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The role of learning in fish behaviour

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Introduction

LEARNING AND BEHAVIOUR

There have been several definitions of learning (Staddon, 1983; Flaherty, 1985), but the term generally refers to a change in behaviour with experience (e.g. Dill, 1983). Inferences about learning are based upon examination of the behaviour of individual animals over time, specifically in reaction to environmental change (Kamil and Yoerg, 1982). As the process by which the effects of experience are recorded, learning has been and remains a phenomenon of great interest, from both proximate and functional viewpoints, being important as a mechanism and providing an animal with behavioural flexibility, especially in changing environments. Therefore, animals living in unstable environments should have more behavioural flexibility.

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LEARNING IN FISH

Fish as a group are the most abundant (more than 20000 species; Huntingford, 1986) and diverse class of vertebrates. They engage in a great variety of activities, among which learning often plays a role. The experimental evidence for learning is widespread and dates back to the late 1800s. Probably the earliest experiment that analysed learning capabilities in fish was the classic work on trial-and-error learning in pike (Esocidae, reported by Mobius in 1873). This paper was unique from the other earlier observations of learning in animals because it involved experimentation to detect the changes in behaviour with experience.

More recently, the learning ability of fishes has been investigated in relation to several subjects, such as foraging behaviour (Godin, 1978; Dill, 1983; Croy and Hughes, 1991a,b; Kieffer and Colgan, 1991), assessment of food nutrient content (Wright and Eastcott, 1982), migration (Hasler and Scholtz, 1983; Dodson, 1988) and social communication (Suboski, 1988) (Table 1). Thorpe (1963) and Gleitman and Rozin (1971) provide excellent reviews of fish learning; both outline the various contributions of learning with respect to the naturalistic and psychological viewpoints. However, since Gleitman and Rozin's paper there has not been a comprehensive review on learning in fishes.

The purpose of this paper is to review the recent literature on learning in fishes. Because this literature is replete, we have selected only representative papers. This review mainly addresses the literature from the early 1970s to the present, as Thorpe (1963) and Gleitman and Rozin (1971) provide earlier accounts. Given the scope of this journal and the many facets of behaviour that learning influences, we chose to focus on the areas that potentially affect a fish's ability to survive and pass on its genes, as in the activities of finding food, avoiding predators, aggression, migration, orientation and recognition. We also consider the human uses of fish learning behaviour, particularly in the improvement of fisheries and hatchery operations.

Migration

Perhaps one of the most widely used definitions of migration is from Dingle (1980): "migration is specialized behaviour especially evolved for the displacement of the individual in space." Dodson (1988) provides an excellent review of the role of learning in migration of fish.

Learning is certainly important in migration; for example, animals may learn the features of a migration route that is regularly travelled. The ability of salmonids to locate their natal streams accurately has been extensively reviewed (Hasler *et al.*, 1978; Hasler and Scholtz, 1983; Dodson, 1988). There is some indication that several species of salmon can return to their home streams, even though as juveniles they were captured and moved several hundreds of kilometres before release (Ebel *et al.*, 1973). It has been hypothesized that the migratory ability of fish is based on ontogenetically fixed sets of environmental conditions (Neill, 1984; Hara, 1986). However, there is evidence that learning has a major impact on homing behaviour in salmonids (Dodson, 1988).

One of the central questions related to homing is 'what features of its home stream has the fish learned that enable it to return successfully'? Evidence for homing and olfaction dates back to the late 1800s and early 1900s. However, most of the information comes from the later work of Hasler (Hasler *et al.*, 1978; Hasler and Scholtz, 1983) which

Table 1. A summary of the role of learning in fishes.

Behaviour	Role	Sources
Migration	Learning features of a migration route (e.g. soil and vegetation)	Quinn and Dittman (1990)
	'Imprinting' to certain stream odours (e.g. odour hypothesis), allowing subsequent return	Hasler *et al.* (1978) Hasler and Scholtz (1983)
	Pheromone hypothesis	Nordeng (1977)
Foraging	Patch choice	Werner *et al.* (1981)
	Prey choice/profitability	Bence (1986)
	Detection/recognition of prey types	Ehlinger (1989)
	Capture/manipulation of prey types	Ehlinger (1989) Kieffer and Colgan (1991)
	Assessment of food sources	Milinski (1984)
	Hunger levels and foraging	Croy and Hughes (1991b)
Landmark orientation	Non-chemical cues (e.g. compass orientation)	Dodson (1988)
	Spatial learning	Reese (1989)
Social learning	Role in activities such as foraging and predator avoidance	Suboski (1988) Suboski *et al.* (1990) Robert (1990) Anthouard (1987)
Recognition processes	Parent–offspring	Hay (1978)
	Mate choice	Ferno and Sjolander (1976) Hollis (1990)
	Rival recognition	Myrberg and Riggio (1985) Losey (1982)
Avoidance learning	Detection of threats	Suboski (1988) Huntingford and Wright (1989)
Human uses of fish learning behaviour	Increased survival rate of hatchery fish when released to the wild	Olla and Davis (1989)
	Imprinting fish increases the potential for conservation and management of endangered fish stocks	Hasler and Scholtz (1983)
	Use of social learning processess in hatchery situations	Suboski and Templeton (1989)

suggests that young salmonids recognize the odour of their home stream. The odour hypothesis postulates that homing is based on imprinting (a rapid and irreversible learning process) that occurs before seaward migration of juveniles (Hasler *et al.*, 1978). Early studies by Hasler (Hasler *et al.*, 1978; Hasler and Scholtz, 1983) suggested that salmon learn the unique odours (from soil and vegetation) of their home stream during the imprinting period (probably at the smolt stage, during which a metamorphosis occurs involving a series of physiological, morphological and behavioural adjustments enabling survival in seawater; Hasler and Scholtz, 1983), and later use this information as a cue to locate their home stream during the spawning migration. Several studies (Hasler and Scholtz, 1983) show the significant role of early experience and olfaction in the development of homing. They also provide vast amounts of information that support the olfactory imprinting hypothesis; the data are remarkably consistent between studies and the effect has been shown in several species of salmonids.

Perhaps the most convincing studies related to the olfactory imprinting hypothesis were carried out by Hasler and his colleagues using synthetic chemicals, morpholine and phenethyl alcohol. For instance, Scholtz *et al.* (1976) performed experiments to test the homing ability of coho salmon (*Oncorhynchus kisutch*, Salmonidae) to the two different chemical cues, morpholine and phenethyl alcohol, as several of the previous studies had shown that some of the morpholine-marked fish were roaming into other streams. These two chemicals were chosen because they are not known to occur naturally and can be detected at relatively low concentrations. Therefore, one group of fish was exposed to morpholine, another to phenethyl alcohol and a third control group was left untreated. This experiment was conducted in two subsequent years. Coho salmon were hatched from eggs and raised for 18 months (i.e. to the smolt stage). Following this, the fish were divided into three groups and held in separate tanks filled with hatchery water which did not provide cues for homing by adults. Fish were imprinted to the chemicals during their pre-smolt and smolt stages. Following the imprinting stage, all groups of fish were transported to, and released in, Lake Michigan, between Manitowoc and Two Rivers. Each of these rivers was to be scented during the spawning migration. During the spawning-season migration (i.e. 18 months later), phenethyl alcohol was put into one test stream and morpholine into the other. The rivers were inspected for marked fish, and other sites were observed to check whether experimental fish were migrating into non-scented streams. In both years about 95% of the captured morpholine-exposed fish were in the morpholine-scented stream and about 92% of the recovered phenethyl alcohol-exposed fish were in the phenethyl alcohol-scented stream. Thus fish learn the odour of the river during the smolt stage. These results also suggest that the fish possess a relatively long-term memory for the odours. Other examples of olfactory imprinting are described by Hasler and Scholtz (1983).

