

# Modification of the Rheotropic Behavior of Male Rainbow Trout (*Salmo gairdneri*) by Ovarian Fluid

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The upstream orientation and frequency of upstream movement of ripe male rainbow trout (*Salmo gairdneri*) in the presence of ovarian fluid obtained from spawning females of the same species were observed and quantified. In a stream tank, male trout moved upstream in the ovarian fluid odor plume. In an optomotor tank, male trout exhibited an increase in the frequency of upstream orientation and movement in the presence of diffuse, nondirectional ovarian fluid. It is concluded that water currents provide directional cues and olfactory stimuli regulate the orientational and kinetic components of the rheotropic response. The significance of this mechanism of orientation in fish migration is discussed.

*Key words:* rheotropism, behavior, olfaction, orientation, migration, ovarian fluid

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Nous avons observé et quantifié l'orientation vers l'amont et la fréquence des mouvements vers l'amont de truites arc-en-ciel mâles matures en présence de liquide ovarien de femelles de la même espèce en voie de fraie. Dans un bassin dans un cours d'eau, les truites mâles se dirigent vers l'amont dans la zone d'odeur du liquide ovarien. Dans un bassin optomoteur, les truites mâles accusent une augmentation de fréquence de l'orientation des mouvements vers l'amont en présence de liquide ovarien diffus, non directionnel. Nous concluons que les courants d'eau fournissent des indications quand à la direction et que les stimuli olfactifs règlent la partie orientation et cinétique de la réaction rhéotrope. Nous analysons la signification de ce mécanisme d'orientation chez les poissons.

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THE term rheotropism describes 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 fish in space (Harden Jones 1968; Arnold 1974). The rheotropic response consists of an orientational and a kinetic component; fish generally orient into a current and adjust their swimming speeds in response to the rate of the current. Several environmental factors affect the orientational and kinetic components of rheotropism and some evidence suggests that such environmental regulation of rheotropism is important in the migration of fish (Dodson and Young 1977).

Olfactory clues have long been implicated in the

migration of fish. The olfactory hypothesis for salmon homing (Hasler and Wisby 1951) has been largely verified by a series of experiments using artificial imprinting to a synthetic chemical (Hasler et al. 1978). However, the natural olfactory cues associated with home streams have not been identified. Hasler and Wisby (1951) postulated that each stream has a different odor due to local differences in soil and vegetation of the drainage basin. Solomon (1973) postulated that metabolic products or race-specific pheromones may be responsible for the homing of Atlantic salmon, and Nordeng (1977) presented a similar hypothesis for migratory Arctic char (*Salvelinus alpinus*). The mechanism(s) of orientation by which fish obtain directional information from such olfactory cues has not been adequately demonstrated.

The behavior of mature male fish is altered by a pheromone associated with the gravid female (Tavolga 1956; Timms and Kleerekoper 1972; Crapon de

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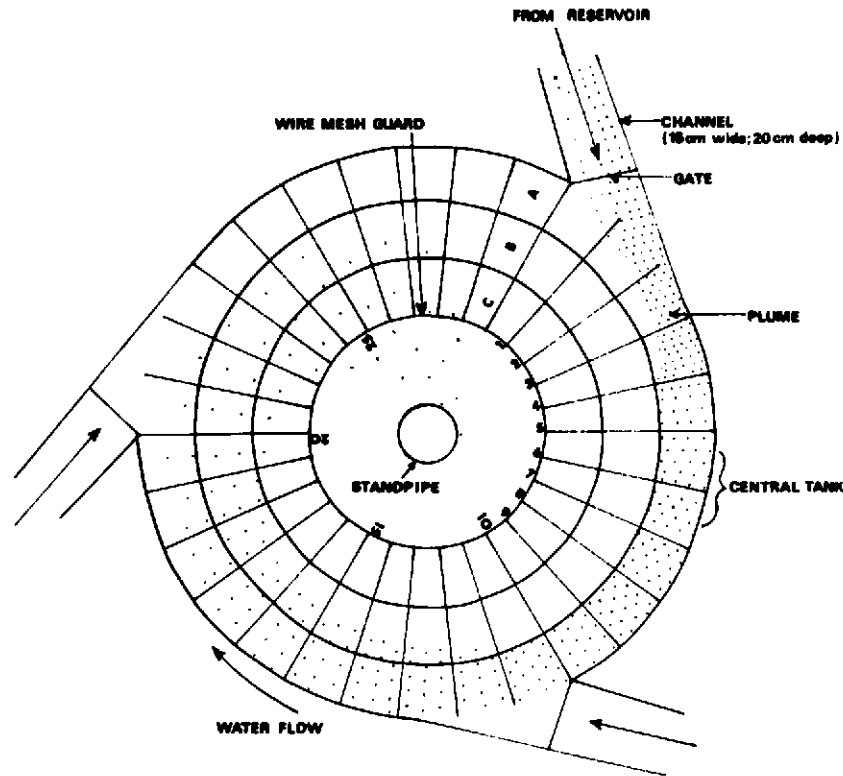


