MODIFICATION OF OLFACTORY-RELATED BEHAVIOR IN JUVENILE ATLANTIC SALMON BY CHANGES IN pH

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Abstract—The hypothesis that low pH modifies the response of salmonids to certain olfactory stimuli was tested. An interactive video–computer system was used to monitor the behavior of juvenile Atlantic salmon (*Salmo salar*). At a pH of 7.6, animals were attracted to glycine and avoided L-alanine. These effects were dose-dependent, with a threshold of 10^{-7} M. The response of the fish to both amino acids changed when the pH of the test chamber was gradually lowered from 7.6 to 5.1; they became attracted to L-alanine and indifferent to glycine. These effects were reversible with a return to pH 7.6. Our findings suggest that acid rain may contribute to reductions in salmonid populations in acidified rivers by impairing the recognition of olfactory cues by salmon during their spawning migration.

Key Words—Acid rain, salmon, *Salmo salar*, pH, olfaction, computer, video, migration, glycine, L-alanine.

INTRODUCTION

Acidification of rivers and streams throughout Europe and North America has been implicated in the decline of anadromous fish populations (Wright et al., 1975; Leivestad et al., 1976; Schofield, 1980). Population decreases have even been observed in rivers where the pH is above levels considered to be lethal[1] (Haines, 1981; Muniz, 1981; Watt, 1981; Watt et al., 1983). Many factors associated with moderately acidified waters may play a role in reducing or, in some cases, eliminating the recruitment of new animals into the population

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[1] The lethal pH level for adult Atlantic salmon is 4.5, parr, 4.0, eggs, 3.5 (Daye and Garside, 1977).

(Neville, 1979a,b; Daye and Garside, 1980; McDonald, 1983; McDonald et al., 1983). We have been testing the hypothesis that changes in pH alter sal-monids' sense of smell and thus may modify their normal migratory behavior.

It is widely accepted that the freshwater spawning migration of salmonids, like many species of anadromous fishes, is controlled to a great extent by ol-factory cues in the environment (Hasler, 1957, 1960a,b; Groves et al., 1968). If the olfactory sense of these animals is altered due to a moderate reduction in the pH of the water (pH 4.5–6.5), migrating fish may not be able to respond appropriately to necessary olfactory cues (Sutterlin, 1974; Fritz, 1980). Al-though there are some field data available which suggest that adult salmon halt upstream spawning migration and may return downstream when presented with copper and zinc pollution (Saunders and Sprague, 1967), little data are presently available concerning the effect of acidic precipitation on homing behavior or salmonid olfaction (Hara, 1976b; Sutterlin, 1974). We have examined the be-havioral response of juvenile Atlantic salmon to amino acids and taurocholic acid, and the modification of their responses by changes in the ambient pH. Our results indicate that pH does have a significant impact on the behavioral response of salmonids to certain olfactory stimuli, and thus it may be a signif-icant factor contributing to the reductions in salmonid populations reported in many moderately acidified rivers.

METHODS AND MATERIALS

Parr-stage Atlantic salmon (*Salmo salar*), approximately 15–20 cm long and 10.0–15.0 g in weight were used in all experiments. Fish were obtained from the Milford State Hatchery in Milford, New Hampshire. They were held in closed-recirculating holding systems at 10°C. Water quality was checked weekly, and the water source was the same as that used in the behavioral ex-periments.

