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TECHNICAL COMPLETION REPORT

Water Resource Research Center
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ABSTRACT

Laboratory and field experiments and field observations were conducted to assess the role of native anuran larvae in several ecosystem processes associated with water quality. We investigated the impacts of these animals on populations of problem-causing toxic cyanobacteria, on rates of sedimentation and water clearing, on rates of decomposition of sediments, and on export of biomass from aquatic to terrestrial systems. Anuran larvae were killed by intraperitoneal injection of the toxic cyanobacteria Aphanizomenon flos-aquae and Anabaena flos-aquae, but were unaffected by injections of Anacystis aeruginosa. All three species of cyanobacteria were effectively ingested by anuran larvae without ill effects; the filimentous forms were quickly exterminated from experimental chambers. Cyanobacteria were not a good ration for the larvae, as they lost weight rapidly on a diet of pure cyanobacteria. Anuran larvae were extremely effective at removing suspended sediments (tripton) from the water column, increasing light transmission through water much more rapidly than would occur through physical settlement. Sediments processed by anuran larvae and released as feces decomposed much more rapidly than unprocessed sediments. These results suggest that anuran larvae could have major effects on algal blooms, water clarity, and decomposition rates.

Estimates of field densities of several species of anuran larvae suggested that some ephemeral species (Bufo americanus and Rana sylvatica) may be major transporters of nutrients from aquatic to terrestrial systems, but that they do not occur in major bodies of water. The species found in major bodies of water (usually Rana catesbeiana) were extremely variable in density over the four years of the study. Restriction to shallow water along the periphery of the lake, as well as the variability in density, decrease the potential importance of anuran larvae to the studied processes in major bodies of water.

ACKNOWLEDGMENTS

We gratefully acknowledge the assistance and encouragement of Dr. John Sasner, without whose help this study would have been impossible. We also thank his numerous work-study students for assisting with the constant task of initiating and maintaining the cyanobacterial cultures. Ann Cleveland assisted with algal culture and counts in the exploitation experiments. Dr. Phil Sawyer gave us the benefit of his vast knowledge of fish, lakes, and other things.

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INTRODUCTION

To many laymen, the only freshwater organisms of any importance are the fish sought after by recreational anglers. However, evidence is accumulating that despite their recreational and economic value, fish may be relatively minor components of many aquatic ecosystems in terms of their ecological function (cf. Seale, 1980; Efford and Mathias, 1968; Neish, 1971). In these systems amphibian larvae, both anuran and caudate, may actually be more important than fish as regulators of primary and/or secondary production, nutrient movement, and energy flow. This putative importance stems from several attributes of amphibian larvae: their populations can be very large, sometimes comprising major components of the biomass in a system, and they are effective consumers, caudates as predators (Neish, 1971) and anurans as non-selective suspension feeders capable of removing surprisingly small particles from the water column (Wassersug, 1973). Furthermore, the amphibian mode of life, leaving the water for a terrestrial or semi-terrestrial existence, reverses the normal ecological movement of matter from land to water. Given these attributes it is surprising that little attention has been given to amphibian ecosystem function and the role such function might play in factors affecting water quality.

It was the purpose of the research reported here to specifically investigate how anuran larvae might affect aquatic ecosystem processes in New Hampshire lakes, particularly those processes associated with water quality. The research comprised laboratory measurement and experimentation, field experiments, and quantitative and qualitative field observation. It was aimed at investigating the effects of anuran larvae on: 1) population growth and production of problem-causing toxic cyanobacteria (blue-green algae);

2) rates of sedimentation or, equivalently, movement of particulate matter out of the water column; 3) rates of decomposition of organic particulate matter; 4) movement of biomass from aquatic to terrestrial systems. In order to evaluate these functions it was also necessary to quantify the behavioral and population biology of the anurans of New Hampshire. The work done actually falls into three distinct classes: work with cyanobacteria; work with sedimentation and decomposition; and work with population abundance, habitat selection, and individual growth. This report is divided according to these three classes, with each class presented separately with its own statement of the problem, methods, and results and discussion. A fourth section comprises the conclusions.

Study Areas

Observations were carried out on many lakes and ponds in New Hampshire, but the major emphasis was on three: Kingman pond, a small farm pond on the agricultural unit of the University of New Hampshire located in Durham; Barbados pond, on the Madbury-Dover border; and Stonehouse pond, in Barrington. Kingman pond is shallow (<3 m), turbid, eutrophic, inhabited by brown bullhead (*Ictalurus nebulosus*), and typical of many farm ponds throughout New Hampshire. Barbados pond is deep (> 13 m), stocked with trout (*Salvelinus fontinalis*) but also inhabited by bullheads, and typical of recreational ponds in the state. Stonehouse pond is also a recreational pond stocked with trout, but somewhat more remote than Barbados.

We also made visits to lakes known to be having trouble with water quality, specifically Kezar lake in North Sutton, and Marsh pond in Alton. Kezar Lake is notorious for its algal blooms and fish kills.

In order to collect anuran larvae of different species we regularly investigated several bodies of water which, for various reasons, were not amenable to direct study. The most important of these ponds was a pond on Adam's Point road and a pond near Foss Farm road, both in Durham, where we studied Rana sylvatica and Hyla chrysocelis; and Turtle pond in Lee, where we studied Rana clamitans.

EFFECTS OF ANURAN LARVAE ON TOXIC CYANOBACTERIA

Some New Hampshire lakes have been afflicted with explosive blooms of blue-green algae. These blooms are often accompanied by massive die-offs of fish, mussels, and other invertebrates (Frost et al., 1972,1973). Some of the cyanobacteria involved can, on occasion, produce toxins that are poisonous to vertebrates; fatalities of livestock, wild animals, and people have been associated with blue-green algal blooms in the northern USA, Texas, Canada, and other countries (Siegmund, 1973). Control of these blooms is as yet an unobtained objective. However, given the ability of anuran larvae to ingest small particulate matter including cyanobacteria (Wassersug, 1972; Gradwell, 1975; Seale and Beckvar, 1979; Seale and Wassersug, 1980) it is possible that they might have potential for use as biological control agents for these toxic cyanobacteria. We therefore initiated an investigation of the ability of anuran larvae to exploit toxic cyanobacteria. This investigation sought to answer three basic questions: 1) Are toxic cyanobacteria toxic to anuran larvae? 2) Can anuran larvae impact on toxic cyanobacterial populations? 3) Do anuran larvae impact on cyanobacterial populations in the field?

We used three species of cyanobacteria known to be capable of toxicity: Anabaena flos-aquae, Anacystis (Microcystis) aeruginosa, and Aphanizomenon flos-aquae. Anabaena and Aphanizomenon are filimentous forms, with many cells joined end to end to form linear trichomes. Each trichome may be 150 µm or more in length. Anabaena flos-aquae is dimorphic: most cells are cylindrical but occasional cells called heterocysts are more rounded. It is thought that the heterocysts are reponsible for nitrogen fixation, as this genus has that rare capability. Individual Anacystis aeruginosa cells are spherical, each approximately 3 µm in diameter. This species may or may not

form loose colonies of approximately 25 cells. These three species give a range of possible interactions with their consumers: they vary in their modes of toxicity (J. Sasner, personal communication), and represent two distinct sizes and morphologies.

Methods and Materials

We used larvae of three species of anuran: Rana catesbeiana larvae were collected from Barbados and Stonehouse ponds; Rana clamitans larvae were collected from Turtle pond in Durham, or were purchased from Connecticut Valley Biological Supply; Bufo americanus was collected from Kingman pond.

All three algal species were cultured in ASM-1 medium (Carmichael, 1973), with the assistance of Dr. John J. Sasner, a physiologist working with the mechanisms of toxicity associated with the algae. The stock for each experiment was initiated from Dr. Sasner's stock cultures, which are carefully maintained under conditions required to keep the algae in toxic modes. Toxicities of stock cultures were regularly assayed by injecting white mice intraperitoneally with 0.1 cc of centrifuged alga; the culture was considered toxic if the mouse died within one hour after injection (T. Foxhall, personal communication). All such mice died within one hour of injection.

Three techniques of quantifying algal density were evaluated: hemacytometer counts, chlorophyll assays, and counts with an automatic Coulter cell counter. Though Seale and Wassersug (1979) and Seale and Beckvar (1980) reported good results using a model B Coulter counter, we terminated efforts to utilize the model A available to us after over four months of inability to substantiate precision and replicability of automated

counts. We also were unable to find consistent agreement between automated counts and direct counts of cell density with the hemacytometer. Chlorophyll assays (American Public Health Association, 1976) were reasonably good predictors of cell density counted on the hemacytometer, using linear interpolation (fig. 1). However, after using this technique in several experiments, and assaying a number of field samples with it, we decided that the technique just wasn't accurate enough: the residual variance in the technique (over 18% of total) might obscure real differences between treatments. (Compare figures 2 and 3 in the results.) We were thus left with no better technique than direct counts of cell densities using the hemacytometer. While accurate, direct counts were tedious and time consuming.

Hemacytometer counts were done in the following way: a drop of sample solution was pipeted onto the hemacytometer and a cover slip put in place. The number of individual algal units (cells or trichomes) on each of ten 0.1 mm grids was ascertained under 400X magnification. If the sample was excessively dense it was diluted serially until the number per grid was less than 100; the counts were then divided by the dilution factor to give standardized relative densities. In the case of the two filimentous species the number of cells per trichome was also counted on at least ten randomly chosen trichomes.

Toxicity of toxic cyanobacteria to anuran larvae was evaluated in two ways: by feeding it to the anuran larvae in exploitation experiments (see below), and by intraperitoneal injection of algal extract at doses similar to those inducing death in laboratory mice. We injected Rana catesbeiana larvae, ranging in weight from 6.5 g to 22.4 g, with hydrolysed Anacystis aeruginosa reconstituted in water to 1 µg dry weight/ml; five received 0.5

