23 September 1960, Volume 132, Number 3430 **SCIENCE**

CURRENT PROBLEMS IN RESEARCH

Guideposts of Migrating Fishes

New findings have added to our knowledge of how fish use olfactory and visual cues to find their way home.

Arthur D. Hasler

Homing in migrating fishes such as the salmon may be defined as a behavior pattern in which an animal spends its early life in one locality and subsequently returns to this locality, after undertaking migratory journeys of long or short duration to areas where the environment is drastically different. Fishes inhabiting smaller bodies of water, such as a stream pool, a pond, or a lake, return readily to a home territory when displaced (*1*), but the homing ability is of far less magnitude in these fishes than in salmon.

The object of this article is to describe and appraise the recent research on homing in fishes, to point up the gaps in knowledge, and to mention a few problems that should be pursued to help clarify differences of opinion. Emphasis is placed on the salmon, for which we have more factual information than for any other group.

There is comparatively good evidence for homing in the Atlantic salmon (*Salmo salar*), the five species of Pacific salmon (*Oncorhyncus kisutch, O. nerka, O. gorbuscha, O. keta, O. tschawytscha*), and the steelhead or rainbow trout (*Salmo gairdnerii*), whose returning migrations constitute a spectacular movement of large numbers of the species as they return to their parent stream to spawn.

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In short, salmon spawn in freshwater streams and spend several years (two to seven, depending on the species), at sea, until they reach sexual maturity. Generation after generation, families of salmon return to the same riverlet so consistently that populations in streams that are not far apart follow distinctly separate lines of evolution. During a spawning movement into a river system the majority of fish swim upstream (Fig. 1) until they locate their home creek, where they spawn. In the genus *Oncorhyncus* the adults die after spawning, while in *Salmo*, spawnings are observed in subsequent years.

For a detailed and comprehensive review of migration of fishes, Scheuring's (*2*) splendid monograph is recommended. For relatively recent accounts of the mechanisms of homing, Scheer (*3*) and Hasler (*4*) may be consulted. The eel's life story has been reviewed thoroughly in the excellent treatise by Bertin (*5*), whose volume is available in both French and English, and the life history of the Atlantic salmon was summarized well by Jones (*6*).

Homing ability may be classified into three principal types (*7*): (i) The ability of an animal to find home by relying on local landmarks within familiar territory and the use of exploration in unfamiliar areas; (ii) the ability to maintain a constant compass direction in unfamiliar territory [this type is called *Richtungsfinden (-fliegen)* by Kramer (*8*)]; and (iii) the ability to head for home from unknown territory by true navigation.

Let us review briefly some of the details of homing in the salmon and eel.

The most overwhelming evidence for the precision of homing in salmon is that of Clemens *et al.* (*9*). They marked 469,326 fingerlings in a stream of the Fraser River system and recovered almost 11,000 when the salmon returned there from the sea. Although traps were placed on nearby tributaries, all of the marked fish were captured in the stream of their origin. There were no strays. Other workers report some straying, an aspect of variation; this is as it should be in a biological system. Nevertheless, one cannot but marvel at the accuracy of the majority, for in this drive to return home there appear to be advantages which are of distinct value for survival.

Seemingly, more spectacular than the migration of the salmon is that of the eel, according to Schmidt (*10*), who could trace the migration of the elvers of *Anguilla* from a spawning ground near the Bahama Islands to North America and Europe. After extensive study of the distribution of *Leptocephalus* larvae of the two species of Atlantic eel, he concluded that the adults migrate long distances at sea to spawn and that the young find their way back to their respective continents. Most recently some inadequacies of Schmidt's explanation have been treated by Tucker (*11*), who has suggested an alternative hypothesis—that there is only one species of Atlantic eel and that the European eel population is derived from American spawn which becomes transported via the Gulf Stream to Europe. He supplies arguments as to why the adult European eel could not migrate so far. D'Ancona (*12*), in a brief note, dis-

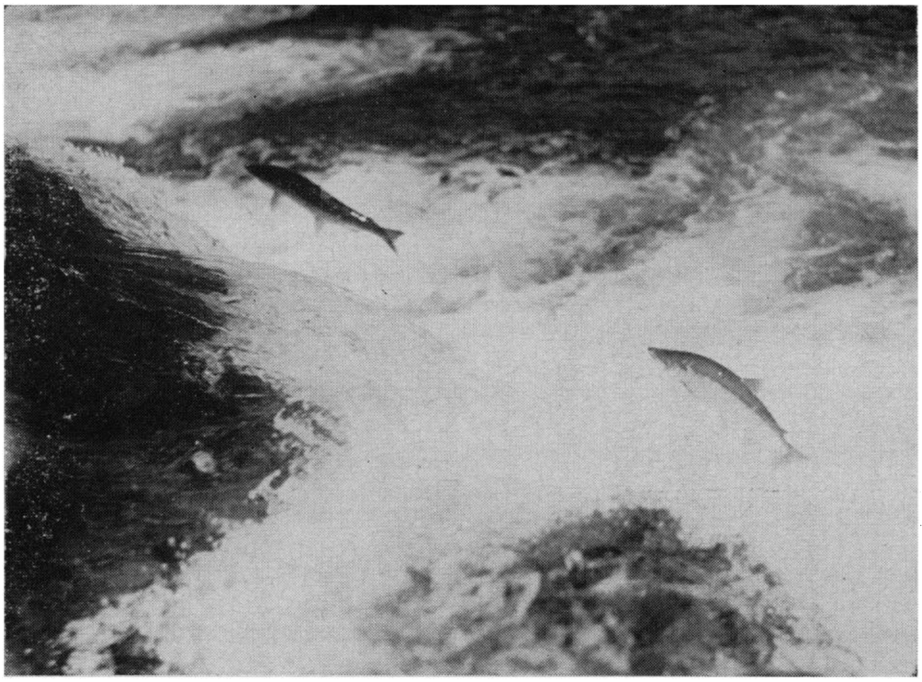

Fig. 1. Salmon ascending falls en route to their home stream to spawn. [U.S. Fish and Wildlife Service]

