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The nature and role of learning in the orientation and migratory behavior of fishes

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Synopsis

Fish migration may be viewed as the product of two processes; the selection and tracking of optimal environmental conditions through time and space, and the use of predictive information about environmental structure to bias movements towards a goal. The establishment and maintenance of directional bias is based on the interaction of experience and instinct. The preoccupation of much fish orientation research with innate fixed patterns of behavior on one hand and hydrodynamics on the other has led us to underestimate the possibility that orientation is a flexible process relying on developmental sequences, calibration of the motor-sensory interaction based on experience and the learning of environmental pattern. Evidence illustrating how experience and learning may influence the direction of movement and how the goal is recognized is presented according to two general categories: (a) imprinting and early experience and (b), spatial learning, including the social transmission of migratory routes and directions. In the first category, the olfactory hypothesis of salmon homing is briefly reviewed and new data presented describing olfactory imprinting in Atlantic salmon, *Salmo salar.* In the second category, evidence is presented demonstrating the modifiability of sun-compass orientation and the ability of some fish species to learn the spatial distribution of landmarks. The role of social transmission in the migration of coral reef fishes is reviewed. The possible role of these learning phenomena in the formation of familiar area maps, route-based and location-based navigation and the critical distance factor is considered. The relationship between life history and the nature of learning in migratory orientation is discussed.

Introduction

Migration is the result of specialized behavior evolved for the displacement of the individual in space (Dingle 1980). Displacement may be viewed as the product of two processes; the selection and tracking of optimal conditions through time and space, and the use of 'predictive' information about environmental structure to bias movements towards a goal (Balchen 1976, 1978, Neill 1979). The first process includes the 'reactive' responses that may simply depend on ortho- and klinokineses. For example, in the case of thermoregulatory behavior, the thermal structure of the environment may be largely unpredictable but fishes can still track preferred temperature through connections between swimming behavior and recent thermal experience (Neill 1979). Such reactions, although released by a stimulus, are not aligned with respect to the stimulus but to the previous course (Schöne 1984). The key element in the class of 'predictive' responses is that the goal bears a spatially predictive relation to the starting position. As some important elements of the environment are scarce and distributed in predictable ways (e.g. spawning grounds), many migratory fishes have come to rely on small parts of the total perceptible spectrum (sign stimuli) to bias their movements in favor of the appropriate heading (Neill 1984). Predictive information about the environment is based on the interaction of personal experience and instinct, although a sharp distinction between the two cannot be made.

The use of sign stimuli to bias movements involves the category of reactions that are directed with respect to the stimulus, the taxes. In the fish migration literature, such reactions are traditionally divided into the three categories of orientation mechanisms proposed by Griffin (1955) and subsequently modified by various authors. The first category includes piloting whereby the goal is reached by referring to familiar landmarks that may be identified by a variety of sensory modalities. This category includes two qualitatively different orientation mechanisms. In its simplest form which I refer to as sequential landmark orientation, an animal can follow a route by reacting to a sequence of stimuli without using spatial stimuli (Thinus-Blanc 1987). In each instance the stimulus controlling the orientation is present at the time of response. However, piloting may also be taken to imply that the animal possesses a familiar area map built on individual experience of the spatial distribution of particular features of the environment. This idea is consistent with the concept of cognitive mapping whereby the knowledge of the goal location is integrated with the knowledge of the spatial relationships existing among various locations (Ellen 1987). In this case, the animal may take short cuts or choose between alternative routes to a goal without having to rely on a particular sequence of locations.

The second category includes compass orientation in which the goal is reached by orienting in a given compass direction without reference to local landmarks. The goal can only be reached when the compass direction leads to home or a familiar area (Able 1980). This will always be the case if the compass direction is simply the reverse of that followed on the outward journey. Such route-reversal is one example of homing based on directional information acquired during the outward journey. This strategy has been referred to as route-based navigation (Baker 1982). Compass orientation may also be used by first trip migrants. There is much support for the notion that migrant birds use innate compass orientation on their first migratory flight, but there is little support for the notion that such migrations are goal oriented (reviewed by Able 1980).

The third category includes true navigation in which the goal is reached by orienting in the appropriate direction when moving over unfamiliar territory in a new and unfamiliar direction. The goal is achieved by using information available at the point of departure independently of the outward journey (location-based navigation; Baker 1982). The migrant may lose contact with a familiar area but uses a bicoordinate map involving at least two large fields of gradients that are established by extrapolation of home-site conditions.

Much of the literature over the past 20 years reflects a fundamental dichotomy in the way students of fish migration view the degree of directional bias necessary to explain migrations and how such directional biases are maintained. On the one hand, the homing migrations of Pacific salmon to their natal streams covering thousands of kilometers have led to the concept of precise distant orientation based on predictive information about the environment (Leggett 1984). This conclusion is based on research suggesting that salmon move in predictable and particular directions at sea and that different populations home with a high degree of spatial and temporal precision to their respective natal streams from common feeding grounds. The rate of homing implies highly directed movement and studies of the early-life history stages of some species reveal celestial and magnetic compass orientation abilities implying that adults possess and use the same compasses (Quinn 1984). In general, proponents of this view emphasize mainly innate mechanisms of orientation as being responsible for guiding fish migrations.

In contrast to this view, some researchers suggest that a limited degree of directional bias may be sufficient to explain long and dramatic migrations. Largely reactive mechanisms may provide such directional bias. For example, Barkley et al. (1978) have proposed that the regular westward migration of large skipjack tuna, *Katsuwonus pelamis,* from the eastern tropical Pacific is due to a size-dependent change in temperature-oxygen requirements. As the fish grow, they must occupy cooler water to avoid metabolic overheating of core tissues and thus must vacate large parts of the eastern tropical Pacific in which required temperatures lie at depths below that at which dissolved oxygen is adequate. Anadromous American shad, *Alosa sapidissima,* approach their natal spawning rivers on the east coast of North America along migratory corridors determined by a specific range of water temperatures resulting in a northward progression in spawning from early spring to late summer (Leggett & Whitney 1972, Neves & Depres 1979). Final identification of the natal river appears to depend on olfaction (Dodson & Leggett 1974).

Drift may also provide the degree of directional bias necessary to explain parts of the migratory cycle of some species. Water motion impinges directly upon fish in the form of long-term drift or short-term advection by currents or tidal flow (Lynn 1984). Both fish larvae and adults (as well as other aquatic organisms) use oceanic and tidal currents to achieve long-range directed movements (reviewed by Miller 1985). Transport can occur by passive drift or by modulated drift if the fish migrates vertically in the water column (Arnold 1981). In such cases, no precise mechanism of distant orientation is necessary although the selection of appropriate currents is essential. Proponents of the view that limited directional bias may be sufficient to explain distant orientation emphasize hydrodynamics as the driving force of fish migration.

The preoccupation of much fish orientation research with innate, fixed patterns of behavior on one hand or hydrodynamics on the other has led us to underestimate the possibility that orientation is a flexible process relying on developmental sequences, calibration of the motor-sensory interaction based on experience and the learning of environmental pattern (Adler 1970). The most extreme manifestation of this view is represented by Baker's (1978, 1982) theory that migration is based on exploration and the development of a general cerebral sense of location among animals. Our ignorance of the role of learning and of development in animal orientation and migration was identified 17 years ago by Adler (1971). In the field of fish migration, not much has changed. Although students of fish migration use learning methods to study the discriminative capabilities thought to play a role in migration and although experimental psychologists have studied the learning ability of fishes in a variety of experimental paradigms (reviewed by Bitterman 1984), the learning components of most hypotheses of fish migratory behavior are still the least investigated ones (McCleave et al. 1984). The purpose of this paper is to review what little we know about the nature and role of learning in the development of orientation mechanisms and migratory pattern and to propose some directions for future research in this area.

Learning and orientation

In its broadest sense, learning is the acquisition of knowledge. In a more operational sense, an animal may be said to have learned something when it behaves differently in the present because of some earlier experience (Staddon 1983). However, some kinds of behavioral changes may be excluded as learning. For example, short-term changes based on the simple innate motor programs involved in kineses may be excluded as the change in behavior depends only on immediate prior experience and is not relatively permanent. For this reason, learning may not be considered to play a significant role in purely reactive processes of fish migration. Thus, for nomadic species such as tuna (Scombridae) for whom 'home' may be a restricted set of ontogenetically determined environmental requirements (Neill 1984), mainly reactive processes may be sufficient to explain the migration with little need of reference to predictive information based on experience. However, the recent demonstration of geomagnetic discrimination training in yellowfin tuna (Walker 1984) suggests that this assumption may be naive.

A consideration of the role of learning in the predictive class of migrations involves two questions: (1) how does experience influence the direction of movement, and (2) how is the goal recognized. I will discuss these two questions in the context of two learning categories: (a) imprinting and early experience and (b) spatial learning (including the social transmission of migratory routes and directions).

Imprinting is a process by which various kinds of preferences can be determined by experience (Bateson 1981). The criteria for imprinting are that it takes place during a restricted period in an individual's life known as the sensitive period, it results in relatively long-lasting memory and it may be completed at a time when the appropriate reaction is itself not yet performed (Immelmann & Suomi 1981). Although the concept of imprinting and the validity of some of the aforementioned criteria are controversial issues, in all phenomena that have been characterised as imprinting, some learning processes are favored during specific, usually early, periods of the individual's lifetime (Immelmann & Suomi 1981). Imprinting is clearly a mechanism by which a young organism can learn to identify characteristics of the home site allowing recognition later in life. Distinct from imprinting is the hypothesis that certain types of early experience influence later behavior by structuring the animal's perceptual capacities (Hebb 1949). This theory predicts animals that have had a large amount of perceptual experience early in life will turn out to be better learners than others deprived of such experience.

Spatial learning in its simplest form involves following a route composed of a sequence of stimuli that must occur in a specific order. Each stimulus encountered along the route may be considered a discriminative stimulus for the next response in the sequence. Spatial learning also includes the perception of spatial relationships and the construction of a representation of the particular set of relationships holding in a given environment. The classic experiment demonstrating this distinction was conducted by Macfarlane (reported in Tolman 1932) who trained hungry rats to swim in a maze to obtain a food reward in the goal box. These rats were then required to run the maze by installing a false bottom submerged several centimeters below the surface of the water. If subjects had learned the route through the maze in the first part of the experiment as a sequence of stimulus-response associations, the qualitative and quantitative differences involved in swimming and running should result in a decrement in performance in the second part of the experiment until new stimulus-response associations are formed. However, if the subjects had learned the route by forming a mental map of the maze, no decrement in performance should be observed. The results of Macfarlane's experiment supported the latter interpretation.