A two-channel preference–avoidance chamber (Figure 1) that included a common area (Greer and Kasokoski, 1978) was used to monitor the behavioral responses of the juveniles to specific olfactory stimuli. At the beginning of each experiment, four fish were placed in the common area for a 15-min acclimation period. The experiment was initiated by removing the barrier and allowing the animals to explore the chamber (Figure 1). The pH was monitored throughout the experiments with an Orion pH meter equipped with an automatic tempera-ture compensation probe. The response to specific olfactory stimuli was deter-mined by recording movements on videotape and then converting these move-ments to digital form using an interactive video–computer system designed in our laboratory (Royce-Malmgren and Watson, 1986). To create a digitized track of the fish, the videotaped experiment was viewed on a high-resolution color monitor with computer generated targeting cross hairs overlayed on the image of the chamber by an Ambico special effects generator (ASEG, Figure 1). The
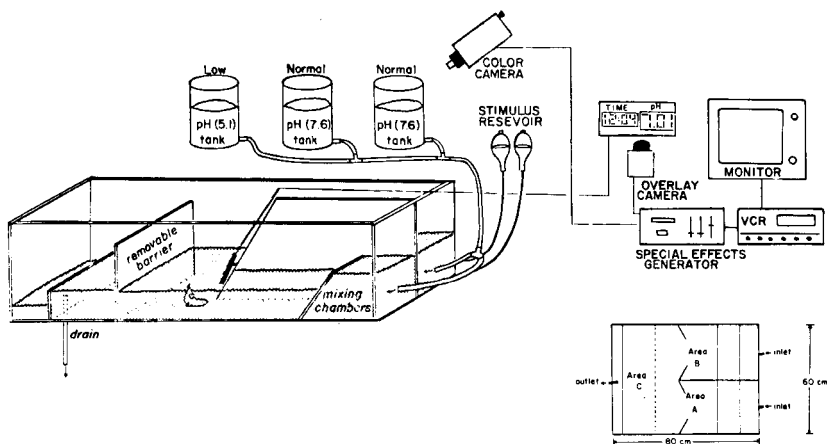
FIG. 1. Test chamber and video–computer data collection system. Fish were introduced into area C of the test chamber, behind the removable barrier. Dechlorinated, aerated tap water (pH 7.6) from overhead storage tanks flowed continuously through the chamber, at a rate of 3 liters/min. Following an acclimation period, the removable screen was lifted to start the experiment. During the control period, no olfactory stimulus was added. During the test period, stimulus was added to area A or B from the stimulus reservoirs. The concentration of stimulus declines as the water from area A and area B mix in area C. This creates a concentration gradient around the tank from the stimulus input to the opposite side. This gradient has been confirmed using dyes with fish present. After 30 min, pH was reduced over a 15-min period, using water from overhead storage tanks whose pH was lowered with a solution of 50% H_2SO_4 and 50% HNO_3 (0.5 M) to simulate the approximate composition of acid rain. Following the acidification, the water in the overhead holding tanks was thoroughly aerated to drive off excess CO_2 and equilibrate O_2 levels between tanks. The pH was maintained for 30 min and then returned to the original level over another 15-min period and held at that level for the remaining 30 min. The pH and temperature of the water were monitored throughout the experiment and stored on videotape by means of an overlay camera. Other physical parameters were determined at the end of the experiment and recorded on the videotape. A Hitachi/Everex model 8A color video camera mounted above the chamber was used to record the experiment, and this video signal along with that of the overlay camera were combined by a special-effects generator and transmitted to a Panasonic NV-8399 video cassette recorder (VCR) for permanent storage. Each fish carried a color coded tag for identification.

targeting cross hairs, controlled by the pen of a digitizer tablet, were used to track individual fish in the experiment.

The computer calculated x–y coordinates, based on information from the digitizer tablet and individual test chamber calibration factors. These coordinates were recorded on data disks at time intervals specified by the technician. The pH information for each experiment was entered into a separate data disk

file. Stimulus concentration, channel with stimulus, and other pertinent information[2] about the experiment were added to the end of the tape to ensure that the technician analyzing the experiment was unaware of the presence, location, quality, and quantity of the stimulus. The digitized tracks of individual animals were plotted and the animal's distance from the source of stimuli, time per area of chamber (both measures of attraction or avoidance) and swimming velocity were measured, at user-determined intervals.

Amino acids have been used successfully to study the olfactory system of various fish (Idler et al., 1956, 1961; Sutterlin and Sutterlin, 1971; Hara, 1973, 1976a) and crustacean chemoreception (Mackie and Shelton, 1972; Derby and Atema, 1978). Initially, we tested the following seven amino acids to determine if they would elicit a consistent response from the Atlantic salmon in our test chamber: L-alanine, glycine, L-leucine, L-serine, L-cysteine, L-glutamine, and L-methionine. All amino acid solutions were prepared fresh daily with double-distilled, deionized water in acid-washed glassware. These compounds were chosen for two reasons: (1) when applied to the nares of Atlantic salmon (*Salmo salar*), they produce consistently large responses recorded from the olfactory bulb (Sutterlin and Sutterlin, 1971); and (2) certain of these amino acids are known to elicit behavioral responses in fish (Hoese and Hoese, 1967; Sutterlin and Sutterlin, 1971; Caprio, 1977; Goh et al., 1979; Goh and Tamura, 1980; Atema et al., 1980) and a variety of other animals (McLeese, 1973; Fuzessery and Childress, 1975; Allison and Dorsett, 1977). Taurocholic acid was also screened due to its implication as a naturally occurring olfactory attractant for Arctic char (*Salvelinus alpinus*) and other salmonids (Doving et al., 1980; Stabell, 1984).

