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Imprinting in Fish: a Little Explored Phenomenon with Possible Implications for Fish Welfare

Luis M Gómez-Laplaza*, **Pura Gil-Carnicero**

Departamento de Psicología, Universidad de Oviedo, Oviedo, SPAIN

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Abstract

Gómez-Laplaza LM, Gil-Carnicero P. Imprinting in Fish: a Little Explored Phenomenon with Possible Implications for Fish Welfare. ARBS Annu Rev Biomed Sci 2008;10:T51-T62. Imprinting, an early learning process that can determine later preferences for particular types of stimuli, is usually not a consideration in many activities related to fish. However, disruption of such learning and/or absence of suitable conditions for the development of preferences are frequent despite the lack of appropriate knowledge regarding the effects that these practices may have on later behaviour and health. The present study reviews the phenomenon of imprinting in fish and discusses its possible influence on fish welfare. Although there is also potential for acoustic imprinting, here we discuss how sexual, filial and olfactory imprinting should be considered when addressing welfare issues in fish. The review focuses on the relatively few fish species in which this phenomenon has been mainly researched, the results often proving that it may affect some behaviour patterns and social preferences. A diversity of factors, including species, context, behavioural repertoire and social systems may affect the actual existence of the phenomenon, although conditions normally prevailing in husbandry and other systems are not adjusted to allow the emergence of the process. Likewise, the effects of imprinting (or its absence) on fish welfare have still to be demonstrated in many fish species and should constitute a matter for further studies. The conclusion is drawn that much more needs to be learned. However, a better understanding of the relationship between this early learning process in fish and welfare is essential if a complete analysis of conditions promoting fish welfare is to be made.

Keywords: imprinting in fish, early learning, social preferences, fish welfare

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[*] **Correspondence**
Luis M Gómez-Laplaza. Departamento de Psicología, Universidad de Oviedo, Plaza de Feijoo s/n, 33003, Oviedo, Spain. E-mail: lmgomez@uniovi.es
Pura Gil-Carnicero: mpgil@uniovi.es

1. Introduction

Addressing issues relative to the welfare of fish is a complex task since it involves dealing with an enormous diversity of species, taxonomic groups and ecological niches. Furthermore, fish are used in a fair number of activities, such as research, fisheries, aquaculture, recreational, ornamental, etc. Despite this complexity, it has been well established that the rearing environment has an enormous impact on later behaviour in many fish species and that it affects the normal development of the young in different ways (Huntingford, 2004). Learning during an early phase of development can shape many behavioural patterns later on in life and is an important component in the acquisition of many behaviour patterns (*e.g.* Brown *et al.*, 2007; Moretz *et al.*, 2007; Salvanes *et al.*, 2007; Chapman *et al.*, 2008). Breeding conditions may thus greatly influence the ability to learn. However, some of the activities mentioned above often subject young individuals to simple social and environmental conditions, as well as to certain levels of stress early in life, including parental and social separation, an impoverished environment or sensory deprivation. These events may reduce learning opportunities and pose lifelong impacts, thereby altering the later behaviour of individuals (Braithwaite & Salvanes, 2005).

By providing inappropriate early social conditions, certain farming techniques, for example, may thus have a profound impact on the welfare of fish, eventually affecting production (Huntingford *et al.*, 2006). It is therefore critical that behaviour promoting welfare is established as early as possible in order to obtain an optimal culture. This requires improved knowledge as to how the early environment influences subsequent behaviour, which is also crucial for the success of programmes that seek the conservation and reintroduction of fish species (Salvanes *et al.*, 2007). However, early social environment and the opportunities it provides to the young are aspects which have frequently been neglected or even ignored when addressing the welfare of fish. The mechanisms of social behaviour of vertebrates are not well understood; as a consequence, diseases associated with abnormal social behaviours may arise. Besides stressed and disease-prone fishes, other appropriate behavioural skills, including mate choice and reproductive behaviour, may be lacking due to the unnatural social and physical environment for incubation and rearing that certain activities involving fish provide and that cultured fish experience (Huntingford *et al.*, 2006). For example, collecting the fry to be housed separately from their parents until they reach maturity is not an unusual practice. Fish raised in this way may be missing a critical part of the environment, as they are possibly not given the opportunity to gain different types of information regarding colour, size, potential mates, etc. Yet little is known about the behavioural and physiological consequences of such practice.