Although imprinting has been demonstrated in fish (Hasler and Scholtz, 1983), there is still some debate concerning the time or the developmental stage in which salmon imprint (Morin *et al.*, 1989a) and the nature of the odours by which salmon identify their natal stream. Quinn and Dittman (1990) outline several studies suggesting that imprinting may occur at times of peak levels of thyroid hormone during smolt transformation (also see Morin *et al.*, 1989b), and that homing may be based on the ability of salmon to recognize a combination of odours from several sources, such as soil and plants. For instance, Quinn *et al.* (1989) provided evidence suggesting that young salmon learn a sequence of olfactory landmarks during their seaward migration. In addition to this, Quinn and Dittman (1990) suggest "that several aspects of the imprinting process, such as the role of population odours and homing, are still unclear under natural conditions."

Despite the acceptance of the olfactory imprinting hypothesis for explaining the homing ability in fishes, other hypotheses have been brought forth, one being the pheromone hypothesis. Nordeng (1977) contends that the guiding cue during river orientation and homing in salmonids may be the result of population-specific pheromones. These pheromones are potentially emitted by juvenile fish (i.e. from their skin mucus) into their freshwater home areas or during their trip downstream to feeding areas, and subsequently attract the migrating adult salmon into their natal stream (details, Nordeng, 1977). Although evidence for the two hypotheses (imprinting and pheromone) frequently conflicts (e.g. Hara, 1986), it is likely that the two are not mutually exclusive. For instance, Hara (1986) suggests that population odours may be only one of the several components in the chemical environment to which a fish imprints as a juvenile and responds as an adult. For further details related to the imprinting v. pheromone hypotheses, the reader is referred to Quinn (1985), Hara (1986) and Stabell (1992).

Piloting and landmark orientation

There is substantial evidence that other non-chemical cues, such as sight, are necessary for orientation in many species of fish. Dodson (1988) reviewed the nature and role of learning in orientation behaviour of fishes, especially compass orientation. As he points out, two important ways that fish learn about the direction of movement are piloting and landmark orientation. Fish often rely on spatial learning, which involves following a course composed of specific cues occurring in a certain order. Because spatial learning often depends on specific landmarks, this type of learning would be important for species that are relatively site-attached, rather than those that home over long distances (Dodson, 1988).

Aronson (1971) showed spatial learning in a gobiid fish, *Bathygobius soporator*, which uses learned information about the spatial relationship of tide pools to orientate accurately. More recently Reese (1989) suggested that certain species of reef fishes (e.g. butterfly fish, *Chaetodon trifasciatus*, Chaetodontidae) base their foraging paths on learned locations of route-specific landmarks. Reese demonstrated this by removing specific areas of the coral reefs (coral heads). The fish would search in the area from which the coral heads had been removed, but after some time would continue their foraging behaviour along the original path. Reese also demonstrated that when pairs of fish were chased from their foraging paths, they escaped into the coral for protection. After a period of time, foraging resumed in the regular pattern as the pairs swam from coral head to coral head. Although the fish are using specific landmarks to orientate, one cannot overlook the possibility that other navigational cues are also being used, such as sun compass navigation (Dodson, 1988). Similarly, Helfman *et al.* (1982) demonstrated that other species of reef fishes (grunts, *Haemulon* spp., Haemulidae) use spatial learning in their migration routes. Further, Teyke (1989) has suggested that the blind cave fish (*Anoptichthys jordani*, Characidae) may be using spatial information about its environment. Teyke (1989) proposes that cognitive maps (mental pictures or representations) may play an important role, but there has been a long debate concerning whether fish in such situations can respond to local cues (the stimulus–response interpretation) or rely on acquired information (the 'cognitive' approach). Similarly, Warburton (1990) demonstrated that goldfish (*Carassius auratus*, Cyprinidae) can learn to use landmarks as indirect spatial reference points.

Feeding

The acquisition of food by fishes is an essential process which requires precision with respect to searching and capturing prey items. Because many foraging environments are complex, and food items change seasonally or spatially, it seems likely that learning plays a role in the foraging flexibility of fishes (Dill, 1983). Learning may affect foraging in two ways: (1) through alterations in a forager's ability to locate and capture prey items (learning 'how') and (2) by providing foragers with additional information about the return rates of habitats (learning 'about') (Krebs *et al.*, 1983).

There are well-documented effects of experience on the foraging behaviour of fishes. Several of these studies have demonstrated that experience influences capture success, profitability of different prey types and habitat-specific foraging. Some of the earliest work on foraging and learning came from Beukema's (1968) study. Beukema noticed that if a new prey item was introduced to threespine sticklebacks (*Gasterosteus aculeatus*, Gasterosteidae), approximately ten encounters with the prey item were needed before it was readily accepted into the diet. Similarly, Ware (1971) showed that changes due to experience increased the capture rate of a specific prey type. It took naïve rainbow trout (*Oncorhynchus mykiss*, Salmonidae) about 4 days, on average, to approach a novel food item. The reactive distance towards a prey item also increased with experience. Godin (1978) showed that the latency time to initial prey capture in pink salmon (*Oncorhynchus gorbuscha*, Salmonidae) decreased over the span of 5 days. Godin also found that the mean percentage capture success increased with experience.

Both Beukema's (1968) and Ware's (1971) studies provided a foundation for other studies on foraging and learning in fish species. However, later studies examined not only the presence of learning, but how this could influence energetic trade-offs and prey selection. Bence (1986) showed that experience affects diet choice. Bence studied the feeding behaviour of young female mosquitofish (*Gambusia affinis*, Poeciliidae). Fish were initially trained on two different diets, either pure copepods (medium profitability) or a mixture of cladocerans (high profitability) and copepods, for 7 successive days. For the experiment, fish originally trained on pure cyclopoid copepods were observed feeding at three different densities of cladoceran; fish trained on the mixture of prey items were observed only at the lowest cladoceran density. During the test period, fish were presented with prey for 10 minutes each day over a 7-day period. Individuals that had had experience with two prey types selected the more profitable over the less profitable prey type more than did fish experienced with only one of the prey types.

