
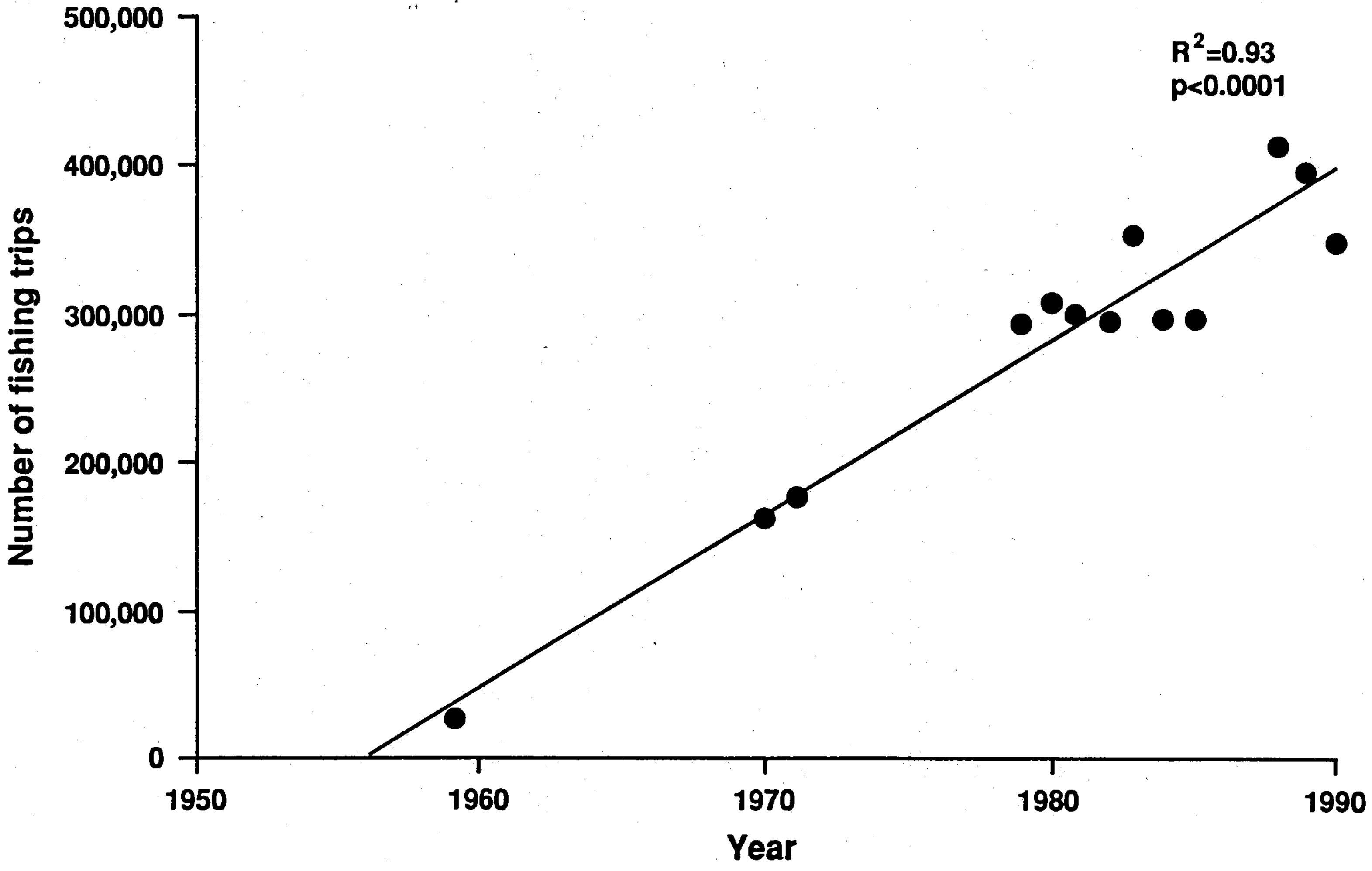

Total
trout
Number stocked
1,500,000
1,000,000
500,000
0
58-60
61-65
66-70
71-75
76-80
81-85
86-90
Five-year period

FIGURE 4. Estimated number of annual fishing trips to Lake Taneycomo from 1959-1990. Data are from the Missouri Department of Conservation.


R^2=0.93
p<0.0001
500,000
400,000
300,000
200,000
100,000
0
Number of fishing trips
1950
1960
1970
1980
1990
Year

exceeding the present carrying capacity of the rainbow trout prey base. Excessive stocking may be reducing food availability and, in turn, food consumption and growth rates.

In a survey of 16 southern states, Swink (1983) found that 3,691,607 salmonids were stocked in 48 tailwater systems representing 940.4 km of waterway length, in 1980. Lake Taneycomo alone received 31.4% (1,159,909) of these stocked fish, while accounting for only 3.4% (32 km) of the total waterway length. This comparison indicates that the Lake Taneycomo system receives a fish stocking burden that substantially exceeds those of comparable systems.

It was also hypothesized that in addition to high stocking rates, seasonally heavy fishing pressure may not allow stocked rainbow trout to remain in Lake Taneycomo for sufficient times to grow to large sizes. The total number of annual fishing trips to Lake Taneycomo has increased from about 24,000 in 1959 to about 400,000 in recent years (Figure 4).

To test Hypothesis 1 concerning whether currently high stocking rates are causing low food availability and low feeding rates for rainbow trout, food consumption rates were estimated monthly over one full year and compared to estimates of their maintenance ration (MR) levels, food amounts needed just to maintain body weight. Food consumption relative to MR was then re-evaluated during the following year after rainbow trout stocking rates had been reduced by 25%, to determine whether food consumption rates increased in response to lower trout densities. To test Hypothesis 2 concerning the sufficiency of rainbow trout residence times for growth to larger sizes, residence times of cohorts stocked in different months during 1991-1993 were directly estimated and compared to a rough estimate of residence time during earlier years when many rainbow trout grew to trophy size. Seasonal trends in present residence times were also evaluated in relation to monthly angling pressure, rainbow trout standing density patterns, and food consumption rates.

STUDY AREA

Background

Lake Taneycomo is a 700-ha hydroelectric power generation reservoir located in southern Missouri on the White River system. Lake Taneycomo was originally a warmwater reservoir formed in 1913 by the construction of Powersite Dam which still marks the impoundment's downstream limit. In 1958 Table Rock Dam was completed and delimits the reservoir's upper end. Hypolimnetic releases through this dam from Table Rock Lake converted Lake Taneycomo into a coldwater system almost immediately. Water inputs from upstream Table Rock Dam affect not only Lake Taneycomo's flow and water levels, but also its water temperature and dissolved oxygen concentrations. The temperatures of water released from Table Rock Lake into Lake Taneycomo range from 3 to 13°C (Weithman and Haas 1984). Water temperatures in the upper 4.5 km of Lake Taneycomo (this project's study area) are strongly influenced by the temperature of waters released from Table Rock Lake. Temperatures in the upper end of Lake Taneycomo are lowest in February and March (typically about 5°C) and then increase through November to about 13°C when temperatures begin to decline. Water temperature in the study area ranged from 5.8-13.8°C over the study period.

30 mi.

The impoundment is 32 km in length with a maximum channel width of 0.5 km. Water depths in the upper 4.5 km show a 3-m range from lowest inflow through highest inflow periods. Water inflow rates from the four penstocks of Table Rock Dam range from 3.2 to 560 m^3/s (U.S. Army Corps of Engineers [USACE] 1985) and can cause rapid water level changes. Water depths in the study area ranged from 0.75 m, 0.25 km downstream from Table Rock Dam, to 3 m at the downstream limit, during sampling times for this study.

113 ~ 19,762 ft^3/s

Dissolved oxygen concentrations in upper Lake Taneycomo are highest in February and March (10-13 mg/L) and typically decline throughout the year reaching levels as low as 1 mg/L for short periods in late October and early November (Weithman and Haas 1984). Dissolved oxygen levels increase again in late November to early December after Table Rock Lake destratifies. Water temperature follows an inverse pattern to that of dissolved oxygen. Dissolved oxygen concentrations ranged from 3.8-14.0 mg O_2 throughout the study area over the course of this study.

Stocked and indigenous fish and prey

To replace the severely degraded warmwater fishery that had existed (Fry and Hanson 1968), stocking of rainbow trout into Lake Taneycomo began in 1959 after Table Rock Dam was completed. In 1961, amphipods (*Gammarus pseudolimnaeous*) were seeded into Lake Taneycomo to provide an additional food source for rainbow trout (Goddard et al. 1988). High densities of amphipods became established and were the primary prey of rainbow trout (Pfleiger 1977a). Limited early evidence suggests that amphipod densities have been declining in recent years (Goddard et al. 1988).

Other salmonid species have also been stocked into Lake Taneycomo (Goddard et al. 1988). Kokanee salmon (Oncorhynchus nerka) were stocked in 1967 to improve fishing in the lower end of the lake. Because these fish showed slow growth and were caught largely in the impoundment's upper end where they might compete for food resources with rainbow trout, stocking of this species was stopped. Steelhead (Oncorhynchus mykiss) were also stocked from 1971-1974, but this was discontinued for fear that diseases introduced via these fish might be detrimental to the rainbow trout population. Brown trout (Salmo trutta) were first stocked in 1980 when evidence of declines in rainbow trout sizes became apparent (Goddard et al. 1988); this species has been stocked continuously since, but in relatively low numbers. Currently, about one million rainbow trout and 10,000 brown trout are stocked annually (Goddard et al. 1988). The ecosystem also contains a large, apparently increasing population of white sucker (Catostomus commersoni) which was been thought to compete trophically with rainbow trout. A recent study (Hansen and Hayward, in preparation), however, suggests otherwise.

Study zones

As stated, the study area comprised the upper 4.5 km of Lake Taneycomo. This area was selected because it is considered the area that contributes most to rainbow trout growth. Food volumes in stomachs of rainbow trout collected from this area in earlier years were higher than those in stomachs of fish collected from downstream areas (Pfleiger 1977a). Densities of amphipods and isopods, historically important prey of rainbow trout (Pfleiger 1977a), are also higher in this uplake area (Pfleiger 1977b). It is generally believed that rainbow trout, regardless of where they are stocked in Lake Taneycomo, tend to situate in this upper area because habitat conditions there are most suitable. For sampling purposes, the 4.5-km study area was considered to consist of three zones (A-C). Zone A began 0.25 km below Table Rock Dam and extended downstream about 1 km, to the Missouri Department of Conservation boat ramp. Zone B consisted of the next 1.25 km, from the boat ramp to the lower end of the riffle below the Scenic Overlook. Zone C consisted of the remaining 2 km, from the lower end of the riffle to the powerlines upstream from Fall Creek. While the three sampling zones differed somewhat in depth and substrate size, all were considered equally important as growth habitat for rainbow trout.

METHODS

Rainbow trout stocking

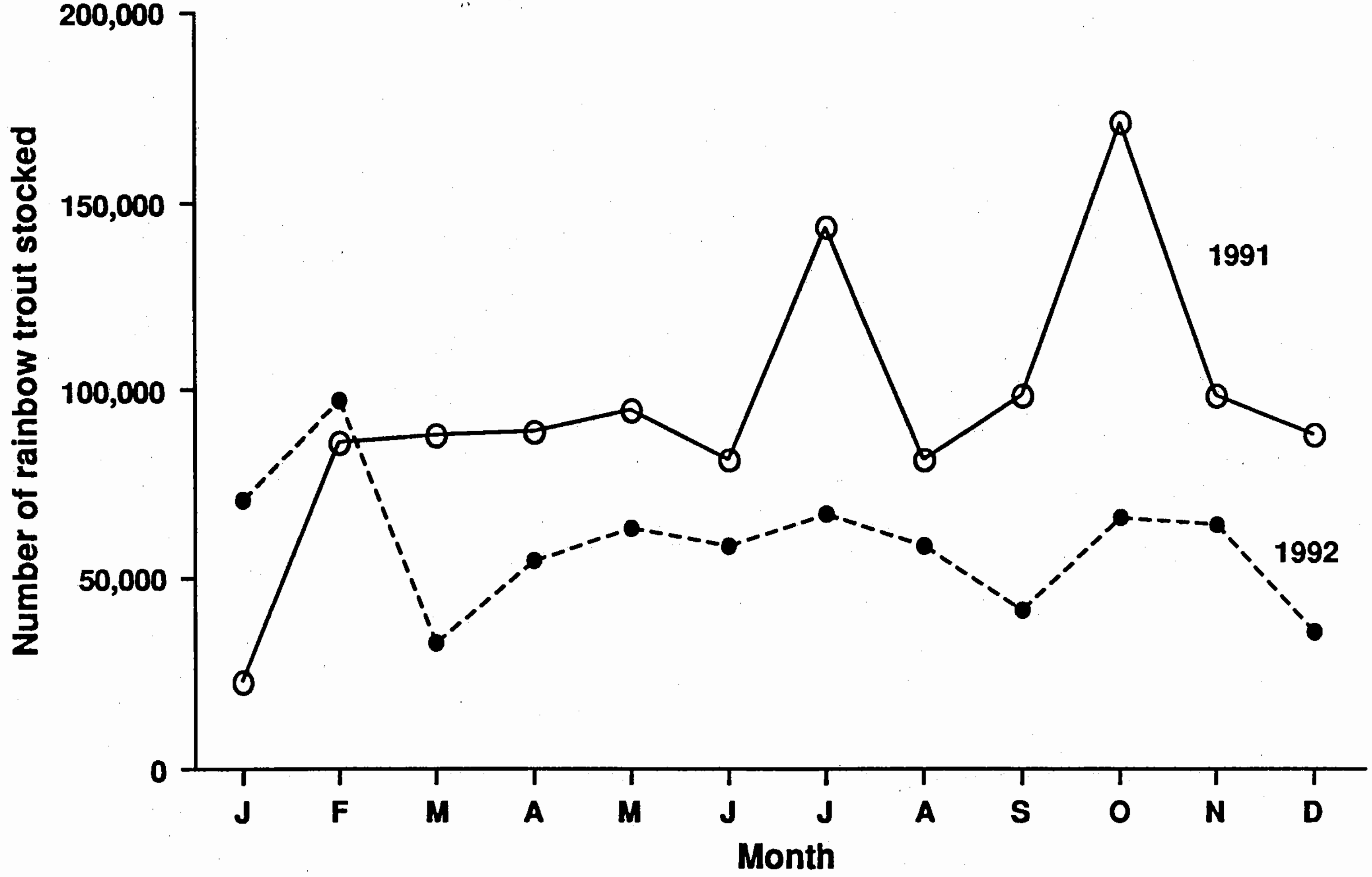
Daily food consumption rates of rainbow trout in Lake Taneycomo were estimated and compared to maintenance rations on a monthly basis in 1991. In 1991, rainbow trout were stocked at rates similar to those in the previous four years (one million total rainbow trout stocked; stocking occurred weekly at a constant rate throughout the year; mean length of rainbow trout stocked was 25.4 cm). To determine if food consumption rates for rainbow trout would increase under lower fish densities, 25% fewer rainbow trout were stocked in 1992 and monthly food consumption estimates were repeated. A total of 750,000 rainbow trout (mean length of 26.2 cm) were stocked in 1992, but weekly stocking rates lower than in 1991 did not begin until March (1992), because of an existing stocking contract with a federal hatchery (Figure 5). The numbers of brown trout stocked (9,000) were the same in both years.

Field Collections

Rainbow trout collection

To estimate food consumption rates, rainbow trout were collected monthly from March, 1991 through November, 1992. Because of strong currents caused by water releases through Table Rock Dam, fish could only be collected in Lake Taneycomo on dates when minimum inflow was guaranteed by USACE. Sustained minimum inflow lasting 24 h could not be

FIGURE 5. Numbers of rainbow trout stocked monthly into Lake Taneycomo in 1991 and 1992.


200,000
150,000
100,000
50,000
0
Number of rainbow trout stocked
J
F
M
A
M
J
J
A
S
O
N
D
Month
1991
1992

guaranteed on dates in all months in 1991 and 1992; in these cases, however, minimum inflow was provided from just before sundown until just after sunup.

Collections of rainbow trout for in situ food consumption rate estimation could be made only in a single sampling zone because of time constraints. Zone B was selected for food consumption work because of its central position in the study area--it and was considered to best represent average conditions. Of the 22 dates on which rainbow trout food consumption was estimated in 1991 and 1992, 13 involved full 24-h sampling while the remaining 9 involved only night sampling (Table 1). On all 22 sampling dates, rainbow trout were collected at four equally-spaced times throughout the night. Night collections would begin at dark and end just before dawn; time intervals between night collections varied seasonally (range = 2.5-3.5 h) according to night length. On dates when day sampling was also done, three daylight collection efforts were made at time intervals ranging from 2.5 to 5.0 h.

All night collections were made by boat electrofishing using pulsed direct current. Because of the high water clarity, electrofishing proved ineffective for collecting rainbow trout during daylight. For day collections, therefore, two experimental gill nets (2.5 m x 61.0 m, 1.3-2.5 cm bar monofilament mesh) were set in a "V" pattern covering about one-third of the channel width (mouth opening

Table 1. Dates on which food consumption data were collected for rainbow trout in Lake Taneycomo.

Date	Samples collected	
	Night only	Night and day
3-2-91		X
3-23-91		X
4-6-91	X	
5-25-91	X	
6-15-91	X	
7-6-91		X
7-27-91	X	
8-24-91		X
9-14-91	X	
10-12-91		X
11-23-91	X	
12-14-91		X
1-25-92		X
2-29-92		X
3-21-92		X
4-25-92		X
5-23-92	X	
7-11-92	X	
8-22-92		X
9-26-92	X	
10-24-92		X
11-21-92		X

downstream). After allowing the nets to set for 20 minutes, the electrofishing boat was run upstream into the "V". Fish were netted as they surfaced, or were caught in the gill nets and quickly recovered. Night sampling involved electrofishing approximately 3 m offshore along the south bank of zone B, until the collection quota of rainbow trout for each sampling time was met. If the collection quota was not met after the entire bank had been covered, effort for that time period ceased. At each daylight sampling, gill nets were set at a single fixed site located about one third of the way downstream in zone B.