FIG. 1. Circular stream tank used to assess the attractiveness of ovarian fluid to male rainbow trout. Letters indicate the 3 radial sections and numbers indicate the 30 angular sections. Stippling indicates the extent and concentration gradient of the odor plume. Supply reservoirs are omitted from the diagram.

Caprona 1974; Partridge et al. 1976), and ovarian fluid contains this as yet unidentified pheromone (Newcombe and Hartman 1973; Partridge et al. 1976). In this study, the rheotropic response of ripe male rainbow trout to a real and simulated water current in the presence of dilute ovarian fluid obtained from spawning females was observed. The purpose of the study was to determine whether ovarian fluid would stimulate the upstream movement of male trout and to describe the mechanism(s) of orientation responsible for any such movement.

### Materials and Methods

In the fall of 1976 ripe male rainbow trout (*Salmo gairdneri*) were obtained from Creekbank Hatchery, Elmira, Ontario, and held in the laboratory in 790-L and 2500-L tanks equipped with fluorescent cool white lighting and time switches set for an 8 h daylength. The tanks were supplied with local well water at a constant temperature of 11°C. The trout were 30–50 cm long (FL) and weighed 200–400 g.

The rheotropic behavior of rainbow trout in the presence of ovarian fluid was observed initially in a circular stream tank (Fig. 1) made of galvanized steel and consisting of three channels 60 cm long attached tangentially to a central tank 152 cm diam and 23 cm deep. Each channel was at-

tached distally to an 80-L supply reservoir and water from the reservoirs flowed down the channels into the central tank at 15 cm/s. The water level was maintained at 18 cm by an adjustable standpipe located in the middle of the central tank. A wire mesh guard 60 cm diam was placed around the standpipe to prevent fish from being sucked down the outlet. Wire mesh gates were placed at the entrance of each channel to the central tank. Therefore, fish were restricted in their movements to a circular channel 46 cm wide. Black curtains surrounded the stream tank which was illuminated from 6 m above by a 7500-W spotlight. All observations were recorded with an XL-400 Minolta Super 8 movie camera at a rate of 1 exposure per minute from the same height.

Groups of five fish each were observed swimming in the stream tank. Each group was allowed 30 min to acclimate following their introduction into the tank. After a 30-min observational period during which time fish movement was filmed, ovarian fluid was introduced at a constant rate into one of the channels and fish movement filmed for another 30 min. The source channel was changed for successive replicates.

Ovarian fluid was collected on several occasions from female rainbow trout being stripped of their eggs during the hatchery spawning period. The fluid as collected was considered to be a 100% solution and subsequent dilutions were made by mixing the ovarian fluid with well water.

Preliminary testing at concentrations of 50, 10, 1, 0.5, 0.1, and 0.01  $\mu\text{L/L}$  in the source channel indicated that obvious changes in rheotropic behavior occurred at the 0.1- $\mu\text{L/L}$  level. Therefore, 15 replicates of five fish each were observed in the stream tank in response to ovarian fluid at a concentration of 0.1  $\mu\text{L/L}$  in the source channel.