Finally, I have included a discussion of social transmission as a subset of spatial learning in the context of a paper concerned uniquely with orientation and migration. Social transmission of behavioral patterns through learning permits the rapid acquisition of advantageous behavior (Helfman & Schultz 1984). In its simplest form, known as local enhancement (Thorpe 1963), the behavior of a model directs the attention of the learner to a particular object or place. The most sophisticated form of social transmission is observational learning and occurs when the learner is simply exposed to a stimulus sequence in the absence of performance of the response to be learned and response-contingent reinforcement (Del Russo 1975).

Learning the direction of movement

Piloting and landmark orientation

The classic demonstration of the role of spatial learning in fish pilotage is provided by the experiments of Aronson (1951, 1971) on the gobiid fish, *Bathygobius soporator*. These tide-pool fish when menaced will jump from their home tide pool to adjacent tide pools with great accuracy. Aronson (1971) hypothesized that fish swim over the pools at high tide and acquire memories of the local topography around their home pools that they can use at low tide to escape from unpleasant situations. To test the hypothesis, three artificial tide pools were constructed within a round concrete tank (Fig. 1).

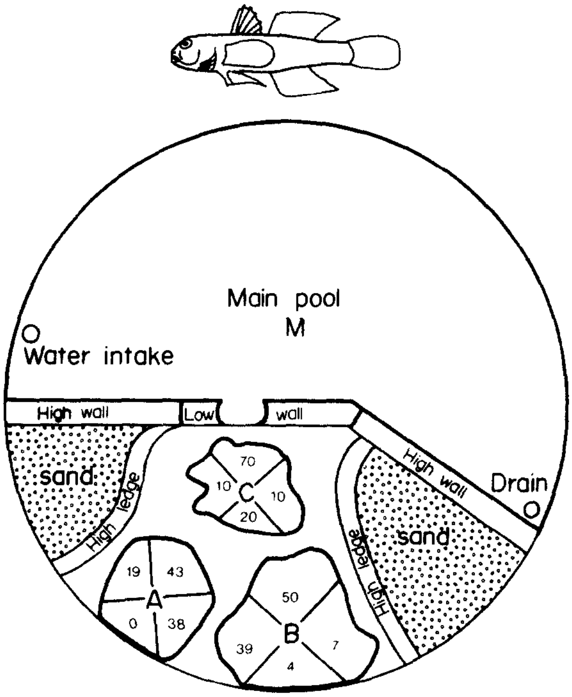

Fig. 1. Topography of tide pools located in a round concrete tank used to test the orientation and jumping behavior of *Bathygobius soporator*. Pools A, B, and C are divided into quadrants and numbers indicate the percentage of successful jumps within a quadrant exhibited by inexperienced fish (modified after Aronson 1971).

Two small pools (A and B) separated by a low ledge were built on the highest level with a maximum water depth of about 8 cm. Eight cm lower a single pool (C) led, via a narrow gap, to the large pool (M) on the lowest level. The outlet tube in pool M could be adjusted to maintain either of 2 water levels, a low tide of about 10 cm in pool M or a high tide when the water level rose to the edge of pool M and flooded the 3 smaller pools. Tests for orientation and jumping were performed by placing individual fish collected in rocky tide pools in either pool A or B. Following a one hour acclimation period, the fish was stimulated to jump by stirring the water close to the fish with a stick. Prodding continued as the fish jumped to neighboring pools but the trial was terminated after several minutes or as soon as the fish reached pool M. At the end of a trial, fish were returned to their home pool. Three trials were conducted daily. Following a series of such trials, one group of fish (experimentals) was permitted to swim throughout the tank overnight during a simulated high tide. Following high tide, fish were generally found in pool M. Each fish was returned to its home pool as low tide conditions were reestablished in the tank and given an additional 3 trials as described previously. A second group of fish (controls) was left overnight in their home pools at low tide conditions and thus did not have the opportunity to swim throughout the tank. Control fish also received an additional three trials.

Orientation and jumping behavior were evaluated by quantifying the number of trials in which the fish successfully reached pool M, the time taken by each subject to reach pool M and a composite 'jumping' score designed to represent the precision of jumping. In the preliminary and control tests, subjects reached pool M in only 15% of the trials. In general, fish exhibited poorly oriented jumps or none at all. After one overnight experience of high tide, the performance of experimentals increased significantly compared to that of the control group. Fish reached pool M in 97% of the trials, and in one quarter the time taken during preliminary tests. Jumps were also more oriented. Experimentals retained their orientation and jumping ability for up to 1 month following training, at which time experiments were terminated. Aronson (1971) also demonstrated that gobies collected in beach areas, where they presumably had no opportunity to acquire jumping experience, also demonstrated significantly improved jumping orientation in the experimental pools after experiencing one high tide situation, although the change was not as striking as with fish collected in rocky tide pools. Thus, the results indicated that gobies rapidly learned the spatial distribution of tide pools and that the predisposition to learn was manifest in gobies with no apparent prior jumping experience.

The landmarks used by gobies to map their familiar area were not established by Aronson (1971), although naive fish with no high tide experience that exhibited some jumping behavior tended to do so when located in areas of the pool adjacent to low edges (Fig. 1). It is not known if experienced fish map visual topographical features relative to an absolute axis such as a compass direction.

An excellent example of the role of social transmission in fish piloting is provided by the grunts (Haemulidae), coral reef fish that exhibit relatively short, highly regular daily migrations in all seasons. Ogden & Quinn (1984) reviewed the evidence demonstrating diel migration routes that lead from patch reefs into surrounding seagrass beds in the Caribbean. In the evening, the routes followed were linear for 50 to 100 m and then migrating groups fragmented in a dentritic pattern until single individuals remained at a particular location to feed through the night on benthic invertebrates. Prior to sunrise, they reaggregated and returned to the home reef along the same route taken the evening before. Fish appeared capable of recognizing a home schooling site on a particular reef.

Helfman et al. (1982) have shown that particular resting sites on coral reefs have persistent groups of juvenile and subadult grunts that are joined by recruiting juveniles. Young fish apparently follow older, more experienced fish thus assuring the persistance of routes. To test the hypothesis that new recruits learn from conspecifics the location of the school site and the migratory route associated with it, Helfman & Schultz (1984) transplanted juveniles between home sites. The experiments involved 3 groups of fish: (1) residents were fish occurring at a site with an established migration route where experiments were conducted; (2) transplants were fish moved from their home site to a resident site where they were held from 3 to 7 days before being released into the resident school. After migrating with the resident school for 2 days, they were tested for learning of the migration route in the absence of resident fish; (3) controls were fish taken from the same home site as the transplants and moved to the resident site after removal of both resident and transplanted fish. Controls were released after 1–7 days of acclimation and their migration on the evening of release mapped.

Learning of the migration route took place after only 2 days of experience migrating with resident fish (Fig. 2). Transplants migrated along compass directions that were the same as those of residents but significantly different from their home migration directions. Controls migrated along the same compass directions as their home migration directions. The conclusion is that the opportunity to learn from residents accounts for the change in migration pattern of the transplants. Controls had no comparable learning opportunity and oriented in a direction appropriate for their home site. Quinn & Ogden (1984) also observed that grunts trapped during morning and evening migrations and displaced up to 100 m or 5 km away in various directions tended to move in the compass direction they were taking when captured. These observations suggest that grunts possess a compass orientation mechanism and that such a mechanism may be modifiable by the behavior of conspecifics. However, because the migratory performance of transplants may have been based uniquely on sequential landmark orientation, transplants would have to be displaced to a second unfamiliar site and released with no opportunity of learning the route to see if they migrate in a direction appropriate for the learned resident site or their original home site.

The learning phenomenon described by Helfman & Schulz (1984) is characteristic of local enhancement. As naive fish migrated with experienced fish rather than simply observing conspecifics, observational learning cannot be considered the mechanism responsible for social transmission. To the best of my knowledge, the question of whether fish can learn migration routes or directions by observation remains unanswered.

Many species of marine and freshwater fish exhibit overlapping age cohorts and migrate along predictable routes, thus providing the opportunity for social transmission of routes and home sites (Helfman & Schultz 1984). For example, Olsen et al. (1978) hypothesized that walleye, *Stizostedion vitreum*, migration between home spawning sites and home feeding areas is an adult-learned behavior. Their hypothesis, although plausible, is based entirely on the results of conventional capture-mark-recapture experiments and requires experimental validation. Nevertheless, the role of social transmission in the feeding and spawning migrations of many species in a variety of habitats is potentially significant.

These examples of piloting may be largely due to sequential landmark orientation, possibly coupled with a compass direction, but cannot be taken as

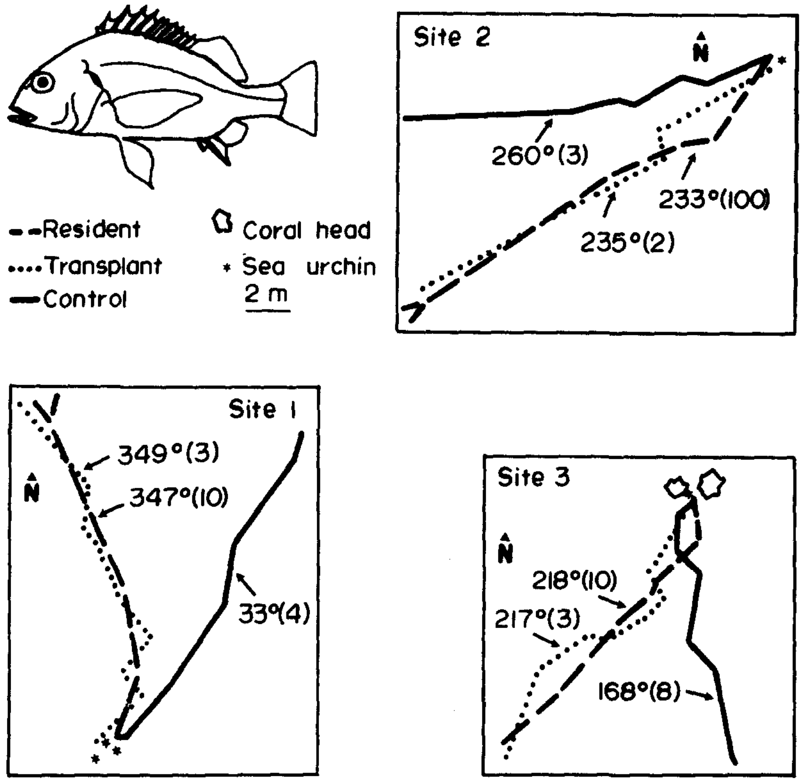

Fig. 2. The evening migration routes of French grunt, *Haemulon flavolineatum,* residents, transplants and controls at three sites, Tague Bay, St. Croix. All migrations start at a daytime schooling site identified by a coral head and/or *Diadema* sea urchin. Direction of movement of each group (numbers of fish in parentheses), as measured between the origin and the point at which groups divided or were lost in darkness, is indicated (modified after Helfman & Schultz 1984).