Werner *et al.* (1981) found similar results in the bluegill sunfish (*Lepomis macrochirus*, Centrarchidae). Bluegills increased their foraging efficiency up to fourfold over the duration of six to eight foraging sessions when feeding on *Chironomus* larvae. Also, when exposed to structured and open-water habitats, the population of fish began to specialize in one habitat or the other. The role of learning in the habitat choice by fish may be critical because the profitability of different habitats may be misjudged by inexperienced fish. Also, being inexperienced could have an effect on the ability to switch between habitats (Werner *et al.*, 1981).

More recently, Ehlinger (1989) performed a number of experiments using open-water and structured habitats to show how learning modifies habitat-specific foraging rates. When bluegills were exposed to open-water habitats, they learned to increase their searching speed, whereas bluegills foraging in the structured habitat learned to search more slowly. Ehlinger also suggested that bluegills varied their searching behaviour to meet the requirements of particular habitats and prey types, which may reflect differences in their learning rates. With experience, bluegill sunfish showed a reduction in the number of times they crossed their search path (Ehlinger, 1986); this suggested that the fish may have learned how to forage more efficiently in specific habitats.

Recently, Colgan *et al.* (1991) and Kieffer and Colgan (1991) have shown that two species of sunfish differed in their ability to learn a foraging task. Colgan *et al.* (1991) demonstrated that individuals that learned quickly to feed on one prey type also learned to feed more quickly on other prey types. This suggested that individual differences in learning persist across learned feeding tasks. Ehlinger (1989) and Colgan *et al.* (1991) proposed that habitat structure and prey types influence learning in sunfishes. Kieffer and Colgan (1991) showed that the order in which habitats are experienced by an animal is important; sunfish whose first experience was with structured habitat and then with an open-water habitat were more efficient feeders than fish experiencing the habitats in the reverse order. These studies provide evidence that the difficulty of the task influences learning.

A task for which learning would be very important is the assessment of food sources. Because of costs associated with remaining in unprofitable patches, it may be important for an animal to 'learn about' the patch before spending large amounts of time foraging there (e.g. Krebs *et al.*, 1983; Croy and Hughes, 1991c). Because resources often have a variable pay-off, learning about the environment may be useful. In his study of the ideal free distribution, Milinski (1984) demonstrated that threespine sticklebacks achieve a stable foraging distribution through learning. Further, his results support the hypothesis that the fish used the relative pay-off sum (RPS) learning rule (details, Milinski, 1984). Godin and Keenleyside (1984) also postulated that cichlid fish (*Aequidens curviceps*, Cichlidae) distributed themselves in the most profitable patch because individual fish varied in their perceptual abilities and in the ability to learn the differences in the patch qualities.

Other factors may play a role in the ability to learn in fishes. For example, Croy and Hughes (1991b) suggested that hunger levels may be important in the foraging levels and the overall foraging efficiency in fifteenspine sticklebacks (*Spinachia spinachia*, Gasterosteidae). They found that fish denied food for a day gained attack and handling skills more quickly than those fish that were fed to near satiation. Also, Croy and Hughes (1991a) showed that over a period of time fifteenspine sticklebacks decreased the handling time of capturing certain prey items. Croy and Hughes (1991a) suggested that learning to improve handling efficiency increased the profitability of specific prey items.

Social transmission of learning

Many animals acquire knowledge by observing other animals. Through their observation, animals may obtain new behavioural patterns or modify existing ones (Thorpe, 1963). In general, there are three mechanisms of social transmission of learning: social facilitation, local enhancement and observational learning (Thorpe, 1963). **Social facilitation** is a process where the behaviour of one individual alters the rate at which another animal performs a particular behaviour (Allee *et al.*, 1950). Similarly, Thorpe (1963) describes social facilitation as 'contagious behaviour' occurring when the behaviour of one animal acts as a releaser for the same behaviour in another. **Local enhancement** is a form of social facilitation which directs the attention of an animal to a particular object or part of the environment (Thorpe, 1963). Although not learning mechanisms, social facilitation and local enhancement are considered a part of social learning as they often bring an animal into situations conducive to learning (review, Suboski, 1988). **Observational learning** can be defined as occurring when an animal copies a specific technique used by a conspecific that is interacting with a specific set of features in the environment (Lefebvre and Palameta, 1988). Similarly, Thorpe (1963) defined observational learning as "the copying of a novel or otherwise improbable act or utterance for which there is clearly no instinctive tendency." Although social transmission of acquired behavioural patterns has been reported in fishes, many of these studies are examples of social facilitation or local enhancement (Magurran and Higham, 1988; Suboski, 1988; Suboski *et al.*, 1990; Ryer and Olla, 1991). However, little is known about observational learning in fish.

In his review, Robert (1990) outlines five possible cases of observational learning in fishes. In one, Helfman and Schultz (1984) examine cultural transmission of migratory and schooling site information in French grunts (*Haemulon flavolineatum*, Haemulidae). They hypothesized that young grunts are capable of learning the migratory routes of older fish if they are displaced to a new home site. When small juveniles were transferred from one site to a new site and were allowed to observe and follow resident adults at the new site, the small fish imitated (i.e. learned) the migratory routes and returned to the new sites in the absence of the adults. A control group, transplanted to new sites but without the opportunity to learn from residents, did not return to the new sites.

Anthouard (1987) provides another case of observational learning. He suggests that in previous studies using fish as subjects, the transmission of behaviour from one individual to another simply entailed the variation of everyday activities. Anthouard proposes that to investigate observational learning, one should study novel behavioural patterns, such as lever-pressing to obtain food. He used an operant conditioning procedure to train sea bass (*Dicentrarchus labrax*, Serranidae) to press a lever for food reward (referred to as the demonstrator group). Based on performance, the demonstrators were separated into either 'good' demonstrators (those showing efficient lever-pushing ability to obtain food) or 'poor' ones (those that responded very little to the operant conditioning procedure). Following the training, two groups of naïve fish (observers) were allowed visual contact with either poor or good demonstrator fish. Fish that were allowed visual contact with a good performer explored the lever earlier and learned to use it to obtain food more quickly than did fish exposed to poor demonstrators.

Other evidence of social transmission has been demonstrated in various species of fish. Magurran and Higham (1988) found that shoaling European minnows (*Phoxinus phoxinus*, Cyprinidae) gleaned information about a predator's advance from changes in the avoidance behaviour of other conspecifics. When minnows had the opportunity to observe, from behind one-way mirrors and out of visual contact with the model, the behaviour of other minnows threatened by a model pike (*Esox lucius*, Esocidae), they decreased their foraging activity and increased hiding behaviour.

Recently, Groten (1990) demonstrated that bluegills fed more quickly at a novel location in a tank after observing a trained conspecific, than did a control group that observed a non-feeding conspecific. Similarly, Templeton (1987) showed that rock bass (*Amploblites rupestris*, Centrarchidae) that had an opportunity to observe a skilled conspecific feeding on a novel prey item, responded to the prey type more quickly than those that did not.

Other aspects of social transmission in fishes are discussed by Wright and Eastcott (1982), Suboski *et al.* (1990), Baird *et al.* (1991) and Ryer and Olla (1991).