Nasal occlusion experiments were conducted to determine the sensory modality involved in the observed behaviors. After running a screening experiment under normal conditions with a stimulus concentration of 10^{-4} M, or 10^{-6} M, the fish were removed and two of the four fish had their nares occluded with Vaseline. The other two fish were sham controls and had distilled water injected into their nares. All four fish were allowed to recover for 1 hr and retested under circumstances identical to the initial testing. This protocol was repeated with five groups of four fish.

The data were analyzed using Student's *t* tests and chi-square tests. Chi-square tests for homogenicity of replicates were performed and accepted for replicates of all tests with the four compounds that elicited reproducible behavioral responses; thus replicates were pooled. Two way analyses of variance (ANOVAs) were performed on the velocity data in order to determine homogenicity of activity levels both between experimental protocols and between fish within a single experiment.

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[2] Physical properties of the water. Temperature 10°C ± 1°, Ca^{2+} concentration 6.8 ppm ± 2.3; alkalinity 12.3 ppm ± 3.2.

RESULTS

Eight compounds were screened to determine if they had an effect on the behavior of salmonids. Fish were attracted to glycine ($>10^{-6}$ M). L-alanine, L-glutamine ($>10^{-6}$ M), and taurocholic acid ($>10^{-6}$ M), all evoked significant ($P \leq 0.001$) avoidance responses when compared to controls. Taurocholic acid elicited the strongest avoidance response followed by L-glutamine and then L-alanine. L-Leucine, L-methionine, and L-cysteine elicited no detectable response (neither attraction or avoidance), and L-serine elicited inconsistent behavior.

We conducted most of our experiments with one compound that produced attraction at a normal pH (pH 7.6, glycine, Figure 2A) and one that fish avoided at a normal pH (pH 7.6, L-alanine, Figure 2B). When glycine was added to one of the channels in the test chamber, fish were attracted to the area of the test chamber containing the highest concentration of this amino acid (Figure 2A). The threshold for this effect was 10^{-7} M ($P \leq 0.001$, Figure 2A, bottom). As the concentration of glycine was increased, the preference of the fish for the side of the chamber containing glycine also increased, up to a maximal preference response at a concentration of 10^{-4} M glycine ($P \leq 0.001$, Figure 2A, bottom). In contrast, L-alanine evoked an avoidance response. The threshold for this effect and the concentration that gave maximal avoidance were very similar to the behavioral threshold and maximal preference response obtained with glycine (Figure 2B).

After having their nares occluded with vaseline, fish which had previously been attracted to glycine spent equal amounts of time in all three areas of the test chamber. Therefore, the amino acids required access to the olfactory receptors in the nares in order to elicit behavioral responses (Figure 3).

The behavioral response of the salmon to L-alanine and glycine changed markedly when the pH of the test chamber was gradually lowered from 7.6 to 5.1 (Figure 4). The initial attraction of fish to glycine changed to a neutral response (Figure 4A). Furthermore, fish that avoided L-alanine at a normal pH were attracted to L-alanine at an acidic pH of 5.1 (Figure 4B). The effect of pH was reversible in all experiments.

Behavior was not altered in response to changes in pH alone. The behavioral parameters of fish in near-neutral water (pH 7.6) was comparable to that in acidic water (pH 5.1, Table 1). When acidic water (pH 5.1) was perfused into one side of the test chamber and near-neutral water (pH 7.6) was perfused into the other side, fish displayed area preference behavior comparable to that observed under control conditions, when identical water was entering both channels (Table 2). In both cases, there was no significant difference in the behavioral parameters of the fish in near-neutral (pH 7.6) and acidic (pH 5.1) water.

