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Cognition: Learning and Memory

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INTRODUCTION

Certain types of behaviour are so fundamentally important to an animal that they become fixed and heritable; for instance, the ritualized zigzag courtship display of a male stickleback, *Gasterosteus aculeatus*, and the female's 'head-up' response (Wootton, 1976). Other behaviours, however, are labile and can be modified and fine tuned to fit a particular situation or environment. An ability to behave in a flexible way, particularly in a changeable environment, requires animals to possess the capacity to learn, remember and update information. There are many examples where learning and memory affect the manner in which fish behave. We will consider some of these in this chapter.

Cognition refers to three processes: (i) a perception phase, where the animal detects and internalizes information through one of its sensory

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systems, (ii) a learning phase where the animal processes the information and (iii) a memory phase, where the animal consolidates what it has learned and establishes some form of memory that it can recover and utilize at some point in the future. Montgomery and Carton (2008) cover topics associated with perception in chapter 1, 'The Senses of Fish: Chemosensory, Visual and Octavolateralis', this book, so here we have chosen to focus more on the second two processes: learning and memory.

Our understanding of fish learning and memory has changed enormously in recent years, and the number of research papers published in this area has seen a dramatic rise (Brown *et al.*, 2006). Prior to this surge in interest, much of the work published on fish cognition came from the laboratories of experimental psychologists where their main interests were in general learning processes. As early as 1971, however, Gleitman and Rozin pointed out that rather than following an argument of phylogeny—where fish are perceived as 'lower' to the 'higher' birds and mammals—a more instructive way of comparing cognition was to actively look for similarities in abilities. When similar abilities are found across species or taxonomic groups, it suggests that there may be common mechanisms underlying them, or perhaps a common ecological background that has shaped those specific abilities. It took some time, but over the last decade, increasing numbers of researchers have used the comparative approach to investigate fish cognition. This has provided quite a turning point in our awareness of what fish are capable of, and at times has demonstrated how similar some of their learning and memory abilities are to birds and mammals (Braithwaite, 2006).

Being able to learn and remember information allows an animal to make informed decisions. As such, cognition can be considered to underpin many aspects of behavioural ecology. Fish are no exception to this. For example, fish learn how to search and forage efficiently on patchy resources (Hart *et al.*, 1994; Noda *et al.*, 1994), and when they have found food they can learn and improve how they manipulate and handle different types of prey (Croy and Hughes, 1991; Hughes and Croy, 1993). Not surprisingly, fish that have learned to respond appropriately in the presence of predators are likely to survive another day (Brown, 2003), but if they are chased then remembering the position of shelter could provide a means of escape (Aronson, 1971; Markel, 1994; Odling-Smee *et al.*, 2006). Within a social setting, being able to recognize and respond appropriately to neighbouring individuals, or other members of a school, allows the fish

to decrease the time they spend being vigilant or aggressive; so they can focus on activities such as foraging and reproduction (Brown and Laland, 2003; Griffiths, 2003; Hoare and Krause, 2003). Thus, there are many ways in which learning and memory can contribute to fish behaviour.

Some forms of learning are time sensitive and occur at a certain stage in a fish's life. Several species of salmonid, for example, undergo a specific phase of learning during their first migration as they begin to move downstream. During this seaward migration, the fish learn the chemical and olfactory signature of their natal stream (Dittman and Quinn, 1996; Hinch *et al.*, 2006). This clearly defined type of learning, referred to as imprinting, allows the salmon to home in on a suitable spawning habitat once they have matured at sea. In other species of fish too, there are periods of learning associated with the transition of juvenile fish to adult habitats. Adult and juvenile fish often live in different environments, and as juvenile fish mature and leave their nursery grounds, they must learn to change their behaviour to adapt to their new environment. For some species, this transition may require very rapid learning, and the ability to recognize and avoid the new array of predators will be a vital part of this learning process. Perhaps, not surprisingly, in some cases anti-predator responses have become innate (Huntingford, 2004; Salvanes and Braithwaite, 2005), although there is good evidence that even these innate responses can be fine-tuned through experience (Kelley and Magurran, 2003; Brown and Chivers, 2006).

In this chapter, we shall consider the manner in which cognitive processes shape fish behaviour. We begin by considering simple forms of learning, and review some of the experimental psychology literature to highlight how even basic learning processes affect fish behaviour. We then focus on how these skills allow fish to discriminate between objects or events. This is followed by an overview of memory processes. In the second half of the chapter, we will focus on more complex learning and behaviour, reviewing how fish learn to find their way around, and how they learn from each other. In the last section, we consider the role of early experience in shaping learning and behaviour in fish.

SIMPLE FORMS OF LEARNING AND FISH BEHAVIOUR

Learning to associate a link between two or more stimuli or events is a simple form of learning, known as associative learning (Pearce, 1997). It is a well-documented phenomenon witnessed in a wide range of species

from invertebrates to vertebrates (Shettleworth, 1998). There are two types of associative learning—Classical and Instrumental Conditioning. In classical conditioning, the animal learns to associate a neutral stimulus with an event or something that affects it. For example, fish can readily learn to associate the delivery of food with a light being switched on. Just like Pavlov's dogs that begin to salivate as they hear a bell ring, fish learn to respond to the light coming on by swimming towards the place where food is delivered. Instrumental conditioning is different in the sense that here the animal learns that a particular action it performs influences the presence of the reward. Here, when the action pushing on a lever directly results in the delivery of a small amount of food, fish learn to associate lever pushing with food delivery.