Some effects that early experience and social environment may have on the development of skills and traits of individuals with long-reaching implications for subsequent adult reproductive performance are highlighted in a study by Fleming *et al.* (1997). These authors reared Atlantic salmon (*Salmo salar*) of the same genetic background either naturally in the river or artificially in a hatchery (sea ranched), depriving the latter of river experience, and then allowed them to grow to maturity naturally in the ocean. Competitive and reproductive abilities were quantified at maturity. Experience-deprived males were involved in more prolonged aggressive encounters and incurred greater wounding and mortality than wild males. They were also less able to monopolise spawning opportunities, this reproductive inferiority varying directly with male density and bias in the sex ratio. Early experience also affected migratory behaviour and female egg production, experience-deprived females producing smaller eggs than wild females. The cited study shows that experience and abilities developed early in life may affect a variety of important behavioural patterns, including mate acquisition and reproductive success. An understanding of the behavioural biology of fish species and their basic needs for optimal survival, growth and fecundity should help to improve the abilities and welfare of fish used in many activities, including aquaculture practice and restocking programmes.

2. Imprinting

Compared to some animal species, mainly birds and mammals, studies on the effects of early experience on the development of behaviour and on adult behaviour are comparatively scarce in fishes. However, there is little doubt that the absence of appropriate stimuli during ontogeny is likely to cause detrimentally disturbed behaviour (Svåsand *et al.*, 1998). Many fish species form social groups and in such shoaling species, early social interactions contribute to the survival of the developing young as well as affecting adult social behaviour. In these species, all events inducing separation from conspecifics, including parents, may have a major impact on their behaviour and social motivation. In many social animal species, the presence of parents and siblings during early life can serve as a model or template for future social and mate choices through a learning process known as "imprinting". Though still poorly understood and controversial, this type of learning takes place during a restricted period known as the sensitive period and produces long-term consequences (Immelmann, 1972).

The opportunity for imprinting may be greater in species with extended parental care, such as birds and mammals, which generally provide a considerable amount of care to their young after birth. In fact, the young and (usually) the mother often show attachment: *i.e.* the offspring and mother bond to one another. This bonding normally keeps them in close proximity. In a number of species, mainly precocial birds, a special form of attachment called imprinting occurs (Bateson, 1966). The process by which young animals develop a preference for following their parents is known as filial imprinting (Bateson, 1966). Other kinds of behavioural responses can also become imprinted. There is, for instance, another type of imprinting, called sexual imprinting, in which the early learning experiences of a young animal regarding parental phenotype affects its choice of sexual partner later when it is mature (Irwin & Price, 1999; ten Cate & Vos, 1999). Sexual imprinting and filial imprinting appear to be two different processes (Vidal, 1980) and the exact timing of the sensitive period differs between species. Furthermore, there is more flexibility in imprinting than was originally thought, which implies greater susceptibility to learning within graded, rather than strict limits. The fact that the limits of the sensitive period are flexible suggests that imprinting is not only determined by a maturational process that unfolds independently of external influence. Other original notions, such as the irreversibility of the initial attachment, have also been questioned by a number of empirical studies suggesting that initial preferences are not immutable, but may be dependent on the ecology of the species under study (Waldman, 1988). Imprinting, therefore, may not be directly comparable among species (Bolhuis, 1991).

Imprinting is adaptive because it is thought to be a reliable mechanism enabling the young to recognise and follow their parents and members of their own species (Irwin & Price, 1999). This possibly ensures that they are fed and protected while providing a model from which to learn the appearance of an adult of their species to guide later courtship and companionship. Therefore, the absence of such stimuli or the disruption of such a learning process may influence learning ability and lead to inappropriate behavioural patterns (*e.g.* Adkins-Regan & Krakauer, 2000).

Imprinting has been extensively studied in certain birds (Immelmann, 1972) as well as in mammals (*e.g.* Kendrick *et al.*, 1998; Bereczkei *et al.*, 2004). Social imprinting has been examined in fish (Colgan, 1983), which, on the other hand, have been shown to be capable of learning in many different contexts (Brown *et al.*, 2003). Here, we briefly review studies on sexual and filial imprinting in fish species together with some evidence of the effects of early learning on later social preferences. The most widely studied type of imprinting in some fish species, olfactory imprinting, is also examined. The situation in fish may not be comparable, in all respects, to imprinting in other animal species, and it may even be thought that newly hatched fish do not imprint in any case whatsoever. Moreover, mixed results have generally been obtained in the few reports dealing specifically with this phenomenon; although evidence of its existence has been shown more clearly in some fish species than in others. Nevertheless, conditions for spawning and rearing such as those generally provided by intensive culture systems or in polyculture practices do not favour imprinting (or favour an out-of-context learning mechanism). This may lead, for example, to subsequent selection of inappropriate sexual mates (misdirected mating), or may even facilitate the formation of new hybrids (by mating with the wrong mate). This can, in turn, have consequences for the production health, success and quality of the stock, as well as for restocking programmes. In fact, the existence, or not, of the imprinting process in individuals is generally not even taken into consideration in most of these practices.