To analyze the movement of ripe male trout in response to ovarian fluid, the stream tank was divided into 3 radial (designated A, B, C) and 30 angular positions (designated 1, 2, 3 . . . , 30) relative to the source channel, thus splitting the central tank into 90 sections (Fig. 1). The films of fish movement were viewed on an editing scope and each fish was placed into one section for each minute of observation. Dye was introduced into each channel on several different occasions and the resultant plume was plotted (Fig. 1). The plume initially moved downstream close to the outer wall of the tank (sections A1-A14) before spreading out and moving toward the center of the tank (sections B11-B23 and C16-C26). The numbers of fish observations before and after the introduction of ovarian fluid were recorded for the upstream end of the plume (defined as sections A1-A14) where the concentration of ovarian fluid was greatest and for the downstream end of the plume (defined as sections B11-B23 and C16-C26) where the concentration declined. Variations occurred in the extent of the plume due to uncontrolled fluctuations in water velocity and minor differences in the geography of the tank between different channels. As it was impossible to monitor the exact position of the plume during each replicate, the plume as defined above represents its minimum extent. Thus we have tended to underestimate the extent of the plume and, as a result, the number of observations of fish in the plume.

The data for the number of observations of fish in the plume before and after the addition of ovarian fluid was analyzed by a 2 factor analysis of variance with interaction and replication. The model was of the form

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

where  $\mu$  is the overall mean

$t_i$  is the effect of the  $i$ th time interval

$i = 1, 2$  (before, after)

$p_j$  is the effect of the  $j$ th plume segment

$j = 1, 2$  (upstream, downstream)

$(tp)_{ij}$  is the time interval  $\times$  plume segment interaction

$\gamma_k$  is the effect of the  $k$ th replicate

$Y_{ijk}$  is the number of observations of fish for the  $k$ th replicate at the  $i$ th time interval in the  $j$ th plume segment

$\epsilon_{ijk}$  is the experimental error corresponding to  $Y_{ijk}$ .

Observations in the stream tank alone did not adequately describe the mechanism of orientation responsible for the movement of male trout responding to ovarian fluid. To investigate this mechanism further, the rheotropic response of ripe male trout in the presence of ovarian fluid was measured in the optomotor tank described and illustrated by Dodson and Young (1977). The optomotor tank did not generate a true current but rather simulated the visual stimuli produced by displacement in a water current by moving a striped background past the fish. Therefore, unlike the stream tank, the ovarian fluid in the optomotor tank was diffuse and nondirectional thus eliminating the odor gradient as an orientational cue.

The rheotropic response consists of an orientational and kinetic component. The orientational component 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) which is equivalent to orienting upstream. The kinetic component of the rheotropic response was quantified by recording the proportion of total observation time that the fish spent swimming faster than the moving background (frequency of gain) which is equivalent to upstream displacement.

Five groups of 10 ripe male rainbow trout each were observed singly in the optomotor tank in the presence of ovarian fluid at concentrations of 0.0 (control),  $10^{-4}$ ,  $10^{-3}$ ,  $10^{-2}$ , and  $10^{-1}$   $\mu\text{L/L}$  and the frequency of positive rheotaxis and gain were recorded for each. Observations were made for 15 min following an acclimation period of 5 min with the background revolving at a rate equivalent to a water current of 15 cm/s. These levels were chosen as indicative of the ovarian fluid concentration in the stream tank plume where the  $10^{-1}$   $\mu\text{L/L}$  solution in the source channel was rapidly diluted upon entry into the central tank.

The data for frequency of positive rheotaxis and frequency of gain were analyzed using simple one-way analyses of variance. Since treatments (ovarian fluid concentration) were qualitatively similar and balanced ( $n = 10$  for all treatments), the experimental error ( $\sigma^2$ ) for each analysis of variance was used to generate the Least Significant Difference (LSD) at the 5% probability level for each of the two behavioral parameters. The means for each treatment were plotted with their appropriate LSD for frequency of positive rheotaxis and frequency of gain to illustrate any differences between the treatment means.