An effort was made to collect 12 rainbow trout during each sampling time, six within each of two size groups, small (<26 cm) and large (≥26 cm). Collected rainbow trout were anesthetized with quinaldine sulfate within 10 minutes of capture and were then bagged and frozen on dry ice. No evidence of regurgitation of food material was found during any sampling.

Water physical-chemical data

Dissolved oxygen and temperature readings were taken on all sampling dates using a YSI meter. Readings were taken at fixed locations in each sampling zone, at the surface and at each meter of depth.

Catch-per-unit-effort

To estimate relative numbers of rainbow trout at large within the entire study area on each sampling date, catch-per-unit-effort (CPUE) data were collected. Rainbow trout CPUE was measured as the number of fish observed in three, 15-minute night electrofishing runs, one each in sampling zones A-C. Night electrofishing runs for CPUE were done separately from, but on the same night as efforts to collect fish for food consumption estimation. Fish were simply counted (using hand counters) as they surfaced during each run and were not removed from the water. The relative numbers of rainbow trout at large in the study area on each sampling date were assumed to be proportional to respective CPUE values.

Residence time

To estimate the residence times of rainbow trout in Lake Taneycomo, cohorts of approximately 20,000 fish each were given distinct marks and were stocked in different months at two sites (upstream site: zone A; downstream site: 6 km downstream from zone C) in 1991, 1992 and 1993. Fluorescent pigment dyes (distinct color for each cohort) were sprayed with compressed air onto and under the skin of batches of these fish using methods described by Pribble (1976). Eight distinctly-marked cohorts were stocked into the impoundment over the three years. Evaluations of mark retention and detectibility through time were carried out for subsamples of fish from each cohort held in hatchery raceways near the shoreline. Mark recognition at night using a black light ranged from 98-100% at 73-122 days after dye application.

Residence times of the eight rainbow trout cohorts stocked into Lake Taneycomo were estimated by collecting fish at night on successive post-stocking dates, by electrofishing and checking all fish for dye marks with the aid of a black light . After stocking a cohort, samplings were made weekly for the first three weeks and then monthly thereafter in conjunction with sampling dates for food consumption. Sampling for dye-marked fish involved night collections within each of the three sampling zones (15 minutes of electrofishing per zone). Consistent with earlier findings (Fry and Hanson 1968), it became apparent that stocked cohorts remained predominantly within, or moved upstream (observed for cohorts stocked downstream) into the study area after being stocked. Occasional efforts to collect dye-marked fish downstream from the study area never showed them to be present there.

Laboratory Procedures

In the laboratory, rainbow trout were thawed, measured to the nearest 1 mm total length (TL) and weighed to the nearest 0.1 g wet weight. Fish stomachs were removed and their contents transferred to a glass dish. Unnatural materials including stones, hooks, and fishing baits were separated from natural foods, recorded as present, and then discarded.

Natural food items were identified and measured, and numbers of individual taxa in a stomach were counted within 2-mm size groups. Total lengths of prey (in the stretched position where appropriate) were measured for all whole animal prey organisms in stomachs. Amphipods were measured from the base of the antennae to the tip of the third uropod (Waters and Hokenstrom 1980); isopods were measured from the anterior of the cephalothorax to the end of the abdomen, not including the telson. Insects with appendages extending beyond the head or abdomen were measured from the anterior of the head to the posterior of the last abdominal segment (Smock 1980; Meyer 1989). Total length was measured for whole prey fish.

For partial organisms, only the heads of invertebrates and the vertebral columns of fish were counted. The total lengths of partial organisms that were commonly encountered in rainbow trout stomachs, which showed considerable variation in size, were estimated from taxon-specific regression relationships. These relationships were established from lengths of selected head portions (nearest 0.1 mm) and total length, established from whole organisms (Appendix A). Total lengths of counted partial chironomids (larvae and pupae) were measured from maximum head widths. Partial amphipods were measured from the front of the eye to the first suture. Maximum width of the cephalothorax was measured for isopods. Vertebral columns of partially-digested sculpins (always intact) were measured. For other taxa that were encountered infrequently or which showed relatively little size variation, the total lengths of counted partial portions were assumed to be equal to the average total length of whole representatives. This assumption was confirmed to be valid and slight discrepancies were negligible in analysis. Counts and total lengths of vegetation in rainbow trout stomachs (almost exclusively filamentous algae), were not determined.

Dry weights of all animal prey material and vegetation in each rainbow trout's stomach were determined separately. Animal and vegetable material from each fish was placed into separate crucibles, dried at 65°C for 24 h, and desiccated and weighed to the nearest 0.0001 g with an analytical balance. Dry weights of whole rainbow trout were estimated from previously-established regressions of dry versus wet whole body weight. These animal prey and rainbow trout dry weights were used to make estimates of specific daily food consumption.

Estimates of the biomass of each animal prey type in individual rainbow trout stomachs were made to ultimately determine the percentages of total prey biomass within rainbow trout groups (i.e., size- or year-groups). For this purpose, mean dry weights of each 2-mm size group of each prey taxon was determined (from dry weight versus total length regressions constructed during lab analysis, or given by Slobodkin and Richman (1961) and Rogers et al. (1976)), these being multiplied by corresponding prey counts. Directly-determined biomasses of vegetation in individual rainbow trout, as previously described, were also used for these assessments.

Analytical procedures

Food consumption

Food consumption by each size group of rainbow trout was estimated on a 24-h basis (g dry weight food consumed/g dry weight fish/24 h) for each sampling date in 1991 and 1992. Comparisons of mean food weights in rainbow trout stomachs from night versus day sampling (from full 24-h sampling dates) showed that their feeding intensity was not different in either period on all but one date sampled for small rainbow trout (paired t-tests, N=7 for small and N=7 for large rainbow trout, P>0.05) (Table 2). A difference was shown on one sampling date for small rainbow trout where mean food weights were higher at night than during the day. Because full 24-h samples were not obtained on a number of sampling dates, and because feeding rates almost never different in day versus night, night data only (present for all sampling dates) were used to estimate daily (24 h) food consumption by rainbow trout. The model of Elliott and Persson (1978) was used to estimate total food consumption by rainbow trout over each night period from four point estimates of food weight in fish stomachs. Food consumed within each of the three time intervals in any given night

Table 2. Comparison, by t-test, of mean food weights (g/g dry weight) in the stomachs of rainbow trout between day and night samples on dates when both small and large rainbow trout were collected during the day and night. Day values are listed first in all cases.

	Small rainbow trout		Large rainbow trout	
Date	Mean food weight ±1 SE	p-value	Mean food weight ±1 SE	p-value
7-6-91	0.0070411 ± 0.0028282 0.0091174 ± 0.0029882	p=0.64	0.0027949 ± 0.0025336[a] 0.0024567 ± 0.0003723[b]	p=0.81
8-24-91	*[a]		0.0022091 ± 0.0009376 0.0024370 ± 0.0010600	p=0.87
10-12-91	0.0010443 ± 0.0001045 0.0013257 ± 0.0004626	p=0.89	*	
12-14-91	0.0010035 ± 0.0002090 0.0008931 ± 0.0003197	p=0.83	0.0003731 ± 0.0000849 0.0005657 ± 0.0001990	p=0.51
1-25-92	0.0002316 ± 0.0001078 0.0004434 ± 0.0001702	p=0.52	0.0001976 ± 0.0001187 0.0002601 ± 0.0001191	p=0.81
2-29-92	0.0040032 ± 0.0022346 0.0010954 ± 0.0003478	p=0.06	0.0012953 ± 0.0003231 0.0023685 ± 0.0007547	p=0.39
3-21-92	0.0098446 ± 0.0040469 0.0051410 ± 0.0019942	p=0.31	0.0116061 ± 0.0036116 0.0081652 ± 0.0025798	p=0.44
8-22-92	0.0038490 ± 0.0003326 0.0038490 ± 0.0005692	p=0.50	0.0006602 ± 0.0005515 0.0016390 ± 0.0003279	p=0.28
10-24-92	0.0001327 ± 0.0000452 0.0011463 ± 0.0003229	p=0.01	*	

11-21-92	0.0005959 ± 0.0001950 0.0006804 ± 0.0003134	p=0.89	0.0001506 ± 0.0001372 0.0004540 ± 0.0003667	p=0.44

---

[a] Not enough fish collected during the day to run t-test.

(four food weight point estimates gives three time intervals) was estimated as

$$C_t = \frac{(S_t - S_o e^{-Rt})\, Rt}{1 - e^{-Rt}};$$

$\underline{C}_t$ is the estimated specific food weight consumed during any single nighttime interval, $\underline{S}_0$ and $\underline{S}_t$ are the median food weights in fish stomachs at the beginning and end of a $\underline{t}$-hour time interval, respectively, and $\underline{R}$ is the instantaneous rate of stomach evacuation for rainbow trout during a time interval. Specific food weights estimated as being consumed during each night sampling interval on any sampling date were summed to get total night consumption. Total night consumption was then expanded to produce a 24-h estimate according to the total hours of night sampling. Filamentous algae was not included in estimates of consumption because its nutritional contribution to rainbow trout was considered very low relative to animal prey consumed (Leibfried 1988).

Instantaneous rates of stomach evacuation ($\underline{R}$) for rainbow trout were estimated from a temperature-dependent equation developed from laboratory evacuation experiments conducted over the ranges of temperature and rainbow trout size observed in Lake Taneycomo during this study (Weiland and Hayward, in preparation). In these experiments rainbow trout were fed 1% body weight meals of chironomid larvae. The resultant equation for estimating instantaneous stomach evacuation ($\underline{R}$) for rainbow trout was

$$R=0.0411e^{0.0871T};$$

T is water temperature (°C) on dates when estimates of stomach evacuation and food consumption rates were made.

Maintenance ration (MR), the food biomass that rainbow trout must consume over 24 h to just maintain body weight, was used as a baseline value against which 24-h food consumption estimates were compared. Daily food consumption values in excess of MR indicated that rainbow trout consumed enough food to grow; values below MR indicated that body weight and condition declined. Specific maintenance rations for rainbow trout were approximated for each food consumption sampling date from the equations of Elliott (1975a) developed for brown trout feeding on invertebrate prey. This was necessary because a similar equation for determining rainbow trout MRs consuming natural prey, is not available. Elliott's (1975a) equations for specific maintenance ration (MR) according to wet body weight (BW) in grams for brown trout, over ranges of water temperature (T) are

$$MR=1.390 \times BW^{0.716}e^{0.224\times T},$$

for T = 3.8-6.6°C, and

$$MR=2.711 \times BW^{0.737}e^{0.105\times T},$$

for T = 6.6-19.5°C.

An equation for estimating the maximum food biomass that rainbow trout would consume in 24 h (C_{max}) under conditions they experienced in Lake Taneycomo, was also developed from laboratory experiments (Weiland and Hayward, in preparation). Thus, in addition to MR, food consumption estimates could be related to the food biomasses rainbow trout would have consumed in 24 h if their food supply was unlimited. The equation estimates absolute $\underline{C}_{max}$ (g food/day) for rainbow trout ranging from 11.6-97.3 g dry body weight ($\underline{DW}$), feeding on chironomid larvae at temperatures ($\underline{T}$) ranging from 7.8-12.8 °C as

$$\underline{C}_{max}=-3.299 + 0.345 \times \underline{T} + 0.131 \times \underline{DW}.$$

Absolute C_{max} estimates were converted to specific C_{max} values by dividing by the mean weight of rainbow trout in a size group on a given sampling date.

Natural logarithms of successive CPUE values for dye-marked rainbow trout from each of the eight stocked cohorts of 20,000 fish were regressed against days post-stocking. Regression slopes provided estimates of the instantaneous total mortality rate (Z) for each cohort, from which their residence times (days until 1% of a cohort remained) could by calculated.

Diet analysis

Diets were evaluated for each rainbow trout size group on each consumption sampling date to assess prey use differences associated with years, seasons and size groups, and to compare present to historical rainbow trout prey use patterns. All food taxa were placed into one of eight food groups: chironomid pupae, chironomid larvae, amphipods, isopods, cladocera, other invertebrates, fish, and algae (Table 3). The "other invertebrates" food group comprised taxa that contributed relatively little to total diet biomass, and consisted mainly of terrestrial invertebrates but some aquatic invertebrates also. The algae group was composed almost exclusively of filamentous algae of the genus _Cladophora_. An index of relative importance (IRI) value was calculated for each of the eight food groups on each consumption sampling date within each rainbow trout size group. Overall IRI values were also calculated for the eight food groups to allow between-year and between-size group comparisons of prey use by rainbow trout, as well as to compare 1991-1992 diets to rainbow trout diet data from the early 1970's (Pfleiger 1977a). The IRI is a composite measure of the relative contribution of any food group to rainbow trout diets (combined diet for various groupings of rainbow trout), and is based on biomass and numbers of organisms in a food group as well as its frequency of occurrence across all rainbow trout in a set group. The _IRI_ was calculated as

$$\underline{IRI}=(\underline{\%N}+\underline{\%B})\times(\underline{\%O});$$

_%N_ is the percent by number of all prey organisms in all fish sampled that was represented by a particular food group; _%B_ is the percent of total food biomass represented by a prey group; _%O_ is the percent of rainbow trout in a sample which contained a particular food group.

Fish relative weight

Relative weights ($\underline{Wr}$) of rainbow trout collected from Lake Taneycomo on each consumption sampling date in 1991 and 1992 were determined to assess their correlation with estimated food consumption patterns within and between years. Relative weight of individual fish was first determined as

$$\underline{Wr} = \underline{W} / \underline{Ws} \times 100;$$

$\underline{W}$ is the fish's weight (ounces of wet weight) and $\underline{Ws}$ is a length-specific standard weight for rainbow trout, derived from the following standard weight equation for rainbow trout

$$\underline{Ws}=0.00683 \times \underline{L}^{2.93058};$$

$\underline{L}$ is in total length in inches (data from Steve Weithman, Missouri Department of Conservation). Relative weight values for individual fish were averaged for all rainbow trout within each size group collected on each consumption sampling date.

RESULTS

Daily ration

Consistent with the hypothesized poor feeding conditions for rainbow trout in Lake Taneycomo, fish from both the small (<26 cm) and large (≥26 cm) size groups consumed less than maintenance rations on sampling dates in most months during 1991 (Figure 6). Small rainbow trout consumed enough prey biomass to grow only on the July and August sampling dates, while large rainbow trout fed only slightly above the maintenance ration level in August.

Despite reduced stocking densities (Figure 5), rainbow trout seasonal food consumption patterns in 1992 were similar to 1991 (Figure 6). Small rainbow trout fed substantially in excess of maintenance rations on only two summer sampling dates (July and August). As in 1991, large rainbow trout showed almost continuous submaintenance daily consumption in 1992 (Figure 6), the exception being in March when threadfin shad (_Dorosoma_ _petenense_) were present in Lake Taneycomo. The threadfin shad were believed to have originated from upstream Table Rock Lake (William Anderson, Missouri Department of Conservation, personal communication).

Prey use

Although numerous prey taxa comprised the diets of rainbow trout in 1991 and 1992 (Table 3), relatively few prey groups were of high importance in diets, according to

FIGURE 6. Estimated daily consumption (±1 SE) (% body weight, dry prey and predator weights) relative to maintenance and maximum daily consumption for small and large rainbow trout in the upper 4.5 km of Lake Taneycomo during 1991 and 1992.

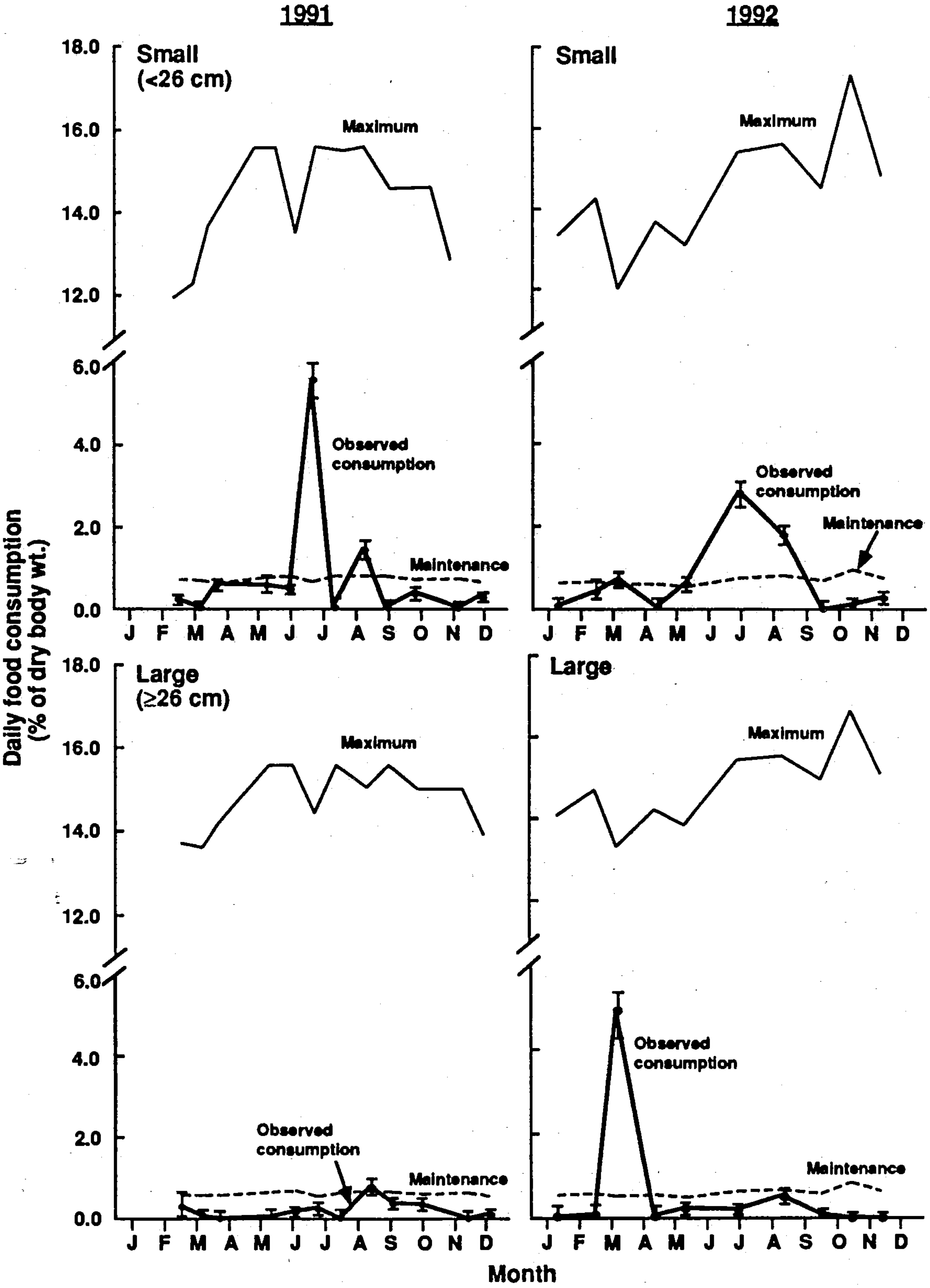

1991
1992
Small
(<26 cm)
Large
(≥26 cm)
Maximum
Observed consumption
Maintenance
Daily food consumption (% of dry body wt.)
18.0
16.0
14.0
12.0
6.0
4.0
2.0
0.0
J F M A M J J A S O N D
Month

Table 3. List of organisms found in the stomachs of rainbow trout in Lake Taneycomo in 1991 and 1992, organized according to designated food groups.

