Temperature and Photoperiod Regulation of Rheotropic Behavior in Prespawning Common Shiners, *Notropis cornutus*

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The upstream orientation and frequency of upstream movement of prespawning common shiners, *Notropis cornutus*, in response to a water current simulated by moving a striped background past the fish were observed at three temperatures (10, 15, 20°C) and two photoperiods (12L:12D and 16L:8D). The greatest frequency of upstream movement was induced by a combination of spring day lengths and warm water temperatures. Further increases in the frequency of upstream movement followed immediate 5°C increases in water temperature. Neither temperature nor photoperiod had a major effect on the frequency of upstream orientation. The significance of environmental regulation of rheotropism as a mechanism of upstream migration is discussed.

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Nous avons observé, à trois températures (10, 15, 20°C) et à deux photopériodes (12J:12N et 16J:8N), l'orientation en amont et la fréquence des mouvements vers l'amont de ménés à nageoires rouges, *Notropis cornutus*, en réponse à un courant d'eau simulé par le déplacement d'un fond de scène rayé près du poisson. La fréquence maximale de mouvements vers l'amont est provoquée par une combinaison de photopériodes printannières et de chaudes températures de l'eau. La fréquence des mouvements vers l'amont augmente encore après augmentations immédiates de 5°C de la température de l'eau. Ni la température ni la photopériode n'ont d'effet majeur sur la fréquence de l'orientation en amont. Nous discutons de la signification du réglage du rhéotropisme dans le milieu comme mécanisme de migration vers l'amont.

THE term rheotropism is used as a portmanteau word to cover all the reactions that a fish might make in response to a current of water, either directly as a response to water flowing over the body surface or indirectly as a response to the visual, tactile, or inertial stimuli resulting from the displacement of the fish in space (Harden Jones 1968; Arnold 1974). The rheotropic response is composed of an orientational and a kinetic component; fish generally turn to head into a current and adjust their swimming speeds in response to the rate of the current.

Several environmental factors have been observed to affect the rheotropic response, either inducing it, reversing the sign of the taxis, or altering the intensity of the kinetic component, but little

more is known about this subject (review by Arnold 1974). As such, environmental regulation of the rheotropic response may play an important role in the migration of fish. This paper reports the results of experiments designed to quantify the orientational and kinetic components of the rheotropic response of the prespawning common shiner, *Notropis cornutus*, a stream-dwelling migratory species, and to assess the role of temperature and photoperiod in regulating the rheotropic response as a mechanism of upstream migration.

Materials and Methods

OPTOMOTOR TANK

A simple and efficient way of observing the rheotropic response is to simulate the visual stimuli produced by displacement in a water current by moving the background past the fish. Responses to displace-

ment of visual images are specifically referred to as optomotor responses (Arnold 1974). All observations were made in the optomotor tank illustrated in Fig. 1 which was fashioned after that described by Harden Jones (1963). The outer tank was constructed of plywood 121 cm square and 43 cm deep. Into this tank was placed a stainless steel drum attached to a central aluminum core. The opposing surfaces of these two concentric cylinders were painted alternating black and white stripes at intervals of 2.5 cm forming an inner and outer striped background. This assembly was attached to a central shaft and rotated within the outer tank by means of a variable speed reversible motor. The inner stationary tank was constructed of two clear concentric plexiglass rings 43 cm high with an outer diameter of 100 cm and an inner diameter of 20 cm defining a circular channel 40 cm wide. The floor of the channel was featureless and constructed of white plexiglass. The inner tank was suspended from the top of the outer tank such that the enclosed channel was surrounded by the inner and outer rotating striped backgrounds. Water contained within the inner tank was thus separate from water in the outer tank and remained calm despite the rotation of the background. A circular sheet of white plexiglass (not shown in the figure) was attached to the top of the central shaft forming a featureless roof. The inner tank was illuminated from above the roof and surrounded with black curtains. Fish were observed through a peephole in the curtains and their responses to the moving background recorded on a eight-channel event recorder.

Water in the outer tank was circulated through a reservoir equipped with cooling coils and immersion heaters. The floor of the rotating striped drum was perforated to permit free circulation of heated or cooled water around the inner tank providing for accurate temperature control. Water level in the outer tank was set by means of an adjustable standpipe and the inner tank was filled with a water to a depth equal to the level of water in the outer tank. Water depth in the inner tank was maintained at 12 cm for all experiments.