agrees with Tucker on a number of points, including his main thesis regarding the effect of temperature on the differentiation in the numbers of myomeres of the two groups of elvers as they are transported to North America and Europe, respectively. D'Ancona concludes that this new interpretation of Schmidt's results "requires so many new hypotheses that it is too difficult to accept it on the basis of present knowledge." It is not the object of this article to appraise the Schmidt-Tucker theories in detail; the true explanation can come principally from recaptures of marked adult eels through intensive hauls at sea made in an attempt to fill in the gaps in our knowledge of the oceanic routes of migration. This is an extremely difficult task and may not be accomplished for a long time. There is need for new questions to be posed and for new tests and experiments to be designed to answer them. If the European eel does not cross the Atlantic to spawn, which Tucker claims, are there yet undiscovered spawning grounds nearer to the European continent? Work needs to be done to determine if there is passive transport, or if there is an inherited migratory behavior pattern which makes possible the return to Europe, or if there is active searching. We greatly need more records of adult eels recaptured at sea to unravel the riddle of the eel's life history.

In spite of the impressive evidence of homing in salmon, we still lack a complete record of the migratory path at sea. So far, only a few salmon have been marked in the home stream, caught and remarked at sea, and recaptured in the home stream (*13*).

Recently the Oregon State Game Commission has released a report of remarkable series of recaptures worthy of special attention.

"April 1958: Steelhead fingerling (probably 6 to 8 inches long) released from Alsea River hatchery on the central Oregon coast; marked by removing both ventral fins and the adipose fin."

"September 5, 1958: Captured 75 miles southeast of Geese Island, which is southwest of Kodiak Island, Alaska; fish was 365 mm. long when marked with a 'spaghetti' tag."

"February 5, 1960: Fish was recovered at Alsea River hatchery; 558 mm."

A. C. DeLacy of the University of Washington states (*14*): "This was one of only 59 tagged on the high seas and . . . two others of the group have been recovered in Washington—one in the Samish River (near Bellingham) and the other at Chehalis on the Washington coast. Of course these last two were not fin clipped but they do suggest that the Alsea return does not represent a freak migration."

Each year, through the self-sacrificing and strenuous efforts of fishery biologists from Japan, Canada, and the United States in the wide expanses of the Pacific Ocean (*15*), the gaps in our knowledge of the routes at sea are being filled in. In summarizing the reports of the International North Pacific Fisheries Commission, W. F. Thompson of the University of Washington comments (*16*): "The red salmon of Bristol Bay feeds in great numbers around Attu Island which is 1200 miles from Bristol Bay. We have a great number of tags from that district retaken in our own North American estuaries, particularly Bristol Bay, but not the Gulf of Alaska. Pink salmon spawning in Kamchatka have been tagged all along the Aleutian Islands to a distance of 1200 miles from their own streams. The chum salmon returning to the Okhotsk Sea have been tagged 1700 miles from their home streams. The same is true of chum salmon spawning in Hokkaido. King and steelhead have been tagged in the vicinity of Adak Island and have returned to the Columbia River system and to Washington streams showing a migration of approximately 2500 miles; but Kings and steelheads are taken in very small numbers along the Aleutians. Their main migration is from the waters of southeastern Alaska southward as far as the Columbia River" (Fig. 2).

Donaldson and Allen's (*17*) recent work nicely confirms the findings of earlier work, that homing is not due to genetic factors but is rather the result of some sort of "imprinting" by environmental factors. They switched salmon stock and let the eggs develop in different waters. The fish returned, as adults, after a sojourn at sea, to the waters in which they had been hatched and in which they had lived as fry, not to the parent stream. In fact, Donaldson has now, in this way, built up a run of salmon to a newly built hatchery at the University of Washington on Lake Union.

A Working Hypothesis on Homing of Salmon

While the details of the routes of salmon are still not fully known, it appears justifiable to accept the home stream behavior as a working base. A leading question is: What cues and mechanisms guide these anadromous fishes in their migration? There are two major parts to this question which require an explanation. (i) How do the salmon recognize the main river as well as the home tributary? (ii)

How do they negotiate the route at sea, without visual landmarks?

In an attempt to answer the first question Wisby and I (*18*) have proposed the hypothesis that young salmon are "imprinted" by or "conditioned" to an organic odor of the home stream during their early fingerling period. To state this in simplest terms, we have proposed that the mature salmon, upon reaching the mouth of the home river, would be stimulated to enter because of a characteristic odor. (That is, each stream acquires a different odor which may be derived from a community of plants or their decomposition products in the stream or in the drainage basin.) Subsequently, the salmon would swim constantly upstream, responding positively to the water current. It would reject tributary after tributary until it began to detect traces of the home stream, to which it would respond positively, owing to the early "imprinting." On the way it might make faulty choices but would continue the search after backtracking— a behavior pattern which is frequently observed (*19*).