3. Sexual Imprinting

Cross-fostering experiments have been employed to study sexual imprinting in fish, frequently using different morphs of the same species; although fostering of young among species (interspecific cross-fostering) has not been unusual. Likewise, species with extended parental care on the part of both parents, or those in which at least one parent cares for the offspring, including mouthbrooding species, have been preferred candidates due to the fact that the opportunity for imprinting may be greater. These conditions are widespread within the family Cichlidae, although other families have also been studied.

Albert (2005) examined the possible existence of sexual imprinting in experiments with threespine sticklebacks (*Gasterosteus aculeatus*, Gasterosteidae), finding no evidence for such a process. In this species, males provide parental care for the fry until they are able to swim freely. Thus, young females can imprint on the appearance of their father, thereby shaping their mating preferences as adults. Albert (2005) used F_1 hybrids of sympatric species pairs consisting of benthic and limnetic sticklebacks, families of F_1 hybrids being fostered to males of both species. When sexually matured, F_1 fostered females were given two no-choice test trials by introducing them into an aquarium in which a nesting limnetic male was present (trial one) and a nesting benthic male was present (trial two). Female nest examination was considered as a measure of female preference. No effect of sexual imprinting on shaping female mate preferences was found. F_1 fostered females raised by males of either type did not differ in their preference for examining the nests of one type of male or the other. The lack of evidence for sexual imprinting in this study does not necessarily rule out its existence, as females were not allowed to choose between males simultaneously, thus possibly masking their preferences. Choice tests are frequently used in this context to determine preferences and are also used for the assessment of fish welfare (Volpato *et al.*, 2007).

Similarly, inconsistency in the effects of early experience with male colour phenotype on adult mate choice decisions has also been reported in female guppies (*Poecilia reticulata*) (Breden *et al.*, 1995). Likewise, results of no clear evidence of an imprinting process have been found in another non-cichlid species. Thus, in an early study in which red and black colour variants of platyfish (*Xiphophorus maculatus*, Poeciliidae) were cross-reared, Fernö and Sjölander (1973) found that males preferred females of the colour variant they were exposed to during two months after reaching sexual maturity. Experience with either colour variants before sexual maturation seemed to be of no importance and no difference was detected between the different colour variants.

In a further study using cichlids, the above authors (Fernö & Sjölander, 1976) cross-fostered convict cichlid, *Cichlasoma nigrofasciatum*, of the normal colour morph (light greyish-blue) and the white morph, which lacks the normal vertical stripes. When sexually mature, pair formation was recorded to assess the influence of parental colour morph on mate choice. In an initial experiment, the white males preferentially formed pairs with normal females, regardless of rearing conditions. This failure was attributed to the possible influence of factors other than experience during early development, such as the establishment of dominance relationships and crowding conditions. It is worth noting that such conditions are frequently encountered in cultured fish and may impair welfare in some species (Huntingford *et al.*, 2006). In a subsequent experiment, Fernö and Sjölander (1976) found preferential mating based on different colour morph experience. However, the results gave no clear indication as to whether imprinting occurred because the experience with the other colour morph was not restricted to any particular period. No effects of early experience on adult sexual preference were found either by Weber and Weber (1976) likewise using male convict cichlids, *Cichlasoma nigrofasciatum*.

Another study addressing imprinting in cichlids was carried out by Siepen and Crapon de Caprona (1986), also using *C. nigrofasciatum*. Their study provided a better control for the influence of the parental colour morph as separated from that of the sibling colour morph, since this factor could have confounded the results in previous studies. They used parents of a colour different from that of the fry (striped or white), the influence of parental colour morph on mate choice being tested in a free choice situation, as well as the stability over time of preferences. The study showed that fish reared by foster parents of their own colour morph and with siblings of their own colour later mated with a fish of the same colour morph. However, only about 9% of the fish cross-fostered by parents of the alternative colour morph and with siblings of their own colour formed mixed-colour pairs, indicating inconclusive effects of the experience with the foster parents colour morph on later mating decisions.