EXPERIMENTAL PROCEDURE

Common shiners were netted in Laurel Creek on the University of Waterloo campus during their spring upstream spawning migrations in 1975 and 1976. In 1975 fish were captured on May 5 at a water temperature of 12°C and in 1976 on April 17 at a water temperature of 17°C. All fish were held in two closed-system, air-lift stream tanks (described by Gee and Bartnik 1969). Water velocity in the stream tanks was maintained at 10 cm/s. Each stream tank was equipped with lights, cooling coils, and immersion heaters for control of water temperature and photo-period. In 1975 two groups of 30 fish each and in 1976 two groups of 50 fish each were held in the stream tanks under a day length of 12 and 16 h, respectively, at a water temperature of 10°C for a period of 2 wk prior to the beginning of observations in the optomotor tank. Fish were fed regularly with frozen brine shrimp. Fish examined ranged in fork length from 8.5 to 10.1 cm.

In 1975, 10 fish from each day-length group were observed singly in the optomotor tank at a water temperature of 10°C. The temperature in the optomotor and stream tanks was then raised to 15°C. After an acclimation period of at least 24 h to the new temperature, 10 new fish from each day-length group were observed singly in the optomotor tank. This procedure was repeated for fish observed at 20°C.

In 1976 six groups of 10 fish each were observed under the same conditions of temperature and day-length as described for 1975. Furthermore, the fishes' responses to immediate increases in temperature were observed. Ten fish from each day-length group held at 10°C were observed singly in the optomotor tank at a water temperature of 15°C. Thus, these fish experienced an immediate 5°C increase in water temperature prior to observation. Similarly, 10 fish from each day-length group held at 15°C were observed singly at a water temperature of 20°C.

In 1975 each fish observed in the optomotor tank was allowed 30 min to acclimate to the tank before the background was rotated. Fish were observed for 5 min at each of seven rates of background rotation equivalent to current rates of 2.5, 5, 10, 15, 20, 25, and 30 cm/s (total observation time = 35 min). The direction of background rotation was alternated between fish.

The rheotropic response exhibited by common shiners in 1975 was highly variable. A major source of this variability was the nature of the experimental procedure. Fish exhibited agitated behavior in response to the initial commencement of background rotation and subsequent alteration of background speeds as well as showing signs of fatigue after 35 min of observation. Therefore, each fish observed in 1976 was placed in the optomotor tank with the background revolving at a rate equivalent to a water current of 15 cm/s. The rate of background rotation
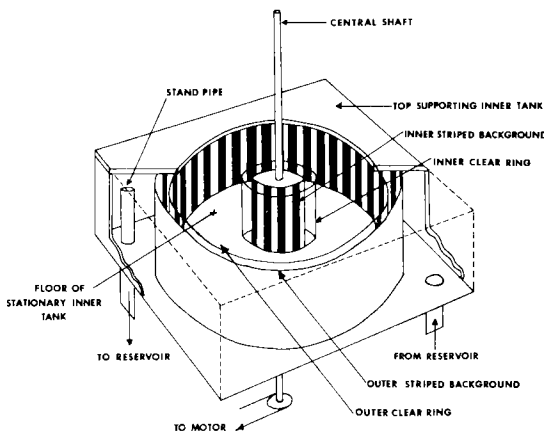

FIG. 1. The optomotor tank used to observe the reaction of common shiners to a moving background. Part of the outer tank is cut away to reveal the outer revolving striped background.

was kept constant for the entire observation period which was restricted to 15 min. Each fish was allowed from 5 to 10 min to acclimate to the optomotor tank. Any fish exhibiting excessively agitated behavior or no response at all to the moving background after 10 min of acclimation was not used in the experiment.

TREATMENT OF RESULTS

The orientational component of the rheotropic response was quantified by recording the proportion of total observation time that fish spent swimming in the same direction as the moving background (frequency of positive rheotaxis). In interpreting the results it must be remembered that swimming in the same direction as the background is equivalent to swimming into a current. The kinetic component of the rheotropic response was quantified by recording the proportion of total observation time a fish spent swimming faster than the moving background (frequency of gain).