Recognition processes

Evidence for the role of learning in individual and species recognition in fish is recent and scanty. The current literature contains papers on parent recognition of fry, fry recognition of parents, recognition of other individuals, rival recognition and mate choice.

PARENT AND FRY RECOGNITION

Noakes and Barlow (1973) provided an excellent example of the ability of parents to learn to recognize their fry. Using the Midas cichlid (*Cichlasoma citrinellum*, Cichlidae), they allowed parents to spawn and raise 100 of their young. Then they took another group of 100 young, from the same clutch, and reared them in a neighbouring aquarium, separated from all but the view of the parents and siblings. Following a period of about 3 weeks, the parents were substituted between the families for about 9 h, after which they were returned to their home aquarium. The results of this experiment suggested that 'foster' parents would accept and care for foreign young about the same age or younger than their own. Noakes and Barlow also demonstrated that the fry would accept the foster parents; after a period of time, the fry began to make contact with the adults. These results suggest that the parents learn to recognize the young and display a moderately short-term memory.

Hay (1978) discussed the role of filial imprinting in the development of recognition of parents by offspring. Such imprinting was demonstrated by presenting convict cichlid (*Cichlasoma nigrofasciatum*, Cichlidae) fry of several age groups with a dummy parent and then testing the fry in a choice experiment between the familiar and a novel dummy. Young fry were very responsive and approached the different parental dummies at a very early age (day 1 free-swimming). Older fry showed similar patterns. The response of the fish to the dummies increased with time, and experience with a single dummy resulted in an increase in responsiveness to the dummies in the preference test. Younger fry appeared to be more sensitive than older fry, but older fry were still capable of learning parental visual patterns. Hay's experiments suggested that cichlid fry learn about the physical and behavioural aspects of their parents; however, this may not necessarily be limited to visual cues. Hay also suggests that the early perceptual learning of the parental characteristics by the fry may be a continuous process.

RECOGNITION OF INDIVIDUALS

Myrberg and Riggio (1985) provide an excellent example of individual recognition in fish: in a field study, they demonstrated that the male bicolour damselfish (*Pomacentrus partitus*, Pomacentridae) learned to recognize neighbours acoustically. Sounds of various male damselfish were recorded and played back to a resident male. Resident males responded less strongly to the playback of sounds produced by their nearest neighbour than to playback of other sounds; they could also distinguish between the calls and other sounds. The authors suggested that learning the sound of a neighbour may be important because damselfish are territorial and that males having a distinct and individually recognizable 'signal' produced throughout the day may reduce the amount of energy used in territorial defence. Other examples of individual recognition where learning may be important are the studies by Fraipont and Thines (1985) using cavefish (*Astyanax mexicanus*, Characidae) and Butler and Johnson (1972) using bluegill sunfish. Butler and Johnson (1972) demonstrated that bluegills in an operant task could discriminate between individuals. Field studies by Fricke (1973) determined that the individual characters of an anemone-dwelling fish (*Amphiprion bicinctus*, Pomacentridae) are learned in 24 h and persist for at least 10 days.

RIVAL RECOGNITION

Another subject that can be placed in the broad category of recognition is rival recognition. In an excellent study relating the effects of learning (experience) to interspecific aggression, Losey (1982) was interested in whether damselfish (*Stegastes fasciolatus*, Pomacentridae) were able to use ecological cues, such as feeding behaviour, in learning to differentiate competitors from non-competitors. Under normal conditions, when a 'competitor' (tilapia, *Sarotherodon mossambica*, Cichlidae, an experimentally introduced, euryhaline species) and a natural competitor (surgeonfish) were exposed to the damselfish, there was little aggression of the damselfish towards the tilapia. Following this, Losey (1982) trained the tilapia to feed like a herbivore (i.e. to mimic a natural competitor) or a zooplanktivore (a non-competitor). Losey then placed bricks of algae turf (which acted as a food patch for the tilapia) just outside the territory of the damselfish. Zooplantivores were trained similarly, but with a surface food. After about 2 weeks of experience with the tilapia, the damselfish's aggressiveness was assessed. Experience with the zooplanktivorous tilapia had little influence on the damselfish. However, experience with the herbivorous tilapia produced defensive reactions from the damselfish towards the tilapia; the response was very similar to that shown to surgeonfish. Losey (1982) suggested that the learning was not an instantaneous effect but rather a cumulative effect. In his conclusions, he suggested that experience with ecological cues, such as feeding, can produce perceptual changes where different species may be recognized as competitors.

Other studies that show how learning is important in rival recognition and territorial defence are represented by the work of Hollis and her colleagues. Hollis used classical conditioning procedures to study behavioural patterns such as parental care and antipredator behaviour in fish (details, Hollis, 1982). **Classical conditioning** in its simplest terms refers to an experimental arrangement whereby a stimulus is made to elicit a response that was not previously associated with that stimulus (i.e. the conditioned stimulus, CS, comes to elicit a response, the conditioned response or CR, similar to the one elicited by the unconditioned stimulus, UCS). From a functional perspective, classical conditioning of aggressive behaviour may give some advantage to a territorial male (i.e. to defend his territory better). Under this viewpoint Hollis (1984a) trained pairs of male blue gourami (*Trichogaster trichopterus*, Cichlidae); one male was classically conditioned (to a signal presentation of a rival male) and the other male was the control (see Hollis, 1984a, for descriptions of control groups). A 10 s presentation of a red light CS was followed by a 15 s presentation of a rival male UCS (details, Hollis, 1984a). Following the training, pair members confronted each other for the first time in a test encounter. For the classically conditioned group, the conditioned males were more aggressive (increased number of bites and tailbeats) than the non-conditioned males when the fish had an opportunity to defend their territories against a signalled intrusion. Hollis (1984a) suggests that the ability to learn in a manner analogous to classical conditioning may serve in nature to allow territorial males to increase their territorial defence. This ability may be a mechanism for an efficient defence strategy.

This approach to the functional nature of classical conditioning (e.g. 'why does classical conditioning result in anticipatory signal-directed behaviour?') has been supported in subsequent theory (e.g. Hollis, 1984b), but little other experimental evidence has shown that conditioning is responsible in preparing animals for important events. Although other studies are needed, the recent work by Hollis and her co-workers (Hollis *et al.*, 1989; Hollis, 1990) should help to establish the biological function of conditioning.