I would like here to object to the often stated hypothesis that an animal "follows a gradient," because, if an animal stayed in the gradient, it would soon become adapted to the odor (*20*) and would be incapable of responding to it. I think it more likely, therefore, that the behavior during the ascent of the river system is analogous to that of a dog following an odor track. The dog does not stay exactly on the track but progresses along it by crisscrossing, responding to the presence and absence of the scent as it follows its prey. According to this theory, a salmon returning to its parent stream reacts differently to the odor of that stream than to that of any other. In order for a salmon to return to its home stream there must be some possibility of a differential reaction, something more than a simple response to a repellent or an attractant. The guiding odor must remain constant from year to year and have meaning only for those salmon which were conditioned to it during their fresh-water sojourn.

This theory presents three distinct problems. (i) Do streams have characteristic odors to which fish can react? If so, what is the nature of the odor? (ii) Can salmon detect and discriminate between such odors if they do exist? (iii) Can salmon retain odor impressions from youth to maturity?

In order to answer the first question, Wisby and I trained a group of blunt-nosed minnows to discriminate between the waters of two chemically different Wisconsin creeks, one in a quarzitic drainage basin, the other in a dolomitic one (*18*). That scent-perceiving organs were the sole means of discrimination in these tests was proved by destroying the olfactory tissue of trained fishes; after this they no longer responded to the training odors. Chemical analysis of the stream waters indicated that the major difference between them was in the total organic fraction. Experimental evidence to substantiate this was obtained by separating the water into various fractions and then presenting these to trained fishes. The fishes trained previously to react to natural water did not react to the redissolved inorganic ash, or to the distillate or residue of water fractionated at 100°C. However, they recognized the distillate, but not the residue, of water fractionated by vacuum distillation at 25°C—a strong indication that the odorous stimulant is a volatile organic substance.

A test was conducted of the retentive capacities of the trained minnow, and it was determined that even this fish, which is not specialized for long migrations, could differentiate between the odors for a comparatively long period after the cessation of training. Learned behavior was found to be retained longer by young fish than by old ones. Numerous examples are known where animals retain imprinting, or early learning, through to adulthood — circumstantial evidence that odor imprinting can be retained for long periods (*21*).

The method of training which had been used with such success with the minnows was then applied to salmon

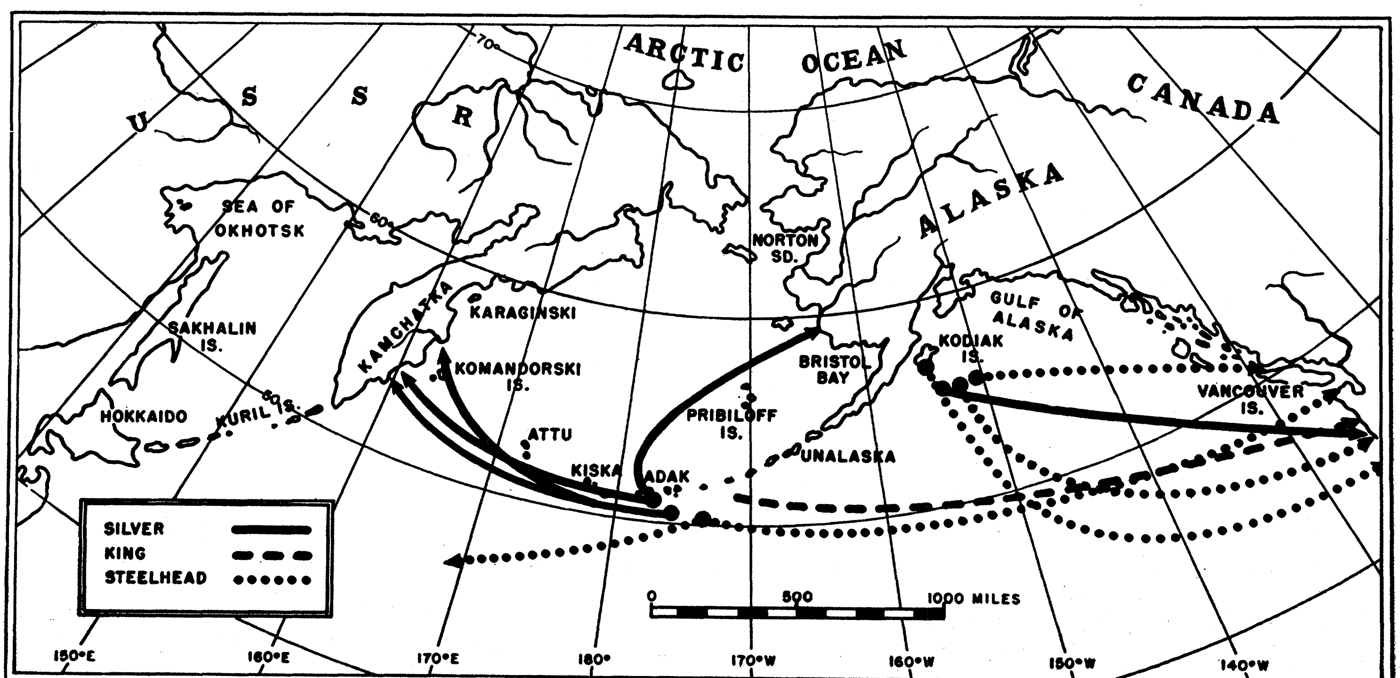

Fig. 2. Generalized distribution of recaptures of king and silver salmon and steelhead trout tagged at sea from 1956 to 1960. The routes shown are the shortest distances between the marking and the recapture points. [International North Pacific Fisheries Commission]