## Results

### STREAM TANK OBSERVATIONS

In the absence of any odorous cues, mature male rainbow trout were observed to swim continuously in the stream tank both upstream and downstream. Agonistic behavior was prevalent with much displaying, circling, and tail-nipping occurring. On addition of the ovarian fluid, a marked decline in agonistic behavior was observed. The orientation of the fish became predominantly upstream as most male trout were observed to move to the outer periphery of the stream tank and upstream into the area of the plume emanating from the source channel. Although one or two trout in some replicates tended to stem the current and remain within the plume, most continued to swim either around the tank and back up the plume along the outer periphery of the tank or in zig-zag fashion across the stream tank in and out of the upstream end of the odor plume. This behavior continued for the entire 30 min that ovarian fluid was present in the tank.

The analysis of the films confirmed quantitatively the behavior described qualitatively above. The total number of observations of 75 fish (15 replicates  $\times$  5 fish) in the upstream segment of the odor plume (sections A1-A14) and in the downstream segment of the odor plume (sections B11-B23 and C16-C26) before and after addition of ovarian fluid were as follows:

	Upstream	Downstream
Before	364	523
After	472	424

The analysis of variance revealed that although the number of observations of fish in the entire plume did not differ significantly between the 30-min time intervals before and after the addition of ovarian fluid, the interaction between time interval and plume segment was significant ( $F_{1/42} = 5.12$ ;  $0.01 < P < 0.05$ ). Therefore, fish observed in the area of the plume spent significantly more of their time in the upstream segment of the plume after the addition of ovarian fluid. No significant variation occurred between replicates ( $F_{14/42} = 1.21$ ;  $P > 0.05$ ).

#### OPTOMOTOR TANK OBSERVATIONS

Variation in the frequency of positive rheotaxis was not significant ( $F = 1.5$ ;  $P > 0.05$ ;  $s^2 = 0.065$ ;  $n = 50$ ) and, therefore, the use of the LSD to detect differences between mean frequencies of positive rheotaxis must be interpreted with caution. However, there is a trend (Fig. 2A) in which the frequency of positive rheotaxis increased to a maximum at an ovarian fluid concentration of  $10^{-3} \mu\text{L/L}$  and then declined at higher concentrations. The frequency of positive rheotaxis at the  $10^{-3} \mu\text{L/L}$  treatment level was significantly greater than that observed at the control,  $10^{-1}$  and  $10^{-4} \mu\text{L/L}$  treatment levels (Fig. 2A).

Variation in the frequency of gain of male trout in the presence of ovarian fluid was significant ( $F = 2.5$ ;  $P = 0.05$ ;  $s^2 = 0.074$ ;  $n = 50$ ). As with frequency of positive rheotaxis, the maximum frequency of gain occurred at an ovarian fluid concentration of  $10^{-3} \mu\text{L/L}$ . The frequency of gain at the  $10^{-3} \mu\text{L/L}$  treatment level was significantly greater than that observed at all other treatment levels (Fig. 2B).

#### Discussion

This study has shown that the rheotropic response of ripe male rainbow trout is affected by dilute ovarian fluid obtained from spawning female rainbow trout. In the circular stream tank, male trout moved upstream in the plume created by ovarian fluid emanating from a source channel. In the optomotor tank, male trout showed an increase in the frequency of upstream orientation and, more significantly, in the frequency of upstream movement in the presence of diffuse, non-directional ovarian fluid at concentrations equivalent to those existing in the plume of the stream tank. These observations demonstrate that the response of trout observed in the stream tank was not solely due to the presence of an odor gradient. Rather, the mechanism of orientation as revealed in the optomotor tank is related to the regulation of rheotropism, whereby the ovarian fluid acts as a sign stimulus regulating the orientational and kinetic components of the response to the water current. A fish using such a mechanism can respond unidirectionally to an attractant odor in a water current when no concentration gradient exists. This would be particularly important to a migrating fish