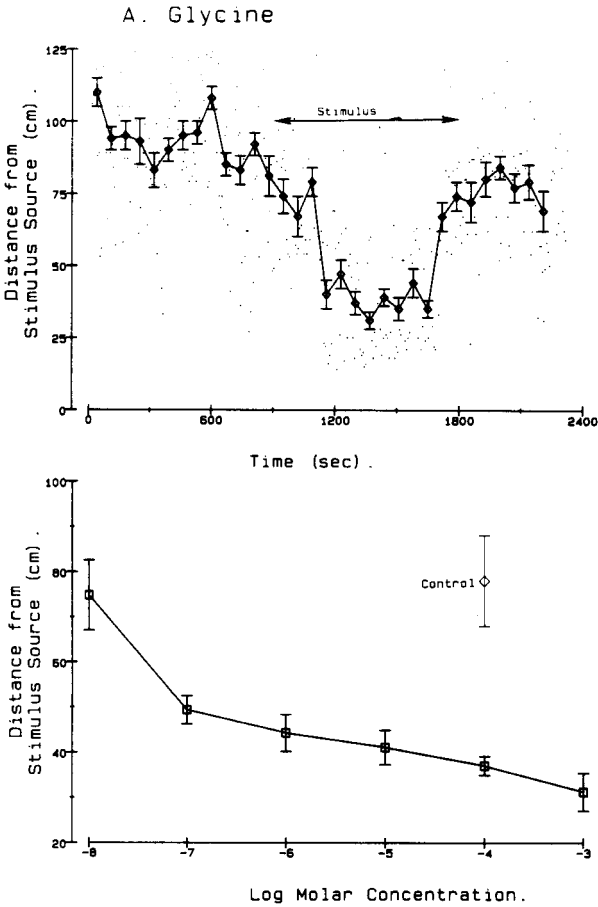The fish did not appear to prefer one area of the chamber over another

FIG. 2. Response of fish to specific amino acids. (A) Top: Response of eight fish to glycine (10^{-5} M, stimulus bar). Distance from the stimulus is used as an indication of preference for, or avoidance of, a particular olfactory stimulant. Diamonds ($\pm$SEM) are means of eight fish, averaged over 200 sec. Dots are mean values of eight fish, averaged every 9 sec. Prior to stimulant introduction, fish did not show a preference for either side of the chamber, but when glycine was added to one side, the fish tended to move into that area and remain there for longer periods of time. Bottom: The attraction to glycine was dose-dependent, with a threshold of between 10^{-8} M and 10^{-7} M ($N = 6$–10 fish/concentration). (B) Top: Response of eight fish ($\pm$SEM) to L-alanine (10^{-5} M). The fish showed no preference for either side of the chamber until L-alanine was added. Fish then moved away from the source of the stimulus. Bottom: The avoidance response was dose-dependent ($N = 6$–10 fish/concentration).
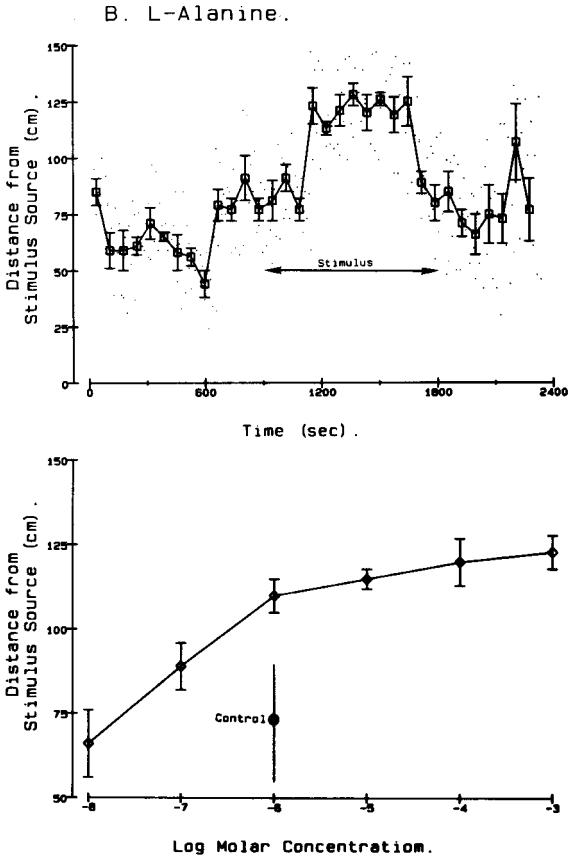
B. L-Alanine.