As early as the 1920s, researchers were investigating classical conditioning in fish. The goldfish, *Carassius auratus*, was often the preferred species, and their abilities to associate light, sound, colour and temperature with cues such as food rewards or punishments in the form of mild electric shocks were studied (McDonald, 1922; Bull, 1928). This work revealed that classical conditioning takes as long to establish in fish as it does in other animals (Voronin, 1962), and that fish can discriminate or generalize between different stimuli with a similar ability to that found in birds and mammals (Yarczower and Bitterman, 1965).

A key turning point in our understanding of classical conditioning and its effects on fish behaviour came from a series of elegant experiments led by Karen Hollis. Hollis and colleagues (1997) demonstrated the adaptive value of the conditioning process and revealed that it not only influenced fish behaviour but it could also affect direct reproductive benefits. Using blue gourami, *Trichogaster trichopterus*, a small territorial, tropical fish, Hollis showed that learning to anticipate events provided a way for the fish to modulate their otherwise very overt aggressive behaviour. A territorial male needs to be aggressive in order to maintain and defend his territory from intruding males, but if the intruder fish turns out to be a female inspecting the territory, then the male needs to switch from aggression to courtship. Typically, males are aggressive towards every intruding fish, and even though a female may adopt a submissive posture, his attack on her is sometimes so severe that she leaves the territory (Daly, 1978). A delay in changing aggressive behaviour into courtship can hinder the mating process and thus presents a cost of reduced mating opportunities for the male (Miller, 1964; Daly, 1978).

Hollis showed that males could learn to reduce their aggression through classical conditioning. In a period of pre-training, males were conditioned to predict the presence of a female by training them so that a few seconds after a light was switched on they could have 5 minutes of exposure to a female. Blue gourami that were allowed to learn this association were then tested and compared with fish that had also been exposed to a female and a light, but where the timing of this exposure did not allow an association to form (i.e., an unpaired control treatment). The results clearly showed that blue gourami males trained to predict the presence of a female decreased their territorial aggression faster and began their courtship activities sooner in response to the light cue (Hollis et al., 1989). Furthermore, Hollis and colleagues went on to show that males conditioned to predict the presence of a female also obtained direct reproductive benefits as they were able to spawn with females earlier, clasp the female more often, and these changes in their behaviour led to them fathering more offspring (Hollis et al., 1997). Clearly, here, the light cue is an artificial signal, but it is possible to speculate that natural cues, such as olfactory signals or even sounds produced by females, might become part of a learned communication system between males and females.

Hollis suggested that classical conditioning provides fish and other animals with the ability to optimize their behaviour in response to biologically important events and she proposed that classical conditioning could provide an important applied tool that would augment certain animal husbandry techniques (Hollis, 1999). Since her work was published, several conditioning paradigms have become part of the day-to-day tools used in aquaculture with sounds and lights frequently used to signal food delivery (Jobling et al., 2001).

Instrumental conditioning has also been investigated in a number of fish species. Here, fish have be trained to push at paddles to obtain food rewards or access to well-oxygenated water (positive reinforcement; Longo and Bitterman, 1959; Hogan and Rozin, 1962; Van Sommers, 1962), or they are trained to swim or shuttle between two sides of a tank as part of a learned escape response to avoid an electric shock (negative reinforcement; Horner et al., 1961). As with classical conditioning, fish respond to instrumental conditioning in the same way that other animals such as rats and pigeons do (Gleitman and Rozin, 1971). For researchers, this type of conditioning provides a useful tool to gauge fish behaviour because it allows us to determine the preferences of fish, or to quantify how motivated they are to have access to certain types of resource.

Recently, there has been renewed interest in conditioning and shuttle-box experimental designs to address aspects relating to fish welfare. In particular, two studies have used instrumental conditioning to determine what fish find aversive (Yue et al., 2004; Dunlop et al., 2006). Yue and colleagues (2004) investigated how aversive a plunging net was for rainbow trout, Oncorhynchus mykiss. Using a shuttle-tank design, fish were conditioned to associate a light cue with the release of the net into the water. After training, most of the fish learned to anticipate the presentation of the net, and when the light stimulus was switched on, they responded by swimming away into another compartment to avoid the net. The authors concluded that conditioning approaches such as this provide a means of quantifying aversion in fish. Quantifying motivation is notoriously difficult (Elwood, 1998), but using instrumental conditioning, we should be able to design experiments that will assess what fish prefer or want within their captive environment—a useful tool with which to address current fish welfare concerns (Dunlop et al., 2006; Huntingford et al., 2006). In designing these types of experiment, however, care needs to be taken when quantifying behavioural states such as motivation and fear. For instance, it is imperative that the design does not use an associative stimulus that is itself aversive. Light can act as an aversive stimulus for some species of fish (Hoar et al., 1957); for many species illumination means greater visibility associated with higher mortality risk, whereas for the predator it might provide a better view of the prey, and it is possible that light may also produce reflex aversion responses.

