For four experiments a highly significant number of exposed compared to unexposed fish was captured at the artificially scented stream: 216 vs. 28, 437 vs. 49, 647 vs. 65 and 439 vs. 55 (Scholz et al.[24,25], Cooper et al.[26-28]; Madison et al.[29]). Fish released as smolts 13 km north of the simulated homestream homed in a similar manner to those released near the homestream. During a third year, morpholine was not added to the stream during the spawning migration and exposed and non-exposed fish returned in equal low numbers (51 vs. 55). These results confirm the existence of odor imprinting and long-term memory in coho salmon.

To obtain more direct information on homing to the imprinted chemical cues, imprinted fish equipped with ultrasonic transmitters were released along the shoreline of Lake Michigan and tracked into an area scented with morpholine (Madison et al.[29], Scholz et al.[24,25]). 20 imprinted fish tracked into this area always stopped migrating and milled around for up to 4 h before leaving (presumably when the morpholine scent had been dissipated by water currents). When no odor was present in this area, 13 imprinted fish moved through without stopping. Non-imprinted fish (14 tracks) moved through the area without stopping. Imprinted fish tracked through the area when a compound closely related to morpholine was used (N-β-hydroxyethylmorpholine) moved through the area without stopping. These results indicated that fish exposed to morpholine recognized the odor and used it for homing in an experimental situation closely approximating natural conditions.

In electrophysiological experiments (Cooper and Hasler[26,30]), EEG responses to morpholine were tested from imprinted and non-imprinted fish captured in the simulated homestream. There was a significant difference in the amplitude of the EEG signals to morpholine for imprinted compared to non-imprinted salmon for 4 experiments. Significant differences were not seen when other substances (N-β-hydroxyethylmorpholine or 1-methionine) were tested. Thus, electrophysiological experiments provide evidence that early exposure to morpholine significantly influences the subsequent responses of these fish.

Experiments on rainbow trout by behavioral (Cooper and Scholz[27]) and physiological (Cooper and Hasler[26]) means indicated that this species also can be imprinted to morpholine and use this scent for homing to a simulated homestream.

In another test of the olfactory hypothesis using the artificial imprinting technique (Scholz et al.[31]), one group of fish was exposed to morpholine, a second group to phenethyl alcohol (PEA) and a third left unexposed. These groups were marked and released into Lake Michigan halfway between two streams. During the spawning migration morpholine was released in one stream and PEA into the other. Census results showed that significantly higher numbers of morpholine-imprinted fish (compared to PEA-imprinted fish) returned to the morpholine-scented stream, while PEA-imprinted salmon homed to the stream scented with this odor. These results verify the original hypothesis that an odor is the basis for identifying 'home' water.

In summary, laboratory and field experiments along seven lines show that odors are the basis for homestream recognition. Juvenile salmon appear to imprint during the smolting to the odor of their homestream, recall this memory during the subsequent adult migration, and use this information to relocate the homestream in the second part of the homing migration.

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Chemical Stimuli in Reproductive Behavior in Fish: Communication

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The importance of chemical stimuli in the behavior of fishes has been widely documented in such areas as schooling, alarm responses, detection and discrimination of plant odors, and in migration. Recent reviews and compilations have given ample testimony to the high degree of sensitivity and discrimination of chemical stimuli by the olfactory system in many teleosts, elasmobranchs, and other fishes[1]. Within the context of reproductive behavior, however, the role of chemical stimuli in fishes has been investigated only sparsely, with few examples reported even in the encyclopedic work by BREDER and ROSEN[2].

Among the reports cited were studies on 'barbel-play' in catfish, and pair formation in the blind goby (*Typhlogobius*)[3]. In these early reports, no specific chemical stimulation was described, and, indeed, olfactory and gustatory chemoreception systems were not separated. Chemoreception experiments were confounded with the presence of tactile and other interactions. In 1939, JASKI[4] postulated the existence of a pheromone, named 'copulin', that was secreted by males of the guppy (*Poecilia reticulata*), and was thought to stimulate receptivity in females. No confirmation of this was ever obtained[5].

In a series of studies on the gobiid fish, *Bathygobius soporator*[6] the courtship behavior and subsequent spawning were found to involve a complex exchange of visual, chemical and acoustic stimuli[7]. *Bathygobius* males were stimulated into courtship behavior through the introduction into the aquarium water of small amounts of fluids from gravid female conspecifics. After testing various body fluids, including skin mucus, urine, blood, coelomic fluid, etc., it was found that the males were specifically sensitive to fluids from the interior of the ovary of a gravid female. These secretions could also be obtained from the opening of the urogenital papilla of gravid females, and extreme dilutions were adequate to stimulate courtship in an isolated male. Plugging the nostrils or cauterizing the nasal epithelium in males eliminated the courtship response, while increasing the tendency of males to aggressive behavior. Castration in males, however, did not eliminate courtship. Rather, castrated males exhibited little or no aggressive behavior while showing an increased readiness toward courtship[8]. It was concluded that some specific pheromone was produced by the ovary of a gravid female, and its effects through the olfactory system of males were to stimulate courtship. The endocrine secretions of the testis may affect olfactory sensitivity. The chemical nature of the ovarian secretions is unknown.