proof that the animals have learned the spatial relationships of their surroundings in the form of a cognitive map. Evidence suggestive of cognitive mapping in fish was provided by Kleerekoper et al. (1970) who observed goldfish swimming in a large $25m^2$ tank with no proximal visual cues which might have affected locomotor behavior. An analysis in 5 min steps of the first hour of tank exploration revealed that specific areas of the tank were explored in succession after an initial grand tour of the entire tank. Kleerekoper et al. (1970) suggested that such behavior would require a spatial memory of topography and a sense of direction, although the landmarks used to establish the spatial memory were not identified. As proximal visual cues were apparently eliminated, I assume that the authors were referring to spatial memory based on idiothetic spatial cues. Such cues are provided by the organism itself and are based on changes in body position (Mittelstaedt & Mittelstaedt cited in Schöne 1984). In a more recent study, the spatial memory capacity of Siamese fighting fish, *Betta splendens,* was tested in an aquatic eight-arm radial maze (Roitblat et al. 1982). The accuracy of performance was greater than that predicted by chance. Fish showed a tendency to choose sequences of adjacent arms and moved about the maze in either a clockwise or counterclockwise direction. However, fish confined for variable periods between the fourth and fifth choice in the maze showed a time dependent decrement in choice accuracy indicating that maze performance had a memory component as well as a stereotypic response component. It is obvious that our knowledge of spatial memory capacity in fish is scanty. We may at present only speculate about its role in fish migration.

Compass orientation

Compass orientation based on celestial and magnetic stimuli has been demonstrated in a number of fish species under laboratory and field conditions (reviewed by Smith 1985). The ability to choose and maintain a compass direction is a component of route-based and location-based navigation. It is also possible that fish using pilotage map landmarks relative to an absolute axis such as a compass direction. Thus the role of experience in establishing compass orientation is central to any discussion of learning and fish migration. Much of the early work demonstrating time-compensated sun-compass orientation used conditioning techniques in which subjects were trained in view of the sun to seek refuge in one of a number of circularly arranged compartments by stimulating them with an electric prod (Schwassmann & Braemer 1961, Hasler 1971). The results of these experiments demonstrated the modifiability of sun-compass orientation without establishing whether such learning plays a role in nature.

A convincing demonstration of the modifiability of a sun-compass reaction by experience and its adaptive significance in nature was provided by Goodyear (1973). Mosquitofish, *Gambusia affinis,* displaced under a clear sky to unfamiliar surroundings use a sun compass to move on a course perpendicular to the shore from which they were captured. In ponds containing predatory fishes, mosquitofish occupy shallow water around the pond margin as protection from predation. In the absence of predators, naive fish occupy deeper waters. To study the learning abilities of mosquitofish in conjunction with these mechanisms, Goodyear (1973) trained fish under the sun in rectangular tanks. The tanks had a sloped gravel bottom such that an emergent shoreline end could be oriented in any direction relative to the sun. A largemouth bass, *Micropterus salmoides,* was placed in each tank as the unconditional stimulus eliciting movement to shallow water. The test arena was a circular wading pool into the center of which individual fish trained for variable periods were placed and observed for directional responses. In one experiment, fish captured from a pond containing predators were trained to learn a new shoreward direction. Fish learned the new direction after 1 day and their performance did not improve on succeeding days (Fig. 3a). Another group of these fish that had been trained to the north for 2 weeks was retrained to a new shore shifted 180 degrees. During testing, these fish were disoriented up to 5 hours but responded to the new shoreward direction after 1 day (Fig. 3b). In a third experiment, fish captured from a pond containing no predators were trained in the presence of a predator to a west shore. Initially disoriented, fish tested in the arena moved in the direction of deep water after 4 days of training. Most fish tested after 10–30 days moved towards the shore (Fig. 3c). Another group of these fish that had been trained to the west for 1 month was retrained to a new shore shifted 180 degrees. These fish responded to the new shoreward direction after 6 days of training (Fig. 3d).

These experiments demonstrate the modifiability of a compass orientation mechanism in the face of environmental experience. The difference between experienced and naive fish may be related to the experience of fish throughout life. Goodyear demonstrated that newborn fish of both naive and experienced fish oriented onshore in the presence of a predator within the first 12–18 h of life and continued to do so after 23 days even in the absence of predators. Adult fish, on the other hand, lost their shoreward motivation only 6 days after removal of the predator from the training arena. This suggests that early experience and the continuity of adult experience with predators may be important in retaining the responsiveness of the learning mechanism.

There is sufficient evidence that experience plays a significant role in shaping compass orientation over short distances, particularly in the case of orienting predator avoidance responses to nearby shorelines. However, its role in long-distance compass-aided navigation is generally discounted. Indeed, the original research into the orientation of sockeye salmon smolts (Groot 1965) and younger juveniles (Brannon 1972) demonstrated stock-specific preferred compass directions corresponding to appropriate migratory directions in lakes. These results and those of subsequent experiments de-

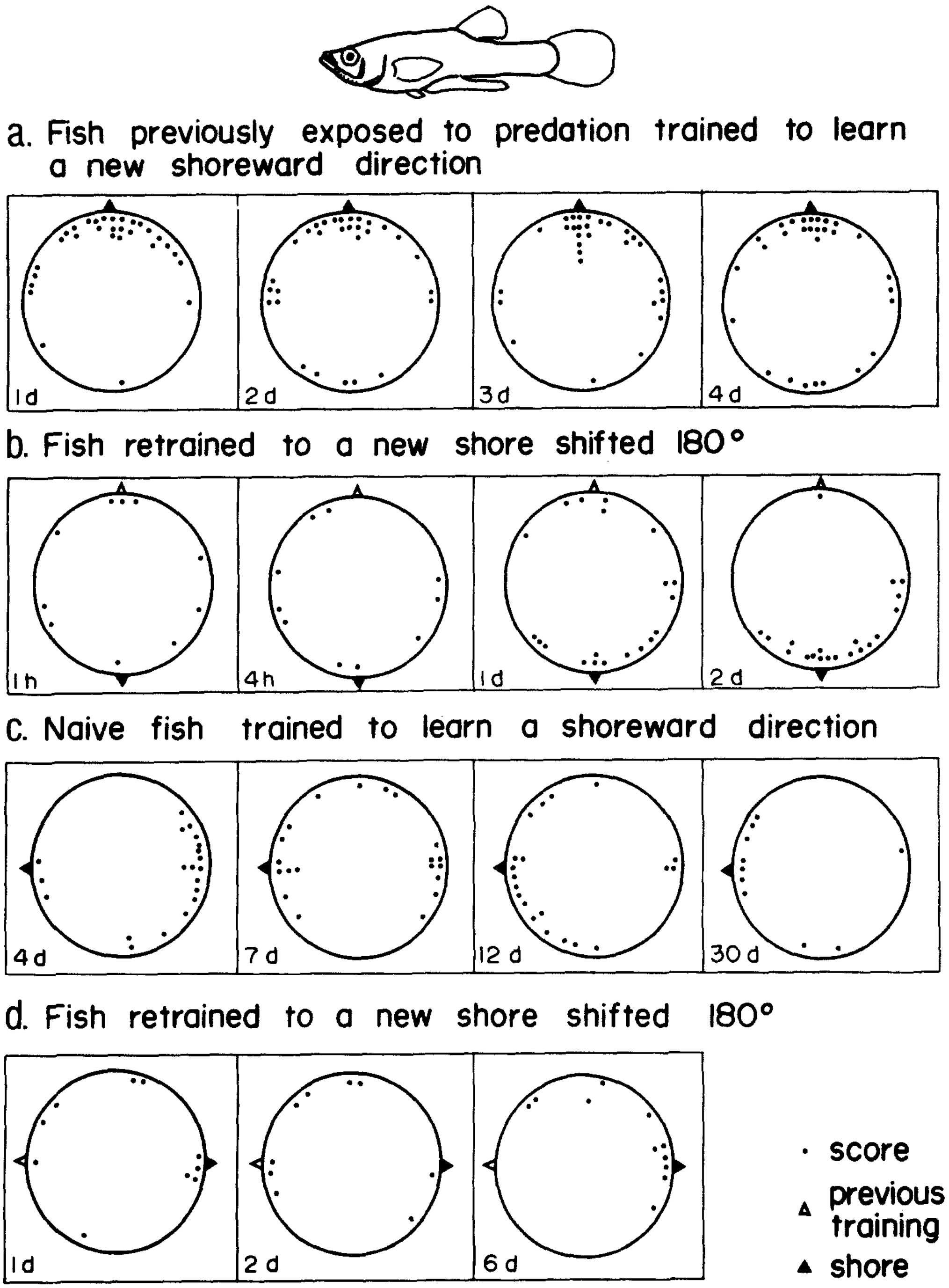

Fig. 3. Orientation tests to determine the time (indicated in lower left corners) for mosquitofish, *Gambusia affinis*, to learn a new shoreward direction. All fish were tested under the sun in a circular arena. a– and b–results of experienced fish at various times after being conditioned in rectangular training tanks with a predator. c– and d–results of naive fish at various times after being conditioned in training tanks with a predator (modified after Goodyear 1973).

signed to define the role of celestial and magnetic clues in the migrations of juvenile Pacific salmon are cited as proof that young orient in directions representing inherited adaptations to the geography of particular lake-river systems (Quinn 1984, Ogden & Quinn 1984). However, a close examination of the data reveals that such a conclusion is not so evident. Table 1 presents the results of experiments conducted outdoors under natural conditions or indoors under a simulated sun to evaluate the role of celestial and magnetic cues on preferred compass directions. Juvenile salmon tested by Quinn (1980) and Quinn & Brannon (1982) were caught during their migrations, and compass directions exhibited by these fish in experimental arenas may have been learned during migrations experienced before capture. In these studies, the occurrence of non-random distributions (Quinn & Brannon 1982), the phenomenon of reverse orientation (bimodal orientation along the axis of migration; Table 1), and the hypothesis of Quinn (1980) that sockeye young migrating south in Chilko Lake in daytime orient to the west at night, all suggest considerable flexibility in compass orientation.

Simpson (1979), Brannon et al. (1981) and Quinn & Groot (1983, 1984) tested juveniles with no prior migratory experience. Of the 5 stocks of sockeye smolts tested by Simpson, 2 showed no preferred compass direction and one showed a geographically-inappropriate compass direction (Table 1). Newly emerged Weaver Creek sockey alevins (Brannon et al. 1981) exhibited a northerly compass direction appropriate for migration in Harrison Lake but inappropriate for the southwesterly migration out of Weaver Creek (Table 1).