Instrumental conditioning has also proved to be useful in the design of feeders for aquaculture (see chapter 17 'Behaviour and Welfare in Farmed Fish' by Brännäs and Johnsson in this book). For example, it is possible to design feeders that release food on demand when a fish sets off a trigger such as pushing against a rod or pulling on a string (Alanärä, 1996; Rubio et al., 2004). Training the fish to use these types of feeder systems, however, can often create its own problems: sometimes only a subset of the population learn the conditioning, and then only a few fish trigger the feeders, in other situations some fish find the physical action associated with triggering the feeder a reward in itself, and this can lead to too much food being released (see Fernö et al., 2006).

Simple forms of learning are an important part of many of the day-to-day behaviours that we observe in fish. It may come as a surprise, but the conditioning responses underlying fish associative learning share many of the same properties that we find in birds and mammals.

DISCRIMINATION IN FISH

Discrimination occurs when an animal detects different stimuli using one or more of its sensory systems and then compares the different stimuli and distinguishes between them. This type of comparative process can be used to help the animal in making decisions. Which potential mate do I prefer? Have I mated with that female before? Which food patch will give me the greatest gain? Is this predator an immediate threat, or is it satiated? Many of these questions are addressed in more detail by other authors in this book. Thus, here we have chosen to highlight just a few examples of how fish use their different sensory systems to investigate differences between stimuli. Although we describe these examples highlighting different sensory systems separately, it is important to remember that in reality cues are likely to be integrated to provide the fish with a more accurate discrimination ability.

Many species of fish can detect small differences in visual phenotypic traits; for example, in both male and female sailfin mollies, *Poecilia latipinna*, body size is an important cue during mate choice (Ptackek and Travis, 1997). Similarly, subtle differences in coloration can influence mate attractiveness; in three-spined sticklebacks, females exhibit a preference for redder males (Milinski and Bakker, 1990), but as the sample males become more similar in their red coloration, females display less discrimination (Braithwaite and Barber, 2000).

Some species can also discriminate between physical structures. For example, bower building Lake Malawi cichlids can discriminate between differently sized bowers (Stauffer *et al.*, 2005). When the bower size was manipulated, Stauffer *et al.* (2005) found that females always selected the male with the biggest bower. Using a non-visual sense, weakly electric fish, *Gnathonemus petersii*, are able to use their electrolocation system to discriminate between objects with different electrical properties (von der Emde, 1990). More recently, this species has also been shown to use its electric sensory system to measure the three-dimensional depth, which they use discriminating between similar-shaped objects (von der Emde, 2004).

There are many examples of fish species that can discriminate between familiar and unfamiliar conspecifics: bluegill sunfish, *Lepomis macrochirus* (Brown and Colgan, 1986), three-spined sticklebacks, *Gasterosteus aculeatus* (Van-Havre and Fitzgerald, 1988), guppies, *Poecilia reticulata* (Magurran *et al.*, 1994) and Panamanian bishops, *Brachyrhaphis episcopi* (Simcox *et al.*, 2005). There would seem to be several reasons as to why

that subtle differences in the calls of *P. adspersus* probably allow fish within this species to individually recognize one another.

Sound discrimination may also play a role in the recruitment of coral reef fish. With evidence that a considerable proportion of demersal spawning reef fish recruit back to their natal reefs (Jones *et al.*, 1999; Swearer *et al.*, 1999), Simpson *et al.* (2005) investigated the use of natural reef sounds in the settling behaviour of juvenile reef fish. By playing recordings of reef sound (such as snapping shrimp and other fish noises) on a subset of artificial patch reefs, they showed that recruitment was greatest on those reefs broadcasting sound. In a refinement of this study, they varied the frequency of sound played on the different reefs ('high frequency' where 80% of the sound was >570 Hz, and 'low frequency' where 80% of the sound was <570 Hz). Their results showed that some fish families discriminated between the sounds, with the pomacentrid species (damselfish) showing a preference for high frequency recordings (Simpson *et al.*, 2005).

Sound discrimination may also be important for reproductive behaviour in Atlantic cod, *Gadus morhua*. Nordeide and Kjellsby (1999) recorded sound on the main spawning grounds off the Lofoten Islands during April 1997 where large numbers of fish from both Arctic cod populations and local coastal cod populations aggregated to spawn. They repeated the recordings in September when the cod were no longer spawning. The analysis revealed differences between the two time periods with the April recordings representing a sound that was between 50 and 500 Hz and transient in character with a 7-18 dB higher sound level. It seems likely that the cod are producing sounds as part of their spawning behaviour; however, the information contained in the sounds and how it is used has yet to be determined.

There are, therefore, many ways in which discrimination ability influences the behaviour and the decisions that fish are able to make. In this section we have also emphasized the need to recognize that many fish are equipped with sensory systems different to our own, and that they can use these very effectively to allow them to discriminate between objects and places in their environments.

MEMORY

Although there have been many studies investigating learning, much less attention has been directed at memory. Curiously, this is not only the case for fish studies, but it is also true for animal behaviour in general

such discrimination ability is important. Fish familiar with each other may be able to cooperate better in terms of schooling behaviour (Griffiths, 2003). Males may want to minimize the time spent courting and mating with females with whom they have previously mated (Kelley et al., 1999; Simcox et al., 2005). An ability to discriminate between an opponent you have never met before, as compared to one that you recently fought, might influence your decision about whether to escalate to a fight or not (Johnsson and Åkerman, 1998). Closer inspection of some of these discriminatory behaviours, however, suggests that individual identity may not always need to be learned. Rather, in some cases, it seems that fish can make generalizations. For example, Ward and colleagues (2004, 2005) have shown that three-spined sticklebacks use odour preferences to allow them to associate with schools of fish that have been recently in the same habitat and eating the same type of diet. Here, the fish seemingly use a general odour cue rather than learning to associate with specific individuals.