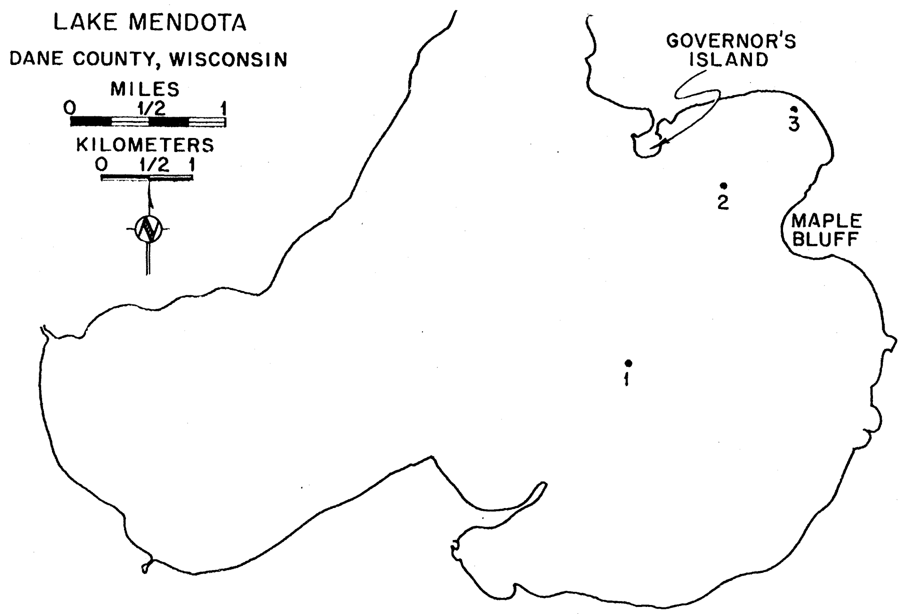

Fig. 3. Map of Lake Mendota. Releases of white bass were made at stations 1, 2, and 3.

fingerlings. After a short period of training it was evident that these fish, too, could discriminate between the odors of water from the two Wisconsin creeks.

Pursuing further this concept of the recognition, by odor, of a home stream, we (*22*) captured sexually ripe coho salmon (*Oncorhyncus kisutch*) at two branches of the Issaquah River in Washington and returned them downstream, below the fork, to make the run and selection of stream again. We plugged the nasal sac of half of the 302 specimens with cotton. The great majority of those recaptured from the other group had again selected the stream of their first choice, while the fish with plugged nasal sacs returned in a nearly random fashion. This field experiment is indicative of the important role that a functional olfactory system has in the orientation of salmon returning to their home stream.

In an effort to further test this hypothesis we proposed to employ an artificial substance to which salmon fry could be conditioned in a hatchery and which could then be used to decoy them, upon their return, into riverlets downstream from the site of conditioning. Moreover, if it proved practical, it might be used to direct fish into rehabilitated streams, formerly dammed or polluted, or to salvage a run which would not be able to pass a newly constructed power dam. Such an odor must be neither a repellent nor an attractant for the unconditioned salmon.

One of my students (*23*) has suggested that the compound morpholine might fit the requirements for this trial. It is soluble in water, thus permitting accurate dilutions; it is detectable in extremely low concentrations, thus making the treatment of large volumes of water feasible; and it is chemically stable under stream conditions. Furthermore, at these low concentrations, it is neither an attractant nor a repellent for unconditioned salmon and thus should influence the behavior of only those salmon that have been previously conditioned to it. Field tests may now be conducted to determine whether salmon fry and fingerlings which have been conditioned to morpholine in a hatchery can be decoyed to a hatchery located on a stream other than that of their birth upon their return to fresh water as migrants. A field experiment of this kind to determine the nature of imprinting is of the highest importance relative to our hypothesis. At least it would be instructive to determine if the "memory" of an artificial odor could be superimposed upon that of the natural odor of the stream. That specific carbon dioxide concentrations in the rivers may serve as guide-posts for migrating fishes has been proposed (*24*). If fishes were found to be attracted or repelled by substances such as carbon dioxide, that would not signify that they were responding to it in homing. Indeed, their homing behavior would seem to preclude the possibility that they are so attracted or repelled. If this were the case, salmon might be expected to follow a chemical track regardless of their origin.

Recently, Teichmann (*25*) has examined the olfactory acuity of the eel with respect to pure chemicals and has found it to be remarkably high. Concentrations of 3×10^{-20} of β-phenylethylalcohol were detected by young eels conditioned by training to these chemicals. If 1 milliliter of the compound were diluted to this concentration, the volume of liquid would be of an order of magnitude 58 times the volume of the Lake of Constance (the Bodensee). Teichmann (*25*) computed that the amount of the chemical in the eel's olfactory sac at this concentration would be as little as two or three molecules.

If and how, in migration, eels use this sense is not known; however, Creutzberg (*26*) suggests that elvers use the olfactory sense in discriminating between the water of ebb and flow tide and are hence able to take advantage of the transport of the flow tide in bringing them from sea to fresh water. In laboratory tests he found that elvers were not able to discriminate between ebb and flow waters after the water had been filtered through charcoal. The odor can be presumed to be organic in nature.

Contemplation of the various roles that olfaction might play in eel migrations is provocative, and the opportunity to discover new mechanisms awaits the imaginative and industrious investigator.