MATE CHOICE

The influence of early experience on mate choice has been extensively investigated. Several studies have suggested that early experience as a fry with an adult may influence its later choice of a mate (Ferno and Sjolander, 1976). Recently, Siepen and Crapon de Caprona (1986) and Siepen (1986) investigated how experience influences mate choice in the convict cichlid. Convict cichlids were appropriate because they occur in two colour morphs, striped and white. Siepen and Crapon de Caprona (1986) allowed each colour morph to spawn, after which the natural parents were replaced by foster parents of the opposite colour morph (test fish) or of the same colour (control fish). Parental care continued for up to about 7 weeks; at this point the foster parents were removed. Following this, juvenile fish were put into a tank until they reached sexual maturity. The experimental design had two groups: a test group (striped and white juveniles that were cared for by white and striped foster parents, respectively) and a control group (white and striped juveniles that were cared for by foster parents of their own colour morph). The test group, which had prior experience with adults of the opposite colour morph and with siblings of their own colour, was compared with the control group, which only had experience with siblings and adults of their own colour. When given a mating choice between the same or the opposite colour morph, the test fish mated with members of the opposite morph (about 9%), whereas the control fish completely separated according to colour. The results of Siepen and Crapon de Crapona (1986) suggested that 'imprinting' may be taking place in the first few weeks of the fish's life. These authors also discuss the implications of learning in assortative mating in cichlids. Further evidence of experience on mate choice was provided by Siepen (1986); his results supported those of Siepen and Crapon de Crapona (1986) on the influence of parental colour morph on mate choice in convict cichlids.

More recently, Hollis *et al.* (1989) used classical conditioning procedures (see p. 134 for definitions) to describe its role in increasing the likelihood of successful mating and reproductive success. The experimental procedures were similar to those of Hollis' previous studies (e.g. Hollis, 1984a, and see above section on rival recognition). The outcome of the experiments suggested that the males conditioned with the presentation of females, as a UCS, respond more quickly in courtship with females than do the unconditioned pairs. Also, Hollis *et al.* (1989) demonstrated that the conditioning procedure may inhibit the initial aggressive behaviour in the males, and courtship may advance more quickly. Subsequently, this outcome of signalling may increase a male's chances of securing a mate, hence influencing reproductive success. In a recent paper, Hollis (1990) discusses the role of learning in mating strategies and sexual selection.

However, not all studies support the conclusion that early experience affects mate choice in adults. For instance, Barlow and Rogers (1978) did not show conclusively that experience of the fry with the parents provided enough evidence for 'imprinting' or 'imprinting-like' learning processes, but their study did not rule out this possibility. Similarly, Weber and Weber (1976) failed to find any influence of early colour experience on adult sexual preference in convict cichlids.

Avoidance learning

Many laboratory and field studies have shown that animals are faced with a variety of hazards, including competition and the risk of predation. With respect to natural hazards, animals should be able to decide when to leave the area of danger (review, Lima and Dill, 1990). Thus animals should possess the ability to learn or modify their behaviour under a particular risk. One of the classic works on avoidance learning in fishes is Goodyear's (1973) study. He showed how mosquitofish could orientate toward the shoreline in the presence of a predator. More recently, Huntingford and Wright (1989) studied how threespine sticklebacks learn to avoid a profitable feeding patch as it becomes dangerous. They compared two populations of sticklebacks, one from a pond with few predators and another from an area with numerous predators, by training sticklebacks to leave a central holding area into one of two adjacent feeding patches. From day to day, during the training sessions, the fish were allowed to swim freely from side to side and eat out of the hoppers (within the feeding patches) that were adjacent to the central holding area. By the end of the training, all the fish could exploit either patch easily, but preferred one side to the other (i.e. they spent most of their time foraging there). Following the training period, each fish was allowed 5 minutes to swim from the central holding area and forage from either food patch. Whenever the fish entered and approached the previously preferred food patch, it was subjected to a strong visual and tactile stimulation (a swinging plastic hammer). Learning had occurred when the fish completely avoided the favoured patch for three consecutive days. About 8 days (trials) were needed for the fish to fully learn about the disadvantage of feeding in the preferred patch. As the number of trials (days) increased, the median number of 'attacks' (by the swinging hammer) decreased. As a result, the fish learned to choose the unfavoured but safe patch. With respect to population differences, the fish from the low-risk population required significantly more 'attacks' before they learned to avoid the previously favoured patch.

Goodey and Liley (1986) provide another example of avoidance learning in fishes. Experiments were used to assess whether visual or chemical cues associated with being chased (by an aerial predator or piscivorous fish) were important in avoidance learning by young guppies (*Poecilia reticulata*, Poeciliidae) when tested as adults under a hazardous situation. Guppies that were chased when young by adult conspecifics required more attacks before they were captured than guppies exposed only to visual or chemical cues associated with being chased. There were also sexual differences in the level of the avoidance response; females often showed larger responses. The authors discussed their results in the light of how early experience of being chased may be part of the learning process.

Other excellent studies on avoidance learning in fishes include those of Kruse and Stone (1984), Coble *et al.* (1985) and Csanyi (1986). For example, Coble *et al.* (1985)

described experiments where 14 species of freshwater fish were trained to perform a simple conditioned response (to move in response to light, so as to avoid an electric shock) in a shuttle box.

Human uses of fish learning behaviour

There are indications that learning may be important in the survival and growth of hatchery stock. Hatcheries produce large numbers of fish species every year at relatively low cost. However, one of the major problems with hatchery programmes is that when fish are released from hatcheries to the natural environment, a large percentage perish because they do not recognize natural prey or predators (Suboski and Templeton, 1989). Evidently, hatchery environments often do not provide the stimuli that allow fish to recognize different food items or predators. Predator avoidance can be enhanced by exposing hatchery fish to predators prior to their release. Olla and Davis (1989) carried out several experiments to investigate the possible role of learning in predator avoidance in coho salmon (*Oncorhynchus kisutch*, Salmonidae). First, they exposed coho salmon to live lingcod (*Ophiodon elongatus*, Gadidae) for 1 h. The surviving experienced fish were removed from the pool, marked for identification and held in tanks for 5 days. Following this, an equal number of experienced and naïve fish were mixed and exposed to lingcod predation. Experienced fish survived in greater numbers than naïve fish by avoiding capture longer and more successfully than naïve fish. These results suggest that learning may explain some of the differences in catchability between naïve and experienced fish. Other factors, such as the selection of faster fish through experience with the predator, may account for the differences between the naïve and experienced fish (Olla and Davis, 1989). To further test whether learning was involved, Olla and Davis (1989) conditioned coho salmon to stimuli that were associated with predation. They placed coho salmon in a plexiglass enclosure which was set in a larger pool, with two lingcod in the area outside the enclosure. Upon presentation, the lingcod lunged at the walls of the plexiglass enclosure in attempts to capture the coho salmon. Because chemical cues are often associated with predation, seawater from a tank that contained injured juvenile coho was pumped into the enclosure. To prevent habituation of the coho to the lingcod, a frozen lingcod was lowered into the enclosure every few minutes. Coho were conditioned for 15 minutes, after which they were housed and fed in a large tank for 5 days. Following this, the conditioned fish were mixed with an equal number of naïve cohorts and subjected to lingcod predation. There were no significant differences in the number of conditioned and naïve fish that were captured. However, when exposed to a second conditioning, fewer conditioned fish were captured. These results clearly show that learning plays a major role in predatory avoidance. They also show that hatchery life may impose a behavioural disadvantage with respect to dealing with predators; to enhance survival in hatchery fishes, a few exposures to a predatory threat may be useful.