Food group	Taxa included	≥1%[a]
Chironomid pupae	Chironomidae	*
Chironomid larvae	Chironomidae	*
Amphipod	*Gammarus pseudolimnaeus*	*
Isopod	*Caecidotea* sp.	*
	Lirceus sp.	
Cladocera	*Daphnia* sp.	
Other invertebrates	Oligochaeta	
	Hirudinea	
	Copepoda	
	Hydracarina	
	Araneae	
	Chilopoda	
	Ephemeroptera	
	Zygoptera	
	Acrididae	
	Gerridae	
	Reduvidae	
	Notonectidae	
	Corixidae	
	Cicadellidae	
	Gyrinidae	
	Lampyridae	
	Staphylinidae	
	Scarabaeidae	
	Carabidae	
	Coccinellidae	
	Trichoptera	

Food group	Taxa included	≥1%[a]
	Lepidoptera	
	Simuliidae	
	Tipulidae	
	Chaoboridae	
	Formicidae	
	Ichneumonidae	
	Apidae	
	Gastropoda	
Fish	*Cottus bairdi*	*
	Dorosoma petenense	*
Plant material	*Cladophora* sp.	*

[a] Taxa indicated by '*' comprised at least 1% of the total prey biomass consumed by all rainbow trout sampled in this study.

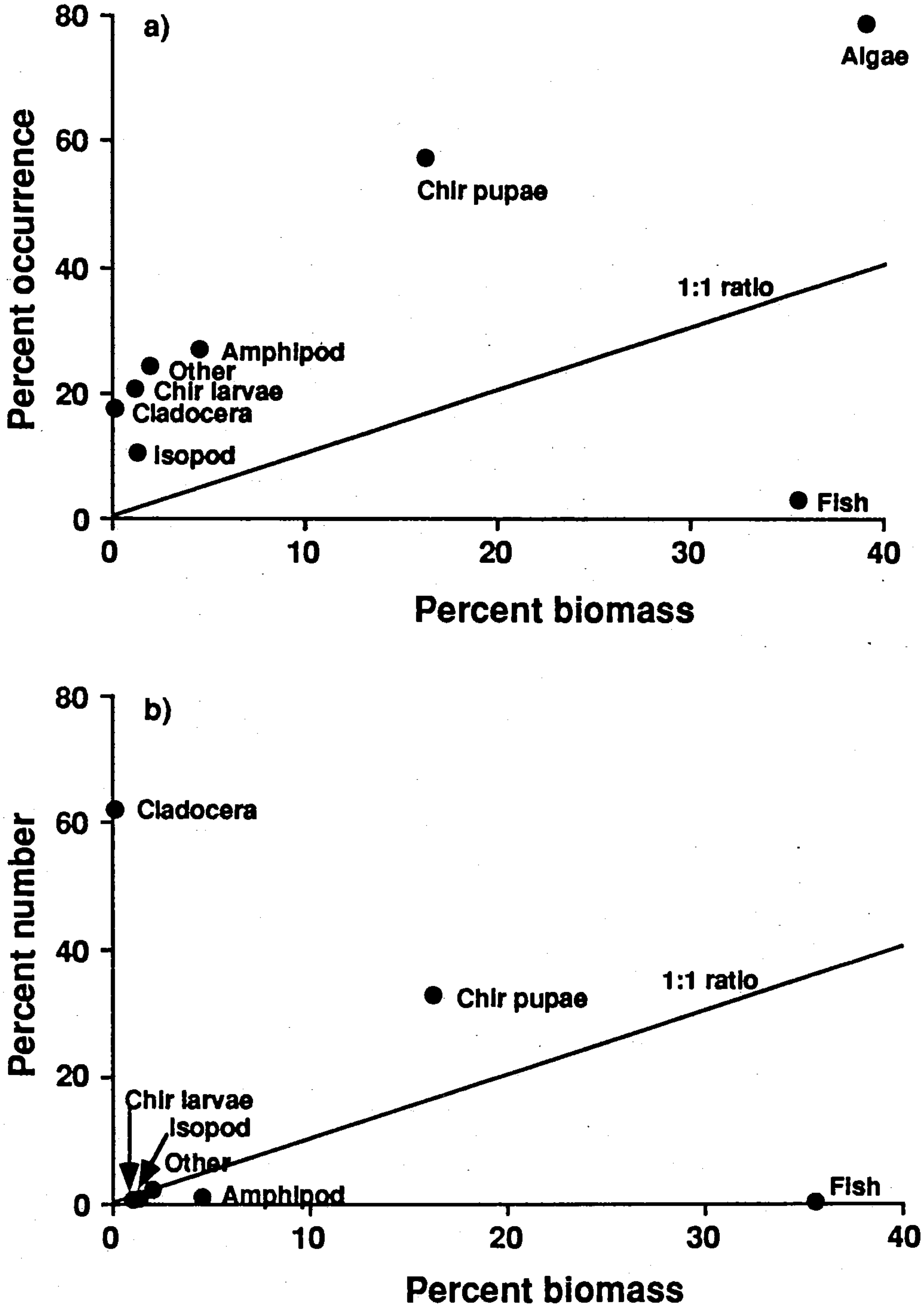
Table 4. Values of the index of relative importance (IRI), percent biomass excluding algae and with algae included (%B), percent occurrence (%O), and percent of total number (%N) for food groups consumed by all rainbow trout collected from Lake Taneycomo during 1991-1992. The index of relative importance was calculated with algae excluded because direct comparison of counts of algae filaments with counts of animal prey were considered inappropriate.

Food group	IRI	%B		%O	%N
		Without algae	(With algae)		
Chironomid pupae	3251	24.1	(16.2)	57.2	32.7
Cladocera	1085	0.1	(0.1)	17.5	61.9
Amphipod	261	8.4	(4.5)	27.1	1.3
Other	130	2.9	(2.0)	24.2	2.4
Fish	199	59.5	(35.6)	3.3	0.2
Chironomid larvae	53	1.8	(1.2)	20.7	0.7
Isopod	41	3.2	(1.3)	10.4	0.8
Algae	-	-	(39.1)	78.8	-

index of relative importance (IRI) values (Table 4). Overall, and among animal prey only, chironomid pupae and cladocerans were the most important food groups in rainbow trout diets in 1991 and 1992, with amphipods ranking third (Table 4). The importance (IRI) of filamentous algae was not calculated because its representation in diets on the basis of numbers (%N), a component of the IRI calculation, was considered incomparable to %N values of animal food groups. Hence, IRI values were computed from among animal food groups alone. However, when compared to all prey groups on a biomass basis (%B with algae), filamentous algae showed the highest value, representing 39.1% of the overall diet of rainbow trout (Table 4). Filamentous algae also showed the highest percent occurrence (%O) value (78.8%) (Table 4).

An inspection of the "evenness" of each food groups' representation in the overall rainbow trout diet (similarity of %B, %O, and %N) was done by first comparing %O to %B values (including filamentous algae) followed by a comparison of %N to %B values (excluding filamentous algae). Most food groups showed %O values in excess of their %B values, the one exception being the fish food group which comprised 35.6% of total diet biomass but occurred in only 3.3% of all fish examined (Figure 7a). Most food groups (algae excluded) showed %N values close to their %B values, exceptions being cladocerans which ranked high in numbers

FIGURE 7. The relationship between a) relative percent biomass and percent occurrence of food groups in the diet of rainbow trout and b) relative percent biomass and percent by number of food groups in the diet of rainbow trout during 1991-1992.


a)
Percent occurrence
Percent biomass
0
20
40
60
80
0
10
20
30
40
Algae
Chir pupae
1:1 ratio
Amphipod
Other
Chir larvae
Cladocera
Isopod
Fish
b)
Percent number
Percent biomass
0
20
40
60
80
0
10
20
30
40
Cladocera
Chir pupae
1:1 ratio
Chir larvae
Isopod
Other
Amphipod
Fish

but low in biomass, and fish, which were quite high in biomass but low in numbers (Figure 7b).

Whether rainbow trout diets differed between 1991 and 1992 (size groups combined) and between the size groups (years combined) was tested using Spearman's Rank Correlation procedure on the IRI values for the seven animal food groups. A lack of correlation was shown between years ($P>0.05$), indicating a significant difference in the diets. This difference was mainly attributable to a higher importance of fish prey (almost exclusively threadfin shad) in the 1992 diet (Figure 8a). A significant correlation was found between small and large rainbow trout size groups ($p<0.05$) indicating no differences in importance rankings of animal food groups. Examination of the data reveals that a higher importance of fish in large rainbow trout accounted for most of the variation between small and large fish diets (Figure 8b). When similar analyses were conducted on the basis of ranked biomass percentages (which allowed inclusion of filamentous algae), the same conclusions resulted (Figure 9a-b). The biomass analysis also showed the higher use of threadfin shad in 1992 as the source of between-year diet differences.

Comparisons of rainbow trout diets with greater resolution (each size group in each year) showed that fish were of higher relative importance (IRI) in the diets of both size groups in 1992 than in 1991 (Table 5), but were of

FIGURE 8. The relationship between a) the ranked relative importance of food groups for all rainbow trout during 1991 and 1992 and b) the ranked relative importance of food groups for small and large rainbow trout in both years and Spearman's Rank Correlation result for each relationship.

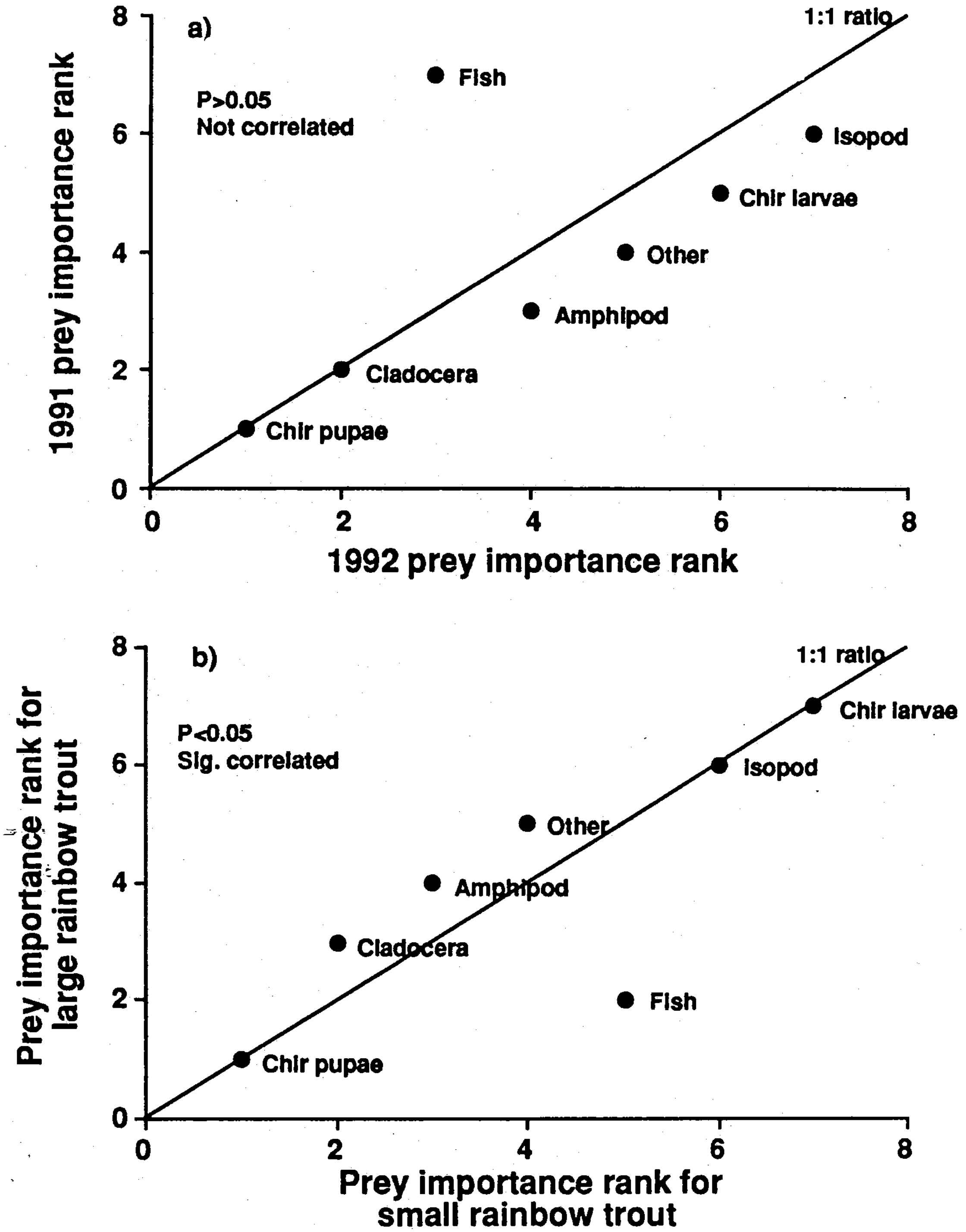
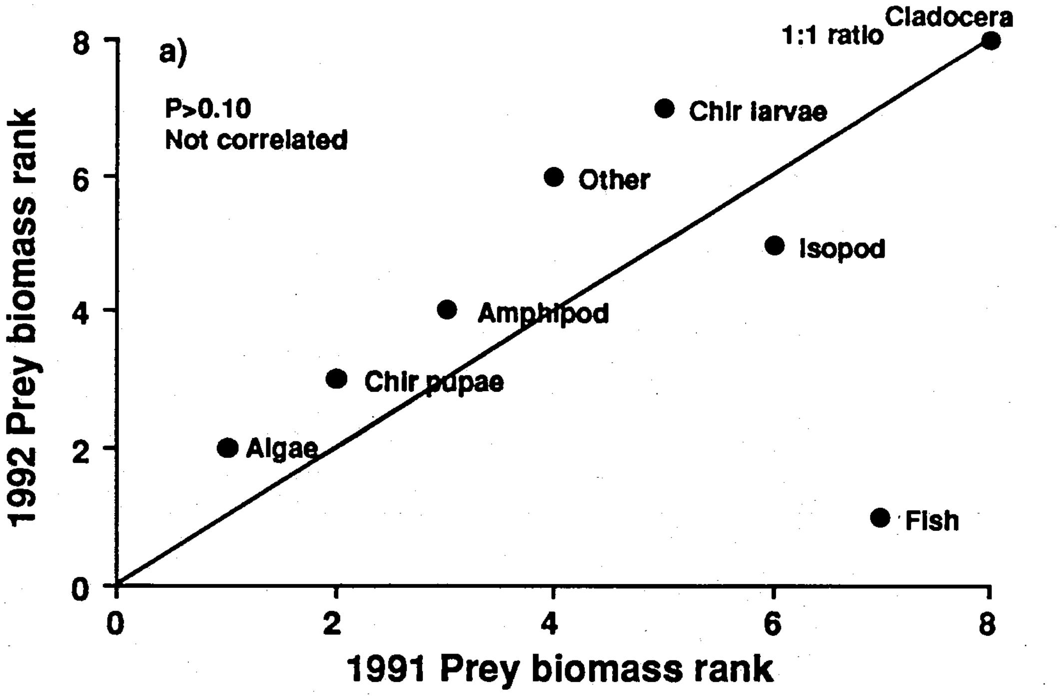

a)
1:1 ratio
P>0.05
Not correlated
Fish
Isopod
Chir larvae
Other
Amphipod
Cladocera
Chir pupae
1991 prey importance rank
1992 prey importance rank
0
2
4
6
8
b)
1:1 ratio
P<0.05
Sig. correlated
Chir larvae
Isopod
Other
Amphipod
Cladocera
Fish
Chir pupae
Prey importance rank for large rainbow trout
Prey importance rank for small rainbow trout

FIGURE 9. The relationship between a) the ranked relative biomass of food groups for all rainbow trout during 1991 and 1992 and b) the ranked relative biomass of food groups for small and large rainbow trout in both years and Spearman's Rank Correlation result for each relationship.