Table 1. Mean bearings (special conditions) of juvenile pacific salmon tested under natural or simulated natural conditions and the expected bearing of the same fish based on their natural migration route. n = number of fish tested, either individually or in groups; n.s. – random distribution of directional responses.

Study	Species	Age	Rearing environ.	Experimental environ.	Origin	Mean bearing (Cond.)	N	Expected bearing
Simpson (1979)	sockeye	1971 smolts	hatchery – identical for all fish	indoor circular tank with simulated sun	Fulton	301	572	325 to 350
					Upper Babine	n.s.	641	350
					Morrison	143–323*1	675	155 to 350
					Lower Babine	n.s.	109	350
					Pinkut	136	81	325 to 350
Quinn (1980)	sockeye	parr	wild caught	outdoor 4-arm arena	L. Washington	349 (night)	3,284	NNW
					Chilko L.	180 (day)	1,354	SSE
						254 (night)	537	WNW*2
Brannon et al. (1981)	sockeye	1979 parr	caught at emergence (wild)	outdoor 4-arm arena	Weaver Cr. (Harrison Lake)	22 (night)	374	SW
		1980 parr				351 (moon present)	827	SW
Quinn & Brannon (1982)	sockeye	1980 smolts	wild	outdoor 8-arm arena	Babine L. outlet	342*3	1,533	NNW
		1981 smolts	wild			161–341*1	8,219	NNW
Quinn & Groot (1983)	chum	1982 parr	hatchery, first generation	outdoor 8-arm arena	Conuma R.	256*4	4,000	SW
Quinn & Groot (1984)	chum	1983 parr	hatchery	outdoor 8-arm arena	Conuma R.	182 (high flow)	15,978	SW
						14–194 (low flow)*1	6,373	SW

*1 – bimodal non-random orientation along the indicated axis

*2 – assuming on-shore orientation at night rather than SSE lake migration

*3 – preference for N and W

*4 – preference for SW and NW

The demonstration of Quinn & Groot (1983) that Conuma R. chum parr tested in 1982 exhibited non-random distributions of compass directions suggests that differences exist between groups of young of the same year class. In addition, Conuma R. chum young observed in 1983 showed a preferred compass direction different from that observed in 1982 (Table 1). Although these studies demonstrate the existence of innate preferred compass directions, the observation of intra-population and inter-year differences is not consistent with the hypothesis of inherited geographically-appropriate adaptations in compass orientation.

Work on pink salmon conducted by Healey (1967) is also cited as evidence for innate compass orientation in directions appropriate for migration. Healey did not provide mean bearings but expressed the orientation of wild young observed in outdoor circular tanks as the number of pointings along and across the axis of migration in the Bella Coola R., British Columbia. Young oriented along the axis of migration for only part of the day; of the 71 tests presented, 33 showed a significantly greater number of pointings along, rather than across, the axis of migration. Another 17 tests showed no significant differences and the remainder were not analysed as they showed more pointings across, rather than along, the axis of orientation. In addition, 50% of the pointings along the axis of migration were cases of reverse orientation.

The observations reviewed above may be analogous to the situation described by Wallraff (1978) who originally introduced the term 'preferred compass direction (PCD)' to describe the loft-specific compass directions exhibited by displaced homing pigeons that deviate in a site-specific manner from the home direction. In a recent analysis of the initial orientation data of inexperienced homing pigeons, Wallraff (1986) recorded several observations reminiscent of the salmon data presented in Table 1. He notes that, even for pigeons from the same loft, the PCD is not constant. Its direction and strength varies considerably in time. In addition, polarity of the PCD seems to be reversible as unknown local features induce some pigeons to produce a reversed PCD. In considering the functional background of the PCD, Wallraff (1986) suggests that it may have no navigational meaning at all. An alternative function might be facilitation of flock cohesion under strange conditions. In such a case, the particular direction would be unimportant as long as all birds take the same direction to prevent dispersal of the flock. The particular direction could be induced by some factor that may be purely genetic, or the result of a self-training process and could involve any environmental feature that includes some directionality. There is evidence for birds that such preferred directions can be overridden by experience or adult example (reviewed by Baker 1982). Baker has suggested that the preferred compass direction is a mechanism by which a bird explores its familiar area and builds a learned familiar area map.

In conclusion, the hypothesis that Pacific salmon young orient in directions representing inherited adaptations to the geography of particular lake-river systems is an oversimplification of a complex orientation process. The evidence presented in Table 1 does not permit us to exclude the possibility that experience plays a significant role in the compass orientation of the early life stages of Pacific salmon.

Early perceptual learning

The role of early perceptual learning affecting adult orientation behavior has not been investigated in fish to the best of my knowledge. However, this may be a fruitful line of research. Bingham & Griffiths (1952) have demonstrated that rats reared from the age of 21 days in the wider environments of experimental rooms equipped with tunnels, inclined planes and swinging doors were superior in maze performance to animals reared in the restricted environments of laboratory cages. The demonstration by Goodey & Liley (1986) that juvenile guppies, *Poecilia reticulata,* chased by adult conspecifics were more likely to survive a predatory encounter later in life suggests that early perceptual learning may affect a variety of adult fish behaviors.

Learning to recognize the goal

Imprinting

Goal recognition in a variety of freshwater, intertidal and anadromous fish species has often been attributed to olfaction. The olfactory hypothesis of home stream recognition by returning adult salmon (Hasler & Wisby 1951) is supported by the results of experiments in which salmonids exposed as parr or smolts to a low concentration of the synthetic chemical morpholine were successfully decoyed to streams scented with morpholine at the same concentration during their homing migrations (Hasler & Scholz 1983). Further support is provided by electrophysiological studies in which the magnitude of the olfactory bulbar response to morpholine of adults exposed as juveniles to morpholine was significantly greater than that of unexposed fish (reviewed by Hasler & Scholz 1983). Although the morpholine imprinting work has been the focus of much controversy due to the high concentrations of morpholine needed to elicit the olfactory bulbar response (Hara et al. 1984), these experiments represent excellent examples of the significant role played by early experience in the development of goal recognition.

Experiments designed to investigate the parent-stream olfactory hypothesis have demonstrated that olfactory learning during smoltification is a relatively rapid process akin to imprinting. However, these investigations have failed to accurately define the sensitive period for olfactory learning. As a result, the link between the classical phenomenon of imprinting and long-term olfactory memory in salmon is speculative. In order to establish this link, Morin et al. (1988) investigated the mechanism of olfactory learning in young Atlantic salmon, *Salmo salar,* undergoing smoltification. Two experiments were conducted using a heart-rate conditioning technique (Morin et al. 1987) to define when the sensitive period occurred during smoltification and to reveal that a sensitive period had occurred by its effects on olfactory recognition following smoltification. In the first experiment, the magnitude of a conditioned cardiac response to L-cysteine was measured during six 10 day intervals during the parr-smolt transition. We postulated that the ability to learn an odor should be optimal during a sensitive period and that the magnitude of the conditioned cardiac deceleration would significantly increase at such times. In a second experiment, retention of an olfactory memory was evaluated by exposing fish to L-cysteine during the same six 10 day intervals of smoltification and measuring their unconditioned cardiac deceleration to the odor after smoltification. Fish decelerate heart rate in response to a recognized odor and we postulated that the magnitude of cardiac deceleration would be significantly greater among fish exposed to an odor during a sensitive period.

Results of these two experiments are summarized in Figure 4. In the upper panel, the percent heart rate reduction of groups of ten fish are presented for the six 8 day age intervals of smoltification. Two groups of fish were tested during each age interval: (1) conditioned fish were presented with the systematic pairing of the odor stimulus and an electric shock. The perfect correlation between the 2 stimuli induces excitatory conditioning and an increase in the magnitude of the conditioned response; (2) control fish were presented with a random sequence of the odor and shock stimuli. Learning does not occur in this group because the presence of the odor is uncorrelated with that of the shock. Therefore, this treatment represents a control procedure with which to assess excitatory conditioning. A multivariate analysis of variance revealed that although fish of all age groups of smoltification exhibited olfactory learning, significantly greater learning performances were exhibited by fish of age groups 3 and 6 (Morin et al. 1988).

The results of the second experiment designed to assess olfactory memory are presented in the lower panel of Figure 4. Groups of fish exposed to L-cysteine during the same six 8 day intervals of smoltification were tested 53 days following odor exposure by measuring the magnitude of the unconditioned heart rate reduction due to L-cysteine. Long term recognition of L-cysteine was more pronounced when age group 3 fish were exposed to the odor. These results show that the effectiveness of an odor stimulus is greater during a particular period of smoltification and are thus consistent with the