With the exception of Olla and Davis' (1989) paper, few experimental data have been gathered on the role that learning plays with respect to hatchery applications. Suboski and Templeton (1989) provide an excellent review of the role of learning in fishes and its potential influence on hatchery success, pointing out that social learning processes (p. 000) could play a large role in enhancing the survival of hatchery-reared fishes. They also provide numerous examples showing that fish learn to recognize features of food, habitat, and predators, and that experienced fish can pass on certain information to other individuals. Social learning may prove to be a very important mechanism that allows hatchery fish to adapt to their new surroundings once they are released from the hatchery.

Other examples showing the influence of learning on fish behaviour, and its potential on fisheries, are described by Hackney and Linkous (1978). Also see the references in Suboski and Templeton (1989). Hackney and Linkous (1978) showed that learning occurred among näive fish exposed to live bait, but not artificial lures, for the first time.

While there is convincing laboratory and field evidence of fish imprinting to natural and artificial odours, the results also provide some practical applications for fish stocks. Hasler and Scholtz (1983) point out that artificial imprinting in hatcheries reduces the need for smolting ponds, therefore providing a controlled environment for the rearing of fish. They also suggest that artificially imprinting fish provides a mechanism for the conservation of stocks, for example selective harvesting of the population or the diversion of fish populations from dangerous situations. Equally, Hasler and Scholtz (1983) briefly discuss how imprinting programmes have taken effect in several countries. It appears, however, that more research is needed in the area of imprinting under natural conditions.

Discussion and conclusions

Although the underlying mechanisms for learning are not discussed, it is apparent that learning plays an important role in the life of fishes in their responses to environmental changes. Despite the fact that animals are innately equipped to recognize certain stimuli, one would expect that animals, including fishes, have developed behavioural mechanisms (including learning) which allow them to fine-tune their behaviour. This may be particularly important in dynamic environments. However, it should be mentioned that behavioural flexibility (i.e. learning) may only be important in changing environments. Behavioural rigidity may be more important in stable or very slow-changing environments. Similarly, if prey items are short-lived it may not be cost effective to learn (through sampling of the environment) new foraging techniques necessary to exploit a novel prey type (see Stephens and Krebs, 1986, for a more theoretical approach to foraging in stable v. unstable environments).

Despite this, however, the degree to which learning is involved in the behaviour of fishes is now being investigated in detail. Many theories of learning are devoted to the understanding of 'what' and 'how' animals learn (Krebs *et al.*, 1983). However, learning capabilities often involve underlying genetic, perceptual, motivational, maturational and motor abilities of animals. Some of these possibilities have been suggested by workers in several species of fish (Goodey and Liley, 1986; Wainwright, 1986; Colgan, 1989), but these areas generally remain unexplained. Similarly, many of the studies that consider learning focus on changing environments. However, more studies should focus on the influence of learning in stable habitats and the choices that must be made in relation to sampling and tracking the environment (Stephens and Krebs, 1986).

Most of the experiments on learning abilities in fishes have been conducted in the laboratory, and the adaptiveness of these results has been extrapolated to the natural situation. Several problems exist when using this approach; under natural conditions animals may face several learning situations concurrently. For instance, animals are often faced with the difficulty of learning to forage from different types of prey organisms while avoiding predation threats. In the laboratory, several of these difficulties are concealed because researchers often use simple learning situations. Therefore, studies of learning in animals, including fish, should be carried out under a more naturalistic surrounding, or complement laboratory results with field evidence, in order to facilitate understanding of learning in natural ontogeny. Also, comparisons of fish populations that are influenced by different selection pressures acting upon them will often be important to help us understand what is learned and the time constraints that are involved in learning under different situations.

Summary

The behavioural patterns of fish are the result of innate ('built-in') patterns of maturation (developmental changes) and of learning processes (imprinting and trial-and-error learning). Innate behavioural patterns are considered to be 'hard-wired' and inflexible. However, through learning, fish can adapt to environmental change. For instance, the homing behaviour of fish may be partly the result of the development of specific parts of the brain and partly because of changes in behaviour with experience. Similarly, one can assume that the feeding mode of fish involving snap-responses is innate, but learning enables fish to modify their foraging behaviour in response to a fluctuating environment. By reviewing these and other examples, such as the role of recognition learning and socially transmitted behaviour, one can illustrate the importance of learning in the everyday life of fishes. Although learning plays a large role in the behaviour of fishes, the learning capacity of fishes may also be useful to fisheries research and hatchery operations.

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References

Allee, W.C., Park, A., Emerson, A.E., Park T. and Schmidt, K.P. (1950) *Principles of Animal Ecology.* Philadelphia, PA: W.B. Saunders. 837 pp.

Anthouard, M. (1987) A study of social transmission in juvenile *Dicentrarchus labrax* (Pisces, Serranidae), in an operant conditioning situation. *Behaviour,* **103**, 266–75.

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.

Baird, T.A., Ryer, C.H. and Olla, B.L. (1991) Social enhancement of foraging on an ephemeral food source in juvenile walleye pollock, *Theragra chalcogramma. Env. Biol. Fishes* (in press).

Barlow, G.W. and Rogers, W. (1978) Female Midas cichlids' choice of mate in relation to parents' and to own color. *Biol. Behav.,* **3**, 137–45.

Bence, J.R. (1986) Feeding rate and attack specialization: the roles of predator experience and energetic trade-offs. In Simenstad, C.A. and Cailliet, G.M., eds. *Contemporary Studies on Fish Feeding.* Boston, MA: Dr W. Junk, pp. 113–22.

Beukema, J.J. (1968) Predation by the three-spined stickleback (*Gasterosteus aculeatus*): the influence of hunger and experience. *Behaviour,* **31**, 1–126.

Butler, M. and Johnson, D.A. (1972) A test of individual recognition in bluegill sunfish using operant procedures. *Virg. J. Sci.*, **23**, 149 (abstract).

Coble, D.W., Farabee, G.B. and Anderson, R.O. (1985) Comparative learning ability of selected fishes. *Can. J. Fish. Aquat. Sci.*, **42**, 791–6.

Colgan, P.W. (1989) *Animal Motivation.* London: Chapman and Hall. 159 pp.

Colgan, P.W., Gotceitas, V. and Frame, J. (1991) Individual variation, acquisition, and re-acquisition in a foraging task by juvenile bluegill sunfish (*Lepomis macrochirus*). *J. comp. Psychol.*, **105**, 78–84.

Croy, M.I. and Hughes, R.N. (1991a) The role of learning and memory in the feeding behaviour of the fifteen-spined stickleback, *Spinachia spinachia* L. *Anim. Behav.*, **41**, 149–59.

Croy, M.I. and Hughes, R.N. (1991b) The influence of hunger on feeding behaviour and on the acquisition of learned foraging skills by the fifteen-spined stickleback, *Spinachia spinachia* L. *Anim. Behav.*, **41**, 161–70.

Croy, M.I. and Hughes, R.N. (1991c) Effects of food supply, hunger, danger and competition on choice of foraging location by the fifteen-spined stickleback, *Spinachia spinachia* L. *Anim. Behav.*, **42**, 131–9.