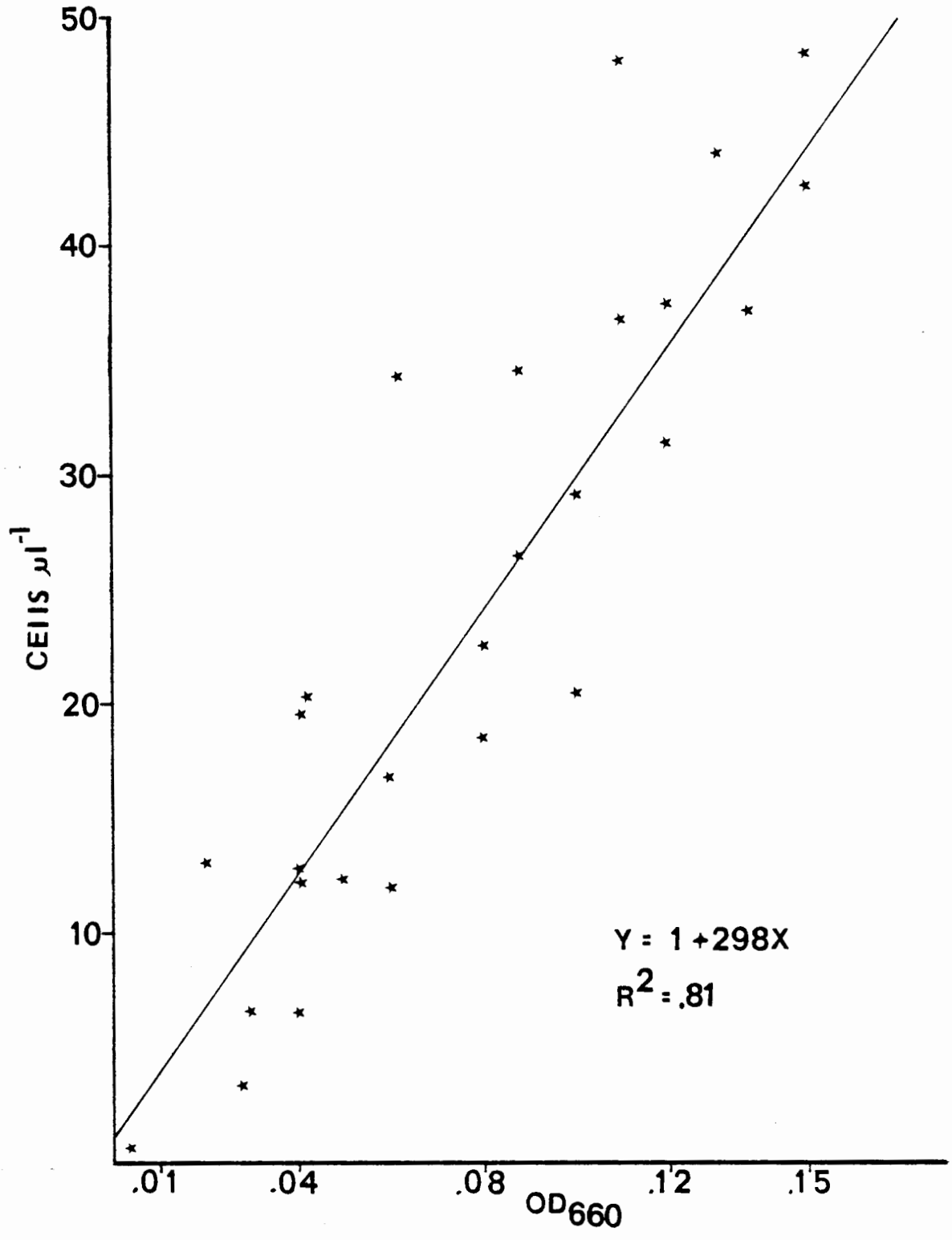

FIGURE 1. Relationship between optical density of chlorophyll extracts and number of cells of Anacystis aeruginosa counted in a hemacytometer. Spectrophotometer set at 660 nm.

ml and 5 received 1.0 ml. This Anacystis had been grown in the laboratory by Dr. Sasner. We also injected Rana catesbeiana larvae, ranging in weight from 13.5 g to 16.9 g, with serial dilutions of hydrolysed Aphanizomenon flos-aquae collected from Kezar Lake, NH, by Dr. Sasner. At the time of each set of injections three laboratory mice (weight ca. 20 g each) were also injected with similar concentrations of the algae.

The first series of exploitation experiments was done using 1000 ml beakers fitted with hardware cloth false bottoms (to prevent anuran larvae from ingesting feces). Eight or twelve beakers received 800 ml of algal culture. Four or six anuran larvae were weighed, then each was assigned to a beaker using a random numbers table. The beakers that did not receive anuran larvae constituted the control. Algal densities in all beakers were ascertained once daily for the duration of the experiment, five to ten days. The anuran larvae were weighed again at the termination of the experiment. This type of experiment was conducted on all three algal species using Rana catesbeiana larvae; on Aphanizomenon flos-aquae using Rana clamitans larvae, and on Anacystis aeruginosa using Bufo americanus larvae. In addition mixed cultures (1:1) of Anacystis aeruginosa and Anabaena flos-aquae, and of Anabaena and Aphanazomenon were used in experiments with Rana catesbeiana larvae. All of the experiments utilizing Rana catesbeiana larvae were replicated at least twice.

To ascertain the status of algae ingested by anuran larvae, some of the animals were placed in dechlorinated tap water in false-bottomed beakers, after weighing at the termination of an experiment. Defecated material was collected and carefully cultured in ASM-1 medium as if it were the stock for initiation of a new culture.

A second series of experiments used six 60 l aquaria also fitted with hardware cloth false bottoms. One l of a dense culture of Anacystis aeruginosa was added to each along with 43 l of dechlorinated tap water. Three aquaria each received ten Rana catesbeiana larvae that had been individually weighed; the other three aquaria served as controls. Algal densities were ascertained daily for five days. This experiment was replicated twice.

We attempted a field experiment: the north end of a pond on Kingman agricultural farm was sealed off with a fence constructed of 1 x 3 pine strapping and 4 mil polyethylene sheeting. The polyethylene was anchored to the pond bottom with rocks and continued as a barrier fence on to land, completely encircling the shore line of the sealed-off area. During construction all anuran larvae fled the area, as underwater searches revealed no anuran larvae within the sealed area, although a few brown bullheads were present. Substantial numbers of Rana larvae were present in the rest of the pond. Algal densities were ascertained regularly from samples taken from both sides of the fence.

We investigated anuran populations at several New Hampshire lakes, those at which anuran die-offs were reported, and some of those at which toxic cyanobacteria were known to occur.

Results and Discussion

All three 20 g mice injected with Anacystis aeruginosa died within 15 minutes. Though several were much smaller than the mice, all of the anuran larvae so injected were still alive one week later, with no sign of ill effects. Anuran larvae are apparently much less susceptible to Anacystis toxins than are mice.

All three 20 g mice injected with Aphanizomenon flos-aquae died within 15 minutes; all of the anuran larvae died quickly also (table 1). One anuran larva managed to last 17 minutes before succumbing but it was given a somewhat smaller dosage than that given the mice. If time to death is the criterion anuran larvae and mice are approximately equally susceptible to injected Aphanizomenon toxin. As might be suspected, response to the toxin appears to be dose dependent.

Anuran larvae could ingest all three species of toxic cyanobacteria, apparently without harm: the majority of the exploitation experiments were carried to completion without loss of any of the animals. However, we must equivocate somewhat on this conclusion, since almost a third of the experiments did result in a significant number of deaths of larvae before the end of the experiment. What killed these larvae? Post mortem dissection revealed no gross pathological conditions, but many of the larvae did have branchial chambers completely stuffed with algae. This, along with the fact that many larvae did survive suggests that the dead animals may have suffocated. They may just have been unable to clear their branchial chambers when exposed to high concentrations of algae.

Figures 2 and 3 illustrate the results of two typical small container exploitation experiments involving Anacystis aeruginosa, and figure 4 illustrates the results of a typical experiment involving Aphanizomenon flos-aquae or Anabaena flos-aquae. The results of the small container experiments that were carried to termination without larval mortality are summarized in table 2. All densities of algae in beakers containing anuran larvae were significantly less than those in equivalent controls. Anuran larvae are effective exploiters of toxic cyanobacteria, in that they can significantly reduce populations of cyanobacteria. This was true of all

TABLE 1. Dose-response of *Rana catesbeiana* larvae injected with *Aphanizomenon flos-aquae*.

Weight (g)	Dose (mg)	Time to Death (min)
16.2	7.0	2.5
16.2		2.9
15.5	5.0	3.5
16.9		3.6
13.5	2.5	4.2
18.4		5.5
15.5	1.25	11.6
16.7		17.0
16.4	0.625	13.6
15.8		9.3

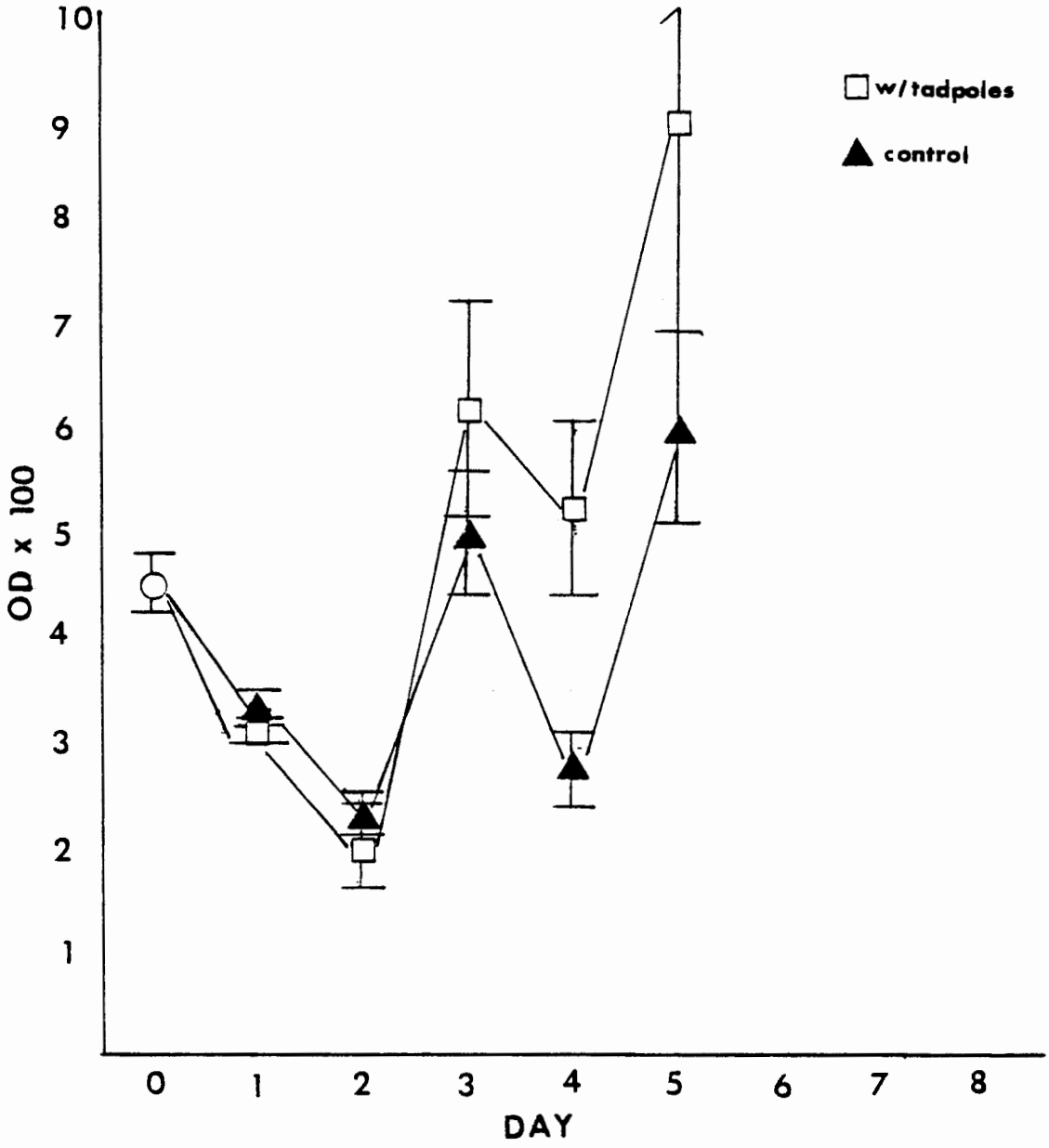

FIGURE 2. Relative abundance of Anacystis aeruginosa in beakers with and without Rana catesbeiana larvae, as measured by chlorophyll assay. Vertical bars represent two standard errors on each side of the mean.