Olfactory information can also be used by some species to discriminate between members of the same species, or a closely related species. As such, olfactory discrimination can play an important role in some speciation processes. For example, McLennan and Ryan (1999) have shown that differences in the olfactory discrimination abilities of different species of the northern swordtails, *Xiphophorus* genus, reflect the degree to which they show reproductive isolation. In discrimination tests where odours from males of three different species were presented to females, McLennan and Ryan (1999) found that *X. nigrensis*, the most reproductively isolated of the three species, had a clear preference for the scent of *X. nigrensis* males. Whereas, *X. montesumae*, in general, exhibited less discrimination and concluded that *X. montesumae* were, therefore, more likely to make mating mistakes based on olfactory cues alone.

Some fish can also discriminate between certain kinds of auditory cue. *Pollimyrus adspersus*, a weakly electric fish, use simple sounds to communicate. The sounds they produce can be classed as grunts or moans, and males alternate between these during their courtship of females (Marvit and Crawford, 2000). Grunts are effectively a series of acoustic clicks with a short inter-click interval, each grunt lasting about 250 ms. Moans are tonal with sharp spectral peaks at 240 and 480 Hz and last for about 800 ms. Using sound patterns of either *P. adspersus* or those from a closely related but acoustically different species (*P. isidori*), Marvit and Crawford (2000) showed that the fish were able to discriminate between species based on their acoustic calls alone. Furthermore, they suggested

(Shettleworth, 1998). Learning and memory are linked: there is little point to learning if the information cannot be recalled and remembered. However, they also represent two distinct processes. Learning is essentially the acquisition of memory, whereas memory has other components such as retention and, if an animal becomes distracted around the time that it is learning, or shortly afterwards, this can lead to interference (i.e., where the strength or validity of the memory becomes impaired). Work directed at quantifying memory duration—how rates of forgetting progress, or what factors cause variation in forgetting rates—is far less common than studies investigating the acquisition of information (Shettleworth, 1998).

Until recently, forgetting was believed to represent a failure of the memory, but it is now proposed that the ability to forget might be advantageous (Kramer and Golding, 1997). For example, forgetting the locations of previously rich but now poor feeding sites will benefit individuals. As such, forgetting is increasingly considered an adaptive trait rather than a flaw associated with failed memory processes (Kramer and Golding, 1997). For instance, foraging nine-spined sticklebacks, *Pungitius pungitius*, select the specific site to feed based on information that they have learned and remembered about food patch profitability, but their tendency to use this information decreases over a period of time, especially if they have not recently been able to sample the food patches directly. When this happens, they start to pay attention to what other fish around them are doing (van Bergen *et al.*, 2004). This may demonstrate flexible memory use, depending on the perceived reliability of current information, and could be an example where forgetting is adaptive under certain circumstances. However, an alternative explanation for this observation is that the fish may forget about their own experiences, and so have to rely on watching others.

In a different study on sticklebacks, Mackney and Hughes (1995) explored whether environmental variation affected memory duration. Here, they quantified how memory for prey handling skills differed between closely related species of sticklebacks. A fully marine population, *Spinachia spinachia*, had a memory window of 8 days, whereas a population that migrated from the sea into freshwater to breed (G. *aculeatus*) retained the memory for 10 days, but the longest memories (25 days) were found in a fully freshwater pond population (G. *aculeatus*). The pond environment was landlocked and structurally simple, and Mackney and Hughes (1995) suggested that their diet would be consistent over a period of time. Therefore, in this habitat, longer memory duration for particular prey handling would be useful. The population from the more variable

(spatially and environmentally changeable) marine environment are more likely to encounter a wider diversity of prey, promoting shorter memory durations and an ability to learn how to exploit whatever prey type is available at the immediate time.

Utne-Palm and Hart (2000) studied how individual fish learn and remember each other. They investigated the buildup and breakdown of familiarity in groups of 12 three-spined sticklebacks by measuring the levels of aggression between pairs of fish as they competed for access to food. Utne-Palm and Hart found that after being housed together over a 4-week time-scale, the fish were less likely to chase each other. They proposed that this reflected an increase in the familiarity and recognition of individuals in the group. In a second part to the experiment, they also quantified the breakdown of familiarity, by splitting the familiar groups in two so as to create smaller groups of 6 fish. Individuals from these two groups were then brought together and allowed to compete for access to food after they had been separated for either 2 weeks or 4 weeks. The results showed a slow breakdown in the familiarity: after 2 weeks the fish were twice as likely to chase the other member of the pair, after four weeks the level of chasing more than quadrupled. This suggests that the memory for individual fish identity is forgotten if the fish do not interact on a regular basis.

Even now, a great deal remains for us to discover about memory duration and how this varies across species and between populations. However, in the same way that fish have provided excellent model systems for studying the adaptive nature of learning, it seems likely that similar species could be used to study the adaptive value of memory (Braithwaite, 2006).

