FINAL REPORT

EFFECTS OF NUTRIENT ENRICHMENT ON BENTHIC ALGAE, MACROINVERTEBRATES, AND YOUNG-OF THE-YEAR CUTTHROAT TROUT (ONCORHYNCHUS CLARKI)

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Effects of nutrient enrichment on benthic algae, macroinvertebrates, and young-of-the-year cutthroat trout (Oncorhynchus clarki)

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Abstract

Two nutrient enrichment experiments were conducted in stream-side artificial channels during 13 August-29 October 1990 and 10 July-20 August 1991 to assess the effects of inorganic fertilization on populations of benthic algae, macroinvertebrates, and juvenile cutthroat trout. Artificial channels were enriched with either nitrate, phosphate, or both nutrients to 2-4 times background levels in the Clark Fork River. Channels that received nitrate additions, both singly and with additional phosphate, supported significantly greater benthic chlorophyll a (32-65%) than control channels after 10 and 20 days in the 1990 experiment and after 10 days in the 1991 experiment. Initial differences did not persist beyond 20 days, however, indicating that factors in addition to nitrogen influenced periphyton biomass. Nitrate-enriched treatments, with or without phosphate, also supported significantly greater invertebrate densities after 77 days of enrichment in 1990. No differences in invertebrate densities among treatments were apparent after 41 days of enrichment in 1991. Growth of juvenile cutthroat trout was unrelated to nutrient regime in the 1990 experiment. These results suggest that the growth of benthic algae in the Clark Fork is likely to be nutrient-limited during at least part of the year and that nitrogen is the probable limiting nutrient. Nitrogen may also indirectly influence the density of grazing invertebrates by increasing the primary production of benthic algae. Increases in invertebrate densities as a consequence of fertilization may potentially enhance growth and survival of juvenile salmonids, but we were unable to demonstrate a relationship between juvenile fish growth and invertebrate abundance in this study.

Increases in stream algal production in response to nutrient enrichment have been well-documented, and both nitrogen and phosphorus have been shown capable of stimulating the growth of stream periphyton (Stockner and Shortreed 1978, Peterson et al. 1983, Grimm and Fisher 1986, Lohman et al. 1991). Limitation by either nitrogen or phosphorus depends both on the absolute and the relative concentrations of the two nutrients. In streams where the concentrations of both N and P are low, the addition of both nutrients may be required to produce a measureable change in algal biomass (Tate 1991). In contrast, in streams where both N and P are abundant, other factors limit primary production and the addition of either or both nutrients will have no effect on algal growth (Wuhrmann 1974, Bushong and Bachmann 1989, Munn et al. 1989). The relative concentration of N and P becomes important in streams where the abundance of both nutrients is below levels that would preclude nutrient limitation. In such cases, N:P ratios have been successfully used to predict which element limits algal growth. Based on the molar tissue concentrations of N and P for marine algae determined by Redfield (1958), N is assumed to be the potentially limiting nutrient at N:P<16, and P is predicted to limit growth when N:P>16.

Low streamwater N:P and, consequently, nitrogen limitation of stream algae seems to be a more common phenomenon in the western and midwestern than in the eastern United States (Thut and Haydu 1971, Gregory 1980, Marcus 1980, Grimm and Fisher 1986, Hill and Knight 1988, Coleman and Dahm 1990, Lohman et al. 1991, Lohman and Priscu 1992). The higher occurrence of nitrogen limitation in streams of the western United States has been ascribed to watershed geology and the abundance of watersheds that are rich in edaphic sources of phosphorus (Thut and Haydu 1971, Munn and Meyer 1990, Lohman and Priscu 1992). In Montana, nitrogen limitation has

been reported in both lakes (Dodds et al. 1989) and streams (Marcus 1980), including the upper Clark Fork of the Columbia River (Lohman and Priscu 1992).

Stream enrichment may also increase secondary production by aquatic invertebrates by increasing food availability through either autotrophic or heterotrophic sources. Increases in weight and abundance of benthic invertebrates have been demonstrated in response to organic enrichment with cereal grains (Mundie et al. 1983) and sucrose (Warren et al. 1964). Similar increases in the size of larval blackflies (Peterson et al. 1985) and chironomids (Hershey et al. 1988) have been shown in response to inorganic nutrient enrichment. Because resource limitation of grazing invertebrates seems to be common (Gregory 1983), increases in their abundance as a consequence of increased primary production stimulated by inorganic enrichment should be expected.

In many aquatic systems, fish production may be highly dependent on the abundance of the invertebrate food supply; relationships between fish production and indices of trophic status have been documented in both lakes and streams (Northcote and Larkin 1956, Egglishaw 1968, Ryder et al. 1974, Jones and Hoyer 1980). Warren et al. (1964) demonstrated increased growth of cutthroat trout in response to sucrose enrichment, and fertilization of oligotrophic nursery lakes and streams in British Columbia by either organic enrichment (LeBrasseur et al. 1978), or by the addition of inorganic nutrients (Hyatt and Stockner 1985, Johnston et al. 1990), has enhanced salmonid production.

We studied the effects of nitrogen and phosphorus enrichment on the abundance of benthic algae, invertebrates, and juvenile cutthroat trout in experimental streams set up beside the Clark Fork of the Columbia River near

Missoula, Montana. Our objectives were to determine 1) whether benthic algae were nutrient-limited and, if so, whether limitation was by nitrogen or phosphorus, 2) whether additions of nitrogen or phosphorus would influence the abundance and biomass of benthic invertebrates, and 3) whether additions of nitrogen or phosphorus would stimulate the growth of juvenile cutthroat trout.

Methods

Experimental Streams and Nutrient Regimes

Two nutrient enrichment experiments were conducted using experimental streams set up beside the Clark Fork River on the grounds of Stone Container Corporation near Missoula, Montana. In the first experiment, we assessed the response of benthic algae, invertebrates, and juvenile cutthroat trout to additions of nitrogen and phosphorus for 77 days during 13 August-29 October 1990. We repeated this experiment for 41 days during 10 July-20 August 1991, addressing only the response of benthic algae and invertebrates to nutrient enrichment. Experimental streams consisted of eight wooden troughs, each 4.3 m long, 13 cm wide and 25 cm deep. Using an irrigation pump, water from the Clark Fork was continuously pumped into a large holding tank and then through each trough at a rate of 0.4-0.6 $L \cdot s^{-1}$. Depth was maintained at 18-23 cm and current velocity was 5-10 $cm \cdot s^{-1}$.

Nutrients were dripped from 20 and 50 L carboys into the head of each trough and baffles were used to insure mixing. Two troughs received nitrate additions, two received phosphate, and two received both nitrate and phosphate. The remaining two troughs served as controls. Nitrate was added as HNO_3 and phosphate as H_3PO_4. Stock solutions of 400 $\mu g \cdot L^{-1}$ PO_4^{-3}-P (+P),

600 $\mu g \cdot L^{-1}$ NO_3^--N (+N), and 200 $\mu g \cdot L^{-1}$ PO_4^{-3}-P plus 600 $\mu g \cdot L^{-1}$ NO_3^--N (+NP) were dripped at rates of 2-10 $ml \cdot min^{-1}$. Nutrient concentrations in the Clark Fork and in the troughs were monitored every few days during the course of each experiment and drip rates were adjusted to elevate NO_3^--N and PO_4^{-3}-P to roughly 2-4 times background levels in the Clark Fork.