The data for the frequency of gain were analyzed by a standard two-way analysis of variance with interaction. The model was of the form:

$$Y_{ijk} = \mu + t_i + p_j + (tp)_{ij} + \epsilon_{ijk}$$

where, μ is the overall mean; t_i is the effect of the ith temperature treatment $i = 1,...,5$; p_j is the effect of the jth photoperiod $j = 1,2$; $(tp)_{ij}$ is the photoperiod $\times$ temperature interaction; Y_{ijk} is the observed frequency of gain for the kth ($k = 1,...,10$) fish at the ith temperature and the jth photoperiod; ϵ_{ijk} is the experimental error corresponding to Y_{ijk}. Prior to detailed analysis, the residuals from the model (the estimates of the ϵ_{ijk}'s) were checked for normality and constant variance. There was no evidence to suggest that these basic assumptions were broken; thus, the experimental error $s^2 = 0.0592$ with 90 df is used throughout the analysis of the kinetic component of the rheotropic response as the best estimate of the common experimental error.

To get a more exact understanding of the significant effects, the Student-Newman-Keuls test and orthogonal contrasts were used.

Data on the frequency of positive rheotaxis were such that neither normality nor constant variance could be assumed and data were split into three categories and analyzed by means of contingency tables.

Results

QUALITATIVE OBSERVATIONS

During the 1975 experimental series, common shiners were observed to rest on the bottom of the optomotor tank and exhibit an optokinetic nystagmus (Arnold 1974) at background speeds < 5 cm/s. This behavior involved movement of the head and eyes in the same direction and at the same speed as the moving background followed by rapid recovery movements of the head and eyes in the opposite direction. At background speeds > 5 cm/s, this behavior was replaced by a full optomotor response in which fish left the

bottom of the tank and swam parallel to the moving background. In 1975 four distinct types of optomotor responses were observed.

1) Fish swam round the outer periphery of the tank in the same direction as the moving background (positive rheotaxis). The proportion of time fish spent swimming faster than the background was similar at each rate of background rotation but this frequency differed widely between individual fish.

2) Fish swam round the outer periphery of the tank in the opposite direction to the moving background (negative rheotaxis).

3) Fish swam rapidly back and forth over short distances at the outer periphery in an apparent attempt to intercept the moving stripes.

4) Fish swam tail-first round the outer periphery in the same direction as the moving background. This unusual behavior involved flexing the caudal fin far to one side and short strokes of the pectoral fins. The more powerful strokes of the caudal and pectoral fins were towards the head. This response generally did not persist at background speeds > 10 cm/s.

Individual fish tested in 1975 exhibited all four optomotor responses in widely varying proportions.

During the 1976 experimental series common shiners exhibited positive rheotaxis immediately upon being introduced into the optomotor tank with the background revolving constantly at 15 cm/s. Negative rheotaxis was rarely observed and optomotor responses (3) and (4) were not observed.

The pattern of swimming exhibited by common shiners in both years varied with temperature. At 10°C fish swam close to the bottom of the tank and maintained the same depth while swimming round the tank. At 20°C fish swam from the surface to the bottom of the tank in sine wave fashion never maintaining the same depth while swimming round the tank. Both patterns of swimming were observed at 15°C.

The 1975 experimental series indicated that the frequency of positive rheotaxis and the frequency of gain exhibited by common shiners varied according to temperature and day length. However, both of these frequencies were highly variable among fish of the same experimental group. As a result, differences between groups were obscured and no definite conclusions could be reached regarding the nature and extent of the regulation of rheotropism by temperature and photoperiod.

QUANTITATIVE RESULTS

The frequency of positive rheotaxis and the frequency of gain did not vary as greatly among fish

of the same experimental group in 1976 as in 1975. This reduction in within-group variation permitted a complete quantitative analysis of the 1976 data. These results are summarized in Table 1. The analyses of the orientational and kinetic components of the rheotropic response are dealt with below.

Kinetic component — The significant sources of variation between observed differences in the frequency of gain were temperature ($F = 13.0$, $P < 0.001$) and an interaction between temperature and photoperiod ($F = 3.3$, $P < 0.01$).