FIG. 2. Continued

under all control conditions, and we randomly introduced stimuli into one of the two input areas (A or B) during our experiments (Figure 1, see stimulus source arrows Figure 4A and 4B, top). In addition, each fish appeared to behave as an individual, rather than as a member of a school. This was apparent from visual inspection of the videotaped experiments, and it was confirmed statistically using a two-way ANOVA analyzing the velocity of all four fish at different pH levels in each pH modulation experiment. While there was no significant variation in velocity for individual fish between pH levels, there were significant ($P \leq 0.05$) differences between velocities of different fish at the same pH level, thus demonstrating that no schooling was occurring.
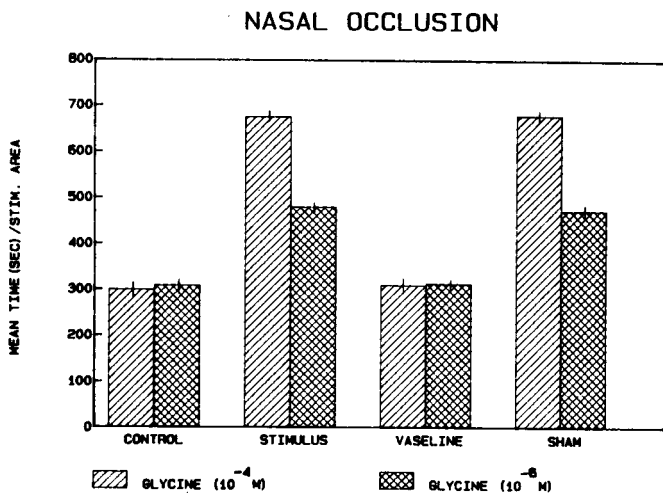
NASAL OCCLUSION

FIG. 3. Response of fish to glycine with and without nares occluded using Vaseline. Under control conditions, with no stimulus present, fish moved randomly about in the test chamber. When glycine was present (stimulus) fish spent more time ($\pm$SEM) in the area of the chamber with the highest concentration of glycine. When those same fish had their nares occluded with Vaseline (Vaseline), they behaved as if no stimulus was present. Sham (sham) control fish, with distilled water injected into their nares rather than vaseline, responded to glycine in a normal manner. At both concentrations of glycine, the responses of the Vaseline occluded and control fish were significantly ($P \leq 0.001$) different from the stimulus and sham control fish ($N = 20$).

DISCUSSION

To our knowledge this is the first demonstration that changes in the pH of surface waters, comparable to those documented in nature, are capable of altering the "normal" behavioral response of fish to olfactory cues. The degree to which our findings pertain to fish migration and behavior in the field remains to be determined. One major problem is that the role of specific substances in fish olfaction and homing is not well understood. Overall, with few exceptions, the specific significance of free amino acids to olfactory-related behavior is not known, and the importance, if any, that amino acids play in salmonid fresh water migration has yet to be demonstrated. The environmental cues which make home stream water unique so that returning adults recognize it and departing smolts imprint to it are at best only vaguely defined. It is considered by many to be heat-labile, volatile, neutral, and dialyzable (Ueda et al., 1967; Hara et al., 1973; Hara, 1976a; Idler et al., 1961; Bodznick, 1978). Others believe a nonvolatile fraction to be important (Atema et al., 1973). Amino acids,

usually in mixtures, can elicit specific behaviors such as exploration and feeding in the goby (*Gobiosoma bosci*) (Hoese and Hoese, 1967) and avoidance by Pacific salmon (Idler et al., 1956, 1961). However, the degree to which amino acids influence the homing behavior of salmonids is not known.

We chose to use amino acids for olfactory stimuli because previous electrophysiological data indicated that the olfactory system responded to certain amino acids in a dose-dependent manner and, in our hands, they gave us reliable, quantitative, avoidance–attraction responses. The dose–response curves that we obtained using our behavioral assay are similar to those determined with the same compounds using electrophysiological techniques (Hara, 1973). Experiments are presently underway to determine how pH affects the behavioral response of salmonids to natural stimuli, such as conspecific odors and home-stream water.