Troughs were located in an open area along the river and substrate in the troughs received full sunlight for 4-6 h per day. Water temperature measured between 0800-1000 h varied from a high of 18.0°C at the beginning of the experiment in August 1990 to a low of 6.0°C at the conclusion of the experiment during the last week of October. Little change in water temperature occurred over the period of the experiment in July-August 1991, with morning temperatures ranging from 16.0 to 18.0°C.

Water Chemistry

Water samples collected from the Clark Fork and from the troughs were routinely analyzed for NO_3^--N and soluble reactive phosphorus (SRP). NO_3^--N+NO_2^--N was determined by cadmium reduction (APHA 1984) and, on the assumption that NO_2^--N was negligible, values are reported here as NO_3^--N. SRP was measured by the ascorbic acid method (Prepas and Rigler 1982). Periodic measurements of NH_4^+-N were analyzed by the phenolhypochlorite method (Solorzano 1969).

Benthic Algae

Clean, bare rocks (10-15 cm diameter) from nearby gravel bars were placed in the troughs on day 0 of each enrichment experiment (13 August 1990 and 10 July 1991). On days 10, 20, 30, 52, and 72 in 1990, and on days 10, 20 30, and 40 in 1991, six rocks were removed from each trough for analysis of chlorophyll a (Chl a). Benthic algae was scraped from a 5.3 cm^2 area on each rock and rinsed onto a Gelman Type A/E glass fiber filter. Chl a was

measured spectrophotometrically and corrected for phaeopigments after extraction in a 50:50 mixture of DMSO and 90% acetone in the dark for 24 h (Shoaf and Lium 1976).

Artificial substrates (6.3 cm^2 ceramic tiles) were used to make additional estimates of benthic algal accrual during the first experiment in 1990. Thirty-six tiles were attached to a board suspended roughly 5 cm below the water surface near the end of each trough on 20 September 1990 (day 38). Five tiles were randomly removed from each trough after 8 and 16 days of accrual. Periphyton was scraped from the tiles and analyzed for Chl a as previously described. New tiles were introduced on 6 October 1990 (day 54) and 5 tiles removed after 7 and 16 days of accrual and analyzed for Chl a.

Benthic Invertebrates

Invertebrates in the troughs were sampled after 35 and 77 days of enrichment in 1990 and after 14 and 41 days of enrichment in 1991. To collect invertebrates, flow through the troughs was briefly stopped and the last 30 cm of each trough containing rocks was blocked off with a board. All invertebrates were then removed from water and substrate within the blocked section of each trough. Invertebrates were counted and identified to genus, or family in the case of Chironomidae. In 1990, mean chironomid biomass (dry weight - DW) in each trough was estimated by drying 50 individuals to constant weight at 105°C. In 1991, mean chironomid biomass was determined by drying all chironomids collected on day 14 to constant weight. On day 41, 25 chironomids and 10 mayflies were used to make biomass estimates.

Juvenile Cutthroat Trout

After recording total length and wet weight, 30 young-of-the-year westslope cutthroat trout (Onchorhynchus clarki lewisi) were introduced into

each trough on day 38 of the enrichment experiment in 1990. Total length and wet weight (WW) were measured again at the conclusion of the experiment on day 77. Total length of mortalities that occurred before day 77 were measured and a length-weight regression was used to estimate wet weight at the time of death. On day 77, 5 juveniles from each trough were randomly selected for tissue analysis of particulate C, N, and P.

In 1991, 50 juveniles were introduced into each trough on day 16. Screens at the end of each trough became clogged with sloughing algae on day 20, however, causing water to overflow and allowing most of the fish to escape. Remaining fish were netted and removed.

Tissue Analysis

Tissue concentrations of particulate C, N, and P were analyzed from benthic algae collected on days 58 and 73 in 1990 and on days 10, 20, 30, and 40 in 1991, from chironomids collected on days 35 and 77 in 1990 and days 14 and 41 in 1991, from mayflies collected on day 41 in 1991, and from juvenile cutthroat trout collected on day 77 in 1990. In all cases, samples were dried to constant weight at 105°C, then powdered with a mortar and pestle. Dried samples were analyzed for particulate C and N using a Carlo-Erba elemental analyzer. Particulate P was measured by subjecting dried samples to persulfate digestion, followed by an ascorbic acid determination of P concentration (Prepas and Rigler 1982). Results for particulate C, N, and P are expressed as percent of dry weight.

Results

Nutrient concentrations in the Clark Fork were generally similar over the period that experiments were conducted in 1990 and 1991 (Fig.1, 2; Table 1, 2). NO_3^--N fluctuated much more than NH_4^+-N or SRP in both years, ranging between 16-84 $\mu g \cdot L^{-1}$ in 1990 and between 21-154 $\mu g \cdot L^{-1}$ in 1991. NO_3^--N concentrations were lowest between days 14 and 35 in 1990 and gradually increased over the latter half of the experiment. In 1991, NO_3^--N was highest between days 18 and 31. NH_4^+-N was 8-22 $\mu g \cdot L^{-1}$ in 1990 and <1-25 $\mu g \cdot L^{-1}$ in 1991. Background concentrations of SRP were 2-17 $\mu g \cdot L^{-1}$ in 1990 and 5-12 $\mu g \cdot L^{-1}$ in 1991.

Weighted average ratio of DIN:SRP was slightly lower in 1991 than in 1990 (Table 1, 2), but fluctuation in NO_3^--N concentration caused DIN:SRP to vary substantially during both experiments (Fig. 1, 2). DIN:SRP generally fell below a Redfield (1958) ratio of 16:1 (molar) during the first few days and between days 14-35 of the experiment in 1990, and during the first 14 and last 8 days of the experiment in 1991.

Similar patterns in the accrual of benthic Chl a occurred in both 1990 and 1991 (Fig. 3, 4). In both years, benthic Chl a in all troughs levelled off after the first 10-20 days of enrichment. Benthic Chl a accrual was significantly greater in +N and +NP troughs than in +P and control troughs on day 10 ($F=12.96$, $p<0.05$), and again on day 20 in 1990 ($F=14.89$, $p<0.05$). Benthic Chl a was also significantly greater in +N and +NP troughs than in +P and control troughs on day 10 in 1991 ($F=131.73$, $p<0.01$). Mean benthic Chl a was also greater in N-amended treatments on day 20 but so was the variability between replicates and these differences were not significant ($F=3.41$, $0.10<p<0.50$). No

significant differences were detected among treatments on other dates in either year.