a)
P>0.10
Not correlated
1:1 ratio
Cladocera
Chir larvae
Other
Isopod
Amphipod
Chir pupae
Algae
Fish
1992 Prey biomass rank
1991 Prey biomass rank
0
2
4
6
8
0
2
4
6
8

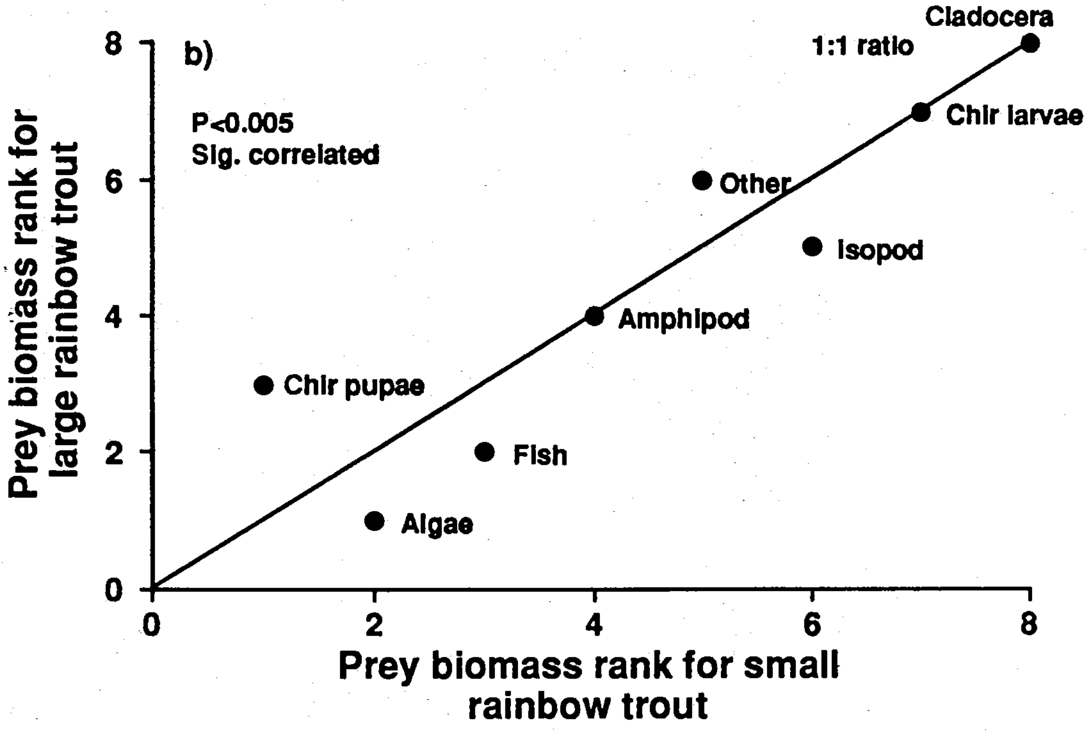

b)
P<0.005
Sig. correlated
1:1 ratio
Cladocera
Chir larvae
Other
Isopod
Amphipod
Chir pupae
Fish
Algae
Prey biomass rank for large rainbow trout
Prey biomass rank for small rainbow trout
0
2
4
6
8
0
2
4
6
8

Table 5. Values of the index of relative importance (IRI), percent biomass excluding algae and with algae included (%B), percent occurrence (%O), and percent of total number (%N) for food groups consumed by small and large rainbow trout (RBT) collected from Lake Taneycomo during 1991-1992. The index of relative importance was calculated with algae excluded because direct comparison of counts of algae filaments with counts of animal prey were considered inappropriate.

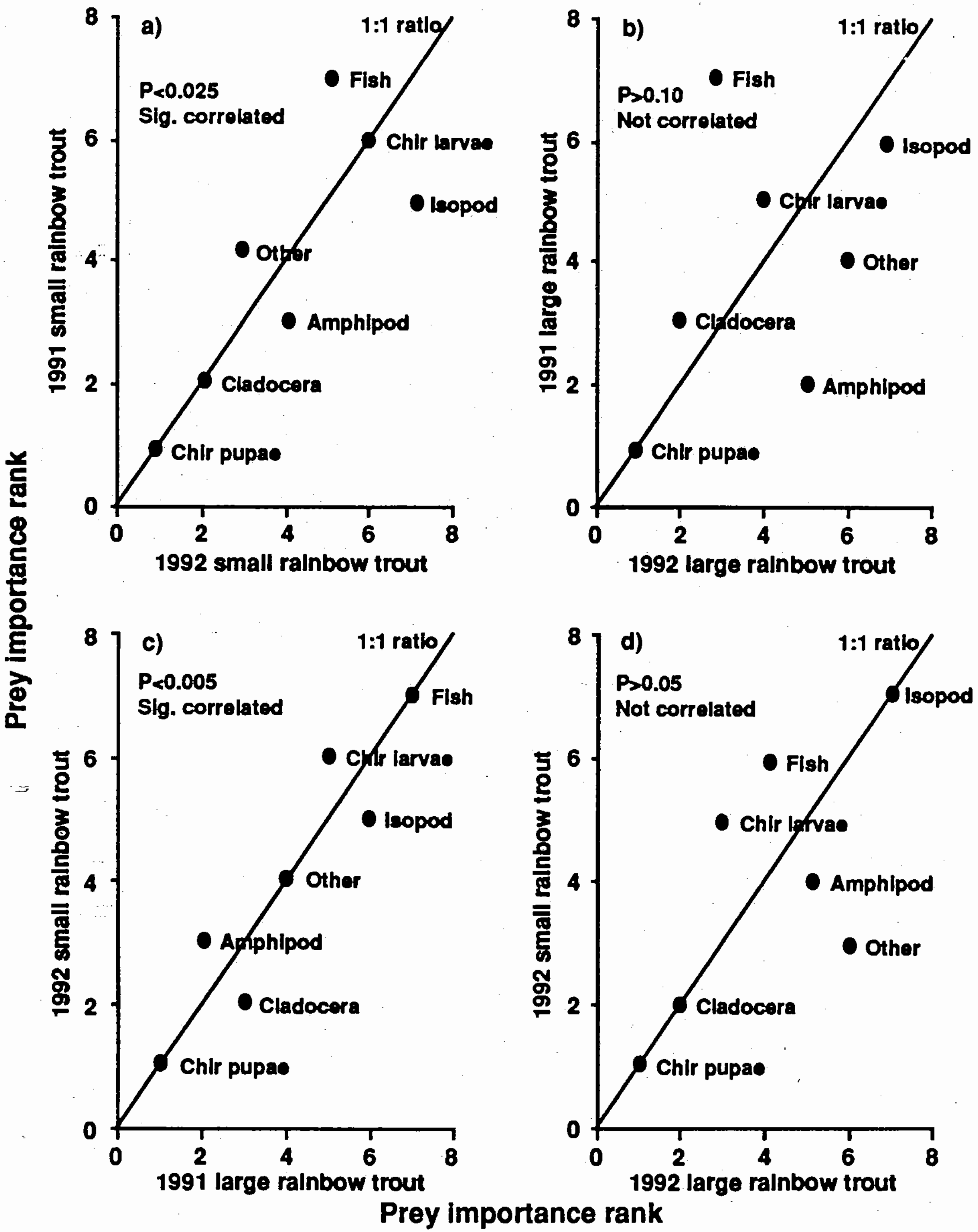
	1991									
	Small RBT					Large RBT				
		%B					%B			
Food group	IRI	Without algae	(With algae)	%O	%N	IRI	Without algae	(With algae)	%O	%N
Chironomid pupae	4537	63.8	(36.0)	47.3	32.1	2244	37.9	(10.6)	41.3	16.4
Cladocera	966	0.2	(0.2)	15.6	61.8	1056	0.4	(0.1)	13.5	77.6
Amphipod	441	16.6	(9.4)	24.6	1.3	1126	35.2	(9.8)	30.4	1.8
Other	308	11.4	(6.4)	20.0	4.1	278	9.9	(2.8)	21.1	3.3
Fish	1	2.2	(1.2)	0.3	0.0	3	4.7	(1.3)	0.1	0.0
Chironomid larvae	21	2.4	(1.3)	7.9	0.3	146	7.3	(2.0)	18.5	0.5
Isopod	38	3.4	(1.9)	10.1	0.4	56	4.6	(1.3)	11.4	0.4
Algae	-	-	(43.6)	72.1	-	-	-	(72.1)	85.0	-

	1992									
	Small RBT					Large RBT				
		%B					%B			
Food group	IRI	Without algae	(With algae)	%O	%N	IRI	Without algae	(With algae)	%O	%N
Chironomid pupae	4909	42.8	(33.5)	65.5	32.1	4825	14.4	(10.1)	74.9	50.0
Cladocera	1450	0.3	(0.2)	22.2	65.1	830	0.1	(0.0)	18.6	44.5
Amphipod	140	5.5	(4.3)	23.3	0.5	77	2.3	(1.6)	25.1	0.7
Other	141	3.7	(2.9)	25.9	1.7	75	0.8	(0.6)	28.3	1.9
Fish	122	45.5	(35.7)	2.7	0.1	613	79.1	(55.4)	7.7	0.5
Chironomid larvae	27	1.1	(0.9)	18.7	0.3	104	1.4	(0.9)	36.0	1.5
Isopod	9	1.1	(0.8)	7.2	0.2	23	1.9	(1.3)	8.2	0.9
Algae	-	-	(21.7)	70.3	-	-	-	(30.1)	86.4	-

substantially higher relative importance for large than for small rainbow trout in 1992. Also shown is that algae, in all cases, occurred in the highest proportion of the rainbow trout sampled (%O). While algae comprised the highest biomass proportion (%B) of rainbow trout diets in 1991, relatively more was present in large rainbow trout diets in both years. Based on the IRI values a Spearman's Rank Correlation procedure ($P \leq 0.05$ indicates significant correlation and hence, no differences in diets) revealed that small and large rainbow trout diets did not differ in 1991, nor did diets of small rainbow trout differ between 1991 and 1992. However, diets of the small and large rainbow trout did differ in 1992, as did the diet of large rainbow trout between 1991 and 1992 (Figure 10). Hence, the major cause of diet differences among the four size year groups was the more distinct diet of large rainbow trout in 1992. The most consistent source of diet distinction for large rainbow trout in 1992 was the high relative importance of fish in their diet. A low relative importance of amphipods for large rainbow trout in 1992 further distinguished their diet from that of large rainbow trout in 1991 (Figure 10).

Seasonal changes in relative importance (IRI) of the most prominent animal food groups (chironomid pupae, cladocerans, and amphipods) as well as the less prominent fish prey group (included because of its effect on rainbow

FIGURE 10. The relationship between the ranked relative importance of food groups of a) small rainbow trout during 1991 and 1992, b) large rainbow trout during 1991 and 1992, c) small and large rainbow trout during 1991, and d) small and large rainbow trout during 1992 and Spearman's Rank Correlation for each relationship.


Prey importance rank
a)
1:1 ratio
P<0.025
Sig. correlated
Fish
Chir larvae
Isopod
Other
Amphipod
Cladocera
Chir pupae
1991 small rainbow trout
1992 small rainbow trout
0
2
4
6
8
b)
1:1 ratio
P>0.10
Not correlated
Fish
Isopod
Chir larvae
Other
Cladocera
Amphipod
Chir pupae
1991 large rainbow trout
1992 large rainbow trout
c)
1:1 ratio
P<0.005
Sig. correlated
Fish
Chir larvae
Isopod
Other
Amphipod
Cladocera
Chir pupae
1992 small rainbow trout
1991 large rainbow trout
d)
1:1 ratio
P>0.05
Not correlated
Isopod
Fish
Chir larvae
Amphipod
Other
Cladocera
Chir pupae
1992 small rainbow trout
1992 large rainbow trout
Prey importance rank

trout diet differences) were examined for 1991 and 1992 (Figure 11). Seasonal patterns of prey group importance were similar for both rainbow trout size groups within years, but between-year differences were apparent. In 1991, IRI values for chironomid pupae were high except in the summer months (May-July). Cladocerans were generally low in importance in 1991, except during summer when chironomid pupae showed low importance values. Amphipods remained low in importance except for a primary peak in May and modest importance from June-August. Fish were of negligible importance in rainbow trout diets throughout 1991. For 1992 chironomid pupae remained higher in importance relative to 1991 diets, showing lowest values in March and April and in October and November. Cladocerans showed a more consistent presence in 1992 than in 1991, while amphipods showed no distinct peaks. Most notable in 1992 was the prominent pulse of fish in diets during February-April (almost exclusively threadfin shad); this prey group was otherwise of negligible importance as in 1991. This pulse of threadfin shad in the diets was the primary source of diet differences among the four size-year groups of rainbow trout throughout the period of the study.

Biomass of algae in the diets of small and large rainbow trout during 1991 and 1992 varied among seasons, fish sizes, and years (Figure 12). Biomass of algae was higher in 19 of the 22 months (significantly higher in 7

FIGURE 11. Seasonal importance of chironomid pupae, cladocera, amphipods, and fish in the diets of small and large rainbow trout during 1991 and 1992.

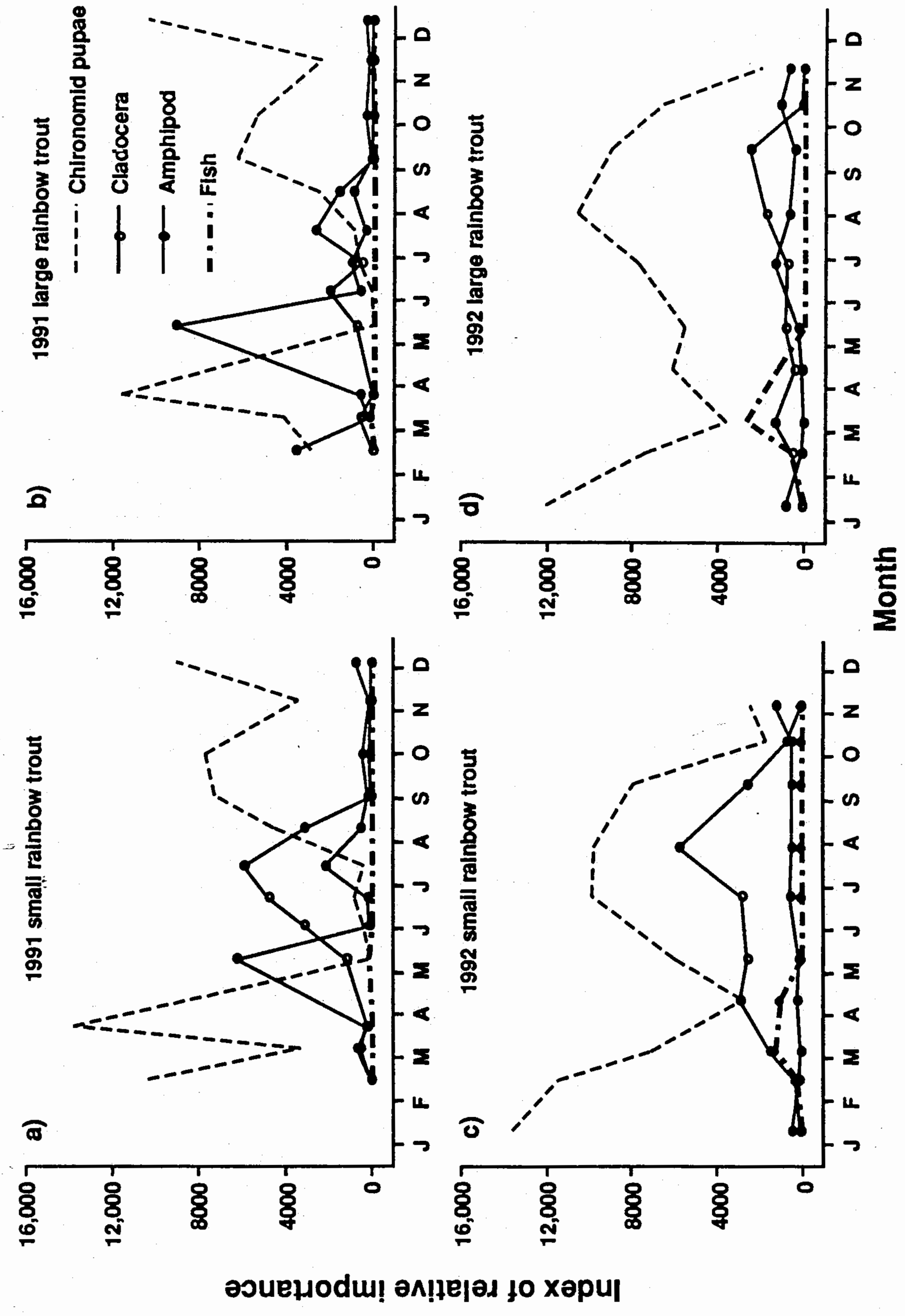
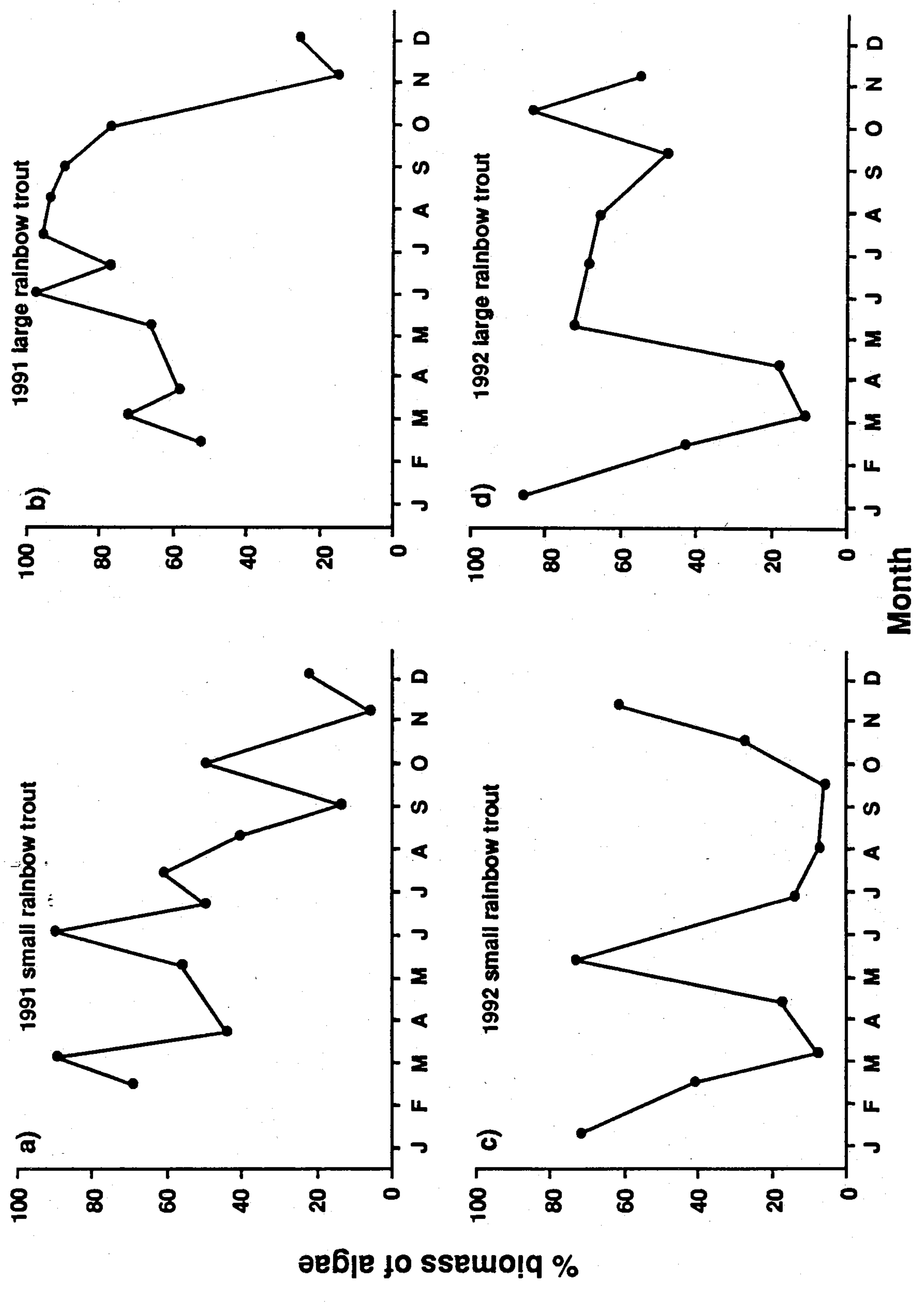