Variation in mean frequency of gain was as follows:

acclimated 24 h			immediate 5°C increase	
10°C	15°C	20°C	15°C	20°C
0.117	0.194	0.517	0.475	0.532

Mean frequency of gain of fish acclimated 24 h to 10 and 15°C were significantly less than the remainder ($P < 0.05$, Student-Newman-Keuls test). Thus, fish observed at 15°C following 24 h of acclimation exhibited a lower frequency of gain than fish observed at 15°C following an immediate 5°C increase in water temperature. Fish observed at 20°C exhibited a similar frequency of gain regardless of acclimation time. The frequency of gain exhibited by fish observed at 20°C after 24 h of acclimation was significantly greater

TABLE 1. The effect of water temperature and day length on the orientational and kinetic components of the rheotropic response of the common shiner, *Notropis cornutus*. $N = 10$; frequency of positive rheotaxis = proportion of 15-min observation time fish spent swimming in the same direction as the moving background; frequency of gain = proportion of 15-min observation time fish spent gaining on the moving background; *fish were acclimated at least 24 h at that temperature; **fish were observed following an immediate 5°C increase in water temperature.

Day length (h)	Temp. (°C)	Mean frequency	
		+ve rheotaxis	gain
12	10*	0.98	0.05
	15**	0.95	0.45
	15*	0.98	0.18
	20**	0.95	0.70
	20*	0.80	0.63
16	10*	0.97	0.18
	15**	0.99	0.50
	15*	0.99	0.20
	20**	0.90	0.36
	20*	0.93	0.40

than the frequency of gain observed at 10 and 15°C after 24 h of acclimation.

The variation in frequency of gain due to the interaction of temperature and photoperiod was analyzed by means of orthogonal linear contrasts. In this case, the first contrast amounted to a comparison of the regressions of frequency of gain on the three temperatures of acclimation for each photoperiod. The contrast showed that the slopes of the two regression lines ($y = -0.583 + 0.058T$ for 12-h day length; $y = -0.065 + 0.022T$ for 16-h day length) were significantly different ($t = 2.34$, $P < 0.02$) indicating a greater increase in the frequency of gain with temperature of acclimation for fish exposed to 12 h of daylight than for fish exposed to 16 h of daylight. This difference is responsible for nearly 50% of the interaction variation. There was no statistical evidence of a significant deviation from linearity in the two regressions.

Another orthogonal contrast revealed that most of the remainder of the interaction variation was due to the differential response to immediate increases in temperature exhibited by fish held under the two photoperiods. Fish exhibited a similar frequency of gain in response to a water temperature of 15°C following an immediate 5°C increase regardless of day length (0.45 for 12-h day length and 0.50 for 16-h day length). However, fish exposed to a 12-h day length exhibited a significantly greater frequency of gain in response to a water temperature of 20°C following an immediate 5°C increase than did fish exposed to a 16-h day length (0.70 for 12-h day length and 0.36 for 16-h day length; $P < 0.02$).

Orientational component — The number of common shiners exhibiting positive rheotaxis 100% of the time, between 90 and 99% of the time, and < 90% of the time at two photoperiods and five temperature conditions is presented in Table 2. Photoperiod was not a significant source of variation between the number of fish observed within each frequency category ($\chi^2 = 1.09$, df = 2, $P > 0.05$), whereas temperature was a significant source of variation ($\chi^2 = 40.22$, df = 8, $P < 0.001$). In particular, fish observed at 20°C following 24 h of acclimation exhibited lower frequencies of positive rheotaxis than fish observed at other temperatures.

Discussion

This study demonstrates that the response of common shiners to a simulated water current is affected by water temperature and photoperiod. Interpreting the experimental variable of frequency of gain as a measure of the frequency

TABLE 2. The number of common shiners exhibiting positive rheotaxis as percent of 15-min observation time at five temperature conditions; *fish acclimated at least 24 h at that temperature; **fish observed following an immediate 5°C increase in water temperature.

Frequency of +ve rheotaxis (% observation time)	No. fish observed at (°C)				
	10*	15*	20*	15**	20**
Fish exposed to 12-h day length					
100	6	8	0	5	4
90–99	4	1	2	4	4
<90	0	1	8	1	2
Fish exposed to 16-h day length					
100	8	7	1	6	2
90–99	0	3	5	4	6
<90	2	0	4	0	2

of upstream movement, the combination of spring day length (12 h) and warm water temperatures (20°C) induced the greatest frequency of upstream movement in the common shiner. Further increases in the frequency of upstream movement followed rapid 5°C increases in water temperature in combination with spring and summer day lengths (Table 1), but most consistently in combination with spring day lengths. Interpreting the experimental variable of frequency of positive rheotaxis as a measure of the frequency of upstream orientation, neither temperature nor photoperiod had a major effect on the frequency of upstream orientation. Although the frequency of this behavior decreased at 20°C in combination with spring and summer day lengths, common shiners continued to exhibit upstream orientation at least 80% of the time (Table 1).