Chl a accrual on ceramic tiles did not differ among treatments in either of the 16-day trials conducted in 1990 (Fig. 5). In both trials, accrual rates were high, averaging 3.7 mg Chl $a \cdot m^{-2} \cdot d^{-1}$ in the first run and 4.0 mg Chl $a \cdot m^{-2} \cdot d^{-1}$ in the second run.

Particulate C and particulate N in benthic algae did not differ among treatments on days 58 and 73 in 1990 (Table 3). Significantly higher particulate P, however, was present in the tissue of benthic algae that received either +P or +NP additions on both dates (day 58: $F=21.32$, $p<0.05$; day 73: $F=15.16$, $p<0.05$). Particulate C:N ratios were similar among treatments, averaging from 11.3 to 12.8 on day 58 and from 12.0 to 12.7 on day 73. Although not statistically different, particulate N:P ratios were slightly higher in benthic algae from the +N treatment on both dates in 1990.

No treatment differences in particulate C, N, or P of benthic algae were apparent on any of the 4 sampling dates in 1991 (Table 4). Particulate C and N were similar to that found in benthic algae on dates in 1990, whereas particulate P was generally greater in benthic algae from all treatments in 1991 than in 1990. Particulate C:N ratios were generally similar to those in 1990, averaging 10.4-16.0. Particulate N:P was somewhat lower than observed in the previous year, averaging 6.3-9.7.

Macroinvertebrate samples were dominated by tube-building chironomids both before (day 35) and after (day 77) the introduction of juvenile cutthroat trout in 1990, making up >90% of invertebrate numbers in all troughs on day 35 and >95% on day 77 (Table 5). Baetid mayflies were the second-most abundant taxa on day 35, but were rare on day 77. Mean individual size of chironomids did not differ among treatments and averaged

230 μg DW on day 35 and 712 μg DW on day 77. Both number and total biomass of chironomids were significantly greater in the +N than in the other 3 treatments on day 35, and on day 77, were significantly greater in both +N and +NP treatments as compared to that in +P and control troughs (Table 7).

Chironomidae was also the most abundant taxa in the troughs in 1991, but Ephemeroptera (particularly Tricorythodes) made up a large proportion of the samples collected on day 41 (Table 6). Fewer macroinvertebrates were collected from troughs in 1991 than in 1990, and densities did not differ among treatments on either day 14 or day 41 (Table 8). Mean individual biomass of Chironomidae did not differ among treaments and averaged 168 μg DW on day 14 and 510 μg DW on day 41. Mean individual size of Ephemeroptera was also similar among treatments and averaged 2510 μg DW on day 41.

Particulate C and particulate N concentrations in chironomids were similar among treatments on days 35 and 77 in 1990 (Table 3), as well as on days 14 and 41 in 1991 (Table 4). Particulate P was significantly greater in chironomids from P-amended treatments on day 35 in 1990 ($F=12.74$, $p<0.05$), but did not differ among treatments on day 77 in 1990 or on either of the 2 sampling dates in 1991 (Table 3, 4). No differences were observed among treatments in the cellular C, N, or P composition of ephemeropterans in 1991 (Table 4). Particulate P concentrations in both chironomids and ephemeropterans were nearly twice as high in 1991 as those of chironomids in 1990.

After 39 days in the troughs in 1990, 84% of juvenile cutthroat trout remained, with mortality ranging from 1-8 fish per trough. Mean length and weight of juveniles did not differ significantly among treatments (Table 9). Overall, juveniles increased in total length by an average of 3.5 mm (8.6%)

and in wet weight by an average of 172.5 mg (34.6%). Net production, calculated as the difference in live weight between days 38 and 77 plus the weight of mortalities over the 39-day period estimated from length-weight relationships, ranged from 3500 to 4600 mg WW per channel. No differences among treatments in cellular concentrations of particulate C, N, and P were apparent (Table 3).

Discussion

Benthic Algae

Benthic algal accrual, measured as Chl a, was initially stimulated by additions of either nitrate or nitrate plus phosphate in both years of study. Elevating nitrate concentrations to roughly twice ambient concentration, with or without the addition of phosphate, resulted in benthic Chl a levels that were 32-65% greater than controls after 10 days of enrichment. From this, we conclude that nitrogen limited the early growth of benthic algae.

Low N:P ratios in streams have been reliable indicators of nitrogen limitation (Grimm and Fisher 1986, Hill and Knight 1988, Lohman et al. 1991). Ambient N:P ratios during the initial period of each experiment were generally consistent with a finding of nitrogen limitation of benthic algae. For two weeks prior to the start and with the exception of two dates (days 9 and 11) after the experiment was begun, molar ratios of NO_3^--N:SRP were below 14:1 until day 32 in 1990. NO_3^--N:SRP remained <12:1 until day 18 in 1991.

Differences in algal biomass among treatments did not persist beyond 20 days of enrichment. In both years, benthic Chl a reached maximum levels on day 20, then tended to decline in +N and +NP and to remain unchanged in +P and control treatments. As a consequence, there was no evidence of

nutrient limitation by either nitrogen or phosphorus after 20 days. Measurements of benthic Chl a on ceramic tiles between days 38 and 70 in 1990 also indicated that nitrate and phosphate additions had no effect on biomass accrual.

Several factors could explain the absence of a nutrient effect on algal biomass in the latter part of each experiment. First, nitrogen and phosphorus concentrations might have been high enough to preclude nutrient limitation. NO_3^--N concentrations steadily increased after day 22 and ranged from 58 to 84 $\mu g \cdot L^{-1}$ during days 50-77 in 1990. In 1991, NO_3^--N rose from 21-32 $\mu g \cdot L^{-1}$ during the first 14 days to 74-154 $\mu g \cdot L^{-1}$ during days 18-31. NO_3^--N concentrations in 1990, however, were also relatively high during days 0-11 (52-72 $\mu g \cdot L^{-1}$). Nitrogen limitation has been reported in streams with NO_3^--N concentrations as high as 55 $\mu g \cdot L^{-1}$ (Grimm and Fisher 1986) and 100 $\mu g \cdot L^{-1}$ (Lohman et al. 1991). In addition, SRP was higher during the first three days (15-17 $\mu g \cdot L^{-1}$) than it was throughout the remainder of the 77-day experiment (2-9 $\mu g \cdot L^{-1}$). Because differences in benthic Chl a were apparent after 10 days of enrichment when NO_3^--N and SRP concentrations were among the highest observed, it seems unlikely that the absence of differences in benthic Chl a among treatments during the latter period of the 1990 experiment can be explained by an overabundance of nitrogen and phosphorus. This could have been the case in the 1991 experiment, however, when background concentrations of both NO_3^--N and SRP were higher during the latter 3 weeks than they were during the first 2 weeks of the experiment.