In the ocean, it seems to me, odor might play a role principally by giving the fish a sign stimulus for home recognition. If the fish were swimming within a water mass, it would have no sense of being displaced, as the mass moved, unless there were fixed visual or tactile features in the environment; (compare the experiences of balloonists in a cloud). On the other hand, in the place of contact of two water masses there might be differences in salinity, dissolved gases, and odor (*4*) that possibly could be perceived. Unpublished data from our laboratory have convinced us that the minnow can smell the difference between water from Georges Bank and samples from the Sargasso Sea. When two water masses met there might be a sliding of one over the other—a "shear effect"—that would help the fish to sense that it had reached the edge of a water mass, stimulating it either to enter the new mass or stay in the water mass in which it had been swimming.

The sensing of salinity, gases, or odors at any one place at sea would appear to me to be signals for recognizing, for example, an oceanic spawning site once the fish had arrived rather than cues for directional orientation.

In this article I may have overstressed the olfactory sense and its importance in migration, but I hasten to acknowledge the many limitations of our results and the need for much more work to fill in the gaps in our knowledge. As I contemplate the role of olfaction in salmon migration I believe it to be, above all, useful to a salmon within a stream system, far less useful in the open sea.

Open Sea Orientation

While home-finding in a stream system may depend upon the recognition of an odor and on other yet undiscovered guideposts, it seemed to me that the olfactory hypothesis was inadequate to explain the movements of salmon in the ocean. Certainly other cues are used.

Since it was abundantly clear that a Wisconsin team would have difficulty in conducting field studies on salmon at sea, I then asked myself the question: Is there a fresh-water fish which must find its spawning ground from open water? If so, then the mechanism of open-lake orientation in such a species might give us a clue as to how the salmon accomplishes these feats at sea.

Our initial attack on this problem consisted of study of a less complex type of homing than that in salmon. For a number of years my co-workers and I (*27*) have studied the natural history of the white bass (*Roccus chrysops* Raf.) in Lake Mendota, Wisconsin; we have been able to locate only two major spawning sites in the entire lake, and these are of very limited area. These spawning grounds, Maple Bluff and Governor's Island, are both on the north shore of the lake and are separated by a distance of 1.6 kilometers (Fig. 3). Here the white bass congregate at spawning time in late May and early June, when temperatures range from 16° to 24°C.

During three different spawning seasons (1955, 1956, and 1957) white bass were captured in fyke nets, marked with numbered disk tags, and transported in open tanks to the different release stations in the lake for daytime releases.

From the start, we observed that a large percentage of the displaced fish returned and were recaptured in nets; moreover, as the observations accumulated we were impressed with the high percentages of recapture (89 to 96 percent) among the Maple Bluff and Governor's Island spawners. They returned to their original spawning site from a release point located 2.4 kilometers from the spawning grounds, in a lake having an area of 39.4 square kilometers and a shoreline of 32.4 kilometers. For tagged fish released on the spawning ground without being displaced the percentages for recapture and for time lapse between release and recapture were of the same order of magnitude as those for fish that were displaced. This would indicate, therefore, that there was an almost complete return of the displaced fish to a spawning ground, it being assumed that mortality of the two groups was similar, that the efficiency of the net was constant, and that the nondisplaced fish remained as a catchable portion of the fish in the spawning grounds.

Subsequently, the "take-off" direction of displaced white bass was observed. To the fish was attached a plastic float (Fig. 4), which could be followed as the fish towed it along. More refined methods of tracking are currently being tested in our laboratory. The releases reported by my co-workers and me in 1958 (*27*), and many additional releases since then, continue to convince us that the course taken upon release is generally north, toward the spawning grounds, on sunny days. On cloudy days, however, the fish swim randomly. It would appear that this tendency to take off toward the north serves the purpose of bringing the fish promptly to shore in the general vicinity of the spawning areas. Once there, they appear to locate their specific spawning areas by other cues. Orientation of type (ii) discussed above appears, then, to characterize the white bass of Lake Mendota.

How might this mechanism of orientation be explained? While we were investigating the field aspects of this problem, the classical studies of von Frisch (*28*) and Kramer (*29*) on sun orientation had been published. I considered it important to explore the possibility that a sun-compass mechanism could be helpful to fish in open-water migration. To expose this notion to laboratory and field tests, new methods and apparatus had to be developed. In addition, we had to determine what fish were most suitable for this type of laboratory experiment.

The principal method which we developed to test for sun orientation relied upon an escape, or cover-seeking, response, which was used for scoring. The fish were tested under the open sky in a specially designed tank (Fig. 5) (*27*). During training the fish usually attempted to seek cover and found it