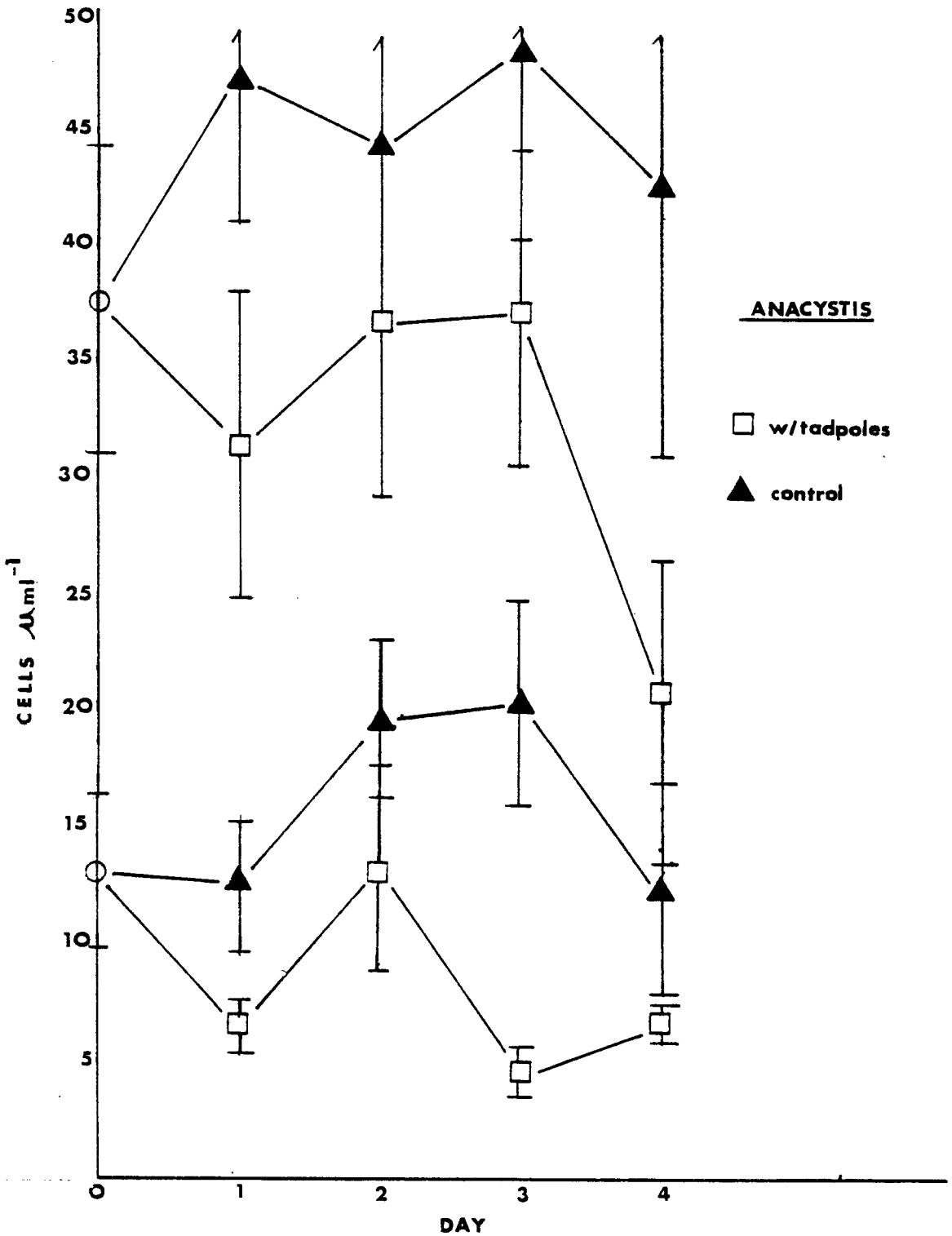

FIGURE 3. Results of two experiments measuring exploitation of Anacystis aeruginosa by Rana catesbeiana larvae.

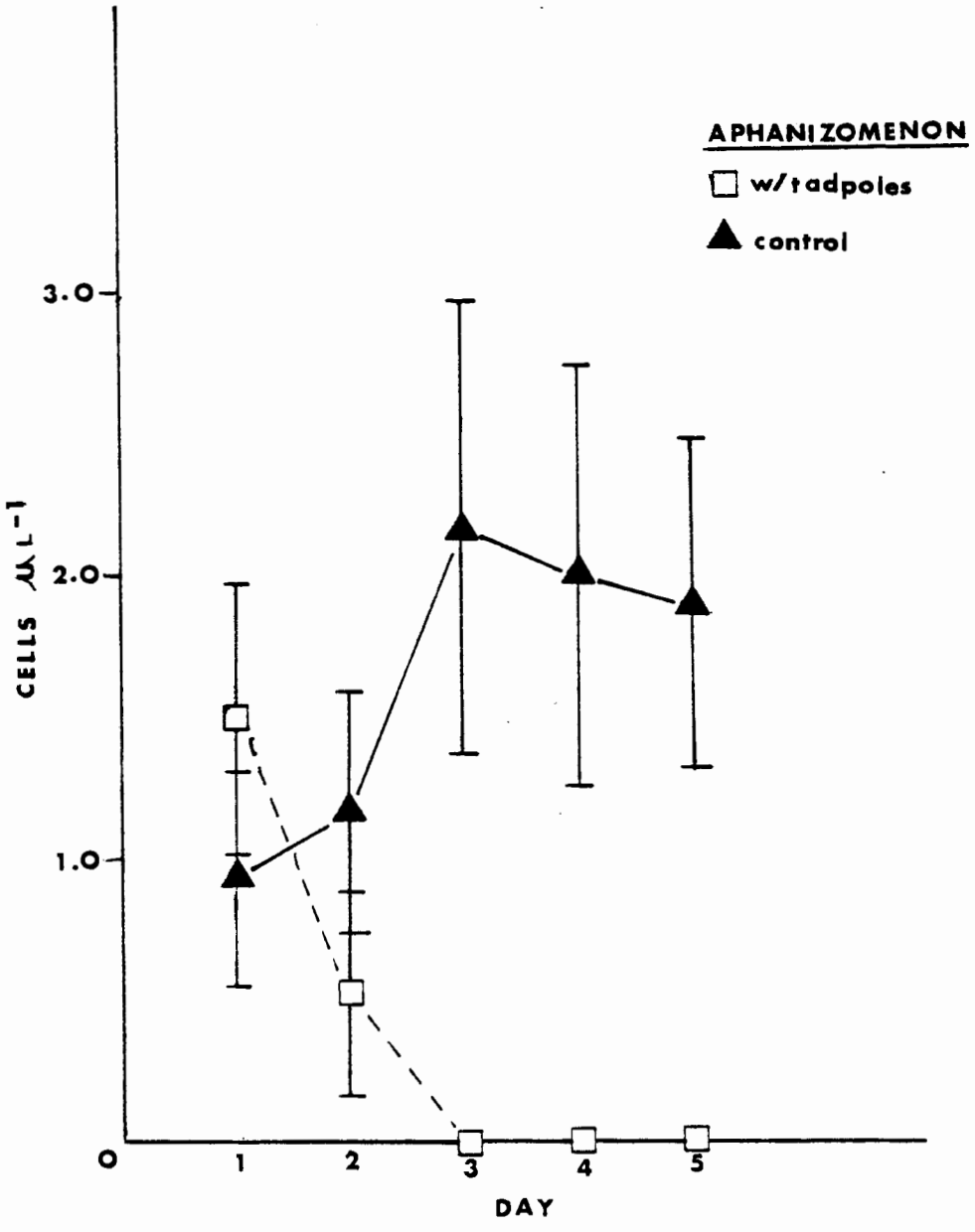

FIGURE 4. Results of a typical experiment measuring exploitation of Aphanizomenon flos-aquae by Rana catesbeiana larvae.

TABLE 2. Summary of experiments evaluating exploitation of toxic cyanobacteria by anuran larvae. Values are means, standard errors are in parenthesis.

	Weight (g)			Relative Algal Density		
Anuran Species	Start	End	Algal Species	Start	End	
					Control	Exp.
R. catesbeiana	4.7(1.2)	4.1(1.3)	Anacystis	13.0(1.6)	12.3(1.6)	6.5(0.4)*
R. catesbeiana	4.3(0.1)	4.1(0.0)	Anacystis	16.8(1.1)	26.4(2.4)	5.0(0.7)*
R. catesbeiana	3.8(0.8)	3.4(0.7)	Anacystis	37.5(2.3)	42.6(4.2)	20.4(2.1)*
R. clamitans	1.8(0.4)	1.5(0.2)	Aphanizomenon	86.8(3.6)	288.3(13.6)	0.1*
R. catesbeiana	13.1(0.4)	11.0(0.9)	Aphanizomenon	2.8(0.4)	13.7(1.7)	0.0*
R. catesbeiana	10.5(0.4)	--	Aphanizomenon	4.5(1.0)	7.7(0.4)	2.3(0.7)*
R. catesbeiana	10.3(1.6)	12.1(1.8)	Anabaena	1.5(0.2)	2.2(0.4)	0.0*
Bufo americanus	0.22(0.02)	0.16	Anabaena	66.8(2.1)	82.5(5.5)	2.1(0.5)*

* Significantly different from control, $p < .01$, unpaired t-test.

three anuran species tested, even for the tiny Bufo larvae. Note that figures 2 and 3 demonstrate the fact that chlorophyll assays gave much less obvious results than did those in which direct hemacytometer counts were made.

Not only could anuran larvae consume toxic cyanobacteria, but processing of the algae by the larval digestive tract killed the algae: no cyanobacteria (or eucaryotic algae) could be cultured from larval feces, using the same techniques that resulted in rapid algal population growth when the innoculum had not been digested by larvae.

There were differences between cyanobacteria in their exploitability: the long filiments of Aphanizomenon flos-aquae and Anabaena flos-aquae totally disappeared from most experimental chambers, while the smaller spheres of Anacystis aeruginosa were never totally exterminated. This was probably merely a result of mechanical efficiency in that some Anacystis were small enough to elude the branchial filtering apparatus of the larvae. This is confirmed by the mixed culture experiment (table 3), as Anabaena disappeared from mixed culture much more rapidly than did Anacystis. Rana catesbeiana larvae did not discriminate between the two filimentous forms, as their relative abundances at the end of the experiment mirrored their relative abundances at the beginning.

There was a physical reduction in trichome length when the filimentous forms were exposed to anuran larvae (table 4). Before extermination the average number of cells per trichome was much reduced in the experimental chambers. This suggests a certain degree of breakage of the trichomes by the larvae. However, the reduction in trichome length was still not sufficient to permit avoidance of consumption, since these forms ultimately disappeared totally from other experiments.

TABLE 3. Exploitation of mixed cultures of toxic cyano bacteria by Rana catesbeiana larvae.

	Starting Densities ul^{-1}		End Densities ul^{-1}	
a)	Aphanizomenon	Anabaena	Aphanizomenon	Anabaena
	9.4 ± 1.0	9.9 ± 1.1	4.5 ± 0.5*	7.5 ± 1.2*
b)	Anacystis	Anabaena	Anacystis	Anabaena
	21.6 ± 3.2	19.0 ± 3.8	6.0 ± 0.9	0.3 ± 0.1*

* Trichomes much fragmented

TABLE 4. Effects of anuran larval grazing on trichome length.

		Cells/trichome			
		Control		Experimental	
Anuran	Alga	Start	End	Start	End
R. catesbeiana	Aphanizomenon	38.1 ± 3.8	33.0 ± 4.0	29.5 ± 4.2	11.3 ± 2.9
B. americanus	Anabaena	21.2 ± 7.0	24.2 ± 6.8	27.9 ± 5.8	8.0 ± 3.9

The large aquarium exploitation experiments were plagued with mortality of the experimental animals (eight of twenty), so the results are somewhat hazy. There were slight, but nonsignificant reductions in algal densities in the experimental aquaria compared to those in the controls. These results are consistent with those of the beaker experiments, and suggest that anuran larvae might impact cyanobacterial populations at biomass densities less than those used in the beaker experiments.

One point that emerges from these experiments is that cyanobacteria are not a good ration for anuran larvae, a point inconsistent with the observations of Seale and Beckvar (1980). Virtually all individual larvae lost weight quite rapidly (cf. table 2) when given nothing to eat except cyanobacteria, suggesting that a complete diet for anuran larvae must include something more. There is some question concerning the degree to which anuran larvae can extract nutrients from cyanobacteria, especially as they often leave the cell wall intact (K. Hoff, personal communication; C. R. Shoop, personal communication).