The differential responses of Atlantic salmon to the same compound at two different pH levels is probably the result of a modification of some component of the olfactory system. The level at which this change takes place is not clear, but it may occur at any one, or a combination of levels; receptor site alteration, stimulus molecule charge distribution, or interaction between the two. These receptors are thought to be membrane proteins with anionic and cationic binding sites (Hara, 1982). Hara (1976b) used olfactory bulb recordings to monitor the response of adult rainbow trout (*Salmo gairdneri*) to numerous amino acids at different pHs. He recorded maximal responses to individual amino acids at their isoelectric points (both glycine and L-alanine have isoelectric points of 6.02; Lehninger, 1982), indicating changes in charge may interfere with normal amino acid-receptor interactions. Since the olfactory receptors are exposed to the environment, with limited protection from a permeable mucus layer, they are subject to changes in the external environment (Brown et al., 1982). The fact that our pH effects were reversible suggests that at pH 5.1 the receptors were not permanently damaged. The manner in which one or more of the components of the olfactory system are consistently and reversibly altered by pH, both in electrophysiological (Hara, 1976b) and behavioral studies, remains to be determined.

Our investigations thus far have been limited to juvenile salmonids. We have tested chinook salmon (*Oncorhynchus tshawytscha*) juveniles as well as Atlantic salmon juveniles, and their responses were similar in all cases. Although we do not presently know the extent to which our data on juveniles pertain to adults, it has been shown that salmon parr have the ability to discriminate between odors in much the same way as adult salmon (Stabell, 1982, 1984), and our preliminary data indicate that pH influences the way adult salmon respond to taurocholic acid (Royce-Malmgren and Watson, in preparation). If low pH alters the manner in which adult fish respond to the odor of their home stream water in the same way it modifies the olfactory-related behavior of ju-
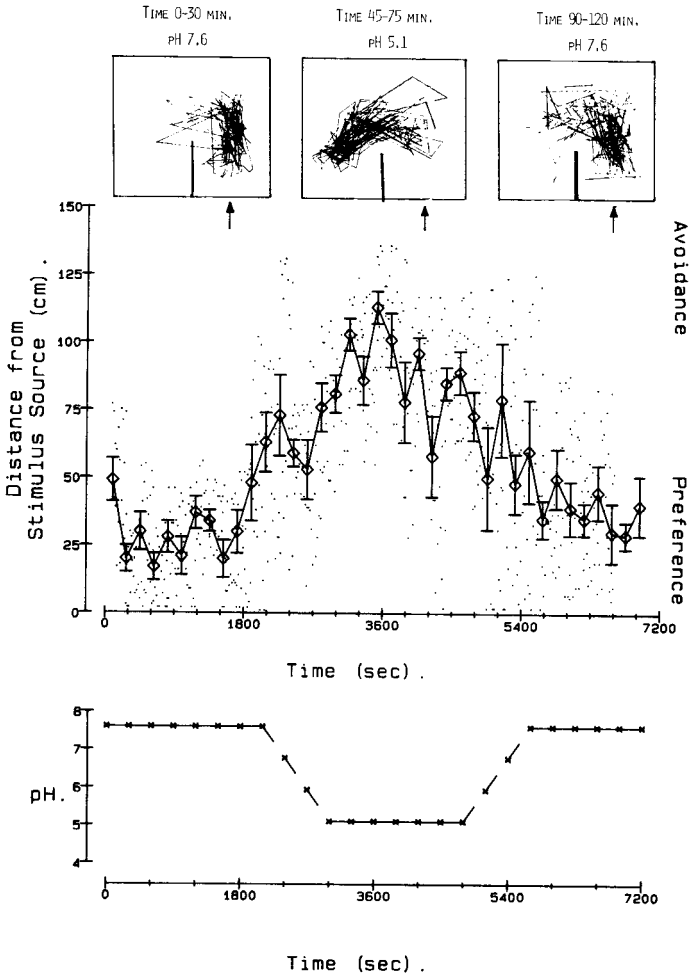
A. Glycine.