Water temperature appears to be an important factor affecting the rheotropic response of juveniles and adults of several species of fish. Keenleyside and Hoar (1954) studied the rheotactic responses of three species of juvenile Pacific salmon (genus *Oncorhynchus*) under varying temperature conditions and demonstrated that rheotaxis was predominantly positive at lower temperatures but became actively negative at higher temperatures. Northcote (1962) concluded that temperature played a predominant role in controlling the rheotropic response of juvenile rainbow trout, *Salmo gairdneri*, migrating into Loon Lake. Of particular interest is the observation that fingerlings subjected to rapid 5°C increases in water temperature exhibited immediate increases in upstream movement. The evidence concerning the influence of temperature on upstream movement in adult salmonids is extensive and conflicting (review by Banks 1969). Lindsey and Northcote (1963) reported that the time of first entrance of adult redside shiners, *Richard-*

sonius balteatus, into spawning streams showed a close correlation with the date at which creek temperatures first exceeded 10°C. Throughout the spawning season, surges of upstream migration were associated with rising water temperatures. MacLean and Gee (1971) have suggested that a positive rheotactic response in association with water temperatures between 15 and 20°C may be the mechanism responsible for the observed migration of prespawning brook sticklebacks, *Culaea inconstans*, into the shallow warm meltwater ponds and ditches where they reproduce. This evidence and that provided by the present study suggest that water temperature is a common factor controlling upstream movements in several species of fish with varying orientational requirements.

The role of photoperiod in regulating the rheotropic response is not well documented. Northcote (1958) demonstrated that fingerling rainbow trout held at a 16-h day length exhibited a strong negative rheotaxis, particularly at low water temperatures, whereas 8-h day length fingerlings exhibited positive rheotaxis at low water temperatures. The results of this study demonstrate that the interaction of photoperiod and temperature regulates the frequency of upstream movement of common shiners. Thus, the mechanism of upstream migration is complex and not regulated only by solitary environmental factors.

A common observation in many studies of rheotropism in fishes as revealed by their reactions to moving backgrounds is the occurrence of wide variations in the optomotor reactions of individual fish of the same species. A number of reasons have been presented to explain this variation. The present study has demonstrated that temperature and photoperiod are two important sources of such variation. Clausen (1931) examined the optomotor reactions of the common

shiner and observed positive rheotaxis, negative rheotaxis, and "tail-first" swimming. Clausen noted an apparent stimulatory effect of the rotation of the background on the occurrence of negative rheotaxis regardless of whether the background was moved quickly or slowly. The results of the 1975 experimental series indicate a similar relationship. Negative rheotaxis, as well as optomotor reaction (3) (see Qualitative Observations), was observed frequently in response to the alteration of the rate of background rotation but independent of the magnitude of rate. In 1976 the rate of background rotation was held constant and common shiners exhibited positive rheotaxis most of the time. As such, alteration of the rate of background rotation may in itself be an important source of variation between the optomotor reactions of individual fish.

The upstream movements of common shiners in this study conform to the general pattern of migratory activity exhibited by common shiners in nature. An inshore migration in lakes and an upstream movement in streams are made by common shiners in early May when the water has reached a temperature of 12–15.5°C (55–60°F) (Raney 1940). Spawning usually begins when water temperatures reach 15.5–18°C (60–65°F) usually in May or June (Raney 1940). The present study has revealed that temperature is more important than photoperiod in controlling upstream migration. This conclusion is supported by the observation that in 1976 shiners were captured in mid-April when water temperatures were already at 17°C due to an early spring heat wave. Water temperatures subsequently declined to 10°C but attempts to capture shiners in May and June failed, a probable indication that spawning had already been completed.

The regulation of the rheotropic response of common shiners by the nondirectional environmental factors of temperature and photoperiod forms the basis of a mechanism of upstream migration that ensures shiners arrive on the spawning site at a time that corresponds with the required spawning temperature. Such a mechanism is of particular adaptive significance in small streams that may be subject to rapid fluctuations in water temperature early in the spring.

Acknowledgments

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