a)
1991 small rainbow trout
b)
1991 large rainbow trout
c)
1992 small rainbow trout
d)
1992 large rainbow trout
Chironomid pupae
Cladocera
Amphipod
Fish
16,000
12,000
8000
4000
0
J F M A M J J A S O N D
Index of relative importance
Month

FIGURE 12. Seasonal patterns of relative "algae" biomass in the diets of small and large rainbow trout during 1991 and 1992.


a)
1991 small rainbow trout
b)
1991 large rainbow trout
c)
1992 small rainbow trout
d)
1992 large rainbow trout
% biomass of algae
Month
0
20
40
60
80
100
J
F
M
A
M
J
J
A
S
O
N
D

months) for large than small rainbow trout, and accounted for over 50% of the total food biomass consumed in most months by large fish. Biomass of algae in 1991 diets was highest early in the year for small rainbow trout and declined throughout the year. It increased during the year for large fish, making up almost 100% of the diet biomass during mid-summer, and did not decline until October. In 1992, algae made up a lower proportion of the food biomass consumed in March and April by both small and large rainbow trout, dates when threadfin shad predominated the diets. Algae also made up a small portion of the biomass consumed by small rainbow trout in July and August when consumption was above maintenance, however, biomass was also low in September when consumption was poor. Hence, there is some evidence that rainbow trout may consume more algae in periods when animal prey are less available, however, this was not always the case.

Comparison of rainbow trout prey use data from this study with comparable data from Pfleiger's (1977a) monthly characterization of Lake Taneycomo rainbow trout diets from May 1970-May 1971 indicates that major structural changes have occurred in the prey community over the past 20 years. Pfleiger (1977a) found that amphipods were, by far, the most important prey group in rainbow trout diets in the early 1970s (Table 6). An IRI value of 16,059 and a %B value of 87.2% was shown for amphipods in his study, while IRI values

Table 6. Values of the index of relative importance (IRI) and percent biomass, and rank, of food groups consumed by all rainbow trout collected from Lake Taneycomo during 1991, 1992, and May 1991-May 1992 compared to historic prey consumption by rainbow trout in Lake Taneycomo May 1970-May 1971 (Pfleiger 1977).

	IRI			
Food groups	1991	1992	May 1991-May 1992	May 1970-May 1971
Chironomid pupae	3228 (1)	4349 (1)	3219 (1)	341 (2)
Cladocera	1035 (2)	1128 (2)	1189 (2)	0 (7)
Amphipod	772 (3)	90 (4)	207 (3)	16,059 (1)
Other	292 (4)	89 (5)	134 (5)	20 (5)
Fish	2 (7)	337 (3)	191 (4)	1 (6)
Chironomid larvae	73 (5)	61 (6)	55 (6)	76 (4)
Isopod	47 (6)	17 (7)	22 (7)	113 (3)

	% Biomass			
Food groups	1991	1992	May 1991-May 1992	May 1970-May 1971
Chironomid pupae	18.5 (2)	15.2 (3)	12.5 (3)	1.0 (6)
Cladocera	0.1 (8)	0.1 (8)	0.1 (8)	0.0 (8)
Amphipod	9.7 (3)	2.2 (4)	4.1 (4)	87.2 (1)
Other	3.9 (4)	1.1 (6)	1.6 (5)	1.3 (5)
Fish	1.3 (7)	51.0 (1)	43.5 (1)	1.4 (4)
Chironomid larvae	1.8 (5)	0.9 (7)	0.8 (7)	0.4 (4)
Isopod	1.5 (6)	1.2 (5)	0.9 (6)	1.5 (3)
Algae	63.2 (1)	28.3 (2)	36.5 (2)	8.0 (2)

of only 772, 90 and 207, and %B values of 9.7, 2.2 and 4.1 were found in the present study for rainbow trout collected throughout 1991, 1992, and from May 1991-May 1992, respectively. Comparisons of rainbow trout diet data further indicate declines have occurred in the availability of isopods. Since the earlier study, major increases have occurred for chironomids (mainly pupae), cladocerans, and filamentous algae in rainbow trout diets (Table 6). Spearman's Rank Correlation procedure corroborated this interpretation (Figure 13) by showing significant diet differences on the basis of ranked IRI and %B values for May-May diets in the early 1970s and 1990s.

Residence times

Estimated loss rates for the eight cohorts of rainbow trout stocked in different months and at different sites over three years, differed significantly (ANCOVA, test for slope heterogeneity, $P \leq 0.05$). Associated residence time estimates (days until 1% of cohort remaining) ranged from 16-194 days (Table 7). The two winter-stocked cohorts (February 1992) exhibited significantly lower mortality rates than cohorts stocked in the late spring and summer (May 1993, June 1992 and August 1991) (ANCOVA pairwise comparisons, $P \leq 0.05$). One of the two cohorts stocked downstream in July 1992 showed no significant difference in loss rate from either of the two cohorts stocked in February 1992 (Table 8).

FIGURE 13. The relationship between a) the ranked importance of food groups for all rainbow trout during May 1991-May 1992 and May 1970-May 1971 and b) the ranked relative biomass of food groups for rainbow trout during May 1991-May 1992 and May 1970-May 1971.

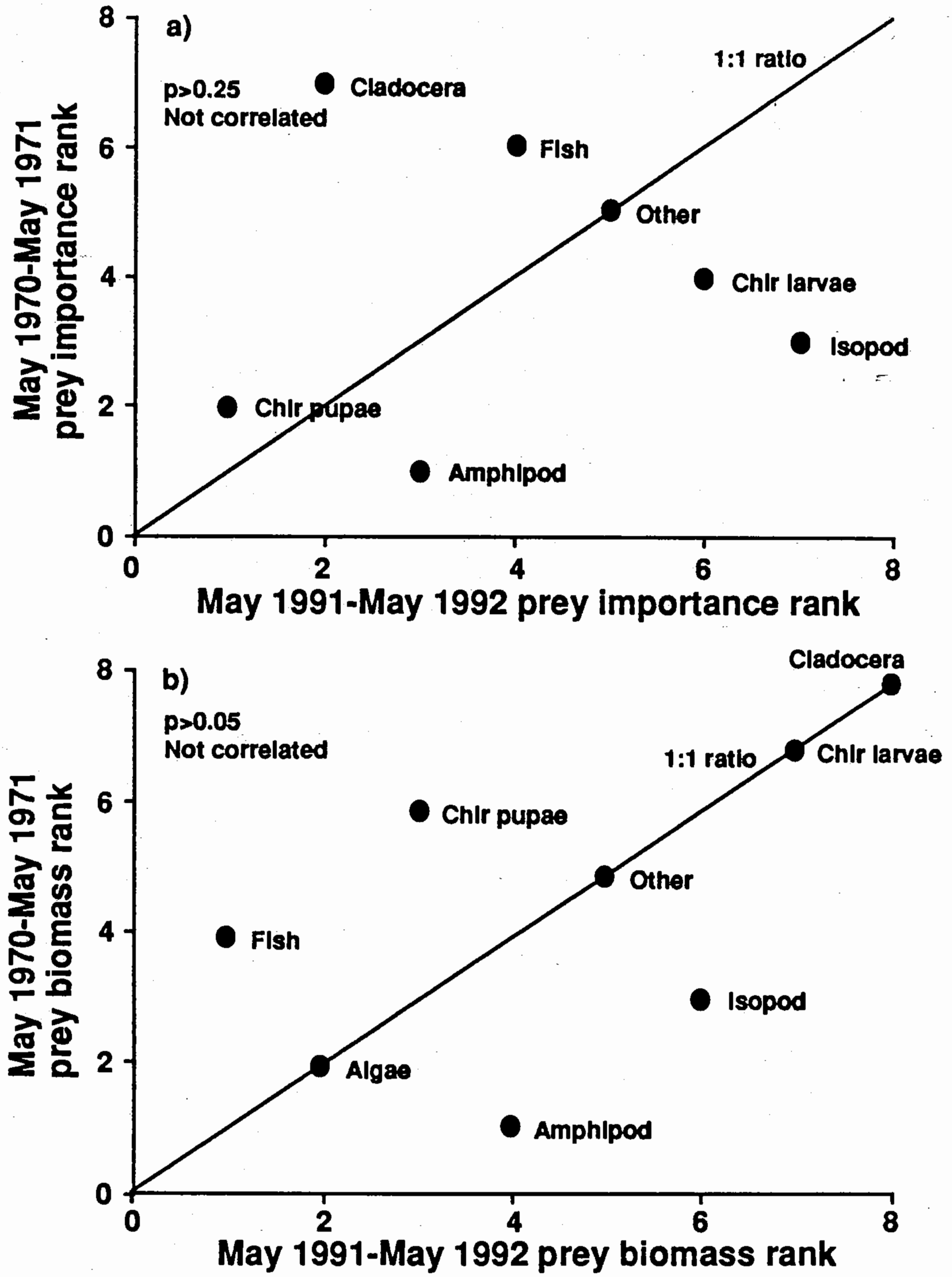

a)
p>0.25
Not correlated
1:1 ratio
Cladocera
Fish
Other
Chir larvae
Isopod
Chir pupae
Amphipod
May 1970-May 1971 prey importance rank
May 1991-May 1992 prey importance rank
0
2
4
6
8
b)
p>0.05
Not correlated
1:1 ratio
Cladocera
Chir larvae
Chir pupae
Other
Fish
Isopod
Algae
Amphipod
May 1970-May 1971 prey biomass rank
May 1991-May 1992 prey biomass rank
0
2
4
6
8

Table 7. Estimated instantaneous total mortality rates (Z) and number of days post-stocking until 1% of marked rainbow trout cohorts remained (residence time) in Lake Taneycomo.

Stocking date	Z	Residence time (Days)	Stocking site
August 12, 1991	0.2968	16	Down[a]
August 19, 1991	0.2750	17	Down
February 19, 1992	0.0158	124	Up[b]
February 6, 1992	0.0145	194	Down
July 20, 1992	0.0469	76	Up
July 13, 1992	0.0340	136	Down
May 24, 1993	0.1569	29	Up
May 24, 1993	0.0872	53	Down

[a] Downstream stocking site was approximately 12 km downstream from Table Rock Dam.

[b] Upstream stocking site was approximately 0.75 km downstream from Table Rock Dam.

Table 8. Pairwise comparisons of instantaneous total mortality rates of stocked cohorts of rainbow trout based on analysis of covariance.

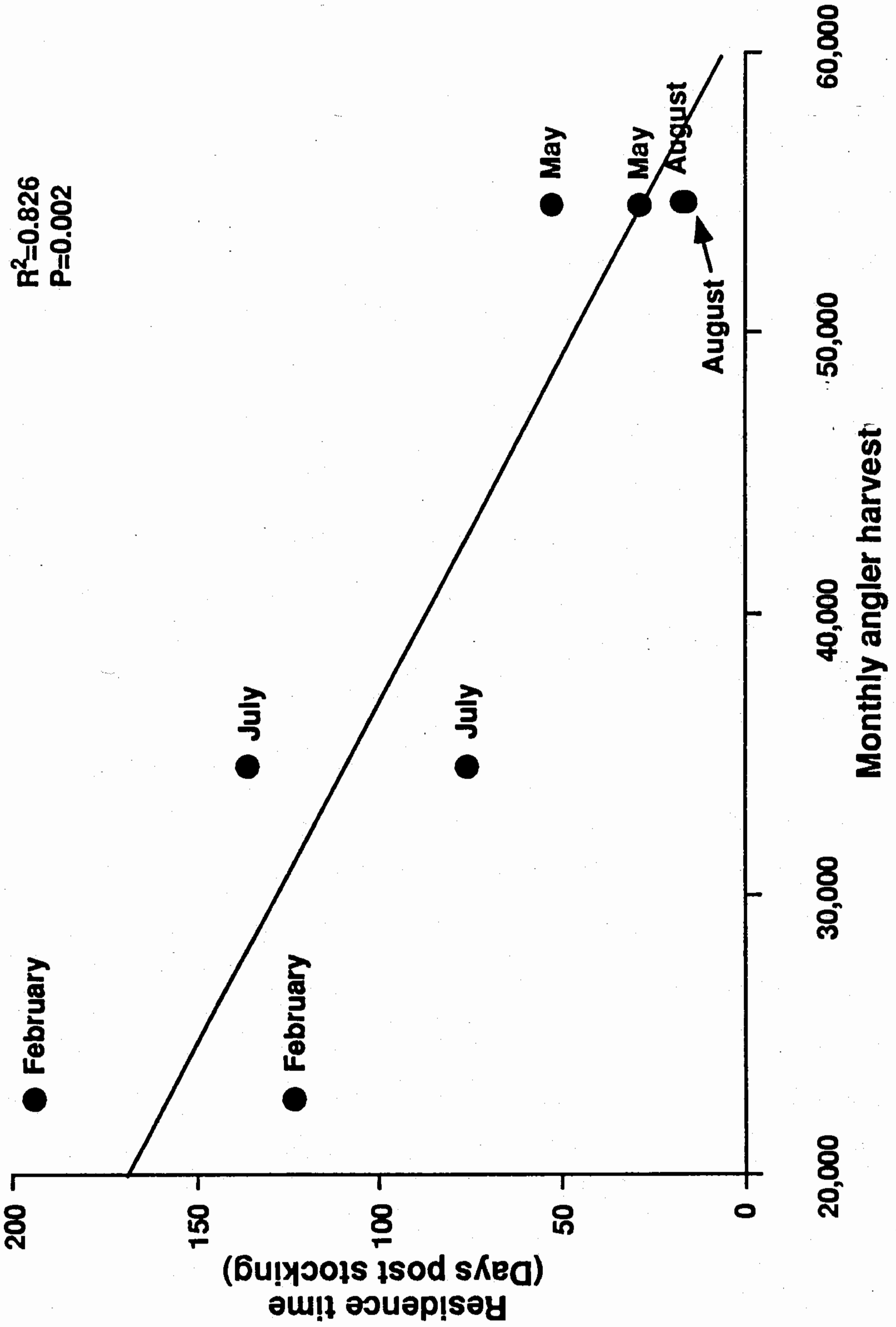
	Month stocked							
Month stocked	Aug. 12 1991[a]	Aug. 19 1991[a]	Feb. 19 1992[b]	Feb. 6 1992[a]	July 20 1992[b]	July 13 1992[a]	May 24 1993[b]	May 24 1993[a]
Aug. 12 1991[a]		NS[c]	*[d]	*	*	*	NS	NS
Aug. 19 1991[a]			*	*	*	*	NS	NS
Feb. 19 1992[b]				*	*	NS	*	*
Feb. 6 1992[a]					*	NS	*	*
July 20 1992[b]						NS	*	NS
July 13 1992[a]							*	*
May 24 1993[b]								NS
May 24 1993[a]								

[a] Stocked at downstream site approximately 12 km downstream from Table Rock Dam.
[b] Stocked at upstream site approximatetely 0.75 km downstream from Table Rock Dam.
[c] 'NS' indicates no significant difference ($P>0.05$).
[d] '*' indicates a significant difference ($P\leq0.05$).