NAVIGATION AND SPATIAL LEARNING

Many studies of animal cognition use assays of spatial ability to investigate learning and memory (Healy, 1998). Most animals need to keep track of their movements and so it is possible to devise experiments that investigate the cues they learn, how well they remember routes, and whether they can calculate short cuts. The study of fish spatial cognition has recently become a very productive area (Braithwaite and Burt de Perera, 2006; Odling-Smee et al., 2006). Spatial behaviour in fish has been measured using a variety of mazes in the controlled conditions in the laboratory, but recent advances in tracking technology have also allowed experiments to be conducted in the field (see Metcalfe et al., 2008 in this book).

These varying approaches have shown a remarkable amount of variation in spatial learning and memory with fish using a variety of sensory systems to encode spatial information, and displaying various adaptations to local environments (Braithwaite and Burt de Perera, 2006). Furthermore, they have also revealed that in addition to long distance migrations that take fish from one part of the globe to another, there are many fish that also undergo vertical migrations moving large distance through the water column (see also chapter 5 'Migration and Habitat Choice in Marine Fishes' by Metcalfe *et al.*, this book).

Many fish need to move between different places in their search for food or as they move into and explore new areas. Most species of fish, therefore, have a basic set of spatial skills that allow them to move around and not get lost (Odling-Smee *et al.*, 2006). To successfully orientate around an environment, fish need to learn and remember their current position with respect to the position of a goal. One of the simplest ways a fish can remember the position of a goal is to learn the position of a prominent landmark that helps the fish return to that place. Warburton (1990) showed that goldfish are able to do this. A number of fish species have also been shown to swim from one landmark to the next, following a chain of landmarks. For example, in laboratory aquaria, three-spined sticklebacks have been shown to follow small plant landmarks to find their way through a series of doors in a maze (Girvan and Braithwaite, 1998). Juvenile Atlantic salmon, *Salmo salar*, can also learn to follow moveable food patches labelled with unique visual landmarks to indicate the position of a food reward (Braithwaite *et al.*, 1996). One or two field observations also indicate that fish are likely to follow lists or sequences of landmarks to help them find their way. For instance, Reese (1989) described how butterflyfishes (family Chaetontidae) follow consistent routes as they swim between feeding patches on their reef. To investigate the types of information that the fish use, Reese changed the appearance of the reef by moving prominent coral outcrops. On approaching the modified area, the fish stopped swimming and began a series of search-like movements before eventually continuing on their route. It was proposed that when the fish reached the manipulated areas of the reef, they were forced to stop following their list and, instead, started looking for the next familiar landmark. Similar observations have been reported in brown surgeonfish, *Acanthurus nigrofuscus*, here the fish can be erroneously led away from their normal route by displacing parts of the reef, again suggesting that they follow lists of landmarks (Mazeroll and Montgomery, 1998).

A recent study using blind Mexican cavefish, *Astyanax fasciatus*, showed that sequences of landmarks are learned, indicating that the lists of landmarks have a specific order (Burt de Perera, 2004). With no eyes to guide them, blind cavefish orient themselves using their lateral line organ which consists of specialized mechanoreceptor cells that measure disturbances in the flow of water that surrounds them (Hassan, 1985, 1989; Montgomery *et al.*, 2001). As the fish swim forwards, they set up a flow field around themselves and objects or surfaces in the environment distort the flow field. These distortions are picked up by the cells in the lateral line organ and relayed to the brain. The fish can, therefore, use the information they get from their lateral line as a way of learning about the layout of their local environment. If a fish encounters something new it begins to swim faster; this is proposed to increase the stimulation of its lateral line organ, and allows the fish to investigate the change in the environment (Hassan, 1989). Swimming speed, therefore, provides a tool with which to measure how familiar the fish are with their environment: they swim slowly when they are familiar with their surroundings but speed up when they detect a change or something new. To determine whether they encode order, Burt de Perera (2004) allowed fish to learn a specific sequence of landmarks arranged in a ring-shaped tank. The order of the landmarks was then switched and this coincided with an increase in swimming speed. As other cues were controlled for, this result indicates that the fish responded to the altered sequence of landmarks.

In addition to learning landmarks and integrating these to form maps, several species of fish are also known to use compasses. There are a wide variety of cues that animals can use as compasses, e.g., the sun, stellar rotation, polarized light, salinity gradients and even the Earth's magnetic field. Compasses provide a relatively stable, unchanging source of spatial information, which can be used either on its own or in combination with landmarks or a map (Goodyear, 1973). Compasses are particularly useful when animals need to travel long distances in a specific direction. Many migrating animals, for example, make use of compass orientation (Dingle, 1996). As Metcalfe *et al.* (2008) discuss elsewhere in this book, determining the orientation mechanisms that migrating fish use is not straight forward, and so our understanding of compass use in fish is scant.

There are a few empirical demonstrations of compass use in fish. For example, when mosquitofish, *Gambusia affinis*, are moved to an unfamiliar location, they use a sun compass to guide them in a direction that is at right angles to the shore from which they were captured. This movement

towards the shallow water close to the shore is thought to help the fish avoid piscine predators (Goodyear and Ferguson, 1969; Goodyear, 1973). Experiments using polarizing filters have demonstrated that like a number of bird species, juvenile rainbow trout can also use polarized light as a compass. Curiously, however, this ability appears to be restricted to juvenile fish (Hawryshyn *et al.*, 1990). The first widely accepted evidence for behavioural and electrophysiological responses to magnetic fields was also documented in fish. In 1997, Walker and colleagues identified an area in the rainbow trout snout where candidate magnetoreceptor cells were located. Their work showed that the trout detect the Earth's magnetic field using magnetite, biogenically produced iron oxide crystals. Since their findings became known, a magnetic compass has been proposed to underlie the ability of salmonids to migrate substantial distances out at sea while maintaining a constant bearing, but this remains mere speculation at this point.

