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THE EFFECTS OF AERATION ON AMPHIBIAN LARVAL GROWTH: AN EXPERIMENT WITH BULLFROG TADPOLES

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ABSTRACT

I conducted an experiment to assess the effects of aeration on the growth of bullfrog tadpoles (*Rana catesbeiana*). Tadpoles in the non-aerated treatment grew slower than tadpoles in the aerated treatment. Tadpoles in the non-aerated treatment were observed at the water's surface more often and on food resources less often than tadpoles in the aerated treatment. Oxygen concentrations in natural aquatic habitats varied greatly (encompassing the range of the experimental treatments), suggesting the results of this study may be applicable to natural situations. The results suggest oxygen content (and/or disturbance) of aquatic habitats may influence the distribution and success of *Rana catesbeiana*.

† † †

The oxygen concentration of aquatic habitats may affect the distribution and abundance of amphibians, particularly through its potential influence on the embryonic and larval stages. The embryonic and larval stages may be particularly susceptible to the effects of oxygen concentration because they are often dependent on diffusion to obtain the oxygen necessary for respiration (Burggren and Just 1992). Several studies suggest that oxygen concentrations are important in embryonic respiration and development (see Seymour and Bradford 1995 for review), however little work has been done on the effects of oxygen concentration on the larval stage, either in the laboratory or in the field. The few available results suggest that oxygen availability can alter physiological/metabolic costs and performance (Feder 1983a, Pörtner et al. 1991, Wassersug and Feder 1983), and some aspects of individual behavior (Dupré and Wood 1988, Wong and Booth 1994). In this paper, I report the results of a laboratory experiment on the effects of aeration on the growth of bullfrog tadpoles (*Rana catesbeiana* Shaw). In addition, I surveyed potential breeding ponds to determine natural oxygen concentrations.

MATERIALS AND METHODS

A single clutch of eggs was collected from the reservoir pond at the Kellogg Biological Station's experimental pond complex, Kalamazoo County, Michigan, on 27 June 1995. Batches of eggs were placed into 12 containers filled with 1 L of pond water (to minimize stress to the eggs, no attempt was made to divide eggs equally among containers). Half of the containers were aerated using aquarium airstones and half the containers were not aerated. Containers were small enough that aeration caused the circulation of the entire water column. After hatching, larvae were maintained in the same containers for 11 d and were fed brine shrimp during this time. Approximately 75% of the water in each container was changed every morning. After 11 d, the number of tadpoles in each container was reduced to five individuals. Thereafter, water was changed every other morning, with feces and excess food removed at the same time. I fed the tadpoles algal fish food in excess (i.e., food remained in all containers after 12 h) every day. Excess food was removed after 12 h to prevent fouling of the water. Beginning 11 d after hatching, tadpoles were measured every 3 d for 15 d, and then weekly until the end of the experiment. I measured standard length (tip of snout to base of tail) to the nearest 0.001 cm using dial calipers. Survivorship was very high throughout the study (only 1 tadpole died 2 d into the experiment, giving a survivorship rate of 98%). Throughout the study, I recorded the number of tadpoles in each container that were first seen (1) on the surface of the water (observations timed so that they were made at several time intervals after water changes ~ 3–4 h), and (2) on the food on the bottom of the container. At the termination of the experiment, tadpoles were released into their natal pond.

Throughout the study I measured the oxygen content and temperature of the water using a YSI Model

58 dissolved oxygen meter (Yellow Springs Instruments, Yellow Springs, Ohio, USA). I also made similar measurements at natural breeding sites in the Kellogg Biological Station's experimental pond complex. These ponds were basically identical when constructed, but subsequent manipulations have caused them to have different levels of vegetation and organic detritus.

I used repeated measures analysis of variance with aeration as the between factor and time (day) as the within factor to compare treatment means for body size and behavioral measures over the course of the study. Oxygen content and temperature of treatments were compared using a series of *t*-tests with a corrected α-value of 0.006 (0.05/8). Means are given ± 1 SE.