The field experiment yielded possibly flawed results. Despite efforts to make the field enclosure anuran proof, the sealed area was invaded by hordes of Bufo larvae; either they or their parents penetrated the barrier. Although these eventually disappeared from the water, there was no difference between the enclosed and open areas in algal density at any time. We could not quantify the densities of Rana larvae in this pond, due to extreme turbidity.

Field observations bearing on the interactions of cyanobacteria and anurans were made at Kezar Lake, a farm pond in Durham, and a farm pond in North Sandwich. In a number of visits we never observed a single anuran, larval or metamorphosed, at Kezar Lake. However, K. Auger (personal

communication) reported seeing a number of dead anurans at this lake during an Anacystis aeruginosa bloom in early July, 1982. In August, 1980, we investigated an algal bloom at Moore's pond in Durham. The algae were subsequently found to be toxic Aphanizomenon flos-aquae. The bloom was accompanied by a massive die-off of pre-metamorphic and early metamorphic Rana catesbeiana larvae (Gosner (1960) stages 25-41: all stages with suspension feeding mode); late metamorphic and fully transformed individuals and adults (Gosner stages 42-46: adult mouth forming or formed and loss of suspension feeding mode) were apparently unaffected. Those larvae that we dissected had their branchial chambers stuffed with filimentous algae. The deaths of these larvae could have resulted from:1) ingestion of toxic algae, in contrast to the larvae's ability to safely ingest it in the laboratory; 2) suffocation due to congestion of the gills in the branchial chambers; 3) anoxia: oxygen concentration in the pond was between 0 and 2 mg/ml during my visits. The details of this die-off are similar to those of two other die-offs in New Hampshire reported to me, but that we were was unable to immediately investigate. These die-offs do suggest that anuran larvae in the field are susceptible either to cyanobacterial toxins, or to the conditions that obtain during cyanobacterial outbreaks. A third die-off, of adult Rana sylvatica in a pond in North Sandwich in April, 1980, did not yield any evidence of interaction with cyanobacteria; the presence of large amounts of decomposing eucaryotic algae and large numbers of phantom midge larvae (Chaoborus) suggested anoxia during aquatic hibernation as an associated factor.

These field observations do suggest the possibility that toxic cyanobacteria may be hazardous to anuran larvae. However, we prefer to emphasize the direct evidence from the exploitation experiments, in which

all three species of toxic cyanobacteria were ingested safely at rather high density. In the case of Anacystis aeruginosa the intraperitoneal injections also suggest lessened susceptibility to cyanobacteria.

EFFECTS OF ANURAN LARVAE ON SEDIMENTATION AND DECOMPOSITION

Seale (1980) and her coworkers (Seale, Rogers, and Borass, 1975; Seale and Wassersug, 1979; Seale and Beckvar, 1980) have demonstrated that anuran larvae may be major determinants of aquatic ecosystem function by virtue of their ability to remove suspended matter from the water column. As relatively indiscriminate suspension feeders (Seale and Beckvar, 1980; but see Hoff, 1981) anuran larvae ingest tripton, the nonliving component of the seston, as well as phytoplankton. If ingested tripton is removed from the water column, rather than resuspended, then suspension feeding by anuran larvae may affect water turbidity and light transmittance, i.e., the compensation point. A change in the compensation point would change the volume of water supporting primary productivity, and therefore affect net primary production itself. Furthermore, the ingested tripton may be changed quantitatively and qualitatively as it passes through the gut, which could affect the rate at which the material falls from the water column as well as its decomposition rate. We here report on experiments designed to ascertain the effects of anuran larvae on: 1) light transmittance through the water column, 2) rate of sedimentation, and 3) rate of decomposition of sediments.

Methods

Rana catesbeiana larvae, all in stage 25 of Gosner (1960), were not fed during the week prior to their use in an experiment. Thirty six hours before an experiment began the animals were placed in dechlorinated tap water in aquaria with 6 mm mesh hardware cloth false bottoms. This procedure allowed much of the gut contents to be evacuated; false bottoms prevented reingestion of feces.

To investigate effects on light transmittance pond sediments were resuspended in tap water in a 92 l garbage can. The sediments were allowed to settle for 36 hours, and the resultant "soup" was decanted into 1000 ml beakers fitted with hardware cloth false bottoms. Anuran larvae of approximately the same weight were randomly assigned to half of the beakers; the other beakers were left as controls. We transferred 10 ml water from each beaker to a 19 mm diameter spectrophotometer tube and measured percent transmittance at 750 nm wavelength on a Bausch and Lomb Spectronic 20 spectrophotometer. This assay was repeated once or twice each day for four to six days. The experiment was replicated six times using anuran larvae of different weights; in two of the experiments there was mortality of some of the experimental animals.

To measure concommitant accumulation of sediments with time, the experiment outlined above was repeated using Imhoff cones (three experimental, three control), also fitted with hardware cloth false bottoms. This experiment was replicated three times.

To determine the degree to which anuran larvae would pass sediments through their digestive tract, 10 R. catesbeiana larvae were placed in individual false-bottomed beakers of tap water for 7 days. They were then weighed and immersed individually in beakers of sediment "soup" for 24 hours, after which they were again weighed, and returned to tap water for three days. Material defecated was dried and weighed, and this weight compared to the final weight of the larvae.

To determine possible contribution of anuran larval feces to sediments, 37 R. catesbeiana larvae were brought into the laboratory from Stonehouse pond, weighed, and placed in false-bottomed beakers of tap water. After three days their feces were dried and weighed.

To measure possible larger scale effects we mixed 1 l pond sediment into 43 l tap water in each of six 60 l aquaria. Three aquaria were chosen as controls with a random numbers table; the other three aquaria each received ten Rana clamitans larvae in stage 25 of Gosner, matched to provide a total weight of 40 ± 1 g. At one end of each aquarium we centered a 26 X 10 mm rectangle of white styrofoam, with a 60 w incandescent light bulb 20 mm directly above it. Each aquarium was regularly checked to determine if the target could be seen from the opposite end when the eyes were directly level with it and the nose was pressed to the glass. The total light path was the length of the aquarium, 60.6 cm. The experimental metric was time required for the target to become visible. At the end of the experiment the liquid was filtered and the accumulated sediments dried and weighed. We replicated this experiment twice.

Neither technique used to assay light transmittance through the water column constitutes nephelometry. However, both give relative measures of light transmittance through water, and conversely, the relative amount of interference due to tripton in the water column. The measure of time for a target to become visible is an analog of Jackson turbidimetry, with a standard target with standard illumination. Rather than varying the length of the light path, however, we used a standard light path and allowed time to vary. The colorimetric technique does not measure light scattered at 90^{o}, as required for nephelometry, but does directly measure light transmitted.

To ascertain effects on decomposition of tripton processed by anuran larvae 5.0 ml of sediment was removed from each of eight beakers (four experimental, four control) at the end of a transmittance experiment. Samples from experimental beakers were collected so as to contain tadpole

fecal pellets. Oxygen consumed by these sediments was measured in a Gilson microrespirometer. During the respirometry the measurement chambers were subjected to light so that any photosynthetic organisms present would not contribute to oxygen consumption; the measurements may therefore underrepresent actual oxygen consumption if photosynthetic organisms were present.

All experiments were conducted at ambient room temperature, 21 $\pm$ 2° C, with one accidental exception: a window was left open and temperature fell below 15° C one night during a transmittance experiment.

Results and Discussion

Changes in light transmittance through water containing resuspended sediments are illustrated in figures 5-8. Water in beakers containing anuran larvae consistently transmitted more light than did water in control beakers, at least up to the time at which transmittance in the control beakers approached 80%. The anomalous behavior of the controls in fig 6 is related to a drop in temperature below 15° C during the first night of the experiment, with subsequent warming; the cooling did not affect the experimental animals's filtration. To test for significance of the different rates of change we performed analyses of covariance on log-log transformed data (table 5), omitting observations after 96 hours when transmittances in control and experimental beakers converged. Residual mean squares of transformed control and experimental observations were homogeneous. Time and treatment effects accounted for most of the variances in transmittance. However, treatment effects were significant only with larger anuran larvae. The small anuran larvae had an insignificant effect (fig 7) possibly complicated by some behavior that retarded rate of change in light transmittance (fig 8).

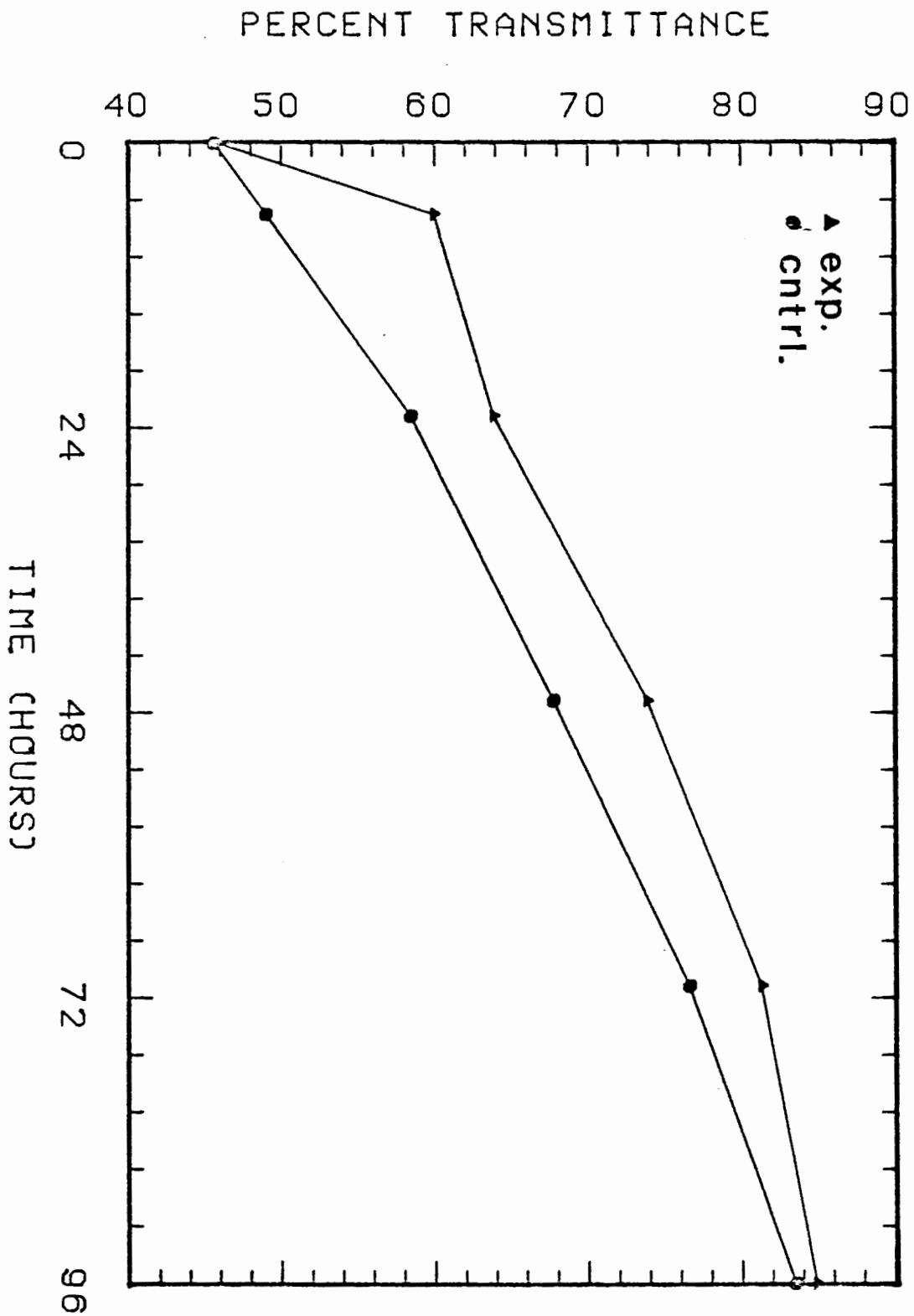

FIGURE 5. Increase in transmission of light through water containing suspended sediments. Animals in experimental beakers were large Rana catesbeiana larvae, average weight 14.4 ± 0.8 g.