Csanyi, V. (1986) Ethological analysis of predator avoidance by the paradise fish (*Macropodus opercularis*): I. Key stimuli in avoidance learning. *Anim. Learn. Behav.*, **14**, 101–9.

Dill, L.M. (1983) Adaptive flexibility in the foraging behaviour of fishes. *Can. J. Fish. Aquat. Sci.*, **40**, 398–408.

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

Dodson, J.J. (1988) The nature and role of learning in the orientation and migratory behavior of fishes. *Env. Biol. Fishes*, **23**, 161–82.

Ebel, W.J., Park, D.L. and Johnsen, R.C. (1973) Effects of transportation on survival and homing of Snake River chinook salmon and steelhead trout. *Fish. Bull.*, **71**, 549–63.

Ehlinger, T.J. (1986) Learning, sampling and the role of individual variability in the foraging behavior of bluegill sunfish. PhD dissertation, Michigan State University at East Lansing.

Ehlinger, T.J. (1989) Learning and individual variation in bluegill foraging: habitat specific techniques. *Anim. Behav.*, **38**, 643–58.

Ferno, A. and Sjolander, S. (1976) Influence of previous experience on mate selection of two colour morphs of the convict cichlid, *Cichlasoma nigrofasciatum. Behav. Process.*, **1**, 3–14.

Flaherty, C.F. (1985) *Animal Learning and Cognition.* New York: A.A. Knopf. 419 pp.

Fraipont, M. de and Thines, G. (1985) Responses of the cavefish *Astyanax mexicanus (Anoptichthys antrobius)* to the odor of known or unknown conspecifics. *Experientia*, **42**, 1053–4.

Fricke, H.W. (1973) Individual partner recognition in fish: field studies on *Amphiprion bicinctus. Naturwissenshaften*, **60**, 204–5.

Gleitman, H. and Rozin, P. (1971) Learning and memory. In Hoar, W.S. and Randall, D.J., eds. *Fish Physiology.*, Vol. 6. New York: Academic Press, pp. 191–278.

Godin, J.-G. (1978) Behaviour of juvenile pink salmon (*Oncorhynchus gorbuscha*) toward novel prey: influence of ontogeny and experience. *Env. Biol. Fishes*, **3**, 261–6.

Godin, J.-G. and Keenleyside, M.H.A. (1984) Foraging on patchily distributed prey by a cichlid fish (Teleostei, Cichlidae): a test of the ideal free distribution theory. *Anim. Behav.*, **32**, 120–31.

Goodey, W. and Liley, N.R. (1986) The influence of early experience on escape behavior in the guppy (*Poecilia reticulata*). *Can. J. Zool.*, **64**, 885–8.

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

Groten, H.F. (1990) The social aspects of place learning in the feeding behaviour of bluegill sunfish (*Lepomis macrochirus*). MSc thesis, Queen's University, Kingston, Canada. 37 pp.

Hackney, P.A. and Linkous, T.E. (1978) Striking behaviour of the largemouth bass and use of the binomial distribution for its analysis *Trans. Am. Fish. Soc.*, **107**, 682–8.

Hara, T.J. (1986) Role of olfaction in fish behaviour. In Pitcher, T.J., ed. *The Behaviour of Teleost Fishes.* London: Croom Helm, pp. 152–76.

Hasler, A.D. and Scholtz, A.T. (1983) *Olfactory Imprinting and Homing in Salmon.* Berlin: Springer-Verlag. 134 pp.

Hasler, A.D., Scholtz, A.T. and Horrall, R.M. (1978) Olfactory imprinting and homing in salmon. *Am. Scient.*, **66**, 347–55.

Hay, T.F. (1978) Filial imprinting in the convict cichlid fish, *Cichlasoma nigrofasciatum. Behaviour,* **65**, 138–60.

Helfman, G.S. and Schultz, E.T. (1984) Social transmission of behavioural traditions in coral reef fish. *Anim. Behav.*, **32**, 379–84.

Helfman, G.S., Meyer, J.L. and McFarland, W.N. (1982) The ontogeny of twilight migration patterns in grunts (Pisces: Haemulidae). *Anim. Behav.*, **30**, 317–26.

Hollis, K.L. (1982) Pavlovian conditioning of signal-centered action patterns and autonomic behavior: a biological analysis of function. *Adv. Study Behav.*, **12**, 1–64.

Hollis, K.L. (1984a) The biological function of Pavlovian conditioning: the best defense is a good offense. *J. exp. Psychol. Anim. Behav. Proc.*, **10**, 413–25.

Hollis, K.L. (1984b) Cause and function of animal learning processes. In Marler, P. and Terrace, H.S., eds. *The Biology of Learning.* Berlin: Springer-Verlag, pp. 357–71.

Hollis, K.L. (1990) The role of Pavlovian conditioning in territorial aggression and reproduction. In Dewsbury, D.A., ed. *Contemporary Issues in Comparative Psychology.* Sunderland, MA: Sinauer, pp. 197–219.

Hollis, K.L., Cadieux, E.L. and Colbert, M.M. (1989) The biological function of Pavlovian conditioning: a mechanism for mating success in the blue gourami (*Trichogaster trichopterus*). *J. comp. Psychol.*, **103**, 115–21.

Huntingford, F.A. (1986) Development of behaviour in fishes. In Pitcher, T.J., ed. *The Behaviour of Teleost Fishes.* London: Croom Helm, pp. 47–68.

Huntingford, F.A. and Wright, P.J. (1989) How sticklebacks learn to avoid dangerous feeding patches. *Behav. Process.*, **19**, 181–9.

Kamil, A.C. and Yoerg, S.I. (1982) Learning and foraging behaviour. In Bateson, P.P. and Klopfer, P.H., eds. *Perspectives in Ethology,* Vol. 5. New York: Plenum, pp. 325–64.

Kieffer, J.D. and Colgan, P.W. (1991) Individual variation in learning by foraging pumpkinseed sunfish, *Lepomis gibbosus*: the influence of habitat. *Anim. Behav.*, **41**, 603–11.

Krebs, J.R., Stephans, D.W. and Sutherland, W.J. (1983) Perspectives in optimal foraging. In Brush, A.H. and Clark, G.A., eds. *Perspectives in Ornithology.* Cambridge: Cambridge University Press, pp. 165–216.

Kruse, K.C. and Stone, B.M. (1984) Largemouth bass (*Micropterus salmoides*) learn to avoid feeding on toad (*Bufo*) tadpole. *Anim. behav.*, **32**, 1035–9.

Lefebvre, L. and Palameta, B. (1988) Mechanisms, ecology, and population diffusion of socially learned, food-finding behavior in feral pigeons. In Zentall, T.R. and Galef, B.G., jun., eds. *Social Learning: Psychological and Biological Perspectives.* Hillsdale, New Jersey: Lawrence Erlbaum Assoc., pp. 141–64.

Lima, S.L. and Dill, L.M. (1990) Behavioural decisions made under the risk of predation: a review and prospectus. *Can. J. Zool.*, **68**, 619–40.