RESULTS

Individuals in the aerated containers grew faster than the individuals in the non-aerated containers (Fig. 1; Date by Treatment effect: $F_{7,70} = 3.29$, $P = 0.004$). Individuals in the non-aerated treatment groups tended to be seen on the surface much more often than individuals in the aerated treatment groups, but the difference decreased as the experiment progressed: 100% in non-aerated groups at surface at beginning decreased to 20% at the end, and virtually no individuals in aerated groups were at the surface throughout the entire study (Date by Treatment effect: $F_{32,320} = 11.82$, $P < 0.0001$). Individuals in the non-aerated treatment groups also tended to be seen on the food on the bottom of the container less often than individuals in the aerated treatment groups, but again the difference decreased as the experiment progressed: 30% in aerated groups on food at beginning decreased to 10% at the end, and <10% of individuals in the non-aerated groups were on the food at any time during the experiment (Date by Treatment effect: $F_{10,100} = 2.36$, $P = 0.015$).

On all days for which data were available, the aerated containers had significantly higher amounts of oxygen in the water (Table 1). Water temperature did not differ between treatments, except for one day on which the aerated treatments were slightly cooler, on average, than the non-aerated treatments (Table 1). Oxygen content varied among the natural breeding sites sampled (Fig. 2). The range of oxygen contents found in the experimental containers was within the range found in the natural ponds (Table 1; Fig. 2). Temperature did differ somewhat among sample sites ($N = 21$; range = 21.9–26.9 C). Oxygen content in the ponds increased with water temperature ($N = 21$, $R^2 = 0.31$, $P = 0.01$; y = -16.45 + 0.82x).

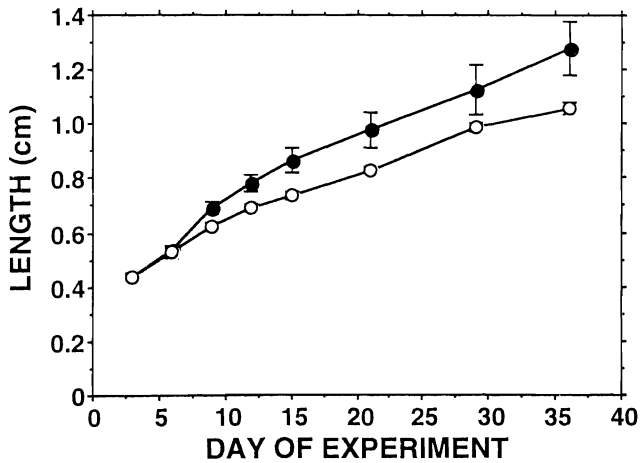

Figure 1. Mean body size of bullfrog tadpoles (all containers) from non-aerated (open circles) and aerated (closed circles) treatments throughout the study. Bars are ± 1 SE, *N* is 6 for each point.

DISCUSSION

For many anuran larvae, the oxygen content of the water they live in can influence physiological as well as ecological performance. Increased aquatic hypoxia caused a decrease in the stamina of three species of anurans, but access to air ameliorated the effects in one species (*Rana berlandieri*) (Wassersug and Feder 1983). In addition, anuran tadpoles may increase their heart rate or ventilation rate in hypoxic conditions (Feder 1983b, Feder and Wassersug 1984). Survivorship and

Table 1. Mean oxygen content (mg L^{-1}) and temperature (C) of the aerated and non-aerated treatment groups. Means are given ± 1 SE, $N = 6$ in all cases. All of the mean oxygen contents are significantly different at the < 0.0001 level, whereas all of the mean temperatures are not significantly different at the corrected α-level of 0.006, except for the August 17 means which are significantly different at the 0.001 level.

Date	Treatment	Oxygen Content	Temperature
3 Jul 1995	Aerated	6.95 ± 0.06	21.17 ± 0.12
	Non-aerated	5.53 ± 0.12	22.30 ± 0.14
21 Jul 1995	Aerated	7.45 ± 0.06	23.40 ± 0.04
	Non-aerated	4.88 ± 0.21	23.45 ± 0.03
24 Jul 1995	Aerated	7.32 ± 0.14	23.42 ± 0.04
	Non-aerated	4.67 ± 0.08	23.55 ± 0.04
17 Aug 1995	Aerated	7.11 ± 0.19	23.97 ± 0.02
	Non-aerated	2.42 ± 0.13	24.15 ± 0.03