Intense grazing by aquatic invertebrates is a more probable reason for the observed patterns in benthic algal biomass in both years. Resource depression by aquatic herbivores, in spite of nutrient enrichment, has been demonstrated in a number of studies (Stewart 1987, Hill et al. 1992). High

numbers of chironomids were present on days 35 and 77 in 1990. Fewer invertebrates were collected on days 14 and 41 in 1991, but on day 41 two species of mayfly that were large in comparison to chironomids made up 69-75% of grazer biomass (Table 8). We speculate that colonization by grazing invertebrates greatly increased between days 10 and 30 in both years, and that beyond 20 days, grazing was more important in regulating periphyton biomass than was nitrogen limitation.

Macroinvertebrates

The abundance of many stream herbivores may be determined by the availability of benthic algae (Gregory 1983). In addition, several studies have demonstrated that either individual growth or population density of stream herbivores can be stimulated by increased periphyton production. Hart and Robinson (1990) reported greater density and mean individual size of two grazing caddisflies in P-enriched flumes that supported greater periphyton biomass than in unenriched controls. Increases in chironomid numbers in response to P enrichment and greater algal biomass have been documented in an Arctic stream (Hershey et al. 1988). Invertebrate communities in our channels were dominated by grazing species in both years. Greater periphyton biomass would account for the higher density and biomass of chironomids that were associated with +N and +NP-amended treatments in 1990, although a similar trend was not observed in 1991.

Differences in the overall densities of grazing invertebrates between the two years may explain why nitrogen treatments supported greater numbers than control and phosphorus-enriched treatments in 1990 but not in 1991. Although levels of benthic Chl a were generally similar between years, colonization of all troughs by benthic invertebrates was much more rapid in 1990 than in 1991. Density and biomass of invertebrates were an order of

magnitude greater on day 35 in 1990 relative to day 41 in 1991 (Table 7, 8). This may suggest that populations of invertebrate grazers in 1991 had not yet reached densities great enough to be resource-limited when the experiment was concluded.

Juvenile Cutthroat Trout

Although increased growth of juvenile salmonids in response to whole-stream fertilization with nitrogen and phosphorus has been demonstrated (Johnston et al. 1990), growth of juvenile cutthroat trout was not enhanced in our artificial stream experiment. Nutrient enrichment had no effect on the growth of juvenile cutthroat trout in the 1990 experiment, in spite of increased numbers of food organisms in +N and +NP treatments. Juveniles grew well in all treatments, with individual weight gain averaging 4.4 mg WW·day^{-1}. Chironomid biomass increased in all treatments following the introduction of juvenile cutthroats, suggesting that fish growth was probably not limited by food supply. If growth of juvenile cutthroat trout is indeed limited by the availability of invertebrates, then differences among treatments might have been observed had fish been stocked at substantially greater densities or had larger fish been stocked.

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Table 1. Weighted average concentrations of NO_3^--N and SRP, and NO_3^--N:SRP ratios in control, +P, +N, and +NP treatments averaged over 77 days of the experiment in 1990. Treatment values are the average of two replicate channels.

	C	+P	+N	+NP
NO_3^--N (µg/L)	53	53	101	98
NH_4^+-N (µg/L)	14	14	14	14
DIN (µg/L)	67	67	115	112
SRP (µg/L)	6	20	6	22
DIN:SRP (molar)	24.7	7.4	42.4	11.2

Table 2. Weighted average concentrations of NO_3^--N, NH_4^+-N, and SRP, and N:P ratios in control, +P, +N, and +NP treatments averaged over 41 days of the experiment in 1991. Treatment values are the average of two replicate channels.

	C	+P	+N	+NP
NO_3^--N (µg/L)	62	62	125	116
NH_4^+-N (µg/L)	8	8	8	8
DIN (µg/L)	70	70	133	124
SRP (µg/L)	8	21	8	26
DIN:SRP (molar)	19.3	7.4	36.7	10.5

Table 3. Cellular concentrations of C, N, and P in benthic algae, chironomids and cutthroat trout collected from experimental channels September-October 1990. Values are the means of two channels per treatment (±1 SD) and are reported as percent of dry weight. C:N and N:P are molar ratios.

	Day	C	+P	+N	+NP
Benthic Algae					
%C	58	9.10±0.86	10.47±0.49	9.56±1.03	9.86±0.11
	73	11.12±0.80	11.68±1.21	11.14±0.71	10.96±0.64
%N	58	0.83±0.08	0.97±0.06	0.98±0.21	1.02±0.09
	73	1.11±0.37	1.12±0.04	1.02±0.06	1.11±0.16
%P	58	0.16±0.00	0.22±0.01	0.16±0.02	0.22±0.02
	73	0.18±0.01	0.22±0.01	0.16±0.02	0.24±0.02
C:N	58	12.8±0.1	12.6±0.1	11.5±1.3	11.3±0.8
	73	12.2±3.2	12.2±0.9	12.7±0.1	12.0±1.2
N:P	58	11.4±1.2	10.0±0.2	13.0±1.2	10.2±1.9
	73	13.9±4.1	10.9±0.6	13.7±1.0	10.4±2.4
Chironomidae					
%C	35	36.83±1.23	34.36±3.12	38.33±2.45	36.42±2.26
	77	46.88±0.60	47.99±0.76	47.10±3.08	49.11±0.20
%N	35	9.84±0.42	9.01±0.71	10.12±0.66	9.67±0.32
	77	9.10±0.34	8.88±0.50	8.80±0.46	8.88±0.85
%P	35	0.57±0.04	0.66±0.03	0.58±0.01	0.64±0.01
	77	0.40±0.08	0.44±0.06	0.36±0.05	0.39±0.01
C:N	35	4.4±0.0	4.4±0.0	4.4±0.0	4.4±0.1
	77	6.0±0.1	6.4±0.2	6.2±0.1	6.5±0.7
N:P	35	38.2±1.2	30.2±1.1	38.2±2.0	33.2±1.5
	77	51.2±9.0	45.4±4.1	53.6±4.4	50.4±6.6
Cutthroat trout					
%C	77	46.99±0.10	46.50±0.10	47.52±0.20	48.44±0.29
%N	77	11.72±0.28	11.43±0.47	11.42±0.30	11.82±0.07
%P	77	2.16±0.02	2.13±0.31	1.86±0.01	1.90±0.10
C:N	77	4.7±0.1	4.8±0.2	4.9±0.1	4.8±0.0
N:P	77	12.0±0.4	12.0±2.3	13.5±0.3	13.8±0.8

Table 4. Cellular concentrations of C, N, and P in benthic algae, Chironomidae, and Ephemeroptera collected from experimental channels in July-August 1991. Values are the means of two channels per treatment (±1 SD) and are reported as percent of dry weight.