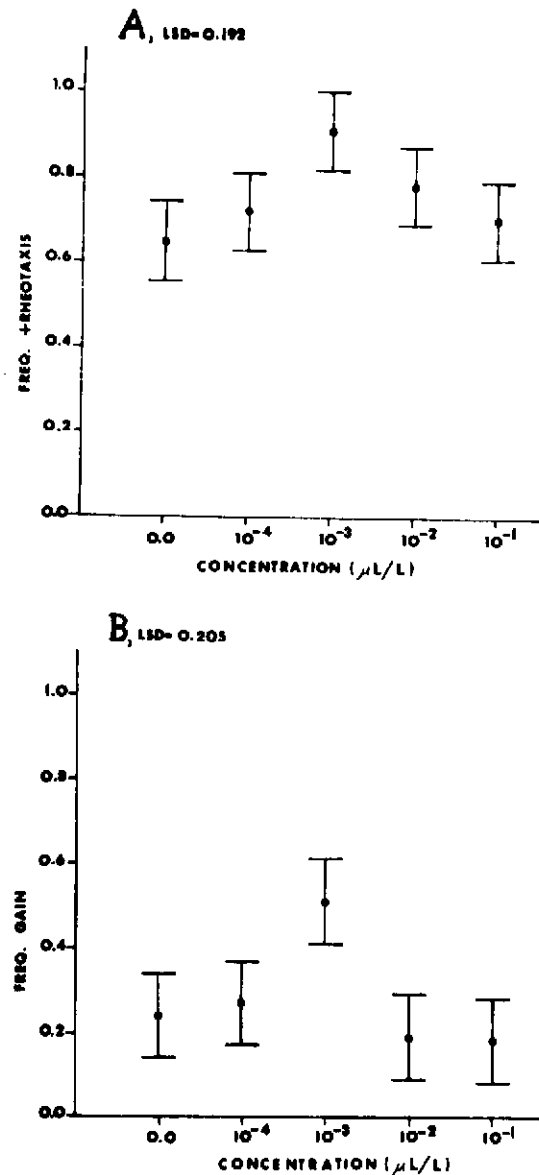


FIG. 2. Effect of dilute ovarian fluid on the frequency of positive rheotaxis (A) and the frequency of gain (B) of mature male rainbow trout. Each point on the graphs represents the mean of 10 fish. Bars across the points indicate the Least Significant Difference (LSD) as calculated from the analysis of variance of each behavioral parameter. Overlapping bars indicate no significant difference between means at the 5% probability level.

far from its goal, where olfactory cues indicative of home may be present but no concentration gradient would exist due to the dilution and dispersion of such cues far from their source.

The majority of male trout observed in the circular

stream tank spent much of their time moving in and out of the odor plume during the period ovarian fluid was present in the tank. This may have represented some kind of gradient or boundary response and suggests that trout are capable of using an odor gradient when present. Another consequence of such behavior was that few trout were exposed constantly to the odor. This may have contributed to preventing the adaptation of the olfactory sense to ovarian fluid over the 30-min observation period.

The optomotor tank observations show a trend in which the frequency of positive rheotaxis and gain is at a maximum in the presence of  $10^{-3}$   $\mu\text{L/L}$  ovarian fluid and decreases at greater or lesser concentrations. Thus it appears that a maximum response occurs at a particular concentration of the odor. A similar situation was reported by Timms and Kleerekoper (1972) from a study of the locomotor movement of ripe male channel catfish (*Ictalurus punctatus*) in response to a sexual pheromone released by a ripe female. They noted that at an appropriate strength of the stimulus the response was a well-defined tropotaxis (simultaneous comparison of the stimulus by lateral receptors) and that when presented with a choice between two concentrations of the pheromone, the catfish were not attracted preferentially to the stronger source. Possibly lower concentrations of the pheromone serve as guides leading receptive males to the spawning areas.

No significant changes occurred in the rheotropic response of rainbow trout at the highest concentration of ovarian fluid ( $10^{-1}$   $\mu\text{L/L}$ ) tested in the optomotor tank. As ovarian fluid plays an important role in sexual behavior (Tavolga 1956; Partridge et al. 1976), the possibility exists that at higher concentrations of ovarian fluid, receptive males may require other cues, such as visual or tactile contact with females, to release the next sequence of behavioral responses. Kleerekoper (1972) has suggested that the same sign stimulus may elicit variable responses in the presence of different cues. Hence in the presence of increasingly higher concentrations of ovarian fluid, the absence of other cues associated with females and spawning may have caused an inhibition of the upstream movement of receptive males. In nature, such a mechanism would prevent males from overshooting nearby spawning grounds where ovarian fluid concentrations would be greatest.