Because fishing pressure was suspected to influence residence times of stocked rainbow trout, estimated residence times of the eight cohorts were regressed on average angler harvest rates for the months in which they were stocked (Figure 14). Average monthly angler harvest rates of rainbow trout were determined from a previous creel survey study conducted on Lake Taneycomo by the Missouri Department of Conservation during 1988-1990 and were assumed to be reflective of monthly harvest trends during 1991-1992. Significant negative correlation was observed between monthly angler harvest values and estimated residence times of rainbow trout stocked in the same month (P=0.002, R=-0.91, N=8) (Figure 14). This result indicates that residence times of stocked rainbow trout differ among months in relation to the fishing pressure exerted shortly after stocking.

In all three cases where separate cohorts were stocked at both an upstream and downstream site within the same month and year, the point estimate of residence time was always greater for the cohort stocked downstream (Table 7). Residence times within these months, however, were only significantly greater for fish stocked downstream in February 1992 (ANCOVA, $P \leq 0.05$) (Table 8). The limited evidence that fish stocked downstream exhibit higher residence times than those stocked upstream seems plausible given that fishing pressure is greater near the upper end of

FIGURE 14. The relationship between residence times of eight marked rainbow trout cohorts and median monthly angler harvest of rainbow trout during the month they were stocked.


R^2=0.826
P=0.002
February
February
July
July
May
May
August
August
Residence time (Days post stocking)
200
150
100
50
0
20,000
30,000
40,000
50,000
60,000
Monthly angler harvest

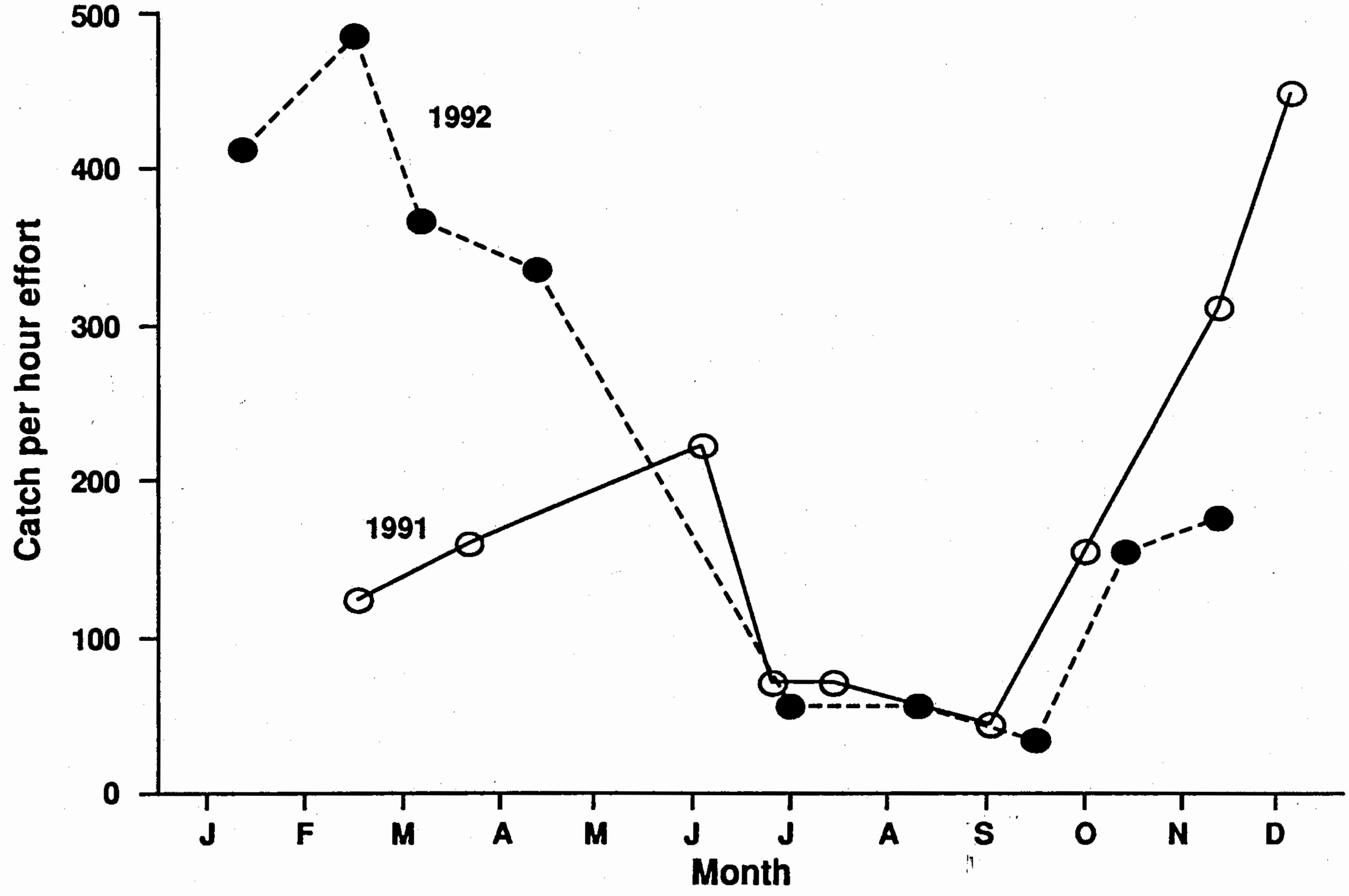
Lake Taneycomo (Michael Kruse, Missouri Department of Conservation, personal communication).

Despite the variation in residence times of rainbow trout stocked in different months, no cohort remained in Lake Taneycomo for more than 6.5 months (Table 7). Even if the relatively high growth rates of rainbow trout that were estimated to have prevailed historically in Lake Taneycomo (1.8 cm/month, Turner 1977) still existed at present, eight months of residence would be required for fish stocked at 26 cm to attain trophy size ($\geq$40.6 cm). Given the evidence that feeding rates of rainbow trout now are generally poor, the estimated current residence times are clearly insufficient for in situ production of trophy-size rainbow trout, no matter when or where they are stocked.

Numbers of rainbow trout at large

Monthly catch-per-unit-effort (CPUE) data over both study years (Figure 15) showed a general pattern of relatively high rainbow trout numbers in the study area during January-early June, relatively low numbers from late June-September, followed by increases through December. Values of CPUE in winter and spring of 1991, though still higher than summer values, were notably lower than winter and spring CPUE values in 1992. These high winter values in 1992 were probably due to higher stocking rates in January and February of 1992 (Figure 5).

FIGURE 15. Monthly catch counts of rainbow trout caught per hour of electrofishing effort (CPUE) in the upper 4.5 km of Lake Taneycomo during 1991 and 1992.


1992
1991
Catch per hour effort
0
100
200
300
400
500
J
F
M
A
M
J
J
A
S
O
N
D
Month

Relative weight

Mean monthly relative weights (Wr) of small and large rainbow trout exceeded values of 100 in all months in 1991 and 1992 (Figure 16), indicating that fish were always in relatively good condition. Rainbow trout Wr's were generally stable and high from March through October in both years, but were markedly lower in winter months (November-February) (Figure 16). Plots of mean monthly Wr of rainbow trout across both size groups and years, versus mean monthly angler harvest (Missouri Department of Conservation data), revealed a significant direct relationship (P=0.033) (Figure 17). Evidence that rainbow trout residence times were inversely-related to harvest rate (Figure 14), indicates that an inverse relationship exists between Wr and residence times of rainbow trout. This provides independent support for our findings of poor growth conditions for rainbow trout because the Wr's of fish stocked in good condition decline with increasing residence in Lake Taneycomo.

FIGURE 16. Estimated mean (±1 SE) relative weights (Wr) of small and large rainbow trout in the upper 4.5 km of Lake Taneycomo during 1991 and 1992.

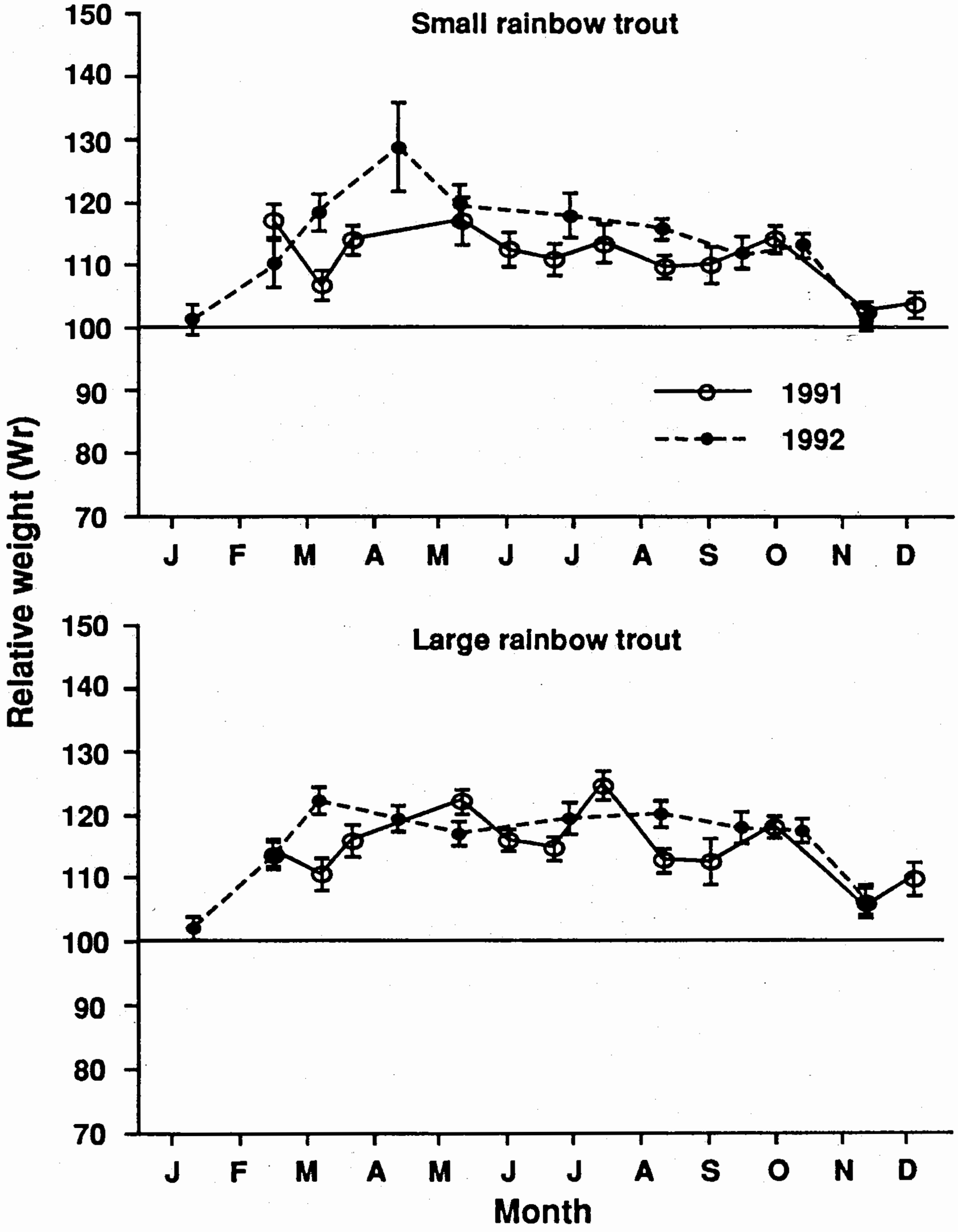
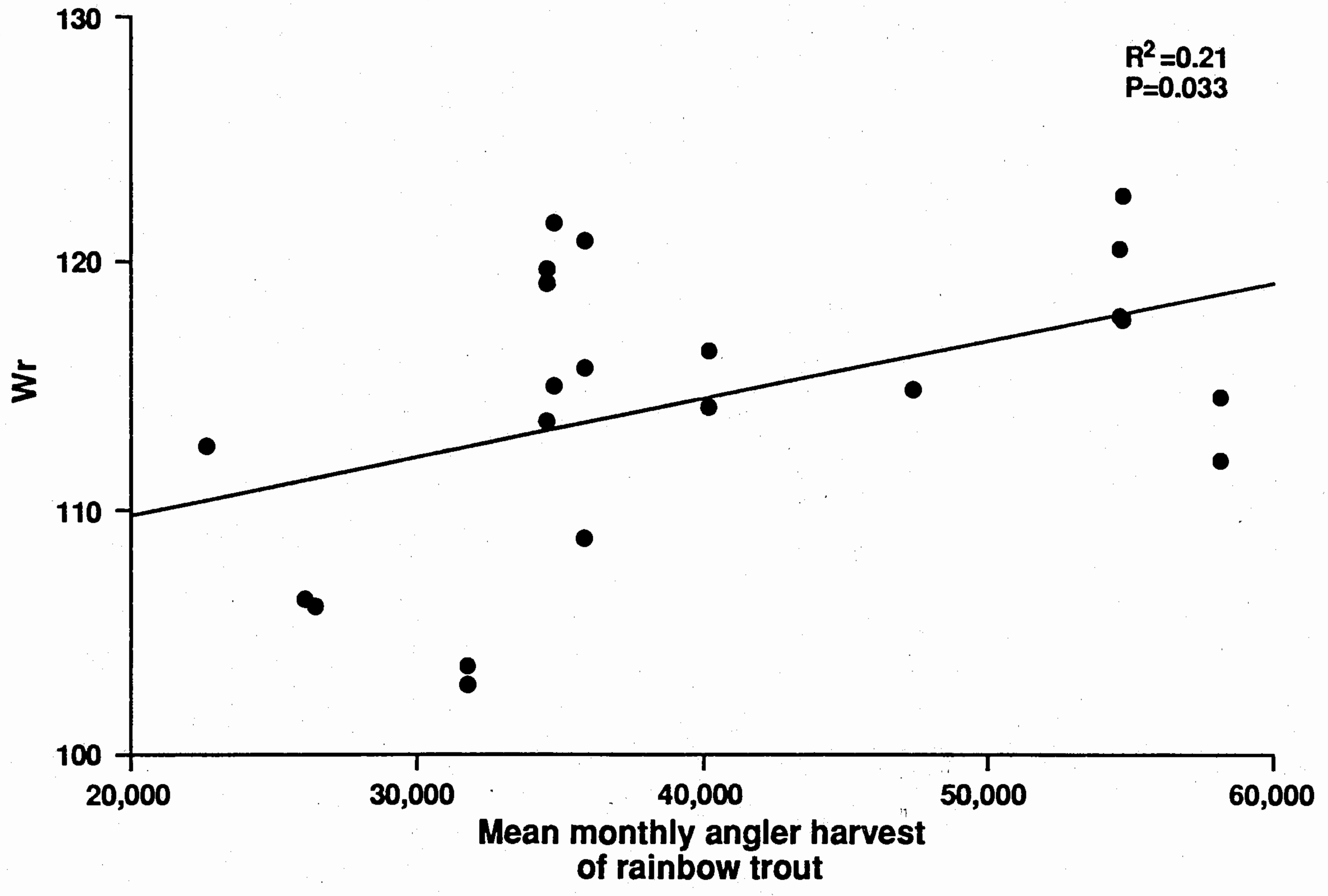

Small rainbow trout
Large rainbow trout
Relative weight (Wr)
150
140
130
120
110
100
90
80
70
1991
1992
J
F
M
A
M
J
J
A
S
O
N
D
Month

FIGURE 17. The relationship between mean monthly angler harvest and condition of rainbow trout in Lake Taneycomo during 1991 and 1992.