FIG. 4. Modification of the behavioral response of Atlantic salmon to amino acids by pH. (A) Response to 10^{-4} M glycine while the pH of water in the test chamber was changed from 7.6 to 5.1 and then back to 7.6. Top: The track of an individual fish during the course of the experiment. Arrows indicate the source of the glycine. During the initial 30 min of the experiment, the fish spent most of its time in the side of the chamber containing the highest concentration of glycine. However, when the pH was gradually lowered to 5.1 (see bottom graph), the fish moved randomly about the chamber. When the pH was returned to 7.6, the fish was again attracted to the glycine. Center: The aforementioned experiment was repeated with 20 different fish and the results were
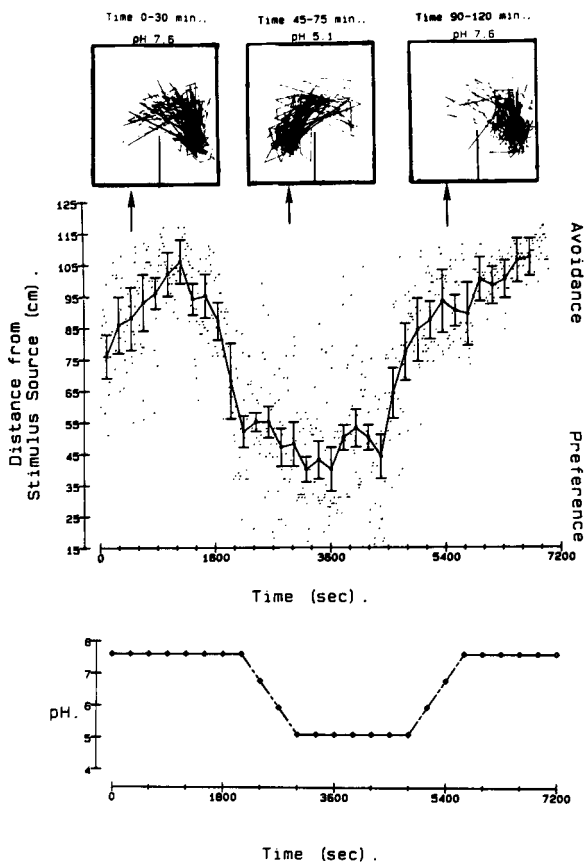
FIG. 4. Continued tabulated and plotted. Diamonds (±SEM) are means of 20 fish, averaged over 200 sec. Dots are mean values of 20 fish, averaged every 9 sec. (B) The response to L-alanine (10^{-4} M) during pH changes. Center: At a pH of 7.6, the fish avoided the L-alanine, but when the pH (see bottom graph) was lowered to 5.1, they were attracted to the stimulus. Note that in the track of the fish shown, the L-alanine was introduced into the left-hand side of the test chamber (in contrast to the glycine experiment shown in A, top). The side of the chamber used for the stimulus source was varied randomly for each set of experiments. The tracks also show that the activity of the salmon remained fairly constant throughout the course of the experiment.

TABLE 1. COMPARISON OF BEHAVIORAL PARAMETERS OF ATLANTIC SALMON IN
ACIDIC (pH 5.1) vs. NEAR-NEUTRAL (pH 7.6) WATER ($N = 20$)

	pH 5.1	pH 7.6
Mean velocity (cm/sec)	7.5 ± 1.3^a	7.7 ± 1.1
Mean distance (cm to stimulus source)	75.9 ± 1.5	74.9 ± 1.5
Mean time (sec)/area with stimulus	592.5 ± 13.5	622.0 ± 16.8

[a] Standard error of means.

TABLE 2. RESPONSE OF ATLANTIC SALMON PARR TO ACIDIC (pH 5.1) WATER
($N = 20$)

Control[a]		Experimental	
Area	Time (sec)/area	Area	Time (sec)/area
A	614 ± 15.8^b	A (pH 5.1)	592 ± 11.6
B	604 ± 10.4	B (pH 7.6)	589 ± 14.9
Common	580 ± 18.9	Common	619 ± 12.2

[a] The pH was 7.6 throughout the test chamber.
[b] Standard error of means.

venile salmon, then their ability to locate a suitable spawning site may be affected. As a result, fish would become dispersed and spawn in areas unsuitable for the development of eggs, fry, and juveniles. This could eventually lead to a reduction in recruitment and a decline in the salmonid population, even at the nonlethal pH levels now common in many New England and Canadian rivers.

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