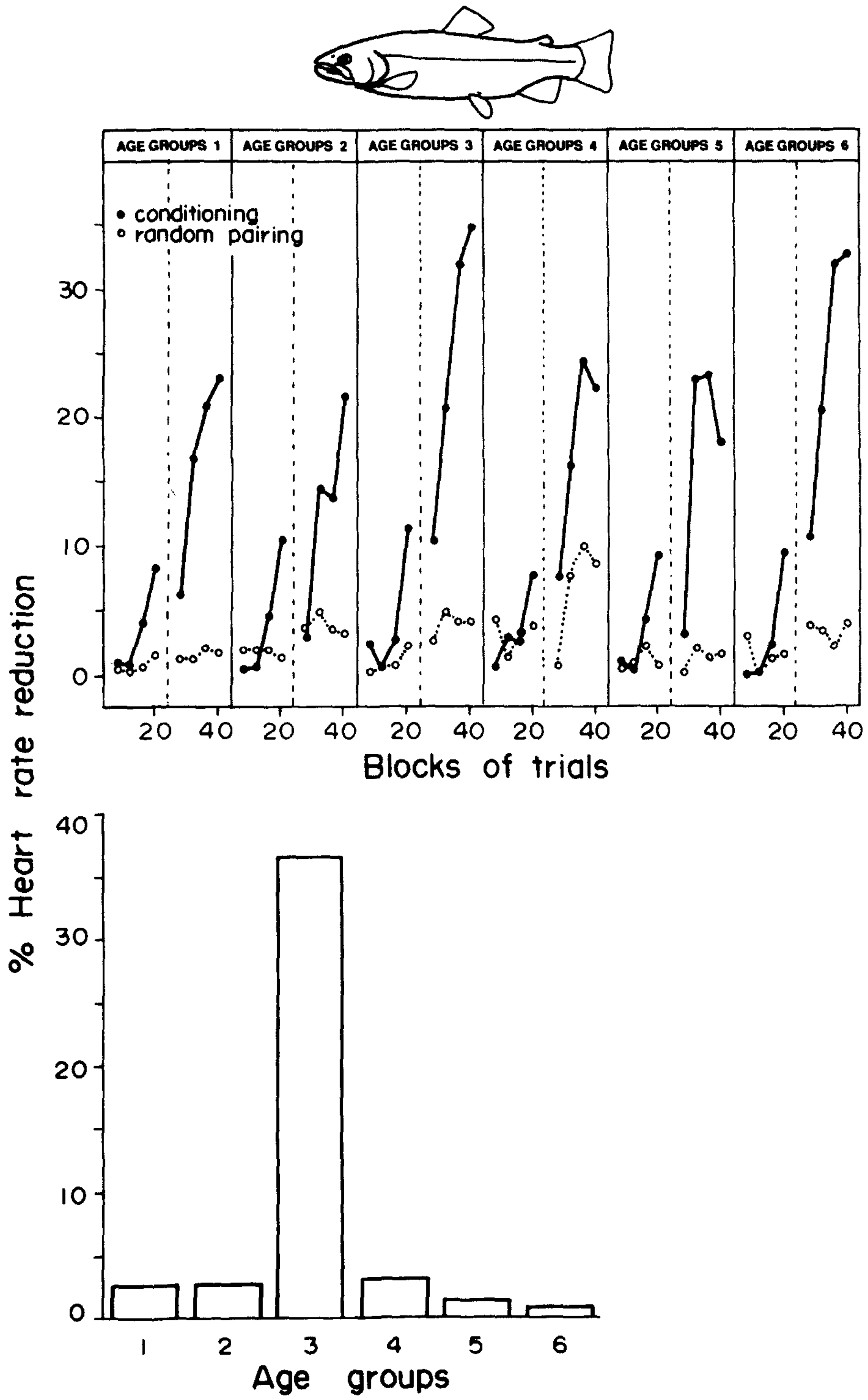

Fig. 4. Upper panel: mean percentage heart rate reduction, per block of five trials, in 2^+ Atlantic salmon, *Salmo salar*, tested in the presence of L-cysteine (3.8×10^{-4} M) during smoltification. Six age groups of 10 fish each were conditioned to the odor followed by a shock and six age groups of 10 fish each were exposed to random odor-shock presentation. Lower panel: mean percentage heart rate reduction, during a 10-day trial session, in 2^+ Atlantic salmon exposed to L-cysteine. Six age groups of 10 fish each were pre-exposed to L-cysteine during an 8-day interval (age groups 1 to 6) and tested 53 days after odor pre-exposure (modified after Morin et al. 1988).

classical imprinting phenomenon. However, an increase in the ability to learn an odor during smoltification does not always result in long term olfactory memory. Age groups 3 and 6 showed significantly greater learning performances whereas long term recognition occurred only when age group 3 fish were exposed to the odor. The nature of the mechanism responsible for olfactory imprinting and the reversibility of its effects later in life remain challenging areas for future study.

Critical distance

Although it is implicitly assumed that homing animals stop migrating when reaching their goal because they recognize local landmarks, Bovet (1987) has argued that an estimation of the distance to be covered to reach home may be useful to animals with only moderate navigational abilities. Bovet (1987) illustrates his hypothesis with the hypothetical example of a migrant that misses the familiar area due to an error in orientation. In such a case, migrants that depend only on familiar landmarks to stop their movement will theoretically continue their migration indefinitely in the wrong direction. However, a migrant using an estimate of distance (or time) to the goal may suspend migration if familiar landmarks are not encountered and use some other tactic such as search in an attempt to locate familiar landmarks. The hypothesis is based on the observations of North American red squirrels, *Tamiasciurus hudsonicus,* who following displacement of various distances from their home sites, tended to move in directions that were nonrandom relative to home but who aborted their homing trip several hundred meters from the release site if home was not encountered. These animals often returned to the release site or closer to it and subsequently made forays of similar length in other directions. Attempts to home apparently ceased after a few days. The length of these forays were similar to normal exploratory forays made outside the home range. Bovet (1987) proposed that the critical distance is a means by which a migrant evaluates whether it has made an orientation mistake and by which it remains within a normal distance of its goal.

In support of the generality of his hypothesis, Bovet cites the work of Veen (1970) who analyzed the results of the extensive capture-mark-recapture program conducted on the plaice, *Pleuronectes platessa,* from 1904 to 1909 in the North Sea. Of nearly 13000 fish tagged and displaced between 11 and 512 km from their place of capture, some 1800 of these fish were eventually recaptured within 100 km of the release site. This distance corresponds to the majority of intercapture distances of control plaice that had been recaptured after release at their original site of capture. Transplantation experiments carried out with immature plaice from 1963 to 1966 (Veen 1978) generally confirmed the earlier findings. The tendency to return to the point of capture in immature plaice stopped working somewhere between displacement distances of 150 to 250 km. Juveniles displaced over longer distances did not home but followed local fish in the new area. Observations of the migrations of mature plaice conformed to the same pattern. The average distance from the release point of recaptured mature plaice tagged on spawning grounds without displacement increased with time to between 160 and 240 km in half a year, but decreased thereafter to reach a minimum distance after 1 year as they homed to the spawning grounds (Fig. 5). Larger fish moved further away than smaller ones. However, mature fish tagged and transplanted between different spawning grounds largely failed to return to their original spawning grounds. Mature fish displaced short or medium distances did no better in returning than plaice displaced long distances; the distance covered back to the spawning grounds after 1 year did not exceed 80 km (Veen 1978).

Another observation that suggests migrating fish estimate the distance to be covered during homing is provided by Ogden & Quinn (1984) who displaced juvenile grunts trapped in a seagrass bed on their dawn migration to their home patch reef. One group of fish was displaced far away to an unfamiliar seagrass bed and immediately released. These fish followed a compass course appropriate to their normal route over a distance approximately equal to the distance at which they were trapped from their home patch reef and then meandered.

These rather anecdotal observations only permit

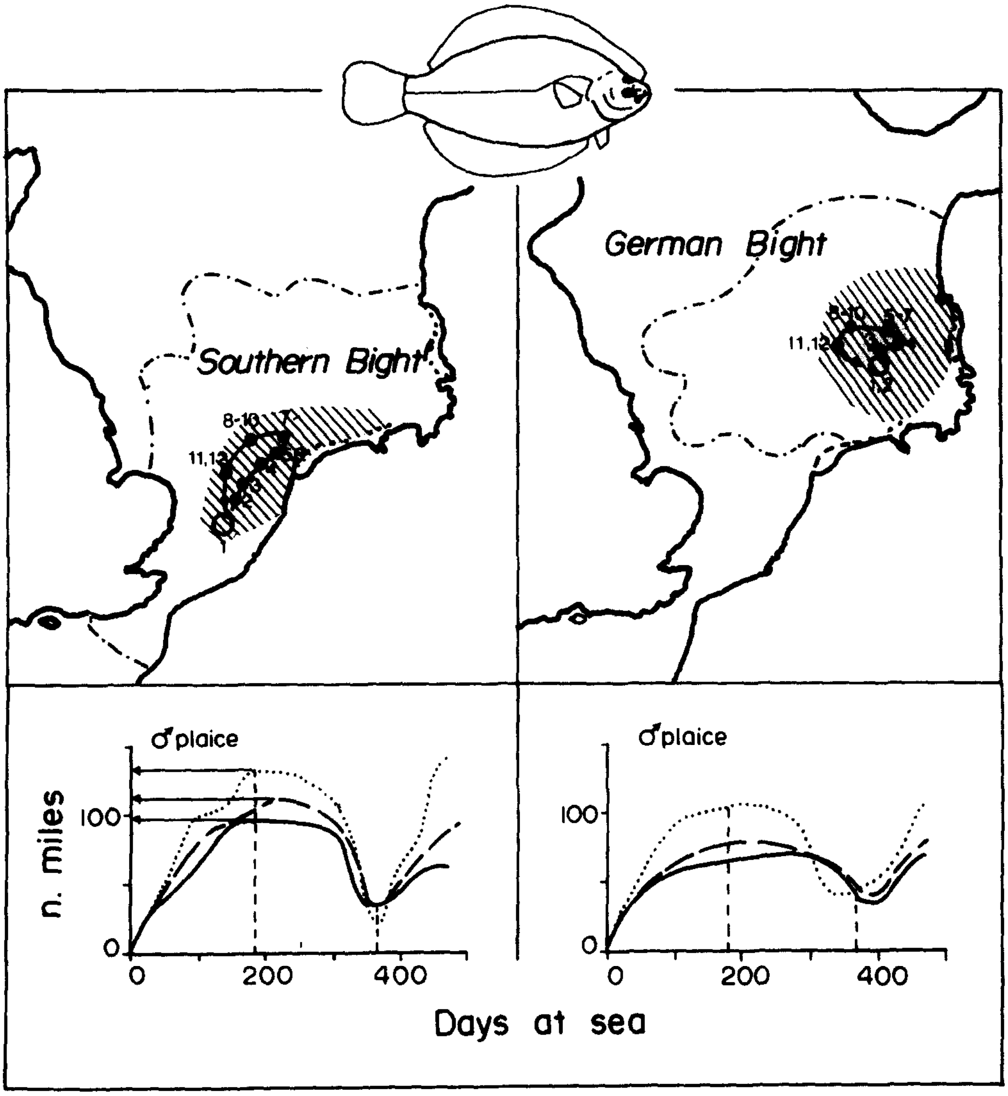

Fig. 5. Upper panel: release positions (open circles) of mature plaice, *Pleuronectes platessa,* tagged in the spawning seasons of 1959 to 1966 on two spawning grounds in the north sea. Tracks of the centers of density of the tagged population throughout the year (numbers denote months), recapture area of the majority of returned fish (shaded area), and the boundaries of the areas of distribution of the two sub-populations (broken and dotted lines) are indicated. Lower panel: average distance from the release point of recaptured male plaice of different lengths as a function of days at liberty. 20–30 cm (solid line), 30–35 cm (broken line), 35–40 cm (dotted line) (modified after Veen 1978).

us to speculate about the use of a critical distance strategy during migration. In the case of plaice using selective tidal stream transport to move between spawning and feeding grounds (reviewed by Arnold & Cook 1984), the existence of such a strategy would explain the behavioral problem of how fish know when to suspend semi-diurnal vertical migrations so as to leave the transport system at the end of the journey. This problem is central to the objections of Veen (1978) who criticized the generality of tidal stream transport on the grounds that the directed and rapid displacement of plaice along tidal stream paths would disrupt the existing structure of North Sea plaice stocks.