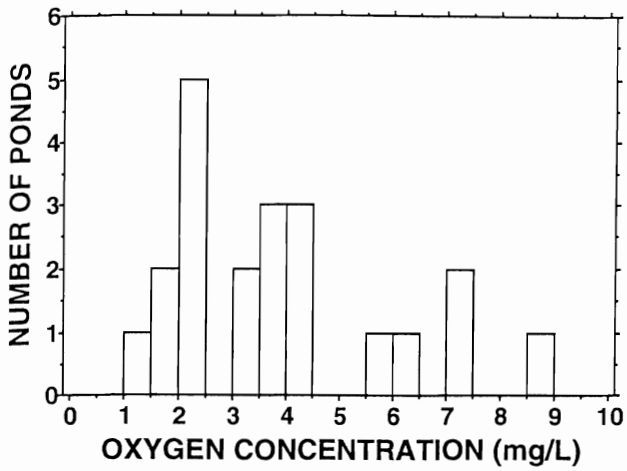

Figure 2. Oxygen concentrations of natural bullfrog breeding sites at the Kellogg Biological Station's experimental pond complex.

growth rates of larval *Ambystoma tigrinum* were highest in areas of high oxygen concentrations (Holomuzki 1986). In this study, I have shown that aeration increases the growth rate of bullfrog tadpoles.

The relationship between growth rate and water oxygen content may be expected to arise for at least two, non-mutually exclusive, causes. First, the physiological costs of breathing air or increased ventilation rates during gill respiration could result in decreased growth performance. In other words, the more energy the tadpoles spend on breathing, the less energy they can spend on growth. Alternatively, increased buccal ventilation may decrease feeding efficiency by interfering with the feeding function of the same surfaces (see Feder et al. 1984). For example, *Xenopus laevis* tadpoles allowed to breathe air grew faster and metamorphosed faster than tadpoles not allowed to breathe air, probably because increased ventilation interfered with feeding, whereas lung breathing did not (Pronych and Wassersug 1994, Wassersug and Murphy 1987).

A second explanation may be that the necessity of breathing air results in behaviors that decrease the amount of time spent foraging. In this study, the proportion of tadpoles seen at the surface was greater in tadpoles from non-aerated containers than for tadpoles from aerated containers. Other tadpoles when exposed to water with low oxygen content also often exhibited increased surfacing behavior associated with aerial breathing (Wassersug and Seibert 1975, Wong and Booth 1994), and *Rana berlandieri* tadpoles increased their use of aerial breathing when oxygen content of the water was lowered (Feder 1983b). The time spent at the surface precludes time spent on the bottom feeding, as evidenced by the small proportion of tadpoles observed on the food resource in the non-aerated containers relative to in the aerated containers.

The oxygen content of the water used in the aerated and non-aerated treatments varied over the course of the experiment, but the aerated treatment was always higher than the non-aerated treatment, and fell within the range of natural variation. My results suggest that oxygen content may be a factor in determining the distribution of amphibians. Indeed, field observations and laboratory studies suggest aquatic amphibian distributions may be affected by environmental oxygen concentrations (Noland and Ultsch 1981, Ultsch and Duke 1990).

My experimental design did not allow for the effect of the aerated treatments to be solely accredited to the effect of oxygen content. Oxygen content is confounded with disturbance: the airstones and aeration constantly disturbed the aerated treatments, whereas there was no disturbance in the non-aerated treatments. However, the observations on tadpole behavior and casual observations of the tadpoles, suggest that the mechanics of aeration in this experiment had a minimal effect on the tadpoles (e.g., tadpoles were not thrown about in the water, nor did they appear to swim more often than in the non-aerated treatments). However, it is likely that the aeration disturbance was greater than the disturbance occurring in natural situations. Also, the effect observed here is the opposite of what might be expected: growth was higher in the more disturbed containers (aerated) than in the undisturbed containers (non-aerated). Thus, I feel the disturbance had little effect on the results of this study, however experiments in which oxygen enriched water is added rather than direct aeration would help resolve this issue.

In conclusion, oxygen content of aquatic habitats appears to be a particularly relevant environmental parameter for the ecology of anuran larvae and possibly all aquatic amphibian larvae. It has the potential to influence distributions, population dynamics, life histories, and community dynamics. Its influence may be especially important in anuran assemblages in which some of the species possess lungs (e.g., Ranids) and some of the species do not possess lungs (e.g., Bufonids).

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