Field studies have also revealed that a variety of animals, including fish, can use the characteristic circulation and gradients of stratified and partially mixed estuaries to help them move or track their movements. In these types of water, there is a seaward flow of low salinity water floating above a denser compensatory landward flow of water. By making vertical migrations at the appropriate times, the animals can use the counter-currents to enable them to either stay in the estuary year-round, or to enter and leave the estuary on a seasonal basis (Mann and Lazier, 1991). For example, Grindley (1964) suggested that copepods remained in the landward-flowing water by ceasing vertical migration when they encountered lowered salinities of the seaward-flowing surface waters. Fortier and Leggett (1983, 1984) reported that herring larvae less than 10 mm long stay in the upper estuary of St Lawrence in the layer of inflowing saline water at c. 40-60 m depth, while larger herring (> 10 mm) made diurnal vertical migrations across the layers but these fish tended to gather and stay at depths where there is close to zero velocity in the water. These examples suggest that complex gradient and current following behaviours are possible even in the youngest and smallest live stages of fish.

With the improvement in modern tracking techniques and tags, and also by using advanced aquaria designs that can track individual responses to environmental stimuli, we can start to learn more about fish movements in the open seas and this should provide us with opportunities to study the compasses that they use to guide their movements. For example, split-beam echo sounders allow the position of a target to be defined in

an acoustic beam, when combined with software allocating subsequent echoes to the same target, so-called 'target tracking' it is possible to gather data on size, 3-D swimming trajectories and swimming speed of individual fish (e.g., Torgersen and Kaartvedt, 2001; Kaartvedt and Klevjer, 2003). New methodology such as this provides us with opportunities for observing detailed individual swimming behaviours even within deep water.

LEARNING FROM OTHERS

Observing and copying others can help individuals find new prey, learn to avoid predators, and even follow migration routes that take them to distant breeding grounds or feeding sites. Social learning works by animals obtaining information from more knowledgeable or more skilled individuals. Copying can save the individual the cost of sampling or, in other words, the cost of trial and error learning. Individuals, therefore, need to decide when and whether it is more cost-effective for them to gain information by copying rather than sampling the environment themselves. For this to work, they need to have some capacity to determine the pay-offs associated with the alternative ways of learning (Laland, 2004), and they need to be able to make sense of and know how to use public information (Valone, 1989). Game theory and population genetics models suggest that animals are selective with respect to the circumstances under which they rely on social learning and which individuals they copy. There are still relatively few empirical examples demonstrating the strategies that animals use when they copy others, but a few studies addressing this have used fish (Laland, 2004). For example, Lachlan *et al.* (1998) demonstrated that guppies were more likely to follow an informed individual through a maze rather than following a naïve fish. This result clearly shows that guppies can discriminate between informed and non-informed individuals, a basic ability for social learning to function.

Learning how to respond to the threat of predation by trial and error could be very expensive given the associated high mortality risk. Thus, we might expect fish to learn about anti-predator behaviours by watching other fish and indeed this has been found in species such as fathead minnows, *Pimephales promelas*, and guppies (Krause, 1993; Chivers and Smith, 1995; Kelley *et al.*, 2003). Socially transmitted information also enables individuals to recognize and respond to threats more quickly than if they independently assess the risks (e.g., Webb, 1980). Members of fish shoals are able to evaluate predation risk by observing the behaviour

of those undertaking predator inspection visits leading to a collective anti-predator response (Pitcher *et al.*, 1986). Fish can also learn to respond to alarm pheromones without having direct prior exposure to such chemical cues. For example, Hall and Suboski (1995) reported that naïve zebrafish, *Brachydanio rerio*, learned to recognize predator cues that were socially transmitted by the behavioural responses of conspecifics that had previously experienced alarm pheromones. Similar findings have also been reported for the arctic charr, *Salvelinus alpinus* (Vilunen *et al.*, 2005).

Several studies report that fish socially learn about location, or quality of food from conspecifics (Laland and Williams, 1997, 1998; Magnhagen and Staffan, 2003). Social learning has a positive effect on growth in young-of-the-year perch *Perca fluviatilis*: here, naïve fish that fed on novel food grew faster in the presence of demonstrators than without (Magnhagen and Staffan, 2003). Sex differences in social learning ability have also been reported: female guppies learn faster than males (Reader and Laland, 2000). Differences between closely related species in their ability to socially learn is also evident. Coolen *et al.* (2003) compared the abilities of three-spined and nine-spined sticklebacks and found that both species use public information to locate food, but only the nine-spined sticklebacks were able to use information from others to also assess the patch quality.