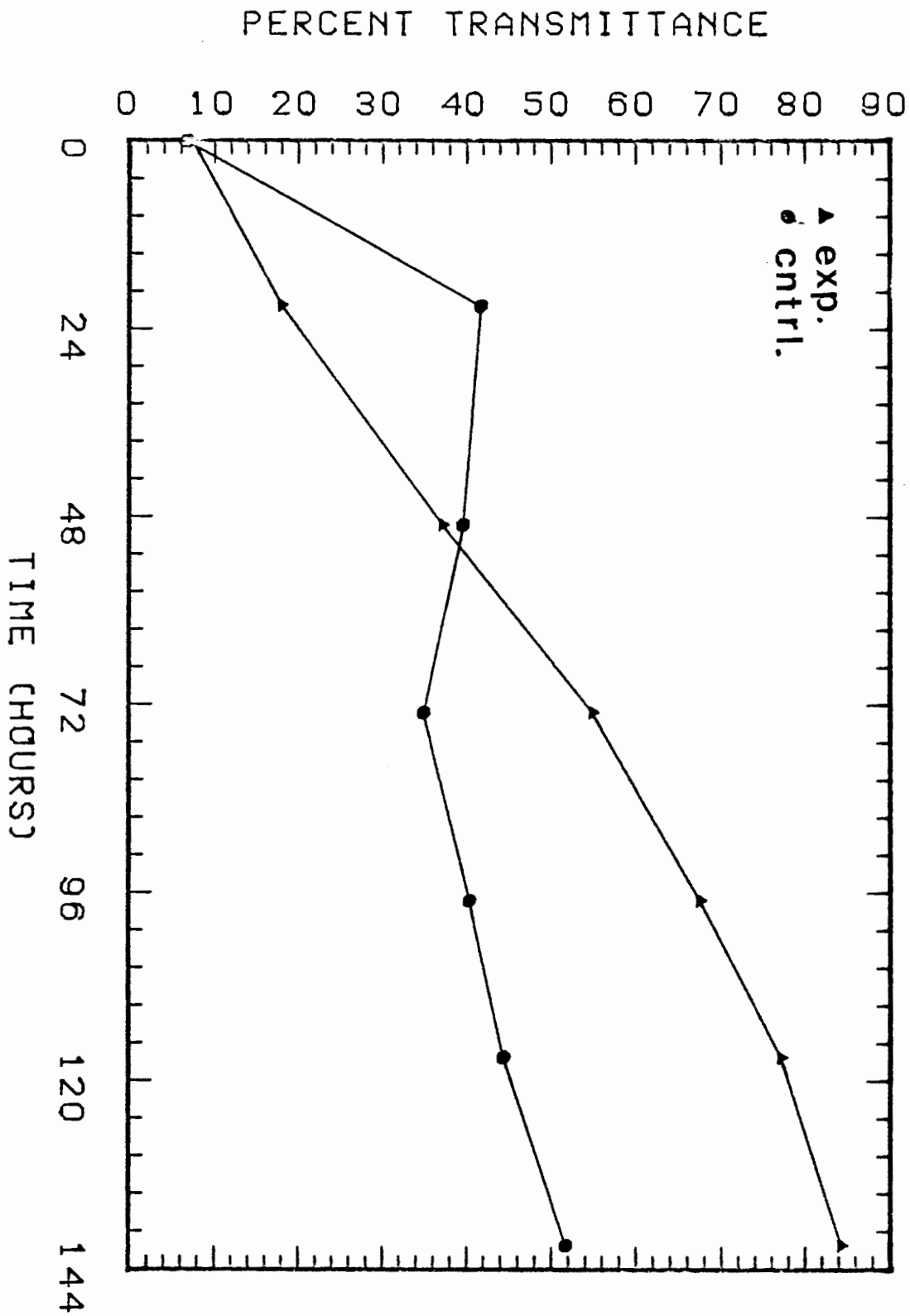

FIGURE 6. Increase in light transmitted through water containing suspended sediments. Animals were medium Rana catesbeiana, average weight 9.9 ± 0.2 g.

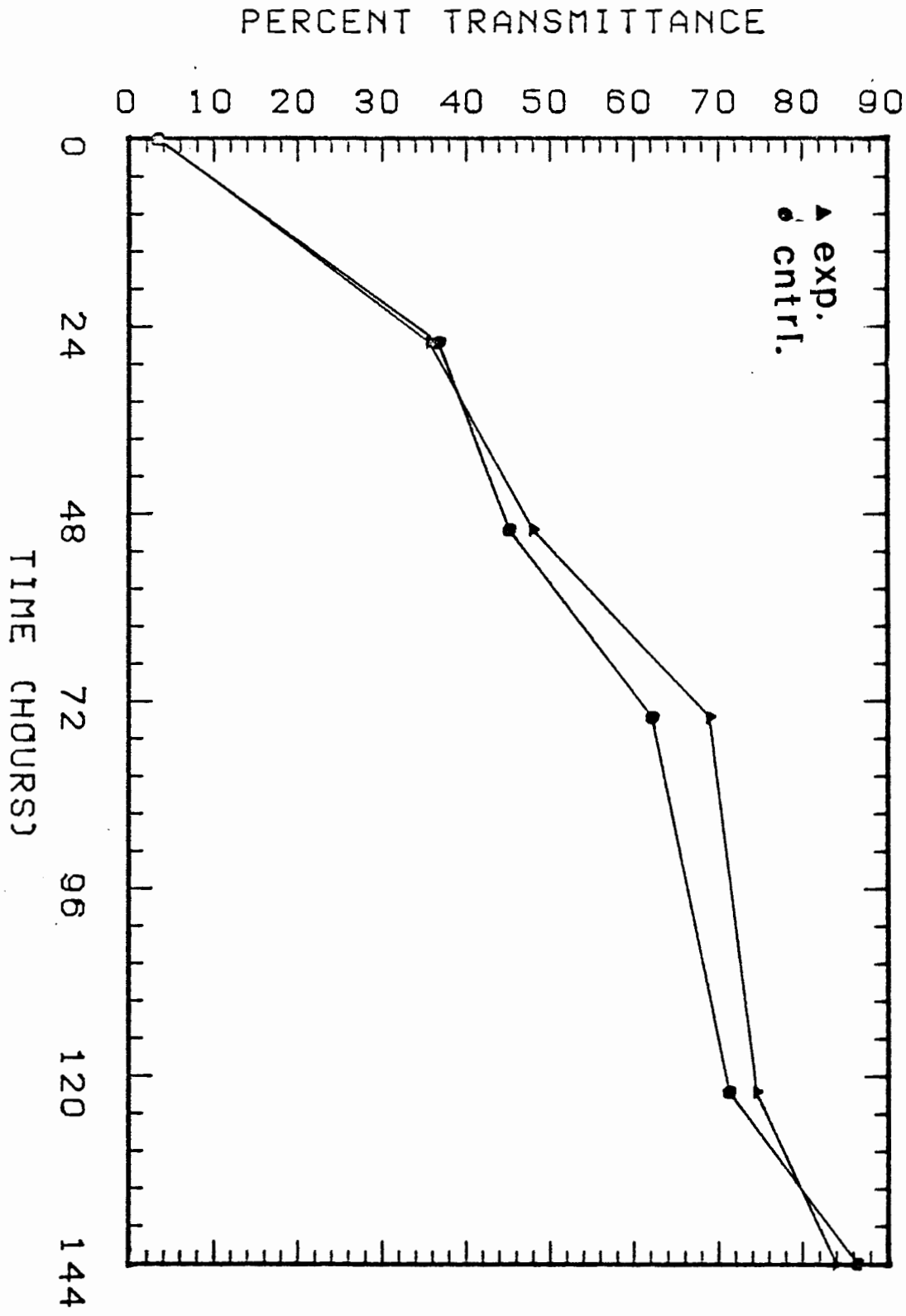

FIGURE 7. Increase in light transmittance in water containing suspended sediments. Animals were small Rana catesbeiana, average weight 3.2 ± 0.7 g.

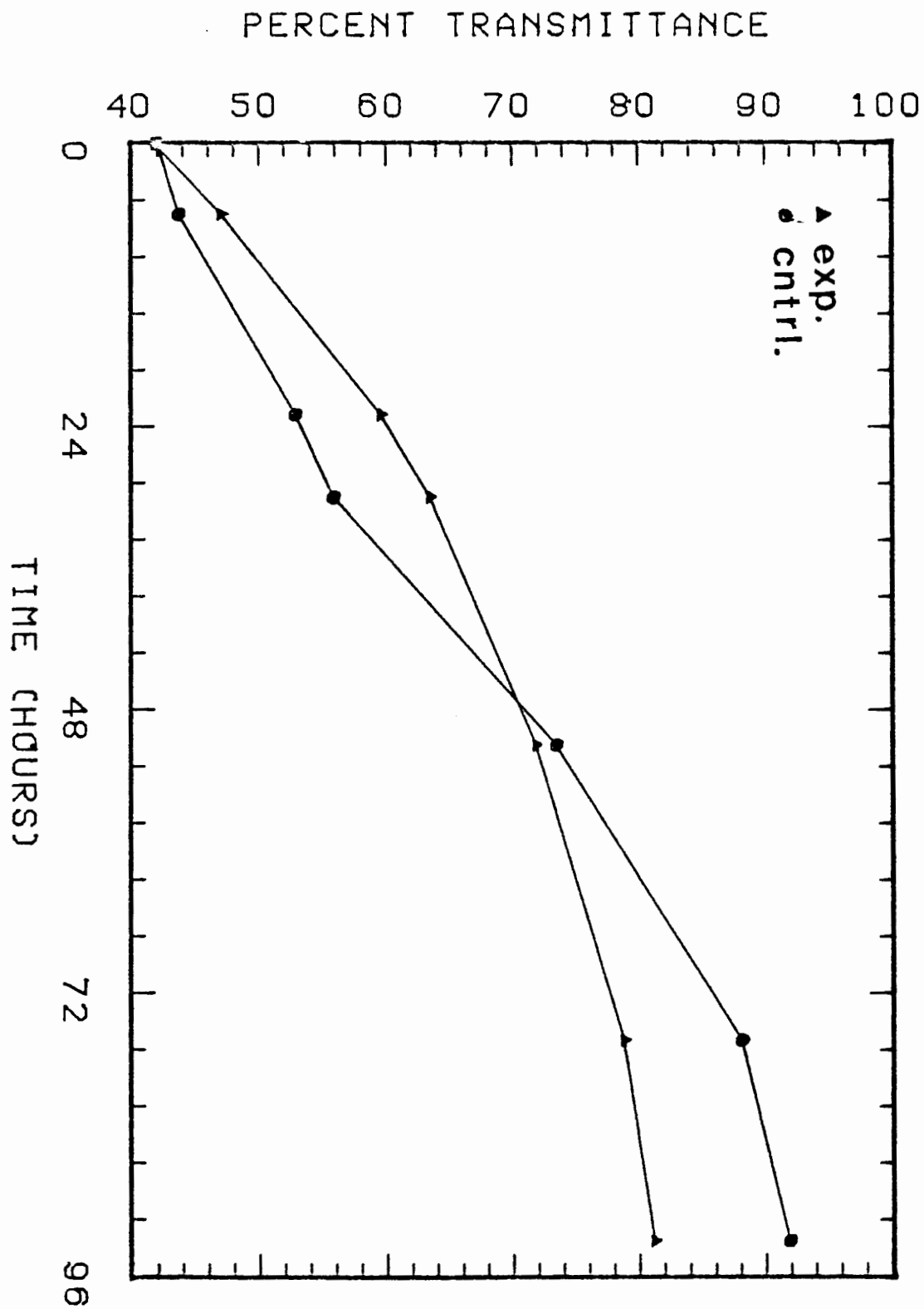

FIGURE 8. Increase in light transmittance through water containing suspended sediments. Animals were small Rana catesbeiana larvae, average weight 2.7 ± .3 g.