	Day	C	+P	+N	+NP
Benthic Algae					
%C	10	11.46±0.81	11.97±0.27	10.52±0.49	10.36±0.62
	20	8.34±0.01	8.58±0.01	9.78±1.50	8.66±0.90
	30	9.46±0.23	10.25±2.04	9.60±1.82	9.96±0.02
	40	10.38±0.12	10.48±0.29	10.87±1.22	11.40±0.25
%N	10	0.96±0.20	1.04±0.11	1.08±0.02	1.03±0.14
	20	0.64±0.21	0.78±0.01	0.88±0.13	0.69±0.01
	30	0.95±0.13	1.00±0.18	0.95±0.23	0.98±0.15
	40	1.02±0.06	0.90±0.04	0.96±0.06	1.02±0.02
%P	10	0.24±0.01	0.28±0.01	0.30±0.11	0.31±0.01
	20	0.17±0.01	0.24±0.01	0.22±0.01	0.24±0.03
	30	0.22±0.02	0.26±0.02	0.27±0.06	0.28±0.05
	40	0.32±0.08	0.32±0.01	0.29±0.06	0.34±0.01
C:N	10	14.2±1.9	13.4±1.1	11.3±0.7	10.4±0.6
	20	16.0±5.3	12.8±0.3	12.9±0.0	14.6±1.2
	30	11.7±1.3	12.0±0.6	11.8±0.6	11.9±1.8
	40	11.6±1.2	12.6±1.1	12.5±0.3	13.0±0.0
N:P	10	9.0±2.1	8.1±0.6	8.6±3.1	7.3±0.7
	20	8.2±2.1	7.2±0.3	9.1±1.1	6.4±0.6
	30	9.7±0.3	8.3±0.8	7.8±0.2	7.9±0.2
	40	7.2±2.1	6.3±0.4	7.4±1.0	6.8±0.3
Chironomidae					
%C	14	35.34	36.52±1.59	36.97±2.60	37.86±2.41
	41	36.20±0.92	34.66±6.27	35.45±3.08	39.82±3.73
%N	14	9.16	9.53±0.58	9.02±1.28	10.14±1.36
	41	7.67	8.88	8.69	8.31±0.11
%P	14	0.94±0.08	0.91±0.06	0.88±0.02	0.91±0.06
	41	1.06±0.10	1.12±0.13	1.00±0.01	1.09±0.06
C:N	14	4.5	4.5±0.1	4.8±0.3	4.4±0.3
	41	5.4	5.1	5.0	5.6±0.4
N:P	14	20.2	23.2±3.2	22.6±2.5	24.7±1.6
	41	15.0	15.2	19.2	16.8±0.7
Ephemeroptera					
%C	41	49.55±0.01	48.36±4.03	45.28	46.62±0.62
%N	41	8.18±1.37	7.90±2.43	8.80	7.18±0.76
%P	41	1.08±0.06	0.95±0.35	0.81±0.00	1.18±0.29
C:N	41	7.2±1.2	8.4±3.2	6.0	7.6±0.9
N:P	41	16.9±3.8	16.7±1.4	24.0	13.7±2.0

Table 5. Number of macroinvertebrates collected from the last 30 cm of channels on days 35 and 77 in 1990. Values are mean ±1 SD.

Taxa	C	+P	+N	+NP
Day 35				
Chironomidae	1244± 21	1152±186	1536± 91	1206±201
Baetis	65± 17	52± 23	38± 12	34± 0
Tricorythodes	2± 3	2± 1	2± 2	1± 1
Hydroptilidae	10± 4	10± 6	8± 2	9± 8
Other	32± 8	12± 3	12± 1	10± 4
Total	1354± 9	1229±167	1594± 81	1260±196
Day 77				
Chironomidae	741± 20	684± 78	915± 30	838± 23
Baetis	1± 0	2± 3	2± 1	0
Hydroptilidae	10± 1	11± 11	11± 13	8± 2
Other	3± 4	4± 6	2± 1	14± 18
Total	755± 17	702± 98	930± 18	860± 7

Table 6. Number of macroinvertebrates collected from the last 30 cm of channels on days 14 and 41 in 1991. Values are mean ±1 SD.

Taxa	C	+P	+N	+NP
Day 14				
Chironomidae	39± 1	50±16	46± 1	54±19
Other	2± 0	1± 1	1± 1	2± 0
Total	41± 1	50± 15	46± 1	56±19
Day 41				
Chironomidae	86±29	118±35	103± 3	110±11
Baetis	8± 4	9± 3	16± 1	4± 1
Tricorythodes	60±51	44±42	52±43	39±25
Other	2± 1	1± 0	2± 1	2± 2
Total	154±77	172±74	172±38	154±17

Table 7. Numbers and biomass of Chironomidae in control, +P, +N, and +NP treatments after 35 and 77 days of enrichment in 1990. Values are means of 2 replicates (±1 SD), * - significantly different from control at $p \leq 0.05$, ** - significantly different from control at $p \leq 0.01$.

	Control	+P	+N	+NP
Number/m^2				
Day 35	34,974± 238	31,757±4312	41,188±2082*	32,558±5080
Day 77	19,509± 438	18,126±2539	24,031± 475**	22,222± 182*
Biomass (g DW/m^2)				
Day 35	8.037±0.055	7.298±0.999	9.465±0.478*	7.482±1.167
Day 77	13.890±0.312	12.906±1.808	17.110±0.338**	15.822±0.130*

Table 8. Numbers and biomass of Chironomidae and Ephemeroptera in control, +P, +N, and +NP treatments after 14 and 41 days of enrichment in 1991. Values are means of 2 replicates (±1 SD).

	Control	+P	+N	+NP
Number/m^2				
Chironomidae				
Day 14	1060 ± 36	1305 ± 383	1202 ± 18	1460 ± 494
Day 41	2210 ± 748	3049 ± 914	2662 ± 73	2842 ± 292
Ephemeroptera				
Day 41	1744 ±1225	1382 ±1005	1744 ±1077	1098 ± 676
Biomass (g DW/m^2)				
Chironomidae				
Day 14	0.178 ± 0.006	0.220 ± 0.064	0.202 ± 0.003	0.246 ± 0.083
Day 41	1.127 ± 0.382	1.555 ± 0.465	1.358 ± 0.038	1.450 ± 0.149
Ephemeroptera				
Day 41	4.378 ± 3.074	3.470 ± 2.522	4.378 ± 2.705	2.756 ± 1.697

Table 9. Mean length and weight of cutthroat trout on Day 77 after 39 days of enrichment in control, +P, +N, and +NP treatments. Values are the means of two channels (±1 SD).

	C	+P	+N	+NP
Length (mm)	44.0±0.1	44.8±1.2	44.8±0.7	43.6±0.3
Length gain (mm)	3.1±0.4	4.1±0.6	3.9±0.3	2.8±0.2
Weight (mg)	660± 18	698± 58	690± 22	636± 16
Weight gain (mg)	148± 32	200± 32	192± 13	150± 11
Net Production (mg/channel)	3500±870	4600±120	4600±280	4160± 10

Figure Legends

Fig. 1. Ambient NH_4^+-N, NO_3^--N, and SRP concentrations in the Clark Fork and control troughs during 13 August-29 October 1990. Ratio of NO_3^--N:SRP is molar and solid line represents 16:1, approximate point of transition from potential N to P limitation.

Fig. 2. Ambient NH_4^+-N, NO_3^--N, and SRP concentrations in the Clark Fork and control troughs during 10 July-20 August 1991. Ratio of NO_3^--N:SRP is molar and solid line represents 16:1, approximate point of transition from potential N to P limitation.