There are many examples in the literature of the attraction of fish by various odorous substances (reviewed for freshwater fish by Solomon 1977). Unfortunately, only a few of these studies have attempted to determine the mechanism of orientation responsible for the observed movement. Mathewson and Hodgson (1972) observed that the lemon shark (*Negaprion brevirostris*) on encountering an olfactory stimulus would swim upstream into the strongest current even when the source of the attractant was placed in the weakest current of an experimental enclosure. They concluded that the attractant odor triggered a positive

rheotropic response with the stronger current providing better orientational cues than weaker currents. Kleerekoper (1967) suggested that an attractant odor released rheotactic responses in several marine and freshwater species observed in an experimental tank, so that the localization of the odor source took place through rheotaxis rather than through orienting cues provided by the odor gradient. Kleerekoper et al. (1975) demonstrated that the nurse shark (*Ginglymostoma cirratum*) required flowing water as a direction vector for the precise localization of the source of an attractant chemical stimulus.

Several investigations into the mechanisms of fish migration have demonstrated mechanisms of orientation involving the modification of rheotropism by olfactory sign stimuli. Creutzberg (1961) demonstrated that the rheotropic response of elvers (*Anguilla anguilla*) changed in response to the tide. On ebb tide the elvers swam against the current whereas on flood tide they rose from the bottom and either swam with or were carried passively by the current, this change in behavior being stimulated by an unidentified chemical characteristic of inland water. Miles (1968) observed a similar rheotropic response to freshwater by elvers of *Anguilla rostrata*. Dodson and Leggett (1973) observed that adult American shad (*Alosa sapidissima*) homing to the Connecticut River from Long Island Sound exhibited different rheotropic responses to ebb and flood tide which resulted in unidirectional displacement, and subsequently demonstrated (1974) this to be dependent on the presence of olfactory cues acting as sign stimuli. Scholz et al. (1972) observed that migrating adult chum (*Oncorhynchus keta*) and coho (*O. kisutch*) salmon responded differently to ebb and flood currents and hypothesized that olfactory mechanisms were responsible for their observations. Atlantic salmon (*Salmo salar*, Stasko et al. 1973a) and pink salmon (*Oncorhynchus gorbuscha*, Stasko et al. 1973b) also exhibit different rheotropic responses to ebb and flood tide currents during their homeward migrations but the mechanism(s) responsible for this behavior has not been described.

In conclusion, this study has demonstrated that dilute ovarian fluid stimulates the upstream movement of ripe male trout. This would likely be of orientational significance only later in the migration after spawning had begun. The olfactory cue(s) responsible for the uniqueness and attractiveness of the natal stream is no doubt a complex of chemical characteristics whose nature remains unclear. Finally, this study has demonstrated that trout can respond unidirectionally to an attractant odor in a water current when no concentration gradient exists. This mechanism of orientation involves water currents providing the directional cues and the olfactory stimuli regulating the rheotropic response.