TABLE 5. Analyses of covariance for sedimentation experiments illustrated in Figs. 5-8. Regression equations are ln (Percent transmission) = a + b (ln (time + 1)).

Figure		Multiple R^2	Residual df	a	b	F values Equal Slopes	F values Equal Intercepts
5	control	.98	54	3.46	0.22	8.07**	0.23
	exp			3.47	0.24		
6	control	.88	80	2.04	0.39	9.92**	3.31
	exp			1.77	0.51		
7	control	.77	80	3.65	0.15	1.30	1.28
	exp			3.58	0.17		
8	control	.88	68	3.73	0.13	0.38	0.28
	exp			3.75	0.13		

* $p < 0.01$; otherwise not significant.

Rates of accumulation of sediments from an Imhof cone experiment are illustrated in fig 9. Sediment accumulation in the control cones was miniscule; sediment accumulation in the presence of anuran larvae was marked, especially at the first of an experiment. The rates of change in light transmittance were consistent with those seen in the first experiments, though significance of treatment effects could not be found with samples of three.

Results of the larger scale experiments with 60 l aquaria are given in table 6. Water in aquaria containing anuran larvae cleared enough for the target to be visible significantly sooner than did water in control aquaria (Wilcoxon rank sum test, $p<0.05$ for both experiments), though there was no significant difference in quantity of suspended matter in the various aquaria. Light transmittance increased more rapidly in the presence of anuran larvae.

That anuran larvae actually do contribute significantly to sedimentation was indicated by the measurement of actual weight of feces produced, as a function of body weight. Seven larvae surviving placement in suspended sediments averaged 18.2 $\pm$ 1.4 g wet weight upon removal from the suspensions; three days later they averaged 12.2 $\pm$ 1.0 g, for a total wet weight loss of 6.0 $\pm$ 0.9 g. The dry weight of their feces averaged 0.92 $\pm$ 0.29 g. Therefore over 15% of the wet weight loss was due to loss of solids through defecation. Field caught animals averaging 11.9 $\pm$ 0.7 g wet weight passed 0.63 $\pm$ 0.09 g dry weigh of feces in three days, some 2% of their wet biomass in solids. There was a relationship between matter egested and size: 63% of the variation in log dry feces weight could be explained by log initial wet weight. Large anuran larvae produce more sedimentation than do small ones, all other things being equal.

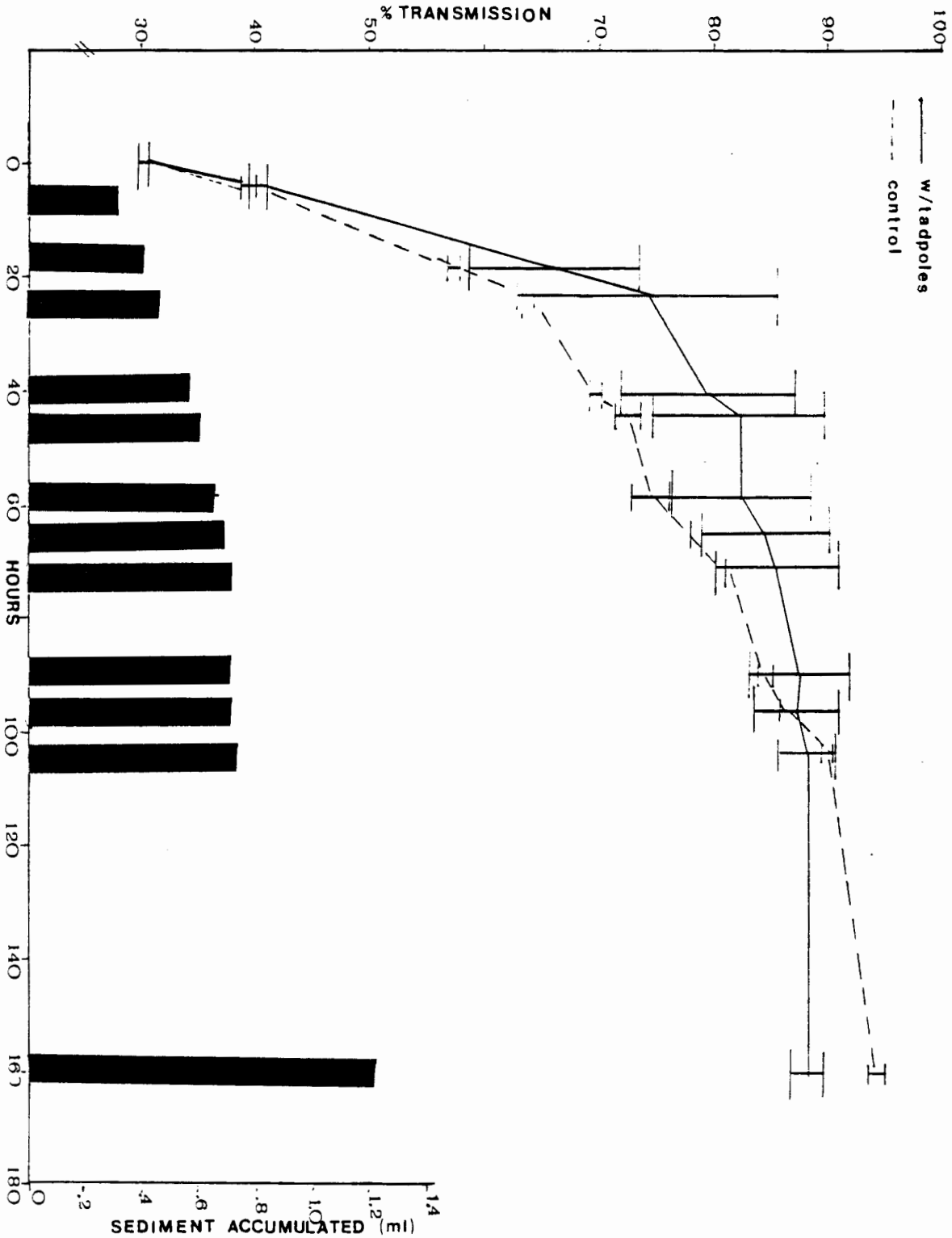

FIGURE 9. Increase in light transmittance and concordant accumulation of sediment, in water containing suspended sediments. Sediment accumulated was that in experimental cones; there was no measurable accumulation in control cones.

TABLE 6. Change in water transparency in 60 l aquaria containing sediments suspended in water. Experimental aquaria contained 10 anuran larvae in a, 2 in b.

a) Weight of Larvae (g)	Time to Clear (hrs) Control	Time to Clear (hrs) Exp.	Weight of Sediment (g) Control	Weight of Sediment (g) Exp.
3.4 g ± 0.1	98.3 ± 2.7	22.3 ± 3.8	94.5 ± 2.0	81.9 ± 5.7

b) Weight of larvae	Day	% transmittance Control	% transmittance Exp.
9.5 ± 0.7	0	48.0 ± 0	49.5 ± 0.9
	1	67.7 ± 2.5	66.3 ± 1.0
8.6 ± 0.7	2	75.3 ± 1.0	83.3 ± 3.9

Figure 10 illustrates oxygen consumption of sediments, some of which had been ingested by anuran larvae, compared with oxygen consumption of sediments not subjected to anuran larvae. Over the time course of the experiment there was virtually no oxygen demand in the control sediments. Oxygen was consumed in the experimental sediments, indicating at least some aerobic decomposition of the material. Clearly, the presence of anuran larvae increased rate of decomposition of tripton falling from the water column as sediment.

It is possible that the increased oxygen consumption of experimental sediments was due to contamination by fecal material allochthonous to the experiment: the larvae used in the experiment may have retained some material in the gut throughout the period of immersion in clear water, and defecated this previously ingested material during the experiment. Ruling out this possiblity will require the ability to insure complete purging of the digestive tract, something we are unable to do (chemical laxatives for humans have little discernible effect on anuran larvae). It is more probable that the major component of increase in respiration in the sediments was due to alteration in the gut of the material ingested during the experiment, in a manner making it more susceptible to aerobic decomposition. This alteration could be through mechanical breakdown, perhaps increasing surface area; chemical breakdown of some of the material into simpler compounds more easily metabolized by decomposers; or by seeding the material with procaryotic decomposers residing in the gut. Alternatively, the increased oxygen consumption in sediments partially processed by anuran larvae could be due to increased availability of ammonia nitrogen excreted by the larvae; nitrogen could be a limiting factor to the decomposers. We were unable to investigate this hypothesis by replicating

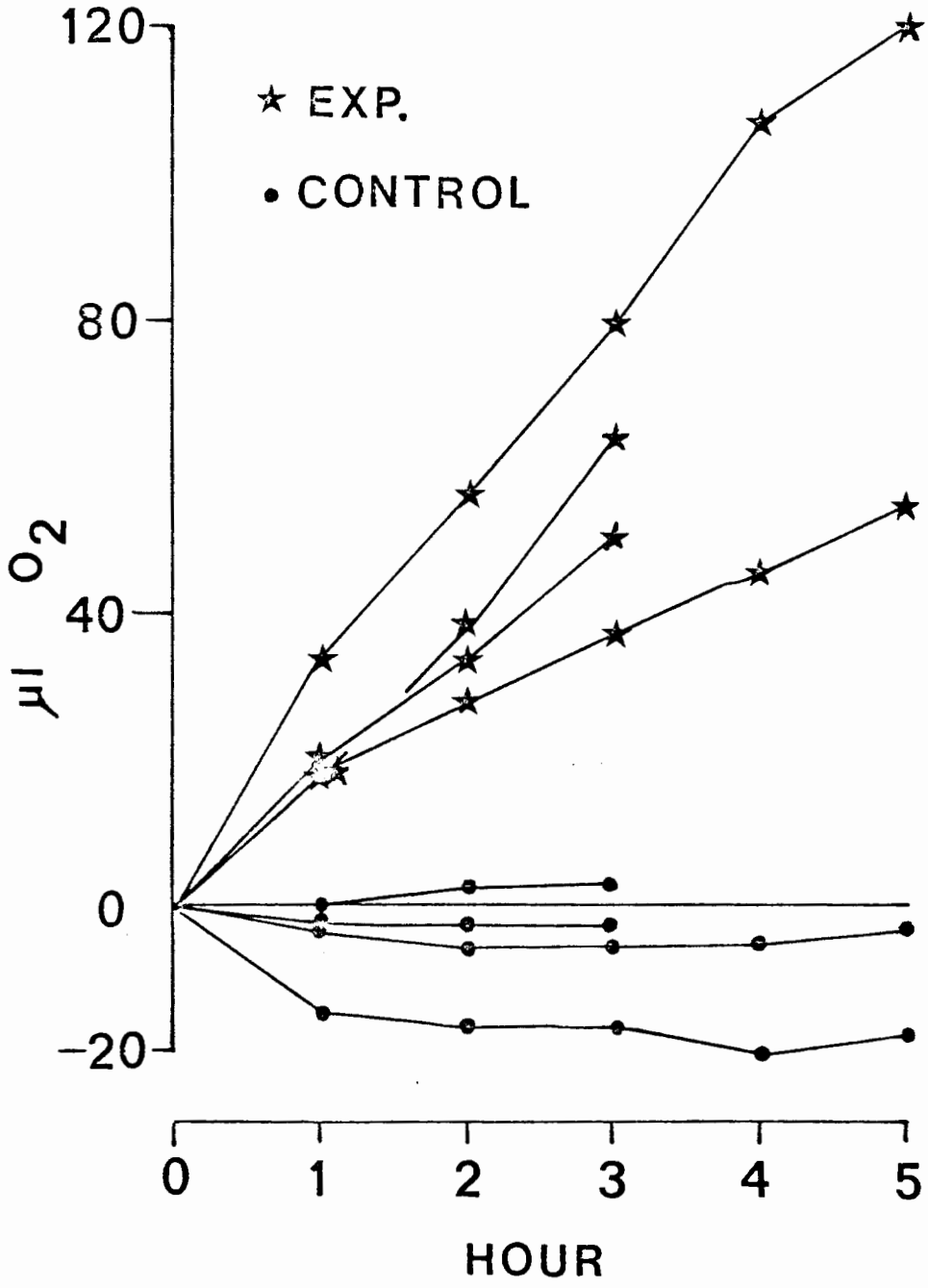

FIGURE 10. Oxygen consumption by sediments processed by Rana catesbeiana larvae (exp) or not so processed (control).

the experiment with excess inorganic nitrogen added to the unprocessed sediments, due to problems with the aged respirometer available to us.