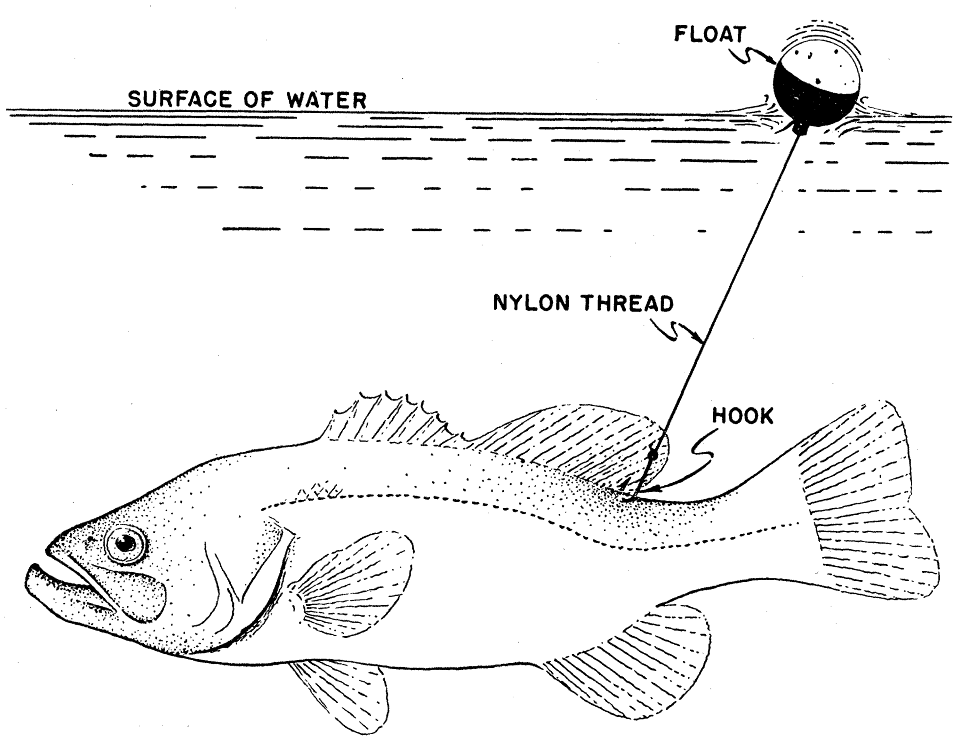

Fig. 4. A method for tracking displaced fish in order to measure the accuracy of their direction of take-off.

in only one of the 16 small compartments, within 360°, the others having been covered by a metal band. The arrangement of the small containers was such that they could not be seen by the fish from its starting point in the middle of the large tank. Training tests were conducted at frequent intervals. In this process the fish was removed from the small container and placed in a cage in the center of the tank. Upon release it was given a small electric shock to frighten it. This resulted in the fish's seeking cover again in the small open container, which was always in the same compass direction.

Tests were then conducted with all 16 of the boxes open and available to the fish. When it was determined that the fish had learned the location of the box which lay in the same compass direction as the training compartment, the critical tests were begun. The tests were made between 0800 and 0900 hours and 1500 and 1600 hours CST. All 16 small containers were available for entry, but usually the fish chose those which lay in the compass direction in which it had been trained to seek shelter.

The trained fish were disoriented when tested under completely overcast skies, at times when the experimenter could not detect the presence of the sun. This demonstrates that the sun was the fish's point of reference and that the fish had learned to seek cover in the same direction at different times of day—that is, to allow for the movement of the sun (see Fig. 6).

The crucial and definitive test was then conducted—namely, substitution of an artificial "sun," indoors, for the actual sun. A sun-compass fish responded as though it were responding to the real sun out-of-doors at that time of day, choosing a hiding box at the appropriate angle to the artificial sun. Hence, the existence of an orientation rhythm which is associated with the so-called "biological clock" has been established.

It now becomes imperative that field studies be made of migrating salmon at sea. Sexually mature salmon should be captured in purse seines near the mouth of a home river, equipped with tracers similar to those described above for the white bass, and displaced several kilometers out to sea, and their "take-off" and swimming direction should then be charted.

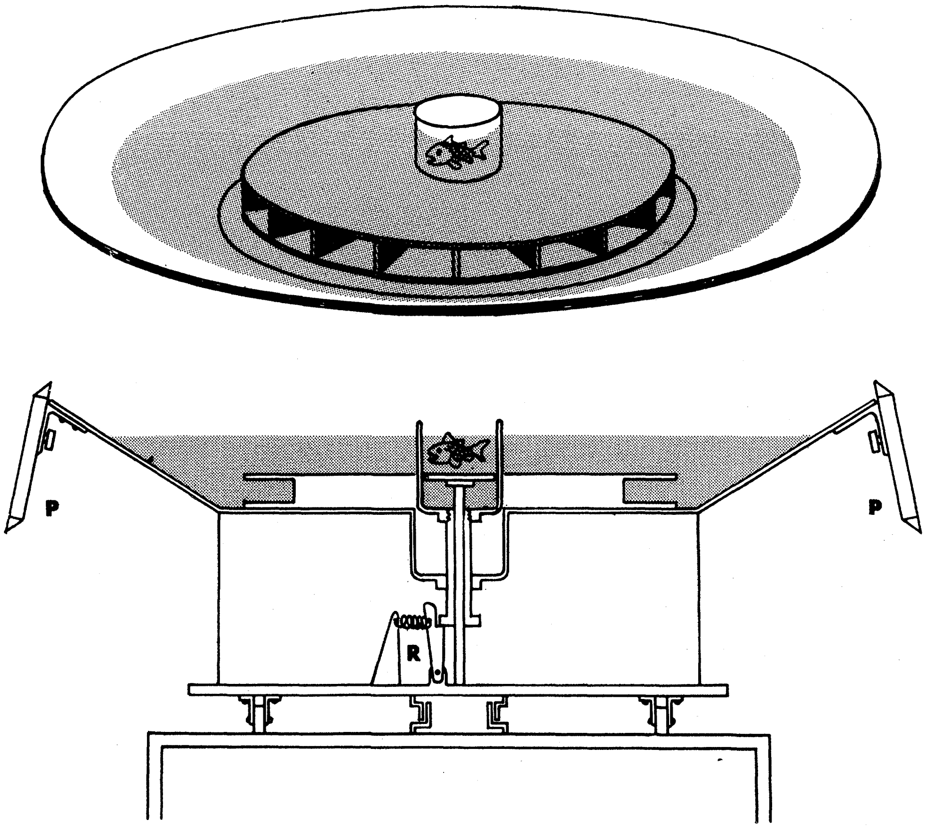

Fig. 5. Tank for training fish to a compass direction. (Top) View from above, showing the hidden boxes. (Bottom) Side view, showing periscopes (*P*) for indirect observation and the release lever (*R*) used to permit the cage to be recessed by remote control when the fish is released.