R^2=0.21
P=0.033
Wr
130
120
110
100
20,000
30,000
40,000
50,000
60,000
Mean monthly angler harvest of rainbow trout

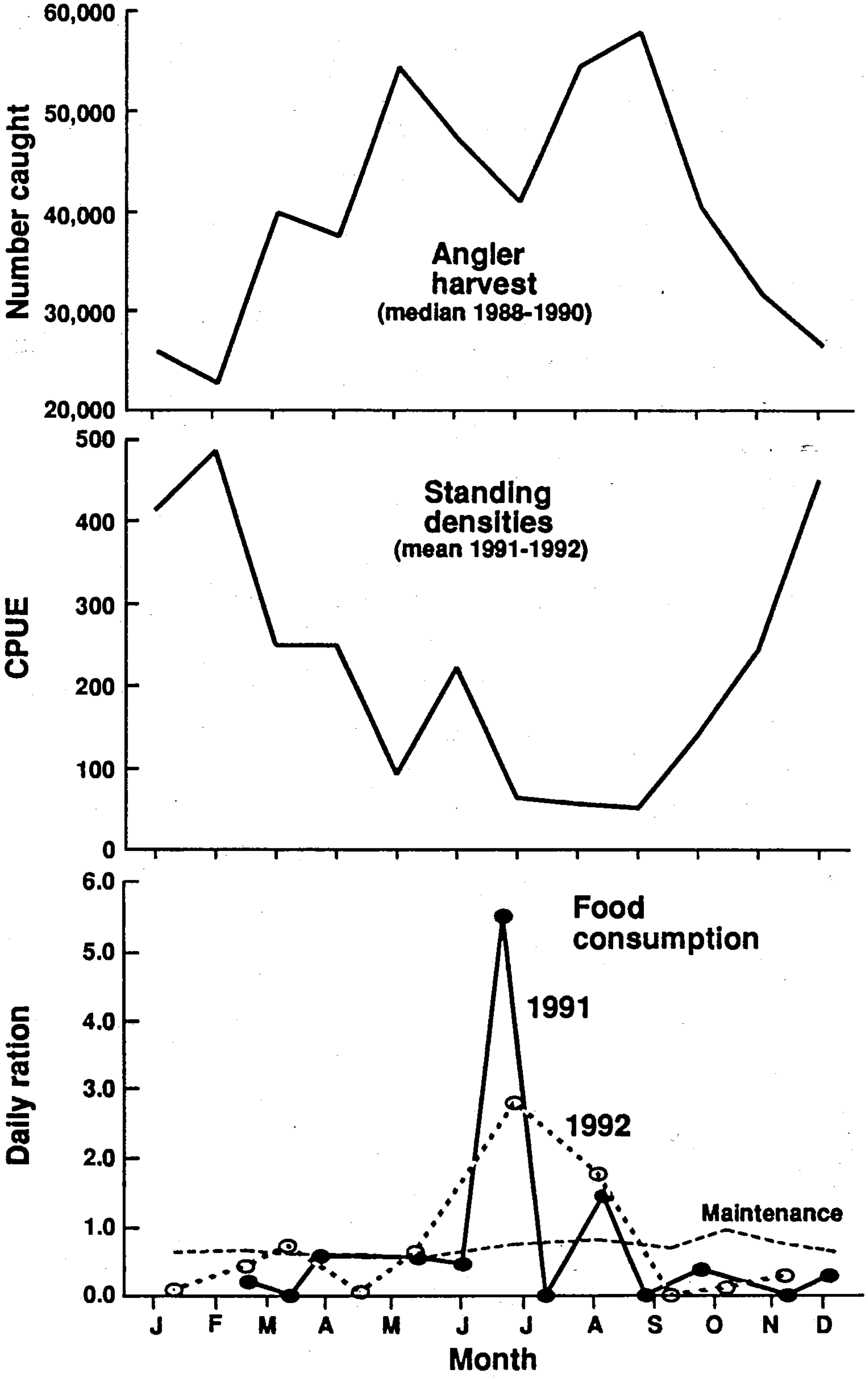
DISCUSSION

The major goal of this study was to identify causes for an apparent loss of large rainbow trout within the Lake Taneycomo ecosystem. Knowledge of these causes should provide a scientific basis upon which a strategy to restore the historical trophy rainbow trout fishery could be developed. After reviewing available background information concerning the decline in numbers of large rainbow trout in Lake Taneycomo (Weithman 1980; Goddard et al. 1988), it was hypothesized that growth conditions for rainbow trout have declined. This was thought to have occurred in connection with a drop in prey availability brought about by excessive stocking, and possibly through a disadvantageous rainbow trout prey base restructuring associated with water quality changes. Limited food availability has been shown to limit growth and condition of salmonids in many streams (Cooper and Benson 1951; Ellis and Gowing 1957; Whitworth and Strange 1983; Wilzbach et al. 1986; Cada et al. 1987; Ensign et al. 1990). Because fishing pressure on rainbow trout in Lake Taneycomo is known to be high at present, it was also hypothesized that residence times of stocked fish are too short for growth to large sizes to occur. Studies in similar systems have found that size structures of salmonid fisheries tend to decline when fishing pressure increases (Ratledge 1966; Wiley and Dufel 1980; Anderson and Nehring 1984).

The first hypothesis was well supported by food consumption findings from 1991 which showed that both small and large rainbow trout consumed less than maintenance rations (MR) in most months (Figure 6). Only small rainbow trout consumed sufficient food biomass to exceed MR during a few summer sampling dates. To test whether poor feeding conditions for rainbow trout could be improved by substantially reducing numbers of trout at large in the impoundment, stocking rates, after February 1992, were reduced by approximately 25% and daily food consumption estimates were made again as in 1991. No appreciable improvement in feeding rates occurred during 1992; small rainbow trout still fed in excess of MR on only a few sampling dates in summer while large rainbow trout showed almost continuous submaintenance food consumption as in the previous year. Large rainbow trout did consume a food biomass substantially in excess of MR in March, 1992, but this was almost solely due to allochthonous inputs of threadfin shad from Table Rock Lake, and was not the result of prey production from within the Lake Taneycomo ecosystem. Thus, the 25% reduction in numbers of rainbow trout stocked did not bring about an improvement in food consumption rates. However, evidence for consistent annual patterns of generally poor food consumption by both size groups of rainbow trout was provided.

Examination of CPUE data throughout 1991 and 1992, however, indicated that the 25% reduction in stocking rates had not brought about lower standing densities of rainbow trout in the system, contrary to expectation. Clearly, this could explain why no improvement in food consumption rates was observed in 1992. Importantly, however, seasonal densities of rainbow trout in both 1991 and 1992 showed a significant inverse relationship ($P \leq 0.05$) to mean monthly angler harvest rates of rainbow trout (acquired from MDC creel data spanning 1988-1990) (Figure 18). This indicates that fishing pressure exerted a much greater influence on monthly densities of rainbow trout than did the 25% reduction in numbers of fish stocked beginning in March, 1992. Yet more interesting was the observation that food consumption rates, at least for small rainbow trout, were in excess of MR (sufficient for growth) during certain summer months in both years when standing densities of rainbow trout were low, apparently in response to the heavy removal effect from fishing (Figure 18). These findings suggest that rainbow trout feeding rates (and growth capacity) in Lake Taneycomo are density-dependent, and that positive growth occurs only when trout densities are reduced to levels that equate to a CPUE value below 100 fish caught per hour of electrofishing effort. Again, it is emphasized that rainbow trout densities sufficiently low for growth to occur, could not be achieved by a 25% reduction in current stocking rates.

FIGURE 18. The relationship between median angler harvest of rainbow trout (from Missouri Department of Conservation creel census data), mean relative standing densities (CPUE) of rainbow trout from 1991 and 1992, and estimated daily food consumption for small rainbow trout in Lake Taneycomo during 1991 and 1992.



60,000
50,000
40,000
30,000
20,000
Number caught
Angler harvest
(median 1988-1990)
500
400
300
200
100
0
CPUE
Standing densities
(mean 1991-1992)
6.0
5.0
4.0
3.0
2.0
1.0
0.0
Daily ration
Food consumption
1991
1992
Maintenance
J
F
M
A
M
J
J
A
S
O
N
D
Month

Just why large rainbow trout did not show feeding rates in excess of MR during periods of low rainbow trout density in summer, as did smaller counterparts, can be explained on the basis of the greater absolute food amounts that larger fish require. It is well known that while larger fish require less food to grow on a weight-specific basis (g food/g body weight/day), more absolute food biomass (g food/day) is needed to surpass their higher metabolic demands (Elliott 1975b). On an absolute basis, large rainbow trout did in fact show higher mean food weights in stomachs than did small counterparts on 16 of the 22 sampling dates (t-tests by month, $P \leq 0.05$). However, the higher absolute food consumption rates by large fish on these dates were almost always insufficient to meet their higher absolute standard metabolic requirements. This result demonstrates that food supply for rainbow trout is currently so limited in Lake Taneycomo that standing densities even lower than those seen in summer months would be necessary to "free-up" sufficient food for rainbow trout in the large size group to grow. Contributing to this more critical feeding problem for large rainbow trout is the lack of scope for feeding niche separation between small and large rainbow trout, creating, in effect, a growth bottleneck situation even when total rainbow trout densities are lowest. Diet analyses indicated strong similarity in prey use between the two size groups of rainbow trout

(Figure 8). Only in the winter months of 1992 when threadfin shad were released into Lake Taneycomo from upstream Table Rock Lake were the diets of large rainbow trout substantially distinct from those of the small size group. In general, environments which support substantial growth rates for a given fish species possess prey bases that allow diet partitioning among fish of different sizes (Crossman and Larkin 1959; Werner 1979; Grossman 1980; Keast 1977); a lack of such predator size-related diet separation leads to stunting or size bottlenecks (Persson 1986; Hayward and Margraf 1987). In Lake Taneycomo, large rainbow trout in most months appear to be competing with smaller counterparts for the same limited food base. Asymmetric competition occurs in such cases (Persson 1988) favoring small over large fish because of the latter group's higher absolute metabolic demands. In addition to simply reducing total rainbow trout densities, therefore, improvement of growth conditions for large rainbow trout in Lake Taneycomo would be facilitated by the establishment of a larger-sized food base component, that would provide more separation of the feeding niches of small and large fish. Again, it is noted that threadfin shad appeared to provide this niche separation in winter during 1992.

As stated, high feeding rates in excess of MR occurred for small rainbow trout only in months when CPUE values for all rainbow trout were below 100 fish/hour electrofishing effort. However, high feeding rates did not occur in every month when CPUE was less than 100 (Figure 19). Finding some low feeding rates during periods of low rainbow trout standing densities would be expected because 1) the recovery of certain heavily-cropped key food groups likely lagged because of the timing of within-year production cycles, and 2) under conditions of higher prey availability when CPUE was low, rainbow trout may have experienced high day-to-day variation in their feeding (as has been shown for white crappie _Pomoxis_ _annularis_ feeding at high rates by Hayward and Arnold, in review); also days of higher feeding may have been missed by the once-monthly sampling regime.

If feeding rates of rainbow trout were truly density-dependent, not only would the highest feeding rates occur when rainbow trout densities were low, but prey densities would also be expected to show an inverse relationship to predator densities; high densities of rainbow trout should be associated with lower prey densities, and conversely. When direct estimates of standing densities of benthic invertebrate food groups within the study area were plotted against CPUE values for rainbow trout on corresponding dates (Figure 20), evidence of inverse relationships were apparent (Robert Hayward, University of Missouri, unpublished data). Estimated densities of chironomid larvae, the precursors of the most important rainbow trout food group (chironomid pupae) were lowest when rainbow trout densities were high,

FIGURE 19. Relationship between daily ration for small rainbow trout, relative to maintenance ration (MR), and relative densities of rainbow trout in Lake Taneycomo during 1991 and 1992.

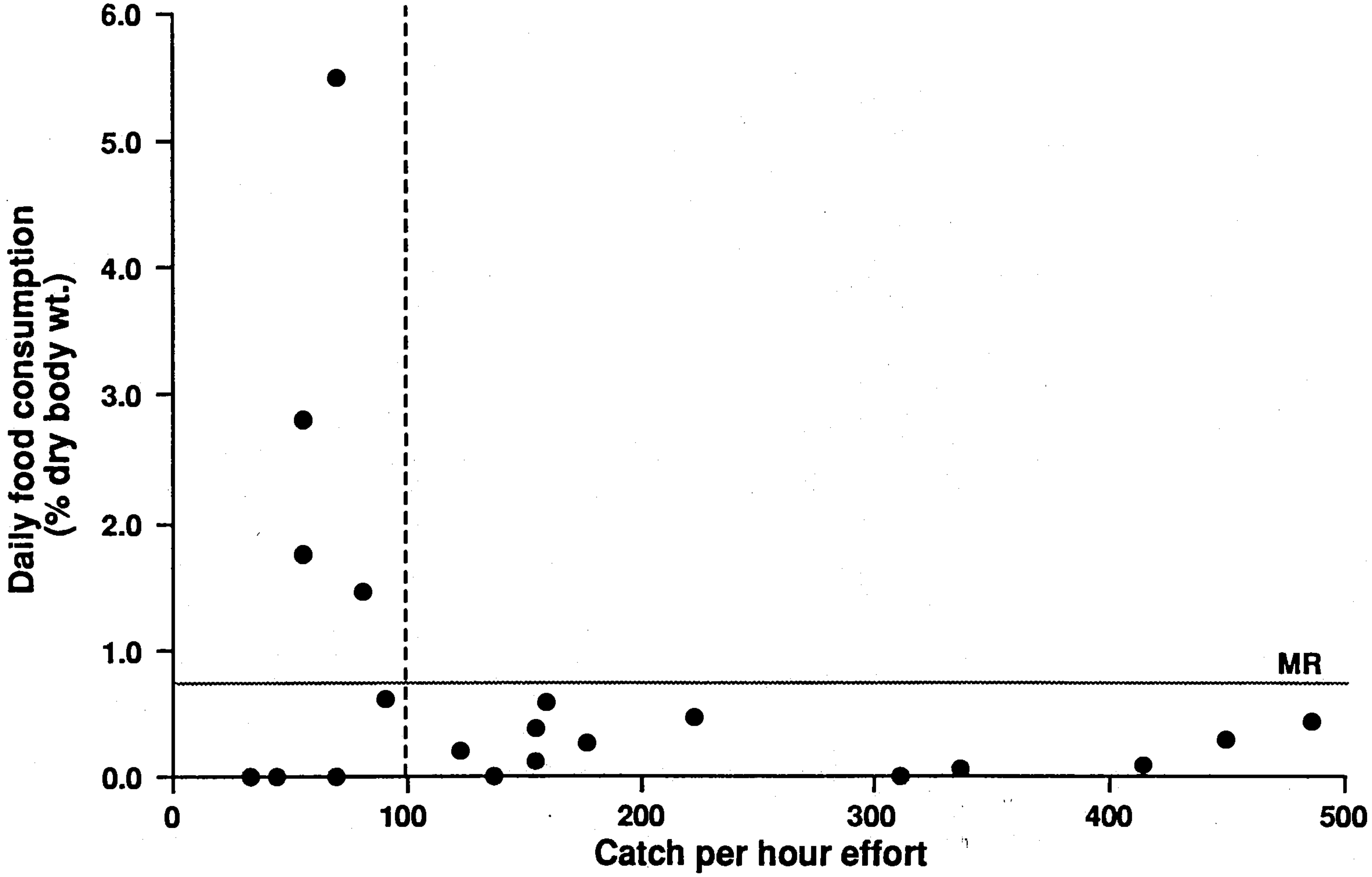
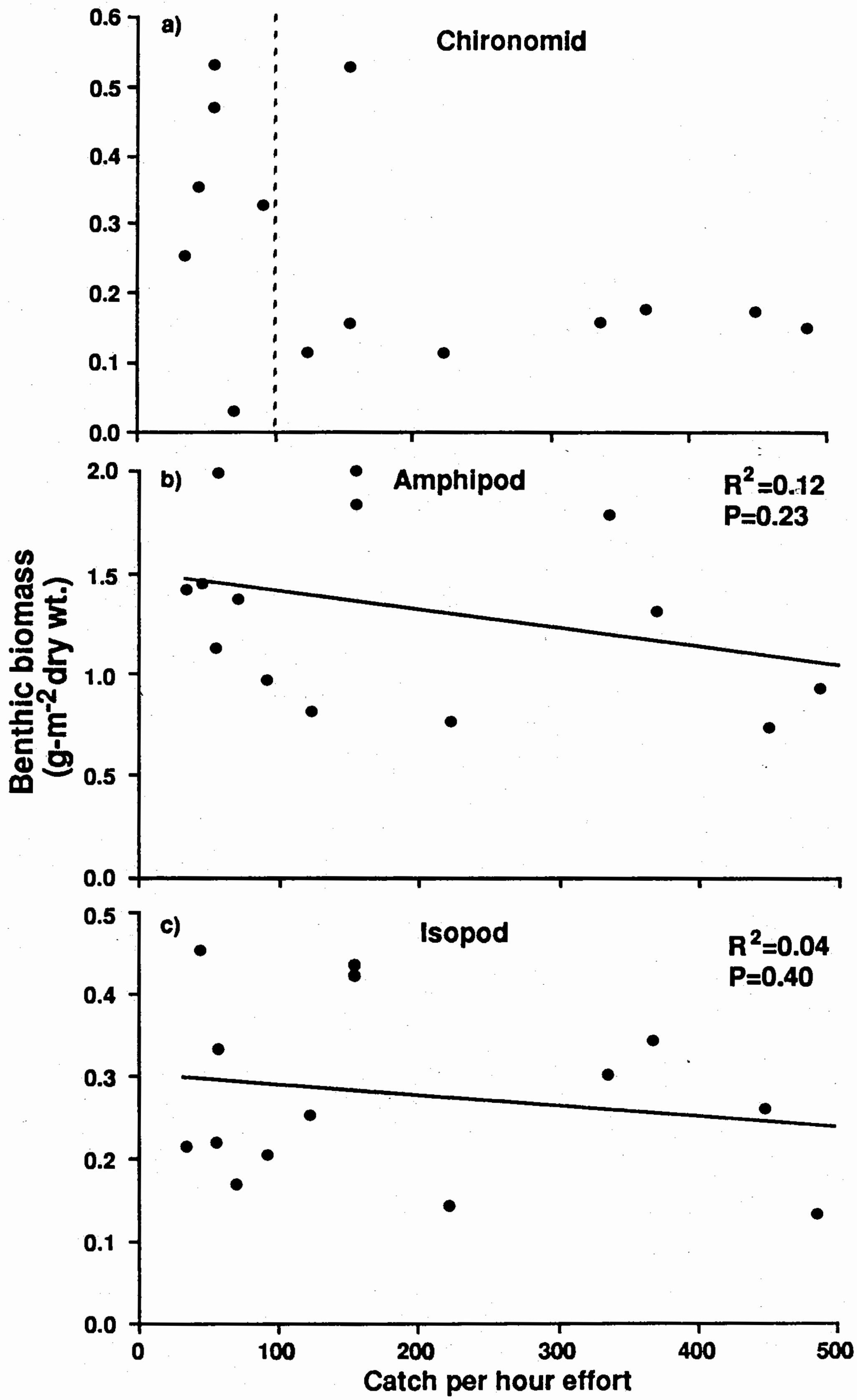

Daily food consumption
(% dry body wt.)
6.0
5.0
4.0
3.0
2.0
1.0
0.0
MR
0
100
200
300
400
500
Catch per hour effort