Mating opportunities can also be learned socially. For example, experiments on guppies suggest that females may use the presence of another female near a courting male when choosing their mate (Dugatkin *et al.*, 1992). Since this first observation, several other examples of mate choice copying have also been reported: for example, Schlupp *et al.* (1994) observed similar behaviour in sailfin mollies, and Grant and Green (1996) reported it again in Japanese medaka, *Oryzias latipes*. In addition to these copying behaviours, male territorial fish can also benefit from socially learned information. For example, Magnhagen (2006) studied whether prior knowledge about an opponent influenced aggression levels during nest competition in the territorial, sublittoral marine species, the common goby, *Pomatoschistus microps*. She found that information about the contestant did not increase the probability of obtaining a nest, but rather males that had seen other males competing were able to use this prior information to adjust their own levels of aggression in later contests with the same fish. Fish that could modulate their aggression in this manner were able to lower the energetic costs associated with nest competition.

Many species undertake long-distance migrations and there are various ways in which the animals find their way between their breeding grounds

(spawning areas) and areas where they feed. Sometimes information about the distance and direction is part of a heritable behavioural program. Other species, however, rely on learning the migration route from older, more knowledgeable individuals. This form of social learning has been observed in some large marine fish populations (Metcalfe *et al.*, 2008). For example, the migration patterns of herring, *Clupea harengus*, typically remain stable and consistent over many years, but from time to time there can be a sudden change in the migratory behaviour and then this becomes the new stable pattern. In a recent study, Corten (2001) analyzed a large data set of case studies of North Sea herring and the Norwegian Spring spawning herring. His analysis suggests that new year-classes learn migration routes from older year-classes. This strategy allows long-term stable migration routes to become established for years on end. Altered routes appear to arise either in response to particular environmental changes, or when social transfer between year-classes is prevented due to separation of the older and younger fish, so that when the proportion of old individuals falls below a certain point, there is a change in the migration route.

There are times when social learning is not adaptive, for example, when information becomes rapidly outdated, or perhaps a maladaptive behaviour is copied and then spreads. An example of the latter was shown in a study by Laland and Williams (1998), who investigated whether social learning could result in the transmission of outdated information. They had small groups of guppies that were trained to take an energetically expensive long route to a feeder even though there was a less costly shorter route available. After completing this training, the knowledgeable founder fish were gradually replaced with new naïve individuals. After all the founders had been removed, the new fish were found to take the longer route even though it was quicker for a single fish to learn to take the short and less costly route. This simple but effective experiment clearly shows that outdated information can be socially learned and persist in small groups.

In this final section on social learning, we highlight a few examples showing that social learning can even occur across species. Three-spined sticklebacks sometimes occur in mixed species schools, and Krause (1993) reported that sticklebacks can learn information about potential predator threats by monitoring the behaviour of chub, *Leuciscus cephalus*, that they school with. Mathis *et al.* (1996) also showed that naïve brook sticklebacks, *Culaea inconstans*, learn to express fright responses to chemical stimuli from pike predators, *Esox lucius*, even when they have

not been previously exposed to stimuli from pike. Their responses are dashing (apparently disoriented swimming), freezing (when the fish drop to the bottom of the tank and remaining immobile for at least 30s) and shelter use. These responses, however, were only seen when the brook sticklebacks had been paired with pike-experienced minnows, *P. promelas*, and did not occur when they were paired with pike-naïve minnows. Mathis and colleagues observed that pike-conditioned stickleback retained their fright response when they were tested alone, and that these fish could also pass on the fright responses to pike-naïve minnows. These few experiments certainly demonstrate that fish are able to socially learn appropriate anti-predator behaviour from other species.

There are also examples of foraging information being socially transferred across species. For instance, Coolen *et al.* (2003) reported how nine-spined sticklebacks refine their estimate of food patch quality based on monitoring the success of other individuals, even when others are the closely related species, three-spined stickleback. In these experiments, Coolen and colleagues found that both species were able to use publicly available information to copy other informed individuals about food locations, but only nine-spined sticklebacks were able to assess the quality of food patches by simply observing others. This indicates there are some differences in the way these two species use socially learned, or privately learned information. The authors proposed that the different levels of body armour and defence found in the two species might explain these learning differences. Three-spined sticklebacks are typically well protected with their plates and long spines, and thus they can perhaps afford to take a few more risks and obtain foraging information through trials and error learning. The less-protected nine-spines, however, typically hide more amongst the weeds and perhaps have more need of observational, social learning strategies.

Recently, a most intriguing example of cooperation and information transfer was reported between two species that inhabit the Red Sea. Grouper, *Plectropomus pessuliferus*, and moray eels, *Gymnothorax javanicus* were observed to communicate their intentions to each other and form alliances to hunt cooperatively. This requires cognitive abilities previously seen in only a handful of animals: chimpanzees, lions, dolphins and hawks. Together, these two species create a formidable predatory team that truly cooperates in hunting. Using video and direct observations, Bshary *et al.* (2006) described how groupers signal to moray eels that they are ready to hunt. They do so by shaking their head in front of the moray eel. In response to this cue, the eel then leaves its cavities and joins the grouper

to jointly begin seeking out their prey. Bshary and colleagues (2006) suggest that joint hunting is beneficial because both species use different hunting techniques and so together these fish have greater success than when hunting for prey alone. For the hunting to work effectively the eel and the grouper need to recognise and understand the intentions of their hunting partner.

There seem to be many situations where it pays for fish to learn from other fish rather than relying on individually acquired information. Although the fish might occasionally end up with outdated information, in many other cases, socially learned behaviours may save individuals from paying a number of costs, and this could be particularly important where assessment of predatory threats is involved.