The concept of a time or distance evaluation in fish is closely related to the theory of inertial navigation. This is homing based on the turns of the outward journey as registered by the semicircular canals, the return path being reconstructed according to these values and their intervening distances (Schöne 1984). This is another example of route-based navigation. The ability of a migrant to maintain a constant course heading in the absence of external clues is often presented as evidence suggestive of inertial, or idiothetic, guidance (e.g. Harden Jones 1984). The observations of Kleerekoper et al. (1970) that goldfish maintained a balance between left and right turns over periods of up to 60 h suggest some form of central nervous system summation akin to the process of inertial guidance. Idiothetic goal orientation and distance measurement, in which the spatial information is provided by the organism itself in the form of changes in body position, has been demonstrated in animals as diverse as spiders, honey bees, crabs and mammals (Schöne 1984). In fish, the existence of inertial orientation and distance measurement remains to be demonstrated.

General discussion

The primary selective advantage of the ability to learn is that it permits adaptation to ecological factors that vary too rapidly to effect adaptive changes in the gene pool (Johnston 1982). As the physical framework that organisms use for obtaining fixed reference points are subject to varying degrees of change on an evolutionary time scale, the existence of purely innate mechanisms of orientation is unlikely (Adler 1970). However, a great deal of evidence indicates that learning, even though it is based on conditioning, is specialized for the tasks that the animal is likely to encounter (reviewed by Gould & Marler 1987). Animals appear to be innately equipped to recognize when they should learn and what stimuli to attend to. Given the great variety of situations and movements that we have considered as examples of migration, we must assume that the nature and role of learning in migratory orientation is equally varied. We may ask if there is any hope of seeking generalities or must each case of migratory orientation be considered as unique. Some evidence exists to demonstrate that the precision of the upstream migrations of anadromous fishes is correlated with life history (Bernatchez & Dodson 1987). Stocks that make long or difficult migrations are more efficient in their use of energy reserves than stocks that make shorter migrations. Improved energetic efficiency was in part explained by a greater degree of precision and persistence of upstream orientation suggesting that the difficulty of migration selects for more precise orientation. Can we hope to establish a similar link between life history and the nature of learning in migratory orientation?

The distinction between fish that make repeated visits to various parts of their habitat and those that may rarely visit more than once any part of their habitat represents two fundamentally different migratory lifestyles in fishes. Orientation mechanisms based on spatial learning are intuitively of greater significance among fishes that pass all of their lives within a well-defined familiar area or make repeated migrations between feeding and spawning grounds. In such cases, natural selection may favor the development of piloting mechanisms based on sequential landmark orientation, cognitive mapping and social transmission. The ontogenetic development of such mechanisms should be open to adjustment based on experience thus permitting the building up of a familiar area based on exploration. On the other hand, fish that traverse largely unfamiliar territory and return to a natal spawning area only once in their life, such as the semelparous Pacific salmon, have little opportunity or need to develop spatial representations of their life-time path based on experience. Such species, however, still must learn site-specific cues permitting goal recognition.

The learning of cues characteristic of home is probably of importance to all species that home to specific areas and provides another example of the relationship between learning and migratory pattern. The importance of olfaction is well established in the reproductive homing migrations of a variety of anadromous species (reviewed by Leggett 1977) that must traverse largely unfamiliar territory during the homing migration. Olfaction is also involved in the homing of the radiated shanny, *Ulvaria subbifurcata*, when displaced from their home sites located in the littoral and sublittoral zones of

Newfoundland (Goff & Green 1978). These fish normally restrict their movements to a relatively small area, less than 3 m^2. In most cases of olfactory orientation, the imprinting process is assumed to be involved but the existence of a sensitive period for olfactory learning is rarely established. One may ask the question whether the classic imprinting process is essential in establishing olfactory memory in all cases where olfaction is involved in homing. There are many examples of long-term memory in vertebrates that do not involve sensitive periods. Large numbers of experiments in classical conditioning are concerned with the development of long-lasting associations between conditional and unconditional stimuli that generally involve some form of rehearsal with no prerequisite of a sensitive period (Mazur 1986). I suggest that the fundamentally different nature of the migrations of shanny and salmon may involve different olfactory learning mechanisms. Shanny spend most their lives in a well-defined familiar area and thus have the opportunity to remain in sensory contact with the home site. I can see no selective advantage to restrict olfactory learning to a brief sensitive period in situations where an animal can constantly update its olfactory perception of home. In such cases, sensitive periods for olfactory learning may not exist or imprinted odors may be subject to modification by association with a variety of other stimuli characteristic of the home site. Migrations such as the repeated movements between adult feeding grounds and non-natal spawning grounds exhibited by some species may also involve such long-term associations between relevant environmental stimuli. In contrast, the long-term olfactory memory of salmon and other species that lose sensory contact with the home site must be resistant to change if the goal is to be successfully recognised at the end of the return migration. Brief, early sensitive periods are essential to insure that the imprinted odor is characteristic of the home site and long-term olfactory memory must be resistant to modification.

The shanny-salmon comparison is an extreme one presented to illustrate possible differences in the nature of olfactory learning in the migration of 2 species with radically different life styles. Among salmonids, however, less extreme differences in life style that may influence the nature of olfactory learning are the time juveniles spend in their natal rivers before migrating to sea and the degree of homing exhibited during the reproductive migration. In pink and chum salmon, *Oncorhynchus gorbuscha, O. keta,* young migrate downstream immediately after emergence. In others such as coho and sockeye,*O. kisutch, O. nerka,* and Atlantic salmon, downstream migration occurs one or more years after alevin emergence and sometimes involves periods of residence in intervening lakes and rivers before migrating to sea. In addition, considerable stock plasticity exists. Various stocks of rainbow trout, *Salmo gairdneri,* exhibit the entire spectrum of downstream migration patterns (Northcote 1984).

Rates of homing and straying to natal rivers also appear to vary between species and populations of Pacific salmon. Although the data are limited, such observations have led Quinn (1984, 1985) to hypothesize that straying is an alternative life history strategy in balance with homing. According to this hypothesis, large stable rivers should have higher proportions of homing salmon than smaller, less stable ones. This in turn would favor the evolution of specialized adaptations increasing early survival in complex freshwater environments. However, the classification of straying and homing as alternative strategies leads to the contradictory notion that selective advantage accrues to salmon that, under certain conditions, make mistakes in home river recognition. A more parsimonious hypothesis is that the selective pressure for precise homing varies according to the stability and complexity of the freshwater habitat. Straying may not be an alternative strategy but simply a manifestation of less precise homing. Although entirely speculative, I suggest that the nature and importance of olfactory imprinting may be correlated with the extent and complexity of early freshwater residence and the precision of homing. For example, species or populations occupying stable streams for long periods of time may exhibit multiple sensitive periods and imprint to a sequence of qualitatively different odors during their freshwater residence. In contrast, populations with brief freshwater residence times will not have this opportunity.

The relative importance of population-specific odors and those emanating from riverine features, often viewed as opposing hypotheses to explain olfactory recognition of the natal stream (Stabell 1984), may also be a function of homing and the extent of freshwater residence. Population-specific odors may be more reliable olfactory markers of home in complex systems of interconnecting tributaries where odors emanating from riverine features may not be readily discriminable. Related to this question is the possibility that salmon may possess innate predispositions to imprint to particular classes of odors. As in the case of song learning in birds, young salmon may possess an empty mental slot labelled 'home-stream odor' and the olfactory imprinting process may serve to fill the slot. Although empty, the slot may not be shapeless. Salmon may imprint more readily to some odors than others. This is the basis for referring to imprinting as template learning, a term originally used to describe song learning in birds (Staddon 1983). We can speculate that the olfactory template of populations exhibiting a high degree of homing may be very narrow, permitting precise olfactory definition during homing, whereas that of populations exhibiting less precise homing may be quite broad leading to a more cosmopolitan preference for spawning rivers. In the future, studies of olfactory-based orientation should demonstrate the occurrence and nature of sensitive periods, the nature of the imprinted odor, the resistance of olfactory memory to modification and the degree of straying. These variables could be compared between species or populations with different migratory patterns to test the hypothesis that the nature of olfactory learning is a function of life history. Such an analysis could be extended to any sensory modality involved in home-site recognition.

Any investigation of how fish in a particular environmental situation establish the appropriate direction of movement to reach a goal must start by identifying possible transport mechanisms provided by water currents. It is untenable to propose the existence of sophisticated mechanisms of route-based or location-based navigation if a fish can complete part or all of its migratory cycle by riding a natural conveyor belt. In such situations, natural selection would most likely favor exploiting appropriate currents. For example, Weihs (1984) has shown theoretically that in areas where tides are directional, fish may achieve considerable energy savings by swimming in midwater at a constant speed relative to the bottom when the tide flows in the direction of migration and holding station on the bottom when the tide flows in other directions. Such behavior, known as selective tidal stream transport, has been demonstrated in plaice, *Pleuronectes platessa* (Greer Walker et al. 1978) and can save up to 40% in energy cost compared with the alternative strategy of swimming continuously in the direction of overall movement. In the case of North Sea plaice, however, swimming continuously in the direction of overall movement involves swimming against tidal currents that exceed the critical swimming speed of 1.4 body lengths per second (Priede & Holliday 1980). As such speeds are exceeded for 3–4 h during each tide during spring tide conditions in the Southern Bight area (G.P. Arnold, personal communication), it seems likely that negatively buoyant plaice attempting to swim against such currents will fatigue and end up on the bottom. Thus, the adaptive significance of selective tidal stream transport concerns not only energy savings that may be invested in present or future reproductive effort, but also reducing the probability of fish exceeding their metabolic limits during migration thus reducing the probability of mortality prior to spawning (Priede 1985).

The use of tidal stream transport raises a number of behavioral problems. For example, when entering or leaving spawning or feeding grounds, the choice of tide is of critical importance if fish are to be transported in the appropriate direction. In addition, some behavioral mechanism must maintain the pattern of semidiurnal vertical migration so that fish repeatedly join the appropriate tide (Arnold & Cook 1984). One possible mechanism is the use of an endogenous biological clock somehow entrained to the local tidal cycle. Such a mechanism has been demonstrated in the case of juvenile American eels, *Anguilla rostrata,* migrating up estuaries by riding the flood tides and settling out on the bottom during ebb tides (McCleave & Wippelhauser 1987). The environmental stimuli responsible for entraining endogenous, circatidal rhythms in juvenile eels are unknown, although tide-specific olfactory cues may play a role (Creutzberg 1961). Hydrostatic pressure cycles can elicit cycles of locomotory behavior in several marine species (Gibson 1984). In the case of plaice larvae entering shallow coastal nursery areas in the North Sea, high concentrations of bottom sediment swept up into suspension by the generally stronger flood tides could indicate both passive vertical transport and represent an entraining cue for active vertical migrations during flood tides (Rijnsdorp et al. 1985).