Future Research on Open-Sea Navigation

From field and laboratory evidence, compiled from four different species of fresh-water fish, it is clear that many fish possess a sun-compass mechanism, and of importance here are the results of our unpublished laboratory tests on young silver salmon, which show that they too have this mechanism for orientation.

We cannot stop here, because a salmon with a sun-compass mechanism needs augmentive sensory and physiological abilities to accomplish the migratory feat it appears to perform.

If it could be shown that salmon do swim in a constant compass direction when the sun shines and that they cannot do so under a completely cloud-covered sky, the evidence would be clear. On the other hand, negative results in both cases could be due to excessive handling, but positive results, with and without the sun, would point toward orienting mechanisms other than our hypothetical sun compass.

If salmon could maintain a compass course in the open sea, even a slight drift with currents would displace them to such great distances that they would be driven to shore hundreds of kilometers from their home-river system (see Fig. 2).

Possible Influence of Sun Altitude

Perhaps there are other cues which are perceived in navigation. Celestial cues may not be the only significant ones.

In seeking an understanding of the mechanism of the sun compass in animals, the application of laboratory methods has been extremely illuminating. Nevertheless, it must be kept in mind that these methods have not provided us with an explanation of navigational ability.

The results from field tests have established navigational ability in birds (*30*), but such ability requires, in addition to the sun-compass type of orientation, some other factors, such as those that enable homing pigeons, for example, to find their home loft after being released at distant, unfamiliar places. For salmon, comparable field tests have not been made, even though oceanic migration appears to demand some type of navigational ability.

The take-off directions of the white bass when released out of sight of shore in the middle of a large lake (*27*) support the view that at least one species of migrating fish uses its ability to maintain a compass direction when the sun is visible. This sun-compass mechanism in fish appears to be quite similar to that found in invertebrates (*28*) and in birds (*29*). Other characteristics of the sun-compass mechanism, as judged from laboratory tests, lead to further fruitful avenues of exploration into the nature of the physiological mechanisms involved.

Braemer (*31*) simulated drastic longitudinal displacements with trained fish by shifting their "time sense." He did this by conditioning them to light cycles which were delayed or advanced from those of their normal day. When these fish were tested out of doors, he found that the compass direction which they now indicated deviated by a definite angle from the previous direction. This deviation was roughly equivalent to the amount of shift in time (or longitude). When testing these fish during the noon hour, he observed that the zenith position of the sun could be correlated with a partial reorientation which resulted in choices that were in the compass direction of take-off of their training period.

This result suggests that the altitude of the sun plays a role in orientation.

In order to shed further light on this point Schwassmann and I (*32*) flew some sunfish (*Lepomus cyanellus*) that had been trained in orientation to the sun for several weeks at Madison, Wisconsin (43°N), to the equator at Belém, Brazil (1°S), where we tested them out of doors in our circular sun-orientation maze (Fig. 5). These fish did not adapt to this new and radically different daily sun movement but continued to make the compensation for the azimuth curve of the sun that would have been "correct" for Madison. One of these sunfish, when flown to Montevideo (30°S) and retrained briefly under the sun (which appears to move counterclockwise in the Southern Hemisphere) continued to make the adjustment that would have been correct for the Northern Hemisphere. What would have been the response of a sexually mature salmon that had moved from one latitude to the other at a normal and gradual rate?

Under the equinoctial sun at the equator a rapid deterioration of the oriented behavior of the displaced fish occurred, and all the fish showed an increasing tendency to maintain one and the same angle to the azimuth position of the sun throughout the day. Because of the somewhat preliminary nature of this experiment, no definite conclusion can be drawn as to the probable cause of this behavior.