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- ARNOLD, G. P. 1974. Rheotropism in fishes. *Biol. Rev.* 49: 515-576.
- CRAPON DE CAPRONA, M. D. 1974. The effect of chemical stimuli from conspecifics on the behavior of *Haplochromis burtoni* (Cichlidae, Pisces). *Experientia* 30: 1394-1395.
- CREUTZBERG, F. 1961. On the orientation of migrating eelers (*Anguilla vulgaris* Turt.) in a tidal area. *Neth. J. Sea Res.* 1: 257-338.
- DODSON, J. J., AND W. C. LEGGETT. 1973. Behavior of adult American shad (*Alosa sapidissima*) homing to the Connecticut River from Long Island Sound. *J. Fish. Res. Board Can.* 30: 1847-1860.
1974. Role of olfaction and vision in behavior of American shad (*Alosa sapidissima*) homing to the Connecticut River from Long Island Sound. *J. Fish. Res. Board Can.* 31: 1607-1619.
- DODSON, J. J., AND J. C. YOUNG. 1977. Temperature and photoperiod regulation of rheotropic behavior in pre-spawning common shiners, *Notropis cornutus* (Mitchill). *J. Fish. Res. Board Can.* 34: 341-346.
- HARDEN JONES, F. R. 1968. Fish migration. St. Martin's Press, New York, N.Y. 325 p.
- HASLER, A. D., A. T. SCHOLZ, AND R. M. HERRALL. 1978. Olfactory imprinting and homing in salmon. *Am. Sci.* 66: 347-355.
- HASLER, A. D., AND W. J. WISBY. 1951. Discrimination of stream odors by fishes and its relation to parent stream behavior. *Am. Nat.* 85: 223-238.
- KLEEREKOPER, H. 1967. Some aspects of olfaction in fishes, with special reference to orientation. *Am. Zool.* 7: 385-395.
1972. Orientation through chemo-reception in fishes. In S. R. Galler et al. [ed.] *Animal Orientation and Navigation*. A symposium held at Wallops Station, Virginia, 1970. Scientific and Technical Information Office, NASA, Washington, D.C.
- KLEEREKOPER, H., D. GRUBER, AND J. MATIS. 1975. Accuracy of localization of a chemical stimulus in flowing and stagnant water by the nurse shark (*Ginglymostoma cirratum*). *J. Comp. Physiol.* 98: 257-275.
- MATHEWSON, R. F., AND E. S. HODGSON. 1972. Klinotaxis and rheotaxis in orientation of sharks toward chemical stimuli. *Comp. Biochem. Physiol.* 42A: 79-84.
- MILES, S. G. 1968. Rheotaxis of eelers of the American eel, *Anguilla rostrata*, in the laboratory to water from different streams in Nova Scotia. *J. Fish. Res. Board Can.* 21: 1591-1602.
- NEWCOMBE, C., AND G. HARTMAN. 1973. Some chemical signals in the spawning behavior of rainbow trout, *Salmo gairdneri*. *J. Fish. Res. Board Can.* 30: 995-997.
- NORDENG, H. 1977. A pheromone hypothesis for homeward migration in anadromous salmonids. *Oikos* 28: 155-159.
- PARTRIDGE, B. L., N. R. LILEY, AND N. E. STACEY. 1976. The role of pheromones on the sexual behavior of the goldfish. *Anim. Behav.* 24: 291-299.
- SCHOLZ, A., D. M. MADISON, A. B. STASKO, R. M. HERRALL, AND A. D. HASLER. 1972. Orientation of salmon in response to currents in or near the home stream. *Amer. Zool.* 12(4): 654 p.
- SOLOMON, D. J. 1973. Evidence for pheromone-influenced homing by migrating Atlantic salmon (*Salmo salar* L.). *Nature, Lond.* 244: 231-233.
1977. A review of chemical communication in freshwater fish. *J. Fish Biol.* 11: 363-376.
- STASKO, A. B., A. M. SUTTERLIN, S. A. ROMMEL JR., AND P. F. ELSON. 1973a. Migration-orientation of Atlantic salmon (*Salmo salar* L.). *Int. Atl. Salmon Symp.* 1972, *Int. Atl. Salmon Found., Spec. Publ.* 4(1): 119-137.
- STASKO, A. B., R. M. HERRALL, A. D. HASLER, AND D. STASKO. 1973b. Coastal movements of mature Fraser River pink salmon (*Oncorhynchus gorbuscha*) as revealed by ultrasonic tracking. *J. Fish. Res. Board Can.* 30: 1309-1316.
- TAVOLGA, W. N. 1956. Pre-spawning behavior in the Gobiid fish, *Bathygobius soporator*. *Behaviour* 9: 53-75.
- TIMMS, A. M., AND H. KLEEREKOPER. 1972. The locomotor responses of male *Ictalurus punctatus*, the channel catfish, to a pheromone released by the ripe female of the species. *Trans. Am. Fish. Soc.* 101: 302-310.