The results of these experiments support the hypothesis that anuran larvae could be important controllers of several physical processes bearing on water quality. They are capable of removing tripton from the water column at a rate much greater than that at which it occurs without biotic intervention. This leads to a more rapid increase in light transmittance through the water column, which could obviously affect primary production. Finally, anuran larvae contribute to increased rates of decomposition in the sediments; such decomposition is the keystone of nutrient cycling, which may also affect primary production. The actual importance of anuran larvae in these processes is of course a function of the actual biomass present (itself a function of abundance and individual size) in any one system. The fact that in one study area, Stonehouse pond, the distinctively semicircular anuran larvae fecal pellets are one of the most prominent structures of the shallow sediments suggests that in this lake anuran larvae are important in these aspects of ecosystem function.

NATURAL HISTORY AND ABUNDANCE OF ANURAN LARVAE IN NEW HAMPSHIRE

The importance of any organism to ecosystem function is a product of the role actually played by the organism and its abundance, measured as either numbers or biomass depending upon the role in question. An important part of any ecosystem study is therefore an assessment of the abundance of the role players, which requires an understanding of their natural history. Ideally, a quantification of the dynamics of the populations should be done, but this is rarely obtainable. Rather, static (state variable) assessments must take the place of dynamic (rate variable) measurements since the latter require observations on a large number of generations. We will never fully understand ecosystem function until the dynamics of the component populations are understood. However, as this study covered only four summers of observations, only short term (within year) dynamics could be ascertained; inferences about between year dynamics could be made only by comparing yearly states.

Methods

Densities of anuran larvae in Stonehouse and Barbados ponds were ascertained on 30 m transects, marked with nylon twine, established in various parts of the ponds. Using skin diving or SCUBA equipment one of us (usually JT) would swim along each transect counting the number of anuran larvae of each species seen within 1.5 m of the transect line; these counts translated in to number per 90 m^2. It was not always possible to differentiate between Rana catesbeiana and Rana clamitans larvae as they differ only in spotting on the tail. For this reason we lumped these two species into a 'large Rana' category, while noting the identities of those individuals we could identify.

Biomass estimates were made by capturing animals from areas other than on the transects and bringing them into the laboratory for weighing. They were usually caught by chasing them down underwater and netting them in a "repeating" net (described in Taylor (1983)). Larger anuran larvae are powerful swimmers for a distance (ca. 3-6 m) but could usually be captured after diligent pursuit by the slower but persistent diver. Some of these animals were used in laboratory experiments, others were released in their natal pond.

Estimates of Bufo americanus larval densities were made by photographing a known area of shallow water and counting the larvae in the photograph. For biomass estimation Bufo could be merely scooped up with a dip net and transported to the laboratory.

We erected drift fences on land to intercept metamorphosing anurans and guide them into pit traps, to provide information on anuran biomass leaving the water. Except at Kingman pond these drift fences were destroyed by vandals or failed to capture any aurans.

Natural history and distribution of New Hampshire anurans was determined by investigating varous bodies of water in the state, at various times of the spring, summer, and fall.

Results and Discussion

Of the ten species of anura occurring in New Hampshire (Conant, 1965) one is exceedingly rare (Bufo woodhousei fowleri) in the state (though extremely common further south) and one (Rana septentrionalis) occurs only in the northern part of the state. The remaining eight species can all be encountered as adults regularly throughout southern New Hampshire. However, we have found larvae of only four of these species in sufficient numbers to be obvious as components of their aquatic communities: Bufo americanus, the

American toad; Rana sylvatica, the wood frog; Rana catesbeiana, the bullfrog; and Rana clamitans, the green frog. In our experience Bufo americanus and Rana sylvatica occur only in small ponds, along with the less numerous Hyla chryscocelis. Rana catesbeiana and Rana clamitans will breed in the larger lakes and ponds as well as smaller ones , along with Rana pipiens, Rana palustrus, and, occasionally, Hyla crucifer. This latter species (the peepah) is noted as a harbinger of spring although it breeds after the wood frogs; it usually breeds in small ponds but we have seen it in larger lakes.

Rana sylvatica breeds immediately after spring thaw, and the larvae have generally completed metamorphosis by June. Given the ephemeral nature of the larvae, and their restriction to "insignificant" bodies of water, the impact of this species on water quality is probably less than that of the other common larvae, even though R. sylvatica larvae occur in enormous numbers: one 30 cm scoop of a dip net in a pond on Adam's Point netted 826 larvae in May, 1979.

Bufo americanus larvae appear in May or June, when aquatic community activity is in full swing. They occur in enormous numbers in shallow water: at Kingman pond average densities before onset of metamophosis were: 1980, 76.2 $\pm$8.4 per 0.1 m^2; 1981, 102.0 $\pm$12.2; 1982, 60.1 $\pm$8.3. Densities in deeper water were apparently not so high, but we could have been deceived: there appeared to be fewer swimming on the surface in deeper water than in the shallows, but in the few centimeters of underwater visibility possible in this pond we could see them massed on the bottom at all depths. Figs. 11 and 12 illustrate biomass trends for larvae and metamorphosed animals. In 1982 larvae were quite smaller than in 1981, but size of metamorphoses was much greater. This is consistent with current knowledge of effects of

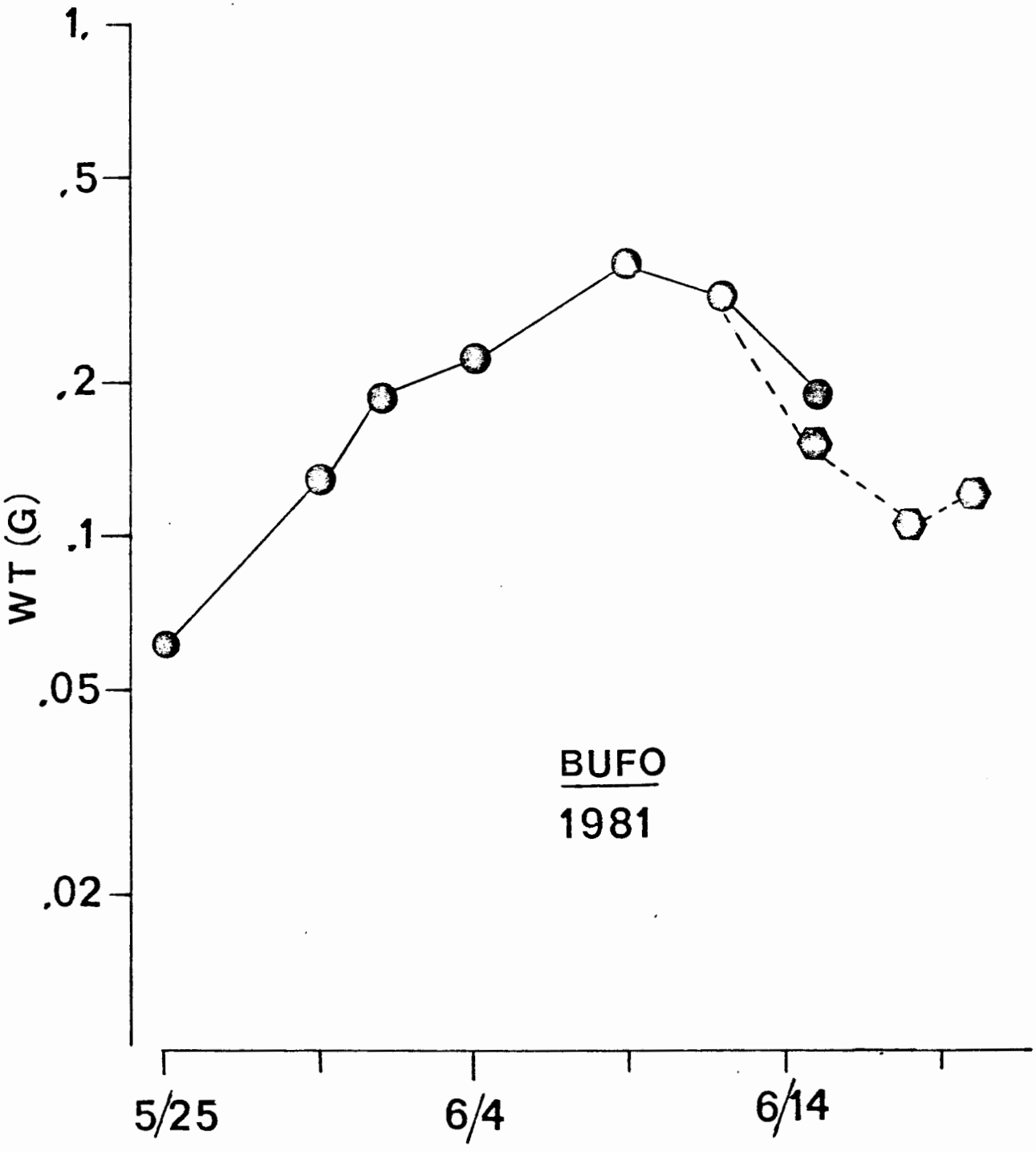

FIGURE 11. Growth of Bufo americanus larvae in May and June, 1981. Dotted lines and octagons refer to metamorphosed individuals.