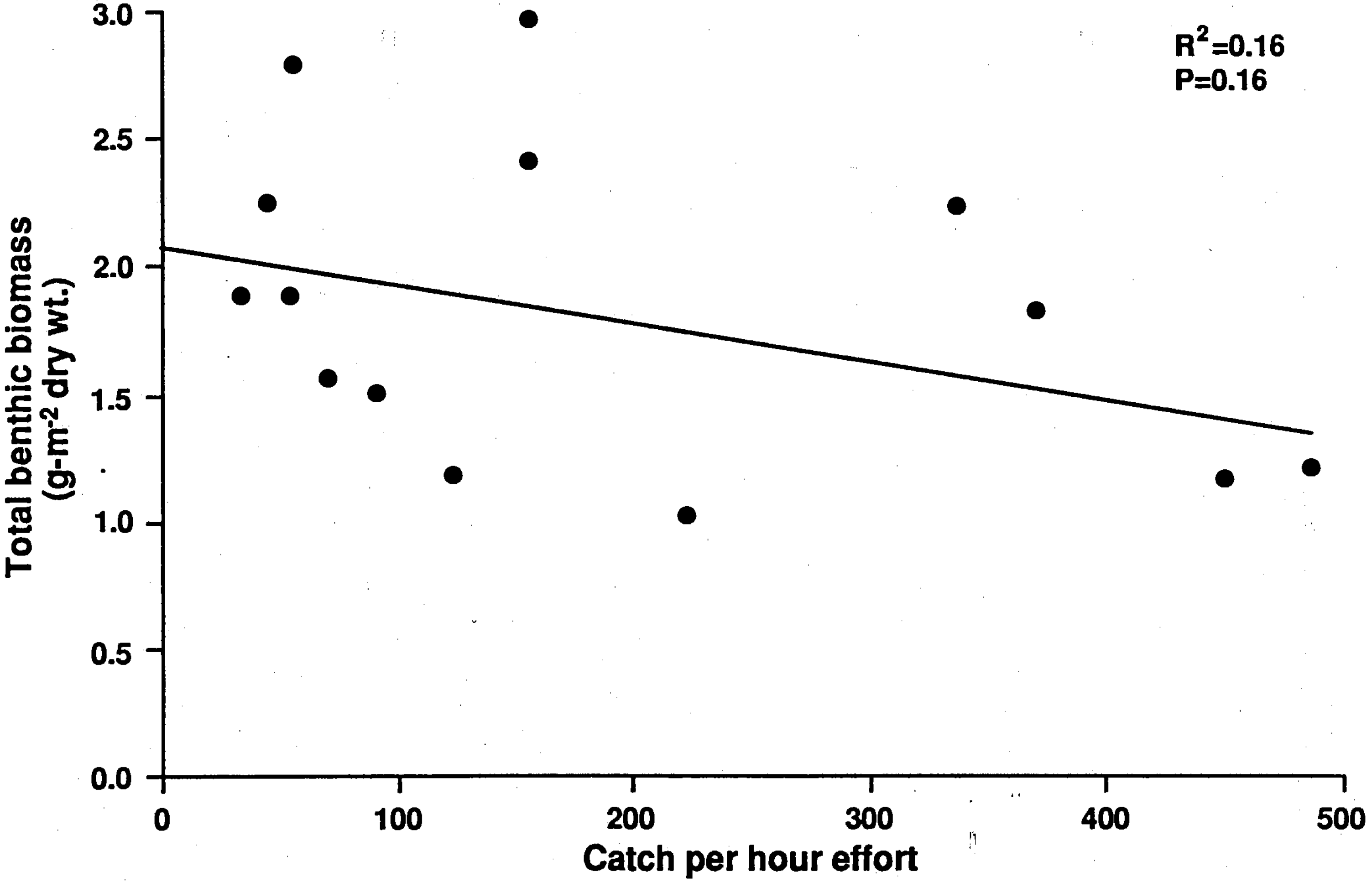
Figure 20. Relationship between standing benthic densities of a) chironomid larvae, b) amphipods, and c) isopods and relative standing densities of rainbow trout in the upper 4.5 km of Lake Taneycomo.


a)
Chironomid
0.6
0.5
0.4
0.3
0.2
0.1
0.0
b)
Amphipod
R^2=0.12
P=0.23
2.0
1.5
1.0
0.5
0.0
c)
Isopod
R^2=0.04
P=0.40
0.5
0.4
0.3
0.2
0.1
0.0
Benthic biomass
(g-m^{-2}dry wt.)
0
100
200
300
400
500
Catch per hour effort

and conversely. In fact, just as was shown for daily ration versus CPUE (Figure 19), high chironomid densities occurred almost exclusively when rainbow trout CPUE values were less than 100 (Figure 20a). It is noted that densities of chironomid pupae were not determined from benthic sampling, as these occurred primarily in the water column. Inverse relationships between standing density and CPUE for the two other directly-sampled benthic food groups, amphipods and isopods (less important prey of rainbow trout), were apparent as well. These relationships, however, were weaker than that shown by chironomid larvae and were less distinctly higher at CPUE values less than 100 (Figures 20b-c). Combined standing densities of the three benthic invertebrate food groups did show an inverse relationship with rainbow trout CPUE, although the relationship was not significant (Figure 21).

Overall, the evidence supports a density-dependent feeding situation for rainbow trout in Lake Taneycomo: high densities of rainbow trout (CPUE) are associated with relatively low prey group densities and low food consumption rates, while months with low CPUEs show higher prey group densities and higher food consumption rates. Fish growth rates have been shown to be density-dependent in other systems (Refstie 1977; Peterman 1984; Hanson and Leggett 1985, 1986; Persson 1986; Mittelbach 1988; Boisclair and Leggett 1989b), and to be positively related to their food

FIGURE 21. Combined standing densities of benthic amphipods, isopods, and chironomid larvae in the upper 4.5 km of Lake Taneycomo relative to CPUE of rainbow trout during 1991 and 1992.


R^2=0.16
P=0.16
Total benthic biomass
(g-m^{-2} dry wt.)
3.0
2.5
2.0
1.5
1.0
0.5
0.0
0
100
200
300
400
500
Catch per hour effort

consumption rates in field settings (Paloheimo and Dickie 1966; Hayward and Margraf 1987; Boisclair and Leggett 1989a, 1989c). Again, the highest feeding rates, including those which exceeded MRs, were seen exclusively when CPUE was less than 100 (Figure 19). This relates to the fact that chironomid larvae densities were high only at CPUEs less than 100 (Figure 20a), and these densities are considered to reflect densities of the most important rainbow trout prey group, chironomid pupae.

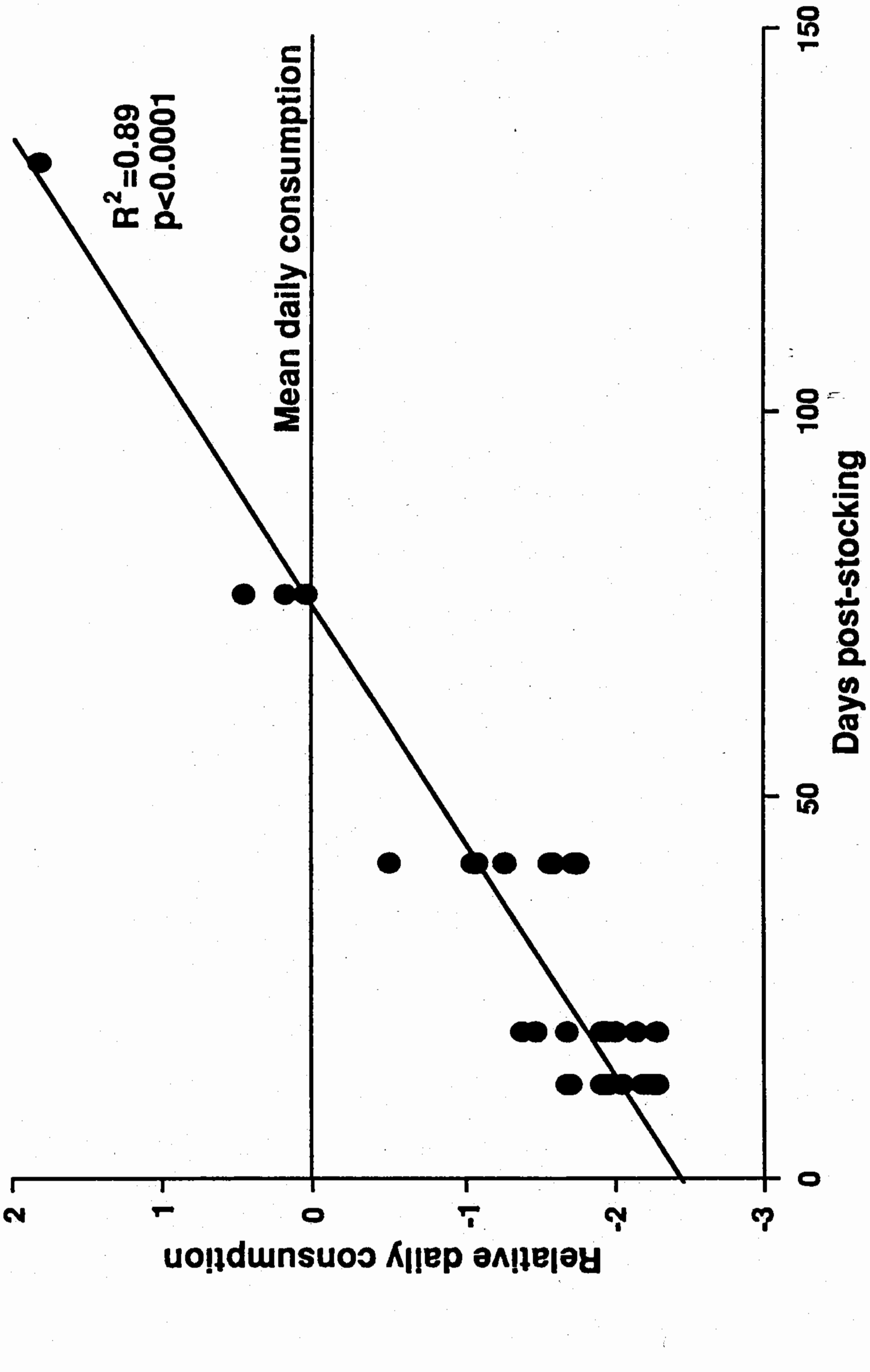
Estimates of loss rates and associated residence times for stocked rainbow trout cohorts differed primarily according to stocking date (Table 7). Cohort residence times were shown to be inversely related to fishing pressure in the month they were stocked (Figure 14). That residence times were negatively correlated with fishing pressure in the same month that stocking occurred demonstrates the immediate and powerful influence that fishing intensity has on the life of a stocked cohort in Lake Taneycomo. This finding is consistent with the observation that monthly angling pressure was correlated with relative standing densities of rainbow trout (CPUE values) in the study area (Figure 18), and with the finding that fishing exerted a more profound influence on standing densities than did the 25% reduction in 1992 stocking rates.

Using a historical growth rate estimate for rainbow trout in Lake Taneycomo of 1.8 cm/month (Turner 1977), it was calculated that a minimum of 240 days of residence in the Lake Taneycomo system was required for fish stocked at an average size of 26 cm to reach trophy size (40.6 cm). Because fish of this size and larger were reported to be common (Hanson 1977; Goddard et al. 1988), it is concluded that residence times in excess of 240 days occurred as well. In contrast, and consistent with the substantially higher fishing pressure that exists, current residence times of rainbow trout ranging from 16 to 194 days were estimated. Hence, even if the historically superior growth conditions prevailed today, fish would not remain for sufficient time in the system to achieve trophy size. When the poor present feeding conditions are also considered, it becomes apparent that more than a single factor is suppressing in situ production of large rainbow trout in Lake Taneycomo.

Of potential significance to the restoration of large rainbow trout production in Lake Taneycomo is the evidence of an interrelationship between a fish's residence time and its effectiveness as a forager. Food weights in stomachs of rainbow trout from the two cohorts stocked in February 1992 were monitored progressively throughout the duration of each cohort's residence. Food consumption estimated for cohort members on successive post-stocking dates were compared to the mean food consumption of all fish at large on the same dates. An increasing linear relationship between food consumption rates by cohort members relative to average rates for all other rainbow trout at large was observed across days in residence (Figure 22). Consumption rate values for fish in the cohort were initially below the mean (shortly after stocking), equal to mean rate after approximately 75 days in residence, and ultimately twice mean levels after 140 days. This observation indicates that rainbow trout remaining in residence longer than about 75 days become more efficient than average feeders. Because food consumption patterns for 1991 and 1992 (Figure 6) were based on results for average feeders, small rainbow trout in residence for more than about 100 days may consume food in excess of MR and begin to show modest growth. Because of the very low mean feeding rates of large fish relative to their MRs, however, extending their residence times will be less likely to result in growth. Whether residence times in excess of 134 days would have resulted in yet higher feeding rates could not be determined, but this warrants further investigation.

The findings of this study confirm that more than a single factor underlies the decline and loss of the trophy rainbow trout fishery in Lake Taneycomo. Steadily increasing stocking rates of rainbow trout since 1959 in response to increasing fishing pressure, have apparently resulted in standing densities of fish that exceed the present capacity of the prey base to support positive growth in most months. Only when rainbow trout densities are

FIGURE 22. The relationship between the rainbow trout residence times and consumption rate relative to the estimated daily food consumption for all small rainbow trout in Lake Taneycomo on that date.



Relative daily consumption
2
1
0
-1
-2
-3
Days post-stocking
0
50
100
150
Mean daily consumption
R^2=0.89
p<0.0001

substantially reduced by heavy fishing in summer is there a sufficient release of predation pressure for the standing prey biomass to support rainbow trout growth. While rainbow trout stocking rates, standing densities, and predation pressures have increased in recent years, there is also evidence that carrying capacity for rainbow trout in the upper region of Lake Taneycomo has declined due to another force. Rainbow trout diets have shifted away from being amphipod- and isopod-dominated, the former being an energetically optimal prey item for this species (Civiello 1989). Diets are presently dominated by chironomids, zooplankton and algae. The second group is likely a suboptimal prey for rainbow trout due to their small size (Pyke et al. 1977; Mittelbach 1983) and the latter likewise, due to a low nutritional value for rainbow trout (Kitchell and Windell 1970; Leibfried 1988).

The shift in the prey community evident from comparing present rainbow trout diets to those in the early 1970s (Pfleiger 1977a) (Table 6), is also shown by comparing benthic invertebrate samples over the same period (Hayward, unpublished benthic invertebrate data from 1991 and 1992 versus comparable data from Pfleiger 1977a). These changes in the benthic community indicate that Lake Taneycomo has become substantially more eutrophic over the past 20 years (Hayward and Margraf 1987), and suggest that changes in trophic status of the Lake Taneycomo ecosystem is also involved in the rainbow trout consumption rate declines observed. Other studies of chemical and biotic trends in Lake Taneycomo support this contention (Knowlton and Jones 1990). Shifts in prey community composition in aquatic ecosystems associated with the eutrophication process have been previously shown to result in poor feeding conditions for resident fish populations (Hayward and Margraf 1987). Hence, it appears that the currently poor feeding and growth conditions for rainbow trout in Lake Taneycomo have resulted, in part, because higher predation pressure (through increased stocking) is being exerted on a prey base that has become less optimal for this species through eutrophication-like effects.

The lack of diet partitioning between rainbow trout size groups (Figures 8 and 9) further exacerbates the problem, in that all rainbow trout, irrespective of size, are competing for the same limited food resources. Energetics data do indicate, however, that positive growth conditions can occur for rainbow trout in Lake Taneycomo if fish standing densities are markedly reduced.

Substantial increases in rainbow trout residence times will also be required for these fish to achieve large sizes, even if the feeding environment is markedly improved. It was shown that current residence times are too short for trophy sizes to be reached (Table 7), even under historical growth conditions which were quite good. As also shown, rainbow trout feeding rates might be expected to improve after about 75 days in residence in Lake Taneycomo (Figure 22). The limited data available on this relationship hint that a doubling of food consumption by rainbow trout could be achieved with longer residence times. However, given the extremely low feeding rates that were measured, particularly for large rainbow trout (Figure 6), extension of residence times alone without improvement of the underlying prey base is not expected to produce growth rates sufficient to restore a strong presence of trophy-size fish.

In conclusion, these study findings indicate that restoration of continuous positive growth conditions for rainbow trout of all sizes in Lake Taneycomo can be achieved through a substantial reduction in the standing densities of rainbow trout coupled with measures that would increase residence times. Establishment of a larger-sized prey component suitable for larger rainbow trout (such as threadfin shad) would facilitate, and may be critical to, positive growth of larger fish by allowing a separation of diets for small and large fish.

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APPENDIX A

Appendix A. Regressions for the calculation of dry weights from wet weights, and total lengths from residual part measurements for rainbow trout and prey organisms. All weight equations involve g dry weight and all length equations are based on length in mm.

Description	Regression or value
Rainbow trout dry weight (DW) from wet weight (WW)	$DW=WW*0.233$
Sculpin DW from length (L)	$\ln DW=-2.222+0.0352*L$
Sculpin length from vertebral column length (VL)	$L=49.427+0.969*VL$
Amphipod total length (TL) from partial amphipods (PA) measured from the front of the eye to the first suture	$TL=-0.554+11.232*PA$
Average amphipod dry weight (DW) for 2 mm length classes (LC) (1=0-2 mm, 2=2-4 mm, 3=4-6 mm, etc.)	$\ln DW=-10.610+0.843*(LC)$
Chironomid pupae total length (TL) measured from head width of partial chironomid pupae (PC)	$TL=0.965+15.164*PC$
Average chironomid pupae dry weight (DW) for 2 mm length class (LC) (1=0-2 mm, 2=2-4 mm, 3=4-6 mm, etc.)	$\ln DW=-12.386+1.0345*LC$
Isopod total length (TL) measured from width of the cephalothorax of partial isopods (PI)	$TL=-0.398+5.321*PI$
Average isopod dry weight (DW) for 2 mm length class (LC) (1=0-2 mm, 2=2-4 mm, 3=4-6 mm, etc.)	$\ln DW=-10.537+0.890*LC$
"Other invertebrate" dry weight (DW) was estimated from a length (L) weight regression for terrestrial insects (Rogers et al. 1976)	$DW=0.030xL^{2.62}$

The cladoceran dry weight (DW) for individual 1.92 mm *Daphnia pulex* was used (Slobodkin and Richman 1961)	$DW=3.6155x10^{-5}$
Threadfin shad dry weight was measured from 6 47-55 mm threadfin shad and an average dry weight was used for individual fish.	DW=0.40