Fig. 3. Benthic chlorophyll a on rocks in control, +P, +N, and +NP treatments during 13 August-29 October 1990. Points are the means of 2 replicate troughs and bars are ±1 SD.

Fig. 4. Benthic chlorophyll a on rocks in control, +P, +N, and +NP treatments during 10 July-20 August 1991. Points are the means of 2 replicate troughs and bars are ±1 SD.

Fig. 5. Benthic chlorophyll a on ceramic tiles in control, +P, +N, and +NP treatments from 2 trials conducted during 20 September-22 October 1990. Points are the means of 2 replicate troughs and bars are ±1 SD.

Fig. 1

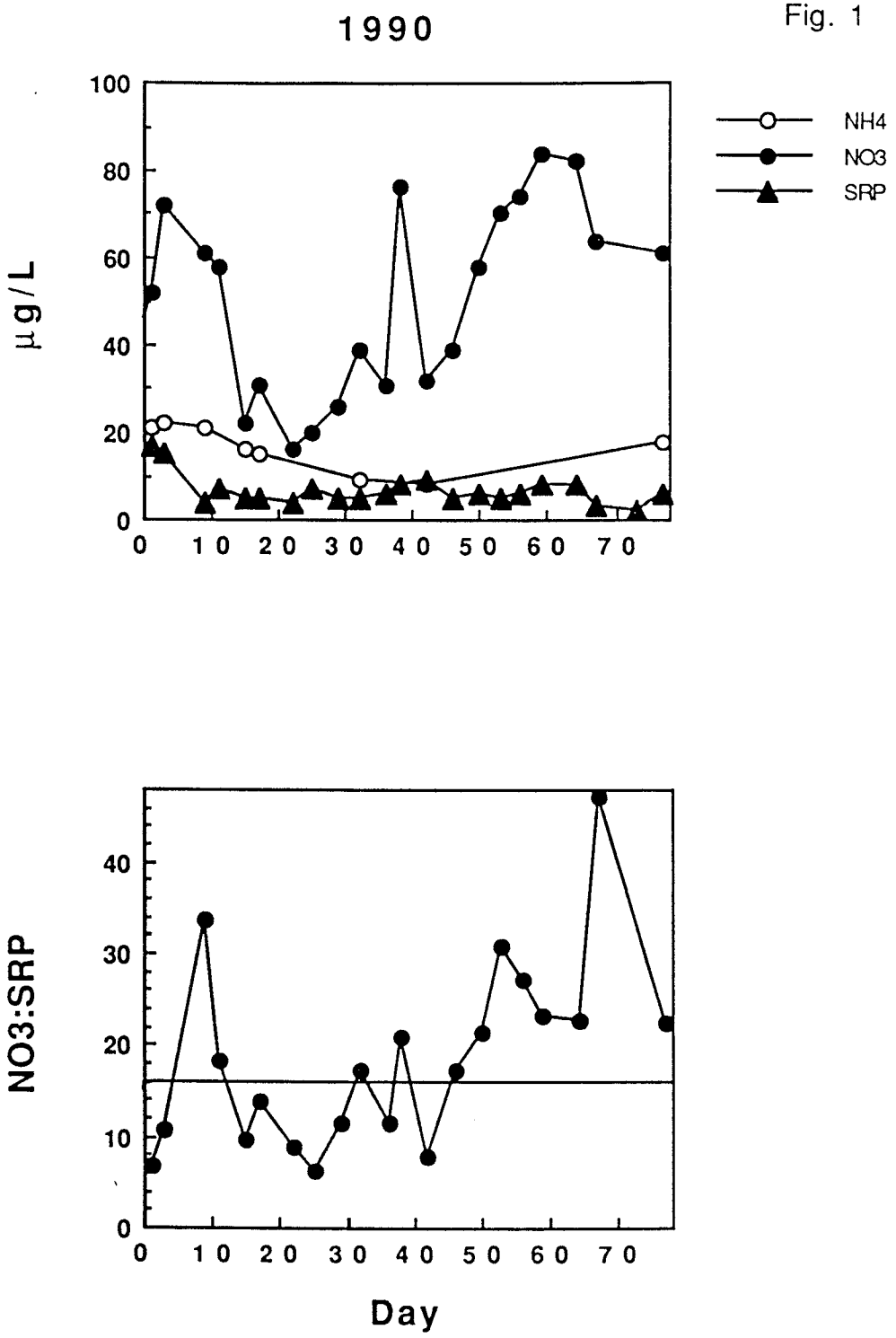

1990
µg/L
100
80
60
40
20
0
0 10 20 30 40 50 60 70
NH4
NO3
SRP
NO3:SRP
40
30
20
10
0
0 10 20 30 40 50 60 70
Day