Losey, G.S., jun. (1982) Ecological cues and experience modify interspecific aggression by the damselfish, *Stegastes fasciolatus. Behaviour,* **81**, 14–37.

Magurran, A.E. and Higham, A. (1988) Information transfer across fish shoals under predatory threat. *Ethology,* **78**, 153–8.

Milinski, M.M. (1984) Competitive resource sharing: an experimental test of a learning rule for ESS's. *Anim. Behav.*, **32**, 233–42.

Mobius, K. (1873) The movements of animals and their psychic horizon. In Hendersen, R.W., ed. (1982) *Learning in Animals.* Stroudsberg, Pennsylvania: Hutchinson Ross, pp. 10–11.

Morin, P.P., Dodson, J.J. and Dore, F.Y. (1989a) Cardiac responses to a natural odorant as evidence of a sensitive period for olfactory imprinting in young Atlantic salmon, *Salmo salar*. *Can. J. Fish. Aquat. Sci.*, **46**, 122–30.

Morin, P.P., Dodson, J.J. and Dore, F.Y. (1989b) Thyroid activity concomitant with olfactory learning and heart rate changes in Atlantic salmon, *Salmo salar*, during smoltification. *Can. J. Fish. Aquat. Sci.*, **46**, 131–6.

Myrberg, A.A. and Riggio, R.J. (1985) Acoustically mediated individual recognition by a coral reef fish (*Pomacentrus partitus*). *Anim. Behav.*, **33**, 411–16.

Neill, W.H. (1984) Behavioral enviroregulation's role in fish migration. In McCleave, J.D., Arnold, G.P., Dodson, J.J. and Neill, W.H., eds. *Mechanisms of Migration in Fishes*. New York: Plenum Press, pp. 61–6.

Noakes, D.L.G. and Barlow, G.W. (1973) Cross-fostering and parent–offspring responses in *Cichlasoma citrinellum* (Pisces, Cichlidae). *Z. Tierpsychol.*, **33**, 147–52.

Nordeng, H. (1977) A pheronome hypothesis for homeward migration in anadromous salmonids. *Oikos*, **28**, 155–9.

Olla, B.L. and Davis, M.W. (1989) The role of learning and stress in predator avoidance of hatchery-reared coho salmon (*Oncorhynchus kisutch*) juveniles. *Aquaculture*, **76**, 209–14.

Quinn, T.P. (1985) Salmon homing: is the puzzle complete? *Env. Biol. Fishes*, **12**, 315–17.

Quinn, T.P. and Dittman, A.H. (1990) Pacific salmon migrations and homing: mechanisms and adaptive significance. *Trends Ecol. Evol.*, **5**, 174–7.

Quinn, T.P., Brannon, E.L. and Dittman, A.H. (1989) Spatial aspects of imprinting and homing in coho salmon, *Oncorhynchus kisutch*. *Fish. Bull., U.S.*, **87**, 769–74.

Reese, E.S. (1989) Orientation behavior of butterfly fishes (family Chaetodontidae) on coral reefs: spatial learning of route specific landmarks and cognitive maps. *Env. Biol. Fishes*, **25**, 79–86.

Robert, M. (1990) Observational learning in fish, birds, and mammals: a classified bibliography spanning over 100 years of research. *Psychol. Rec.*, **40**, 289–311.

Ryer, C.H. and Olla, B.L. (1991) Information transfer and the facilitation and inhibition of feeding in a schooling fish. *Env. Biol. Fishes*, **30**, 317–23.

Scholtz, A.T., Horrall, R.M., Cooper, J.C. and Hasler, A.D. (1976) Imprinting to chemical cues: the basis for home stream selection in salmon. *Science*, **192**, 1247–9.

Siepen, G. (1986) Does breeding under 'forced' conditions affect subsequent mate choice under 'free choice' conditions in the cichlid fish *Cichlasoma nigrofasciatum*? Are animals with different early experience affected differently? In Crapon de Caprona, M.-D. and Fritzoch, B., eds. *Proc. 3rd Workshop on Cichlid Biology, Bielefeld, West Germany, 5–8 February 1986*, pp. 39–42.

Siepen G. and Crapon de Caprona, M.-D. (1986) The influence of parental color morph on mate choice in the cichlid fish *Cichlasoma nigrofasciatum*. *Ethology*, **71**, 187–200.

Stabell, O.B. (1992) Olfactory control of homing behaviour in salmonids. In Hara, T.J., ed. *Fish Chemoreception*. London: Chapman and Hall (in press).

Staddon, J.E.R. (1983) *Adaptive Behaviour and Learning*. Cambridge: Cambridge University Press. 555 pp.

Stephans, D.W. and Krebs, J.R. (1986) *Foraging Theory*. Princeton, NJ: Princeton University Press. 247 pp.

Suboski, M.D. (1988) Acquisition and social communication of stimulus recognition by fish. *Behav. Process.*, **16**, 213–44.

Suboski, M.D. and Templeton, J.J. (1989) Life skills training for hatchery fish: social learning and survival. *Fish. Res.*, **7**, 343–52.

Suboski, M.D., Bain, S., Carty, A.E., McQuoid, L.M., Seelen, M.I. and Siefert, M. (1990) Alarm reaction in acquisition and social transmission of simulated-predator recognition by zebra danio fish (*Brachydanio rerio*). *J. comp. Psychol.*, **104**, 101–12.

Templeton, J.J. (1987) Individual differences in the foraging behaviour of juvenile rock bass (*Am-*

bloplites rupestris): causes and consequences. MSc thesis, Queen's University, Kingston, Canada. 126 pp.

Teyke, T. (1989) Learning and remembering the environment in the blind cave fish *Anoptichthys jordani. J. comp. Physiol.*, **164A**, 655–62.

Thorpe, W.E. (1963) *Learning and Instinct in Animals.* Cambridge, MA: Harvard University Press: 493 pp.

Wainwright, P.C. (1986) Motor correlates of learning behaviour: feeding on novel prey by pumpkinseed sunfish (*Lepomis gibbosus*). *J. exp. Biol.*, **126**, 237–47.

Warburton, K. (1990) The use of local landmarks by foraging goldfish. *Anim. Behav.*, **40**, 500–505.

Ware, D.M. (1971) Predation by rainbow trout (*Salmo gairdneri*): the effect of experience. *J. Fish. Res. Bd Can.*, **28**, 1847–52.

Weber, P.G. and Weber, S.P. (1976) The effect of female color, size, dominance and early experience upon mate selection in male convict cichlids, *Cichlasoma nigrofasciatum* Gunther (Pisces, Cichlidae). *Behaviour*, **56**, 116–35.

Werner, E.E., Mittelbach, G.G. and Hall, D.J. (1981) The role of foraging profitability and experience in habitat use by the bluegill sunfish. *Ecology*, **62**, 116–25.

Wright, D.E. and Eastcott, A. (1982) Operant conditioning of feeding behaviour and patterns of feeding in thick lipped mullet, *Crenimugil labrosus* (Risso) and common carp, *Cyprinus carpio* (L.) *J. Fish Biol.*, **20**, 625–34.

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