DEVELOPMENT, LEARNING AND MEMORY

An ability to learn and generate adaptive behaviour is most apparent in species that experience a variable environment (Papaj, 1986; Odling-Smee and Braithwaite, 2003). Early experience shapes behaviour in fish just as it does in other animals (Bateson and Martin, 1999), and this means that what fish experience during their various life stages contributes to their behavioural development. Increasing levels of complexity in the surroundings lead to more complex individual behaviour being expressed.

Changes from one life stage to the next are often associated with changes in morphology, physiology, habitat characteristics, prey type and mortality risk. These changes create new behavioural challenges for animals as they adapt to their new environment. Although the aquatic medium in many ways is a relatively stable environment, conditions can change dramatically and repeatedly, often as a result of necessary/obligate habitat shifts or seasonal migrations. Illustrative examples here can be seen in fish such as salmonids that change from a more or less solitary, substrate-bound river phase to a schooling, pelagic life-style in the sea. In contrast, species such as cod shift from the characterless pelagic environments to the structurally complex sublittoral habitat where macroalgae, crevices, cobble and gravel create a spatial landscape with landmarks and shelter opportunities. Many environmental factors, therefore, transform with these habitat shifts: the move will generate new social situations, topographic changes, changes in hydrography, novel prey-species and different predators. Apart from the obvious physiological and morphological changes associated with these shifts, an ability to adjust behaviour will be of critical importance. Fish that are faster at adapting

their behaviour to fit their new environment will be more likely to survive. Even though there are likely to be costs associated with learning in environments that are variable, fish having an ability to alter and adapt their behaviour are likely to do better than those that have fixed behavioural phenotypes, or those that are poor learners. Early experience of variability can help promote the capacity to learn and change behaviour (Laviola and Terranova, 1998).

Recent experiments with cod reared in captivity have demonstrated the importance of experiencing environmental variability during the first few months of life. Here, behavioural flexibility of the cod was directly related to their experience of environmental complexity (Braithwaite and Salvanes, 2005; Salvanes and Braithwaite 2005; Salvanes *et al.*, 2007). Cod that experienced variable spatial cues and had a changeable food source were found to be faster in terms of their attraction to, and their consumption of live prey; in their speed of exploration of a new environment; and in their recovery from a stressful experience (Braithwaite and Salvanes, 2005). Fish that were reared in the unchanging, plain hatchery-style tanks spent less time in shelter and showed weaker anti-predator responses than fish reared with access to variable spatial cues. There is also evidence that early experience of complexity affects the ability for social learning and social interactions. For example, Salvanes and Braithwaite (2005) showed that cod with variable spatial cues in their rearing environment directed relatively more agonistic attacks toward fish reared in a plain environment. However, cod from the plain environments showed little discrimination in whom they directed their aggression towards. Exposure to variability in the early rearing environment can therefore promote learning and behavioural flexibility in later life.

Earlier work with cod also found that certain skills could be improved through training. For example, cod reared on pellet food in an outdoor pond environment learned to feed on live gobies (fish prey) when these were first offered, but these fish were still much less efficient in capturing them than wild cod (Steingrund and Fernø, 1997). Experiments conducted by Nødtvedt *et al.* (1999) have shown that cod reared in enclosed saltwater ponds initially had little respect for potentially dangerous predators, and a reduced tendency to inspect the predators and gain more knowledge. Poor post-release survival of hatchery fish has led to a range of rearing studies that have attempted to train hatchery fish for a short period before they are released into the wild (Berejikian, 1995; Olla *et al.*, 1998; Brown and Laland, 2001), but these studies report limited

success on post-release survival. It seems possible that intensive training programs given prior to release may be insufficient to compensate for the hatchery generated behavioural deficiencies. Perhaps, future restocking work could use a combination of these techniques. Thus, fish could be reared in an enriched environment that would promote learning and behavioural flexibility, and then shortly before release the fish could be exposed to a short period of training to teach them about the danger associated with predation, or how to capture and handle live prey.

CONCLUSIONS

In this chapter, we have highlighted a range of issues relating to fish cognition. In several of the examples, we point out how the cognitive abilities that we see are often more sophisticated than we had previously thought possible for fish. However, we also suggest some caution is needed in interpretation, and it is important not to assert complex cognition is occurring when there are more parsimonious explanations. For example, early work by Utne-Palm and Hart (2000) suggested that sticklebacks individually recognize members of a school. More recent work, however, suggests that the sticklebacks often rely on little more than matching olfactory cues based on what the school has been most recently eating, thus, negating the need for individual identification (Ward *et al.*, 2003, 2004).

Many of the cognitive behaviours we report, however, do remain impressive. They indicate that we should consider the cognitive capacities of the species we interact with, and that we should have a good understanding of these if we are to appropriately devise housing and handling protocols for fish that we maintain for scientific research or for aquaculture on farms. With increasing demands for fish welfare, we need to focus on the cognitive capacities of fish to determine whether our interactions with fish have a detrimental effect on their well-being.

Finally, we have emphasized the importance of the early rearing environment for promoting flexible learning and memory and behaviour. The experience of environmental variability during the first few months of life seems to have a profound effect on the behaviour of juvenile and adult fish. If we are to manage populations appropriately, we need to determine what shapes fish cognition and behaviour. A promising way to pursue this research is to investigate how different environments select for fish that exhibit behaviourally flexible responses.

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