Although we may be able to identify environmental stimuli that are associated with specific segments of the tidal cycle, we still do not know how fish using tides for transport know that they are moving in an appropriate direction. For fish larvae or juveniles migrating for the first time to nursery areas, the swimming response may be a simple motor program requiring little experience. In return migrations, olfactory cues indicative of home could permit the choice of the appropriate currents. However, in situations where the cue indicative of home is not uniquely associated with one part of the tidal cycle, some other mechanism must intervene to prevent the migrant from moving back and forth over the same ground. One possible solution is that fish may learn to attend to different stimuli during ebb and flood tides if one tidal state is associated uniquely with an entraining stimulus for at least part of the migration. For example, Dodson & Dohse (1984) hypothesized that rheotactic stimuli associated with the transition between flood and ebb tide may acquire the capacity to elicit swimming behavior initially controlled by changes in olfactory stimulation if the two events are perceived in synchrony at the detectable edge of the diffuse olfactory field. The result of such an association may lead to unidirectional movement within the odor field despite the presence of the olfactory cue during both tidal states and the absence of detectable olfactory gradients.

In cases where migrations cannot be explained by the use of physical transport systems, we may then consider the use of compass orientation, route-based or location-based navigation, or some combination of these mechanisms. The extensive literature concerning the oceanic migrations of Pacific salmon and the influence of meteorological and oceanographic features on their migrations (reviewed by Mysak 1986) indicate that although salmon use ocean currents in their migrations, they also migrate across ocean domains and major current features requiring some mechanism of precise distant orientation. The nature of the orientation mechanism and the environmental stimuli involved are unknown. Orientation based on a magnetic compass, and possibly a geomagnetic map (Quinn 1984), appears to be the most likely candidate at the time being, but little can be said about the role of experience in the development of the salmon's magnetic compass. In migratory birds, the magnetic compass appears malleable during early development and may be modified by visual stimuli that provide information about true geographic directions (reviewed by Able & Bingham 1987). However, experiments designed to specifically examine the ontogeny of magnetic orientation in birds and fish have not been performed. An exciting starting point may be to raise salmon from the egg in the absence of magnetic stimuli and under altered magnetic fields to examine the development of preferred compass directions.

From distant orientation to goal recognition, the mechanisms involved are the products of developmental processes starting at the larval period. Thus, the ontogenetic approach is essential to the understanding of the interaction of experience and genetics in migratory behavior. As stated by Able & Bingham (1987), the manipulation of clues and processes that occur during the development of orientation mechanisms may lead to the discovery of the essential characteristics of them that cannot be clarified in the adult organism. The development of the olfactory hypothesis of salmon homing is an excellent example of the understanding that can be obtained using the ontogenetic approach. I conclude by suggesting that a similar approach applied to the study of such mechanisms as spatial learning, tidal transport, time and distance evaluation and compass orientation will produce equally exciting results.

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References cited

Able, K.P. 1980. Mechanisms of orientation, navigation and homing. pp. 283–373. *In:* S.A. Gauthreaux, Jr. (ed.) Animal Migration, Orientation, and Navigation, Academic Press, New York.

Able, K.P. & V.P. Bingham. 1987. The development of orientation and navigation behavior in birds. Quart. Rev. Biol. 62: 1–29.

Adler, H.E. 1970. Ontogeny and phylogeny of orientation. pp. 303–336. *In:* L.R. Aronson, E. Tobach, D.S. Lehrman & J.S. Rosenblatt (ed.) Development and Evolution of Behavior: Essays in Memory of T.C. Schneirla, W.H. Freeman, San Francisco.

Adler, H.E., 1971. The development and evolution of orientation: panel discussion. Ann. N.Y. Acad. Sci. 188: 393–407.

Arnold, G.P. 1981. Movements of fish in relation to water currents. pp. 55–79. *In:* D.J. Aidley (ed.) Animal Migration, Cambridge University Press, Cambridge.

Arnold, G.P. & P.H. Cook. 1984. Fish migration by selective tidal stream transport: first results with a computer simulation model for the European continental shelf. pp. 227–261. *In:* J.D. McCleave, G.P. Arnold, J.J. Dodson & W.H. Neill (ed.) Mechanisms of Migration in Fishes, Plenum Press, New York.

Aronson, L.R. 1951. Orientation and jumping behavior in the gobiid fish *Bathygobius soporator.* Amer. Mus. Novit. 1486: 1–22.

Aronson, L.R. 1971. Further studies on orientation and jumping behavior in the gobiid fish, *Bathygobius soporator.* Ann. N.Y. Acad. Sci. 188: 378–392.

Baker, R.R. 1978. The evolutionary ecology of animal migration. Hodder and Stoughton, London. 1012 pp.

Baker, R.R. 1982. Migration, paths through time and space. Hodder and Stoughton, London. 248 pp.

Balchen J.G. 1976. Principles of migration in fishes. Foundation for Scientific and Industrial Research of the Norwegian Institute of Technology (SINTEF), Report STF48-A76045, Trondheim, Norway. 25 pp.

Balchen, J.G. 1979. Modeling, prediction, and control of fish behavior. pp. 99–146, *In:* C.T. Leondes (ed.) Control and Dynamic Systems, Vol. 15, Academic Press, New York.

Barkley, R.A., W.H. Neill & R.M. Gooding. 1978. Skipjack tuna, *Katsuwonus pelamis,* habitat based on temperature and oxygen requirements. U.S. Fish. Bull. 76: 653–662.

Bateson, P.P. 1981. Control of sensitivity to the environment during development. pp. 432–453. *In:* K. Immelmann, G.W. Barlow, L. Petrinovich & M. Main (ed.) Behavioral Development: The Bielefeld Interdisciplinary Project, Cambridge University Press, Cambridge.

Bernatchez, L. & J.J. Dodson. 1987. Relationship between bioenergetics and behavior in anadromous fish migrations. Can. J. Fish. Aquat. Sci. 44: 399–407.

Bingham, W.E. & W.J. Griffiths, Jr. 1952. The effect of different environments during infancy on adult behavior in the rat. J. Comp. Physiol. Psychol. 45: 307–312.

Bitterman, M.E. 1984. Migration and learning in fishes. pp. 397–420. *In:* J.D. McCleave, G.P. Arnold, J.J. Dodson & W.H. Neill (ed.) Mechanisms of Migration in Fishes, Plenum Press, New York.

Bovet, J. 1987. Cognitive map size and homing behavior. pp. 252–265. *In:* P. Ellen & C. Thinus-Blanc (ed.) Cognitive Processes and Spatial Orientation in Animal and Man, Vol. 1, Experimental Animal Psychology and Ethology, Martinus Nijhoff Publishers, Dordrecht.

Brannon, E.L. 1972. Mechanisms controlling migration of sockeye salmon fry. Int. Pac. Salm. Fish. Comm. Bull. 21: 1–86.

Brannon, E.L., T.P. Quinn, G.L. Lucchetti & B.D. Ross. 1981. Compass orientation of sockeye salmon fry from a complex river system. Can. J. Zool. 59: 1548–1553.

Creutzberg, F. 1961. On the orientation of migrating elvers (*Anguilla vulgaris* Turt.) in a tidal area. Neth. J. Sea Res. 1: 257–338.

Del Russo, J.E. 1975. Observational learning of discriminative avoidance in hooded rats. Animal Learning & Behavior 3: 76–80.

Dingle, H. 1980. Ecology and evolution of migration. pp. 1–101. *In:* S.A. Gauthreaux, Jr. (ed.) Animal Migration, Orientation, and Navigation, Academic Press, New York.

Dodson, J.J. & L.A. Dohse. 1984. A model of olfactory-mediated conditioning of directional bias in fish migrating in reversing tidal currents based on the homing migration of American shad (*Alosa sapidissima*). pp. 263–281. *In:* J.D. McCleave, G.P. Arnold, J.J. Dodson & W.H. Neill (ed.) Mechanisms of Migration in Fishes, Plenum Press, New York.

Dodson, J.J. & W.C. Leggett. 1974. Role of olfaction and vision in the behavior of American shad (*Alosa sapidissima*) homing to the Connecticut River from Long Island Sound. J. Fish. Res. Board Can. 31: 1607–1619.

Ellen, P. 1987. Cognitive mechanisms in animal problem solving. pp. 20–35. *In:* P. Ellen & C. Thinus-Blanc (ed.) Cognitive Processes and Spatial Orientation in Animal and Man, Vol. 1, Experimental Animal Psychology and Ethology, Martinus Nijhoff Publishers, Dordrecht.

Gibson, R.N. 1984. Hydrostatic pressure and the rhythmic behavior of intertidal fishes. Trans. Amer. Fish. Soc. 113: 479–483.

Goff, G.P. & J.M. Green. 1978. Field studies of the sensory basis of homing and orientation to the home site in *Ulvaria subbifurcata* (Pisces: Stichaeidae). Can. J. Zool. 56: 2220–2224.

Goodey, W. & N.R. Liley. 1986. The influence of early experience on escape behavior in the guppy (*Poecilia reticulata*). Can. J. Zool. 64: 885–888.

Goodyear, C.P. 1973. Learned orientation in the predator avoidance behavior of mosquitofish, *Gambusia affinis*. Behavior 45: 191–224.

Gould, J.L. & P. Marler. 1987. Learning by instinct. Sci. Amer. 256(1): 74–85.

Greer Walker, M., F.R. Harden Jones & G.P. Arnold. 1978. Movements of plaice (*Pleuronectes platessa* L.) tracked in the open sea. J. Cons. int. Expl. Mer. 38: 72–100.

Griffin, D.R. 1955. Bird navigation. pp: 154–197. *In:* A. Wolfson (ed.) Recent Studies in Avian Biology, University of Illinois Press, Urbana.

Groot, C. 1965. On the orientation of young sockeye salmon (*Oncorhynchus nerka*) during their seaward migration out of lakes. Behav. Suppl. 14: 1–198.

Hara, T.J., S. Macdonald, R.E. Evans, T. Marui & S. Arai. 1984. Morpholine, bile acids and skin mucus as possible chemical cues in salmonid homing: electropysiological reevaluation. pp. 363–378. *In:* J.D. McCleave, G.P. Arnold, J.J. Dodson & W.H. Neill (ed.) Mechanisms of Migration in Fishes, Plenum Press, New York.

Harden Jones, F.R. 1984. Could fish use inertial clues when on migration? pp. 67–78. *In:* J.D. McCleave, G.P. Arnold, J.J. Dodson & W.H. Neill (ed.) Mechanisms of Migration in Fishes, Plenum Press, New York.