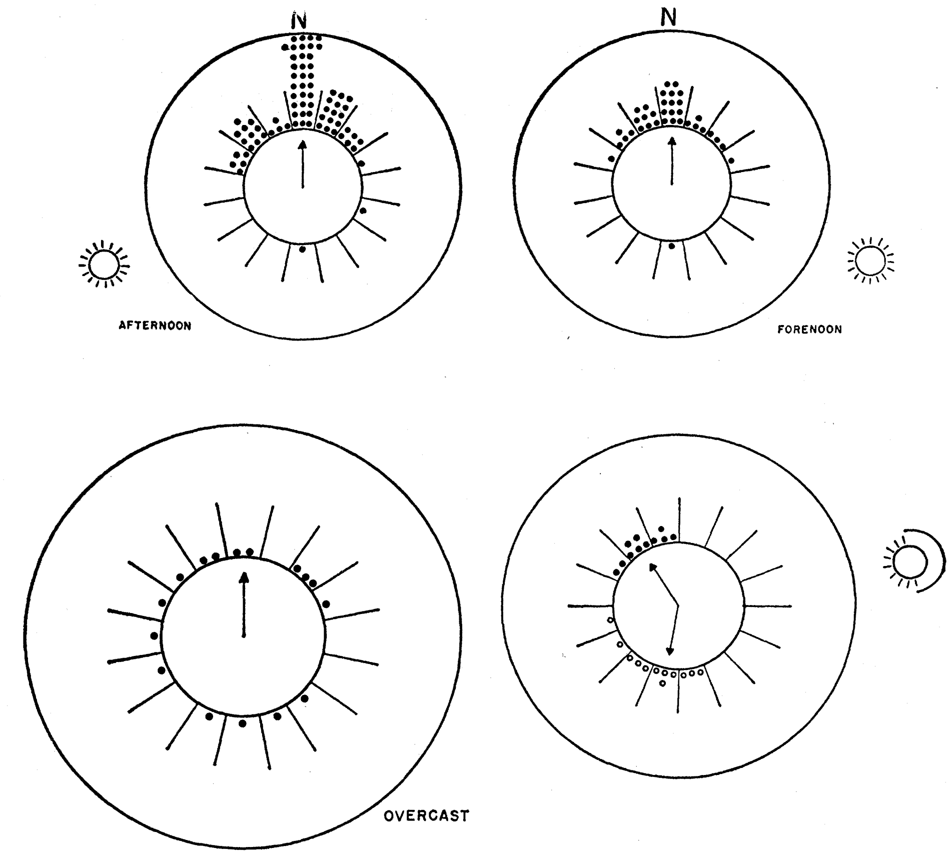

Fig. 6. Scores of a fish trained to north. Scores of the fish (top left) tested in the afternoon, with 16 possible choices; (top right) tested in the forenoon, with 16 possible choices; (bottom left) tested under completely overcast skies on two different days; (bottom right) tested with an artificial light, the angle of altitude being the same as for the sun (solid circles, scores in the forenoon; open circles, scores in the afternoon).

It is clear that other types of studies must be undertaken in order to solve the riddle of the salmon's migratory accomplishments. Certainly we must be boldly imaginative in approaching the problem, by going to sea with new techniques and logical hypotheses to be tested and returning to the laboratory to elaborate on the mechanisms used by the fish to find its way.

Is it possible that the salmon, upon reaching sexual maturity, accumulates a certain temperature budget within a water mass in which it is swimming, as it obeys direction from its sun compass? Its subsequent deviation from this course might take place only when this budget was exceeded. At this point the fish might take another angle to the sun in order to correct its course and keep from being drifted too far off course. This is no doubt too bold a hypothesis, but it is this type of thinking which will be required as we take the next step of the many which will be necessary before the complete behavior pattern is deciphered.

Adult salmon are known to move during the night in the sea. In order to take advantage of this activity the gill-net fishermen set their nets at night. Clifford Barnes of the University of Washington (*33*) observed salmon migrating at right angles to his oceanographic research vessel, which was on course at night in the northeastern Pacific. Because of a luminescent sea, this school of large salmon could be seen clearly. The fish swam on a fairly straight course until they were out of sight. We need to know more about the directed movements of salmon at night. We badly need a technique for tracking them, in order to gain knowledge of their night activities at sea. The work on night migrating birds (*34*) and the possible influence of star patterns as beacons for orientation suggest new points of reference for fish.

The tuna constitute another group of fishes which make long migrations in the open sea. Transpacific and transatlantic (east-west) migration of marked and recaptured tuna are on record. Field data are accumulating rapidly, owing to the efforts of Japanese and North American workers as they add knowledge about the migratory routes. Soon, enough information will have accumulated so that experimental work can be planned. We have here opportunities of unlimited potentiality, exciting to contemplate.

Summary

The pertinent literature regarding the mechanisms employed by sexually mature salmon in order to return from the sea to their home stream or rivulet is the subject of this article. Emphasis is placed on the Pacific salmon as reported in the American literature. Although the migrations of the eel are alluded to briefly, the new theories of odor and sun orientation and their possible role in homing of salmon are reviewed in somewhat greater detail.

In salmon two main phases of homing are stressed: (i) the finding of the home stream or rivulet after the main river has been reached and (ii) migration from long distances at sea to the rivers. The oceanic migration seems to demand an ability to navigate—that is, to return home from a distant place in an oriented fashion and not by random searching.

In the river system, it is proposed, a young salmon becomes "imprinted" or conditioned to the odor of its parent stream. After three to five years at sea and during the return river migration, it swims against the current, rejecting all odors, until it arrives at the home tributary to which it has been initially conditioned. Circumstantial evidence is cited in support of this hypothesis: (i) from training experiments in the laboratory, in which it was shown that fish can discriminate the scents of streams and that a fish may retain the odor of a stream in its "memory"; (ii) from field studies, which showed that after normal salmon and salmon with plugged nasal sacs had been displaced, the latter were unable to return accurately to the home stream.

Additional experiments are suggested for definitive tests of the theory.

Recent studies by Dutch and German researchers on the olfactory sense of eels points up the importance of this sense in orientation, particularly as an aid for locating a river inlet.

At sea, it is proposed, the salmon may possess, among other capabilities, a sun-compass mechanism for orientation, as first described by von Frisch for bees and by Kramer for birds. Recent work has shown that a pelagic American lake fish employs the sun in order to strike a compass course when displaced from its spawning ground near shore. Laboratory experiments prove that several fresh-water fish, in addition to young salmon, have a sun-compass mechanism, but true navigation in fish has not yet been demonstrated by field studies.

Some of the unsolved problems are stressed here, and suggestions are made for future observations and for experiments which should be performed in future investigations of the remarkable feat of homing in the salmon. An increased effort, by the International North Pacific Fisheries Commission to capture and mark thousands of Pacific salmon on the high seas is filling the gaps in our knowledge about the routes of salmon at sea. Comparable efforts are needed in order to obtain records of the oceanic movements of eels, tuna, and other fish which migrate long distances.

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