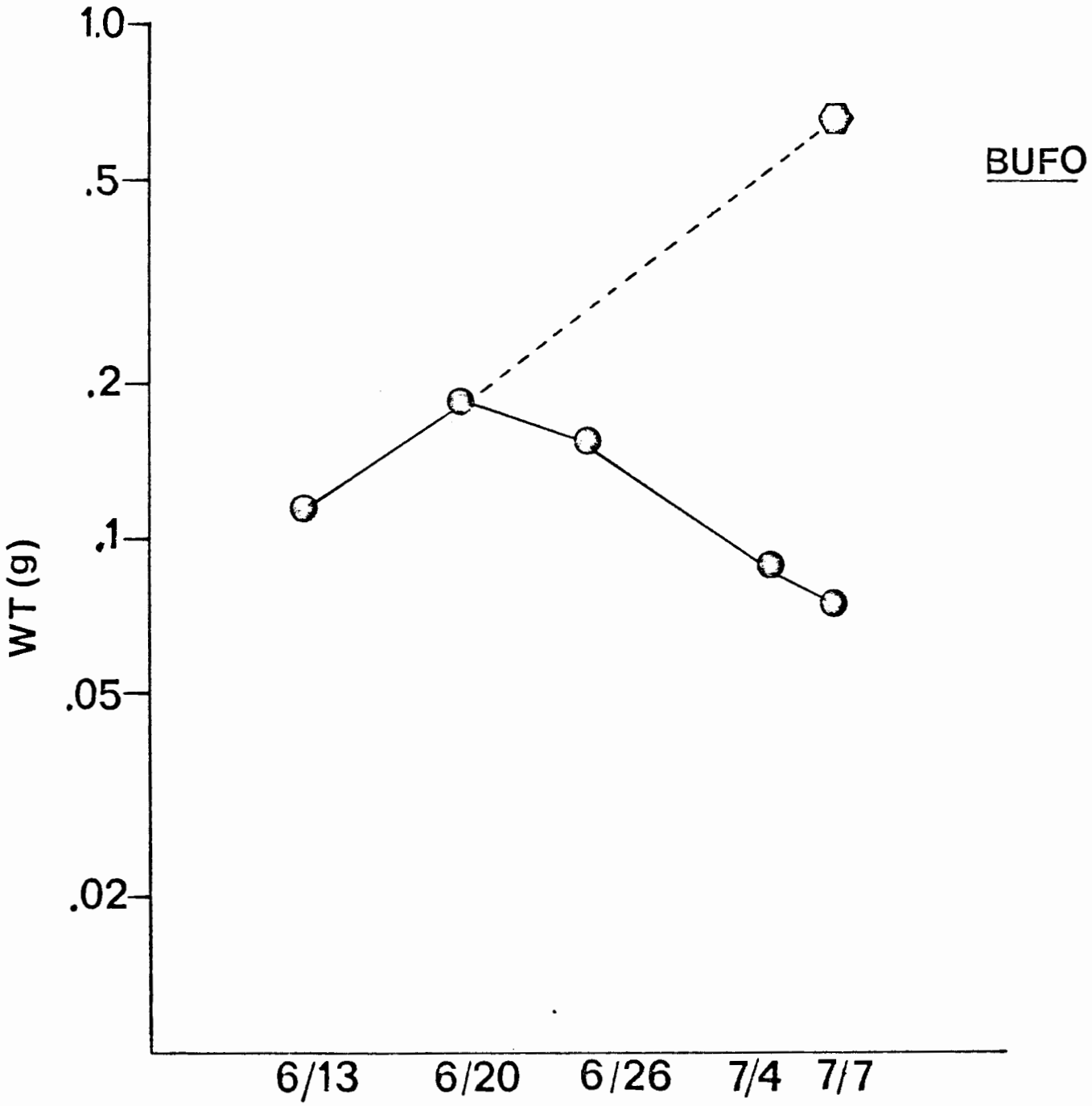

FIGURE 12. Growth of Bufo americanus larvae, June and July, 1982. Octagon refers to metamorphoses.

competition between anuran larvae (Brockelman, 1969; Wilbur, 1976). Assuming that anurans are 95% water (a value determined by weighing some Rana catesbeiana larvae, drying them, then weighing again) and that half of the larvae metamorphose (a figure consistent with captures in pit traps and number of dead larvae not metamorphosing) a rough estimate of biomass export due to Bufo americanus metamorphosis may be obtained: in 1981 2.6 g of biomass (dry weight; wet weight= 51 g) left the water for every square meter of shallow area; in 1982 the figures were 9.0 g dry and 180 g wet. This is a substantial amount of biomass reversing the normal movement of nutrients from land to water. We suggest that the large numbers of Bufo americanus larvae that occur in some ponds may have a significant effect on ecosystem function in those ponds.

Rana clamitans larvae did not occur in any great number in any of the intensively studied bodies of water (Barbados, Stonehouse, Kingman ponds). We did find them to be the principal large Rana in several other bodies of water; they were abundant enough to be readily netted in these lakes.

Rana catesbeiana was the most abundant anuran larva in both Stonehouse and Barbados ponds. As reported for most northern populations the larvae apparently overwinter in both ponds; large individuals (> 10 g) could be found in May and June. These overwintering individuals metamorphose in their second summer. This observation is supported by table 7 which also indicates the patterns of growth through the summer of 1980. By virtue of their large size (greater than that of the common mice, Peromyscus in the adjoining terrestrial systems), the larvae of this species might be expected to exert some influence on their ecosytem if they occur in any abundance.

Rana catesbeiana larvae were abundant in the shallow littoral zones of Stonehouse and Barbados ponds in 1979 (table 8); they were somewhat less

TABLE 7. Weights of Rana catesbeiana larvae from Stonehouse Pond.

	WEIGHT (g) ± S.E.			
GOSNER STAGE	22 June	21 July	11 Sept	26 Sept
25-35 (No Feet)	14.7 ± 0.57	16.8 ± 1.74	3.18 ± 0.14	4.12 ± 0.14
36-40 (Rear Feet)	19.38 ± 0.62	17.98 ± 0.67	4.55 ± 0.13	4.78 ± 0.39
41 (Front Limb Buds)	22.04 ± 0.92	19.08 ± 1.35	---	---
42 (Front Legs)	17.2 ± 0.75	11.63 ± 3.91	---	---

TABLE 8. Densities of Rana catesbeiana on 90 m^2 transects.

	1979	1980	1981	1982
Stonehouse Pond:				
Deep	0	0	0	0
Shallow -- stone cliff	31.0 ± 11.0	19.5 ± 6.0	7.2 ± 4.4	3.8 ± 1.3
Shallow -- debris	42.4 ± 7.4	24.3 ± 6.0	9.2 ± 5.1	5.8 ± 1.5
Shallow -- vegetation	21.8 ± 6.3	---	9.3 ± 3.9	7.2 ± 1.3
Barbados Pond:				
Deep	0	0	0	0
Shallow -- sand	38.9 ± 8.1	17.1 ± 5.5	0.4 ± 0.1	0
Shallow -- mud	7.6 ± 4.0	3.2 ± 1.1	0	0

abundant in 1980; they virtually disappeared from Barbados pond in 1981 and 1982, and were not particularly common in Stonehouse during the same period. We have no explanation for this decline, but it does demonstrate that populations of anuran larvae in these ponds are probably not at any type of equilibrium.

Both of these ponds contain trout, which eat anuran larvae (Fraser, 1978; personal observation) (contrary to the assertion of a New Hampshire fisheries professional). It is therefore not surprising that anuran larvae in these ponds were found only in the shallows along the periphery, a refuging effect reported for a number of species in the presence of fish predators (Macan, 1965, 1966; Goodyear, 1973; Taylor, 1983). This means that any effect anuran larvae may have on ecosystem function would be restricted to the shallows if fish predators are present. Though locally abundant in the shallows, populations of anuran larvae are not large in Stonehouse and Barbados ponds, relative to the total area of the ponds.

Other than restriction to the shallows, Rana catesbeiana larvae in Stonehouse pond displayed no other form of habitat selection, inhabiting mud, rocky areas, vegetation, and litter at approximately the same density. Larvae in Barbados pond did prefer sandy beach areas to mud areas, at least during the summer. This latter form of habitat selection would also alter the generality of ecosystem effect due to anuran larvae.

One final point must be made with regard to anuran larvae distribution and the presence of predatory fish. While anuran larvae were present in ponds stocked with trout, we were unable to find anuran larvae in the so-called warm-water ponds supporting pickerel, yellow perch, and centrarchids ("sunfish" and "bass"). While adult anurans could sometimes be found along the shores of such ponds, we never found any evidence of breeding, though we

did hear a report of anuran larvae being found dead on the shores of one lake. It is very likely that the fish found in the warm-water lakes exterminate any anuran larvae present. While there may be no relationship, we must also point out that the problem lakes in New Hampshire are warm-water ponds devoid of suspension feeding anuran larvae.

CONCLUSIONS

Several recent publications (Seale, Rodgers and Boraas, 1975; Seale and Wassersug, 1979; Seale and Beckvar, 1980; Seale, 1980) have demonstrated that anuran larvae may have considerable impact on both procaryotic and eucaryotic algae in aquatic ecosystems. We have demonstrated that this impact could possibly be applied to the cyanobacteria that cause problems in New Hampshire lakes and ponds. Native anuran larvae have some resistance to cyanobacterial toxins; they are at least able to ingest the three common species of toxic cyanobacteria, and in the case of Anacystis aeruginosa are apparently immune to intraperitoneal injections that kill mammals of equivalent size. Furthermore, anuran larvae are efficient exploiters of these cyanobacteria, capable of exterminating filimentous forms (Aphanizomenon flos-aquae and Anabaena flos-aquae) and reducing the smaller spherical forms significantly. This suggests that auran larvae have potential as biological control agents for noxious cyanobacteria. The problems with their use in biological control are: 1) problem lakes are warm-water lakes supporting fish that prey upon anuran larvae and anuran larvae do not now occur naturally in many of these lakes. 2) Large densities and biomass of anuran larvae reported by others in other areas (Calef, 1972; Arnold and Wassersug, 1978; Werner and McCune, 1979) have not been found in the more important ponds in New Hampshire. Extremely high densities of Bufo americanus and Rana sylvatica do occur, but only in farm ponds and woodland pools. Large biomass of anuran larvae would be required for them to serve as biological control agents. 3) Toxic cyanobacteria are not a good ration for anuran larvae, as they lose weight rapidly when fed nothing else. This effect could prevent anuran larvae from being effective control agents; alternative rations might be necessary to sustain a

population. We would like to attempt a large scale release of allochtonous anuran larvae in a farm pond suffering from an algal bloom, just to see what would happen. Such an introduction would have to be conducted first on a relatively unimportant body of water since there is a potential for untoward effects also: increase in algal production due to increased availability of nitrogen from the ammoniotelic larvae is one possibility (cf. Meyer et al., 1983), as is anoxia due to increased aerobic decomposition of egested algae. Use of anuran larvae as biological control agents could also be complicated by competitive interactions (cf. Smith-Gill and Gill, 1978; Steinwascher, 1978; Wilbur, 1976, 1977).

Anuran larvae can also have significant effects on water clearing, sedimentation, and decomposition. By serving as little biological filters, anuran larvae clear water, leading to increase in the depth of the compensation point and thus increasing the volume of water supporting net primary production. Whether or not this might lead to increase in noxious vegetation (e.g. european water milfoil) is a moot point. Like all effects of anuran larvae, this one would be biomass dependent, and the low biomasses found in the larger study lakes suggest that this effect might at present be minor.

The accelerated decomposition of sediments processed by anuran larvae is interesting. In the larger study lakes it would be confined to the shallow areas inhabited by the animals. In these shallows feces of anuran larvae were one of the most noticeable features of the sediments; they are everywhere. The increased decomposition would have two major effects: increased oxygen consumption, which might lead to reduced oxygen concentration, and increased flux of nutrients tied up in the sediments. As this effect is concentrated in the shallows, it probably has little effect

on oxygen concentrations in the lake as a whole, but the increased nutrient flux might affect productivity in other parts of the lake.

The removal of nutrients from aquatic ecosystems by amphibian metamorphosis has been commented on by others while this study was in progress (Werner and McCune, 1979; Seale, 1980). In New Hampshire this effect appears to be concentrated in farm ponds and woodland pools where sufficient anuran larval biomass occurs to be significant. Whether or not anuran larvae could be used to remove eutrophying nutrients from other bodies of water is unknownn. Given the possibility of predation by fish in many lakes, there is a distinct possibility that many anuran larvae, if introduced into such lakes, would never leave.

In summation, anuran larvae can have significant effects on standing crop of toxic cyanobacteria, transparency of water, rates of sedimentation, rates of decomposition and nutrient flux, and removal of nutrients from aquatic systems. In New Hampshire these effects are minimal in most lakes due to the relatively small biomass of anuran larvae present.

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