Hasler, A.D. 1971. Orientation and fish migration. pp: 429–510. *In:* W.S. Hoar & D.J. Randall (ed.) Fish Physiology, Vol. 6, Academic Press, London.

Hasler, A.D. & A.T. Scholz. 1983. Olfactory imprinting and homing in salmon. Springer-Verlag, Berlin. 134 pp.

Hasler, A.D. & W.J. Wisby. 1951. Discrimination of stream odor by fishes and relation to parent stream theory. Amer. Nat. 85: 223–238.

Healey, M.C. 1967. Orientation of pink salmon (*Oncorhynchus gorbuscha*) during early marine migration from Bella Coola River system. J. Fish. Res. Board Can. 24: 2321–2338.

Hebb, D.O. 1949. The organization of behavior. Wiley, New York. 335 pp.

Helfman, G.S., J.L. Meyer & W.N. McFarland. 1982. The ontogeny of twilight migration patterns in grunts (Pisces: Haemulidae). Anim. Behav. 30: 317–326.

Helfman, G.S. & E.T. Schultz. 1984. Social transmission of behavioral traditions in a coral reef fish. Anim. Behav. 32: 379–384.

Immelmann, K. & S.J. Suomi. 1981. Sensitive phases in development. pp. 395–431. *In:* K. Immelmann, G.W. Barlow, L. Petrinovich & M. Main (ed.) Behavioral Development: The Bielefeld Interdisciplinary Project, Cambridge University Press, Cambridge.

Johnston, T.D. 1982. Selective costs and benefits in the evolution of learning. pp. 65–106. *In:* J.S. Rosenblatt, R.A. Hinde, C. Beer & M.-C. Busnel (ed.) Advances in the Study of Behavior, Vol. 12, Academic Press, New York.

Kleerekoper, H., A.M. Timms, G.F. Westlake, F.B. Davey, T. Marlar & V.M. Anderson. 1970. An analysis of locomotor behavior of goldfish (*Carassius auratus*). Anim. Behav. 18: 317–330.

Leggett, W.C. 1977. The ecology of fish migrations. Ann. Rev. Ecol. Syst. 8: 285–308.

Leggett, W.C. 1984. Fish migrations in coastal and estuarine environments: a call for new approaches to the study of an old problem. pp. 159–178. *In:* J.D. McCleave, G.P. Arnold, J.J. Dodson & W.H. Neill (ed.) Mechanisms of Migration in Fishes, Plenum Press, New York.

Leggett, W.C. & R.R. Whitney. 1972. Water temperature and the migrations of American shad. U.S. Fish. Bull. 70: 659–670.

Lynn, R. 1984. Measuring physical oceanographic features relevant to the migration of fishes. pp. 471–486. *In:* J.D. McCleave, G.P. Arnold, J.J. Dodson & W.H. Neill (ed.) Mechanisms of Migration in Fishes, Plenum Press, New York.

Mazur, J.E. 1986. Learning and behavior. Prentice-Hall, Englewood Cliffs. 387 pp.

McCleave, J.D., F.R. Harden Jones, W.C. Leggett & T.G. Northcote. 1984. Fish migration studies: future directions. pp. 545–554. *In:* J.D. McCleave, G.P. Arnold, J.J. Dodson & W.H. Neill (ed.) Mechanisms of Migration in Fishes, Plenum Press, New York.

McCleave, J.D. & G.S. Wippelhauser. 1987. Behavioral aspects of selective tidal stream transport in juvenile American eels. American Fisheries Society Symposium 1: 138–150.

Miller, J.M., L.B. Crowder & M.L. Moser. 1985. Migration and utilization of estuarine nurseries by juvenile fishes: an evolutionary perspective. *In:* M.A. Rankin (ed.) Migration: Mechanisms and Adaptive Significance. Contr. Mar. Sci. 27: 338–352.

Morin, P.-P., J.-L. Verrette, J.J. Dodson & F.Y. Doré. 1987. Computer-automated method to study cardiac conditioning to a chemical cue in young salmon. Physiol. Behav. 39: 657–664.

Morin, P.-P., J.J. Dodson & F.Y. Doré. 1988. Behavioral evidence of a sensitive period for olfactory imprinting in young Atlantic salmon, *Salmo salar*. Can. J. Fish. Aquat. Sci. (in press).

Mysak, L.A. 1986. El Nino, interannual variability and fisheries in the northeast Pacific Ocean. Can. J. Fish. Aquat. Sci. 43: 464–497.

Neill, W.H. 1979. Mechanisms of fish distribution in heterothermal environments. Amer. Zool. 19: 305–317.

Neill, W.H. 1984. Behavioral enviroregulation's role in fish migration. pp. 61–66. *In:* J.D. McCleave, G.P. Arnold, J.J. Dodson & W.H. Neill (ed.) Mechanisms of Migration in Fishes, Plenum Press, New York.

Neves, R.J. & L. Depres. 1979. The oceanic migration of American shad (*Alosa sapidissima*) along the Atlantic coast. U.S. Fish. Bull. 77: 199–212.

Northcote, T.G. 1984. Mechanisms of fish migration in rivers. pp. 317–355. *In:* J.D. McCleave, G.P. Arnold, J.J. Dodson & W.H. Neill (ed.) Mechanisms of Migration in Fishes, Plenum Press, New York.

Ogden, J.C. & T.P. Quinn. 1984. Migration in coral reef fishes: ecological significance and orientation mechanisms. pp. 293–308. *In:* J.D. McCleave, G.P. Arnold, J.J. Dodson & W.H. Neill (ed.) Mechanisms of Migration in Fishes, Plenum Press, New York.

Olson, D.E., D.H. Schupp & V. Macins. 1978. A hypothesis of homing behavior of walleyes as related to observed patterns of passive and active movement. Amer. Fish. Soc. Spec. Publ. 11: 52–57.

Priede, I.G. 1985. Metabolic scope in fishes. pp. 33–64. *In:* P. Tytler & P. Calow (ed.) Fish Energetics: New Perspectives, Croom-Helm, Kent.

Priede, I.G. & F.G.T. Holliday. 1980. The use of a new tilting tunnel respirometer to investigate some aspects of metabolism and swimming activity of the plaice (*Pleuronectes platessa* L.). J. Exp. Biol. 85: 295–309.

Quinn, T.P. 1980. Evidence for celestial and magnetic compass orientation in lake migrating sockeye salmon fry. J. Comp. Physiol. 137: 243–248.

Quinn, T.P. 1984. Homing and straying in Pacific salmon. pp. 357–362. *In:* J.D. McCleave, G.P. Arnold, J.J. Dodson & W.H. Neill (ed.) Mechanisms of Migration in Fishes, Plenum Press, New York.

Quinn, T.P. 1985. Homing and the evolution of sockeye salmon (*Oncorhynchus nerka*). *In:* M.A. Rankin (ed.) Migration: Mechanisms and Adaptive Significance. Contr. Mar. Sci. 27: 353–366.

Quinn, T.P. & E.L. Brannon. 1982. The use of celestial and magnetic cues by orienting sockeye salmon smolts. J. Comp. Physiol. A 147: 547–552.

Quinn, T.P. & C. Groot. 1983. Orientation of chum salmon (*Oncorhynchus keta*) after internal and external magnetic field alteration. Can. J. Fish. Aquat. Sci. 40: 1598–1606.

Quinn, T.P. & C. Groot. 1984. The effect of water flow on bimodal orientation of juvenile chum salmon, *Oncorhynchus keta*. Anim. Behav. 32: 628–629.

Quinn, T.P. & J.C. Ogden. 1984. Field evidence of compass orientation in migrating juvenile grunts (Haemulidae). J. Exp. Mar. Biol. Ecol. 81: 181–192.

Rijnsdorp, A.D., M. van Stralen & H.W. van der Veer. 1985. Selective tidal transport of North Sea plaice larvae (*Pleuronectes platessa*) in coastal nursery areas. Trans. Amer. Fish. Soc. 114: 461–470.

Roitblat, H.L., W. Tham & L. Golub. 1982. Performance of *Beta splendens* in a radial arm maze. Anim. Learn. & Beh. 10: 108–114.

Schöne, H. 1984. Spatial orientation. The spatial control of behavior in animals and man, Princeton University Press, Princeton. 347 pp.

Schwassmann, H.O. & W. Braemer. 1961. The effect of experimentally changed photoperiod on the sun orientation rhythm of fish. Physiol. Zool. 34: 273–326.

Simpson, K.S. 1979. Orientation differences between populations of juvenile sockeye salmon. Fish. Mar. Serv. Tech. Rep. 717. 114 pp.

Smith, R.J.F. 1985. The control of fish migration. Springer-Verlag, Berlin. 243 pp.

Stabell, O.B. 1984. Homing and olfaction in salmonids: a critical review with special reference to the Atlantic salmon. Biol. Rev. 59: 333–388.

Staddon, J.E.R. 1983. Adaptive behavior and learning. Cambridge University Press, Cambridge. 555 pp.

Thinus-Blanc, C. 1987. The cognitive map concept and its consequences. pp. 1–19. *In:* P. Ellen & C. Thinus-Blanc (ed.) Cognitive Processes and Spatial Orientation in Animal and Man, Vol. 1, Experimental Animal Psychology and Ethology, Martinus Nijhoff Publishers, Dordrecht.

Thorpe, W.H. 1963. Learning and instinct in animals. Methuen, London. 558 pp.

Tolman, E.C. 1932. Purposive behavior in animals and men. Irvington, New York. 463 pp.

Veen, J.F. de, 1970. On the orientation of the plaice (*Pleuronectes platessa* L.) 1. Evidence for orientation factors derived from the ICES transplantation experiments in the years 1904–1909. J. Cons. int. Explor. Mer 33: 192–227.

Veen, J.F. de, 1978. On selective tidal transport in the migration of North Sea plaice (*Pleuronectes platessa*) and other flatfish species. Neth. J. Sea Res. 12: 115–147.

Walker, M.M. 1984. Learned magnetic-field discrimination in yellowfin tuna *Thunnus albacares*. J. Comp. Phys. A 155: 673–679.

Wallraff, H.G. 1978. Preferred compass directions in initial orientation of homing pigeons. pp. 171–183. *In:* K. Schmidt-Koenig & W.T. Keeton (ed.) Animal Migration, Navigation and Homing, Springer-Verlag. Berlin.

Wallraff, H.G. 1986. Directional components derived from initial-orientation data on inexperienced homing pigeons. J. Comp. Physiol. A 159: 143–159.

Weihs, D. 1984. Bioenergetic considerations in fish migration. pp. 487–508. *In:* J.D. McCleave, G.P. Arnold, J.J. Dodson & W.H. Neill (ed.) Mechanisms of Migration in Fishes, Plenum Press, New York.