Fig. 2

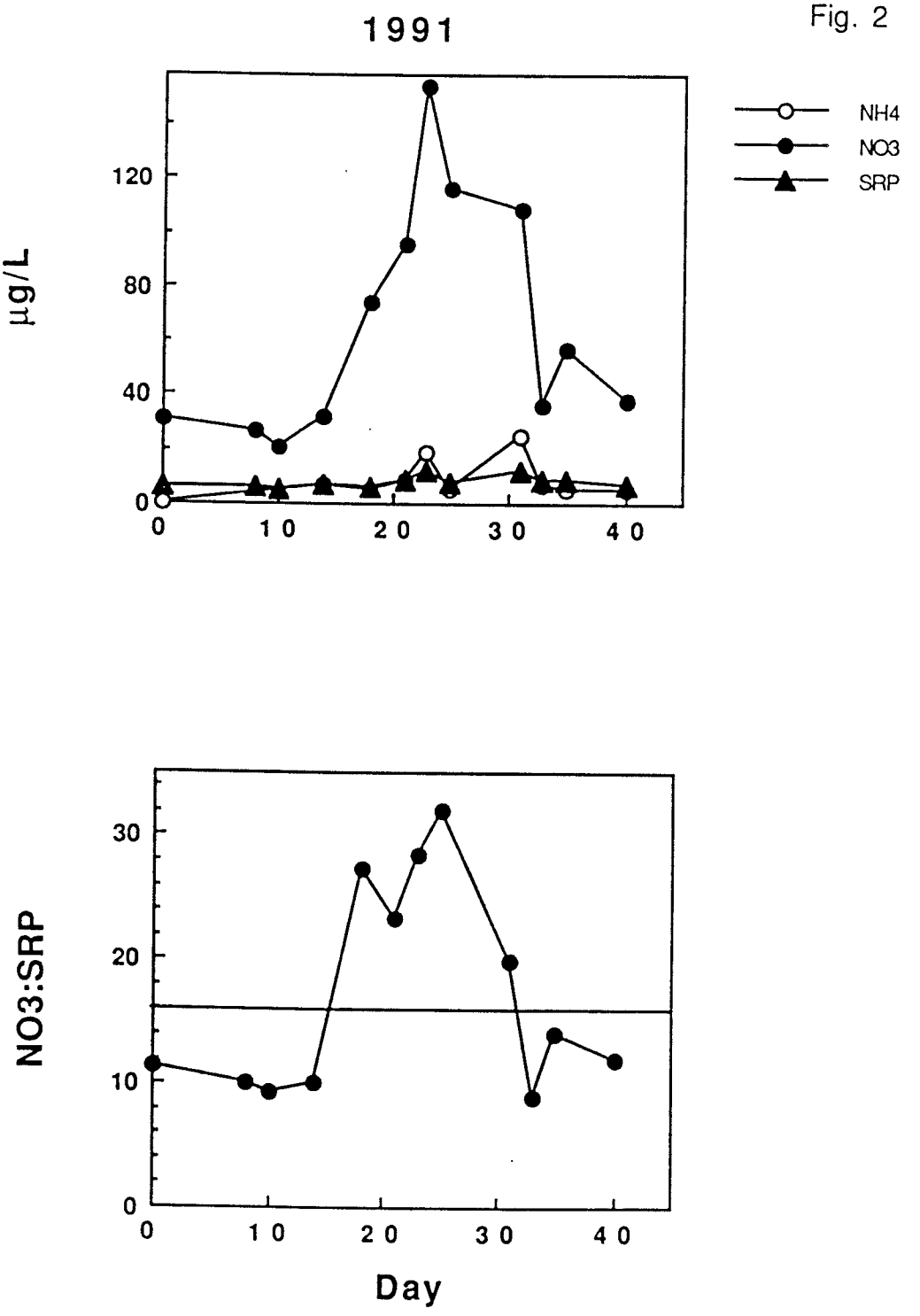
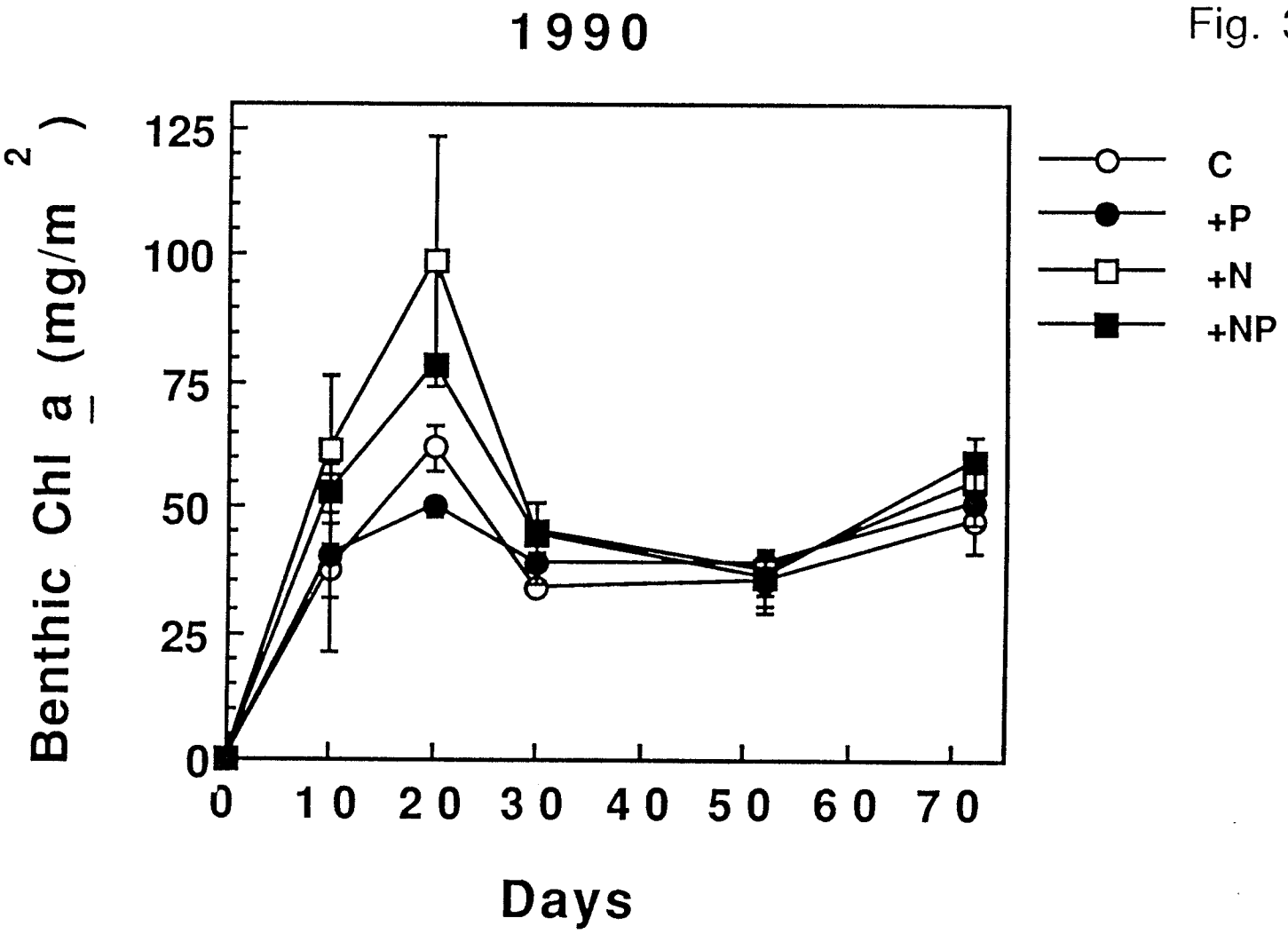

1991
µg/L
120
80
40
0
0
10
20
30
40
NH4
NO3
SRP
NO3:SRP
30
20
10
0
0
10
20
30
40
Day

Fig. 3


1990
Benthic Chl a (mg/m 2)
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100
75
50
25
0
0 10 20 30 40 50 60 70
Days
C
+P
+N
+NP