A significant conclusion of the above study[7] was to emphasize the multi-modal nature of interactions in reproductive behavior. A number of sensory modalities function in concert to elicit, channel and modulate the responses of one animal toward another. Redundancy increases the efficiency and accuracy of the interactions.

Comparable studies in other species indicate a wide variety of mechanisms among the few teleostean species investigated. In a blenniid fish (*Hypsoblennius*), for example, it appears that chemical exudates from courting males can arouse other males into courtship[9]. Water from gravid females appears to increase the appearance of nesting and other activities associated with reproduction in anabantid and cichlid species[10]. In these reports, however, the specificity of the chemical and of the response are as yet unclear.

Reproductive behavior can be extended to include parental behavior, and parent-young interactions in fishes can sometimes include chemical stimuli. The ability of parent individuals of the cichlid fish *Hemichromis* to recognize their own young was first described in 1939 by NOBLE and CURTIS[11]. Since then, many confirmations of this study have appeared[12], curiously however, all restricted to members of the Cichlidae. These experiments have demonstrated that parents of several cichlid species are capable of discriminating among the chemical exudates produced by young of alien species and of different conspecific parents, and can correctly select their own spawn by means of such chemical stimuli. Although the error rate is often high (estimated at 20 to 30% from data reported by MYRBERG[13]), the discriminatory behavior is significant. When visual stimuli are added, the error rate is dramatically reduced, showing that more than one sensory modality is used.

General conclusions from these reports would seem to indicate that the function of pheromones in reproductive behavior in fishes is probably restricted to a few species. This would be even more restricted if the term 'pheromone' were defined in a limited fashion, i.e., to include only such instances where it can be demonstrated that particular, species typical chemical secretions evoke predictable, stereotyped responses. The rarity of such instances in fishes appears curious, because chemical sensitivity in fishes is known to be high, and has been well-documented in other behavioral contexts. It is hard to believe that this particular field of study has been so badly neglected. Since only a few species of fishes have been shown to depend on chemical signals in reproductive behavior, it would be parsi-

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monius to assume that such instances are indeed rare, rather than just neglected. One generalization that can be made is that chemical communication in general among fishes may be on a low level of organization in terms of the hierarchy of levels[14]. Because of the critical position of reproductive behavior in species survival, it is normal to find that interactions during reproduction include the highest levels of organization and behavior of which the species is capable. In the case of chemical stimuli, reproductive behavior in fishes does not attain the level of signal or communication (as defined by Tavolga[14]), with a very few exceptions.

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Electroencephalography of the Olfactory Bulb in Relation to Prespawn Homing

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The purpose of this brief survey is to place in perspective electroencephalographic (EEG) responses of the olfactory bulb as they relate to prespawn homing behavior of salmon. No attempt will be made to review the numerous experiments in this area since they have been recently reviewed by Hara[1,2].

EEG and behavior

Spontaneous electrical activity in the brain was first observed by Caton in 1875 (Brazier[3], 1961) and first recorded from humans by Berger[4] in 1929. Continuous oscillations in electric potential can be measured between electrodes placed on the brain. Oscillations differ in frequency and amplitude from region to region and the parameters of frequency and amplitude can be altered by sensory input, hormones, metabolites, blood gas level, etc. In theory the EEG might serve as a direct measure of the qualitative aspects of brain activity, but in fact the relationship between behavior and EEG is not understood. However, in humans some states of altered brain function may be diagnosed by EEG. Relative to an actual behavioral response the EEG response must be considered to be very crude in terms of yielding qualitative information. For example odiferous substances which evoke behavioral responses in fish do so at concentrations several orders of magnitude below that required to evoke a change in the EEG of the olfactory bulb. This is not surprizing when one considers that changes in EEG require the simultaneous firing of complex networks of neurons.

Bulbar EEG evoked by natural waters

Having recognized the great disparity between evoked changes in EEG and actual behavioral responses the question arises as to whether it is meaningful to draw any behavioral conclusions from EEG studies. To address this question, the relationship between prespawn homing behavior and evoked bulbar EEG responses to natural waters will be discussed. The focus is on studies of homing salmon (various species of *Oncorhynchus*) since more detail is available from these studies. As discussed earlier in this article, the homing salmon is dependent upon olfaction. Hara et al.[5] first showed that when the olfactory epithelium of salmon *Oncorhynchus tshawytscha* and *O. kisutch* was irrigated with water taken from the home stream a high amplitude, synchronized response was recorded from the surface of the olfactory bulb. Originally it was found by Ueda et al.[6] that *only* water from the home stream evoked the high amplitude synchronized bulbar response as shown in Figure a. Ueda et al. showed that waters transversed during migration were stimulatory, but the evoked bulbar response was much less than when home stream water was used as the stimulant.

Subsequently Oshima et al.[7] showed that the bulbar response to natural waters in homing salmon was not the 'all of none' situation which was suggested from earlier studies of Ueda et al.[6]. Oshima et al.[7] found that, although a high amplitude bulbar response always occurred when home stream water was profused into the nasal cavity, all natural waters evoked some response and in some instances non-home water evoked a response similar to the response to home water, Figure b. Oshima et al.[8] also showed that bulbar re-

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