Fig. 4

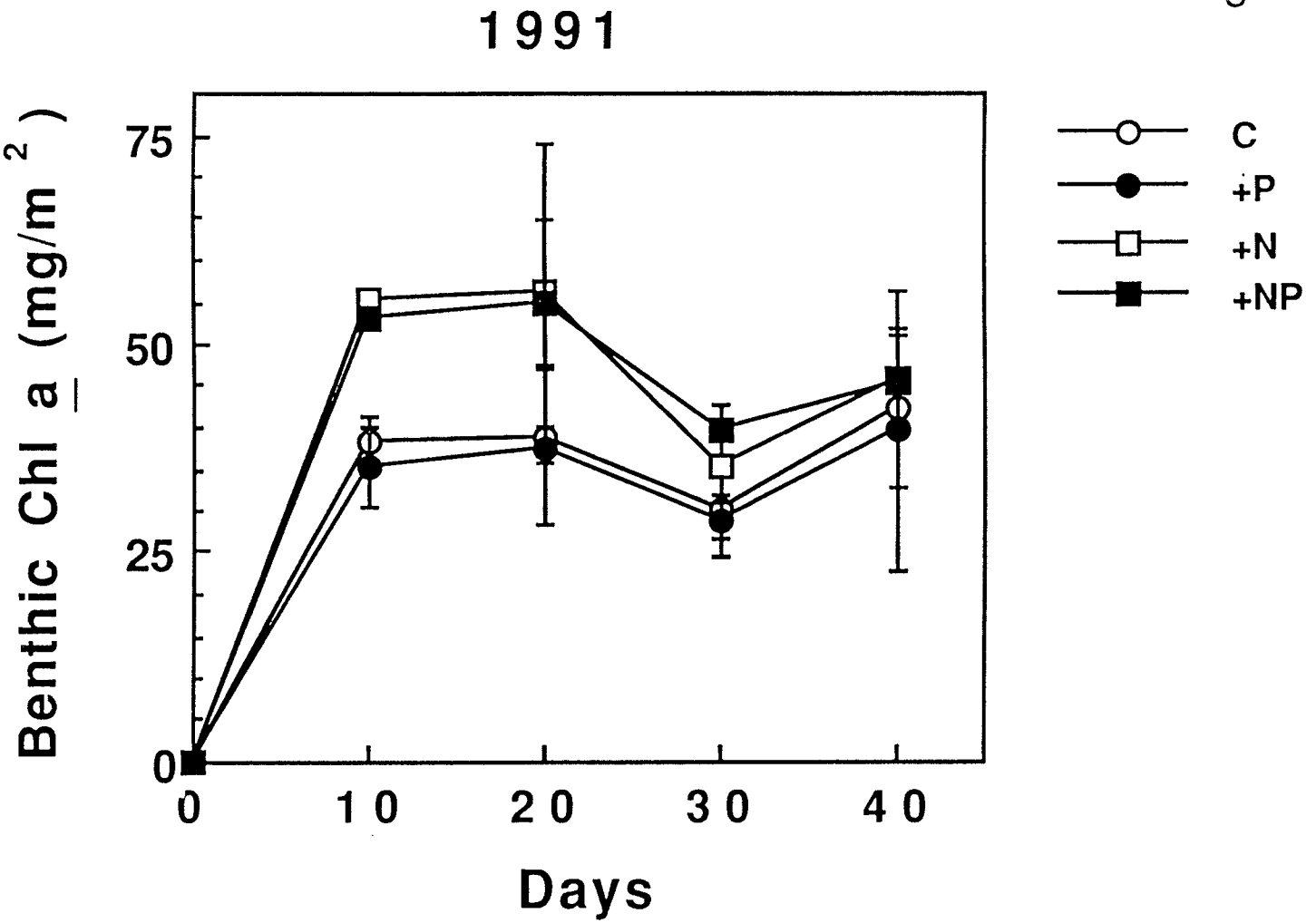
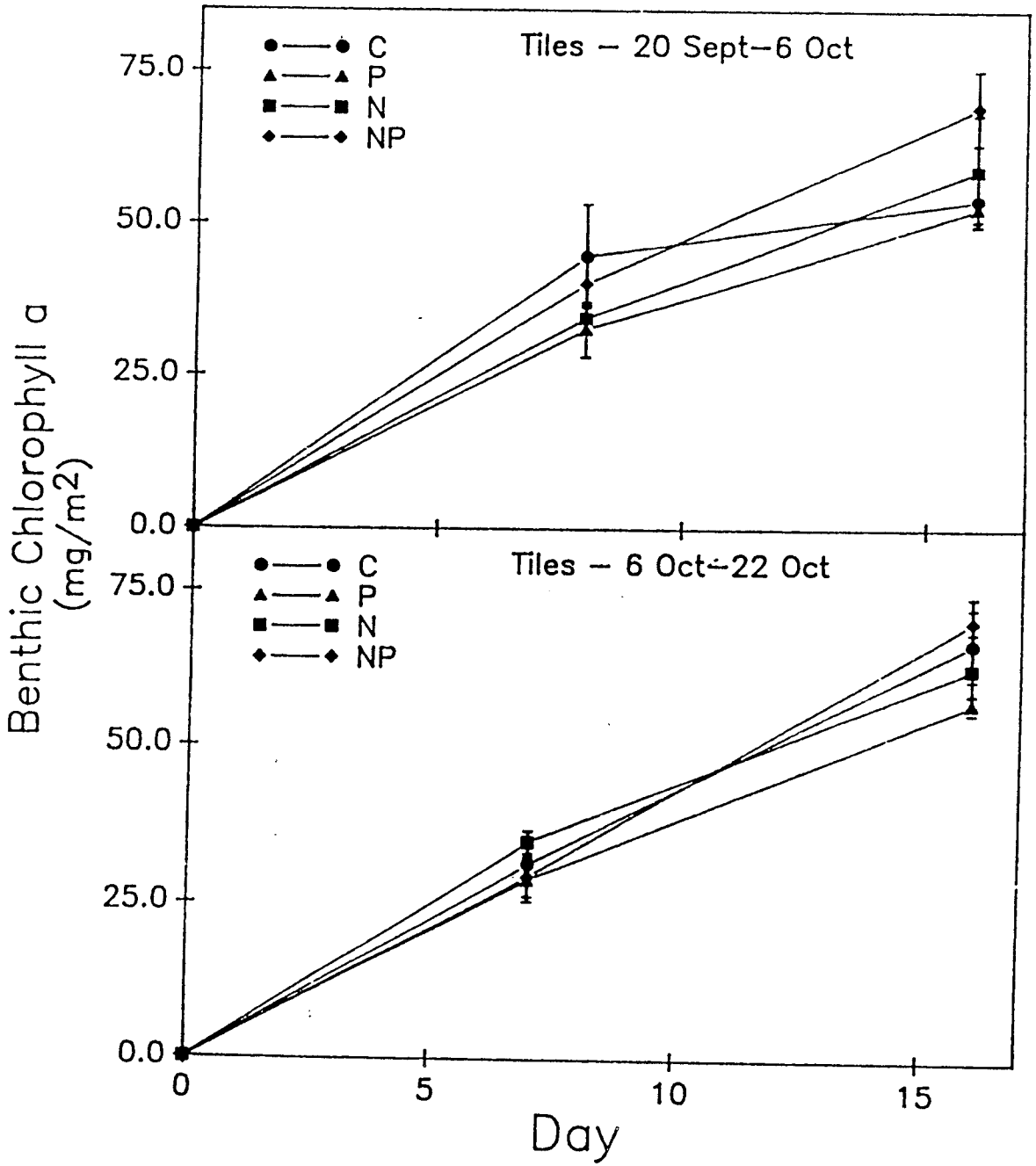


Fig. 5


Tiles – 20 Sept–6 Oct
C
P
N
NP
75.0
50.0
25.0
0.0
Tiles – 6 Oct–22 Oct
C
P
N
NP
75.0
50.0
25.0
0.0
0
5
10
15
Day
Benthic Chlorophyll a
(mg/m2)