Also using different colour morphs, Barlow *et al.* (1990) studied the possibility of sexual imprinting in the Midas cichlid (*Cichlasoma citrinellum*), a naturally polichromatic fish species. These authors used females of the normal and gold morphs and constituted different groups, including cross-fostering treatments. Females were given a binary choice between two males, one gold and one normal, placed at each end of the test apparatus. Aggressive and courtship behaviour towards and time spent close to the males were considered as criteria for preference. No consistent results were obtained and, as in the study by Siepen and Crapon de Caprona (1986), the colour of the foster parents had no clear effect on mating in this species. Female choice of males did not agree with the colour of foster parents (sexual imprinting).

However, in a recent study using two Lake Victoria related cichlid species, *Pundamilia pundamilia* and *Pundamilia nyererei*, Verzijden and ten Cate (2007) were able to show sexual imprinting between these two mouthbrooding sympatric species pairs. These authors cross-fostered *P. pundamilia* and *P. nyererei* to test whether mate preferences in the females of these species were affected by their mothers' appearance, since only females provide continued protection of the brood after hatching. Females preferred to approach a quivering male of their foster species, which appear to confirm that early learning of the maternal appearance acts as a model in these species for later sexual preference. No species differences were found in this early learning and the authors suggest that imprinting may be a more common mechanism than previously recognised among mouthbrooding cichlids in the great lakes of East Africa. In fact, in a later interspecific cross-fostering study on another haplochromine cichlid species pair, also from Lake Victoria, females of *Mbipia mbipi* and *Mbipia lutea* showed the same foster mother effect on their mate preferences (Verzijden *et al.*, 2008). Female sexual preference was strongly influenced by early learning about their mothers' phenotype, thus indicating that the females actually imprinted on their mothers. In addition, the sexually imprinted preference was not affected by later social experiences with males of the alternative species to that of their foster mother.

These studies show that sexual imprinting can potentially be an important learning process in fish in the forming of mate preferences and that the importance of parental appearance is likely to vary in cichlids depending on whether the fish are substrate spawners (generally both parents take care of the brood) or mouthbrooders (one parent takes care of the brood). The similarity between the results in related cichlid species of Lake Victoria indicates that they share the imprinting process. It would be interesting to investigate whether males in these species also learn mate preferences in this way. Besides, more studies are needed to examine specific factors affecting the occurrence of sexual imprinting in a species, the extent of the sensitive period, or the retention interval and possible reversal. Since the adaptive function of this type of learning is to select suitable mates, it may be a priority in this context to investigate the consequences that the absence of this process may have for fish production and welfare. Imprinting is frequently disrupted under unnatural conditions such as those found in hatcheries and may have consequences for the welfare of disturbed fish. However, as evidenced from above, this learning has been studied only in a few fish species and a need to broaden the range of species in which it is studied appears to be fundamental in order to further our knowledge of its influence on welfare. Given the considerable scope for parental effects on young behaviour, the presence of parents and parental care may be necessary if welfare is not to be potentially compromised. However, whether this is so has not yet been specifically investigated and remains an objective for future research.

4. Filial Imprinting and Early Learning Processes

As with studies on sexual imprinting, little work has likewise been carried out on filial imprinting in fish. The relative paucity of studies of this kind may be due to the greater difficulties in demonstrating this type of learning in fish (*i.e.* evidence that the fry learn parental characteristics). Once again, cichlid fish species have been primarily studied. In an early study, Baerends and Baerends-van Roon (1950) reported specific preferences of cichlid fry for certain features of parents and parental dummies (form, movement, colour). Some of the responses presented similarities to the phenomena associated with filial imprinting. Subsequently, in a study designed to investigate specifically filial imprinting, Hay (1978) used the convict cichlid fish *Cichlasoma nigrofasciatum*. Field observations indicated an effect of age on the range of stimuli effective in eliciting approach and following of parents and dummies by fry. Fry of less than 5 days free swimming were likely to approach and follow a diversity of "dummy" parents. Older fry, however, though they still followed their parents, fled the dummies, thus developing fear responses to other stimuli. Further laboratory experiments using preference tests supported the hypothesis that fry learn parental characteristics. Results indicated the existence of a brief period (less than 6 days free swimming) when the fry are maximally responsive to parental dummies, responsiveness showing a decrease with age. Experience with parental cues resulted in increased responsiveness and the findings seem to be consistent with the hypothesis that fry of this species learn visual characteristics of their parents, which results in the maintenance of approach and following responses during the period of parental care. These results suggest that some of the general characteristics of filial imprinting may also apply to filial responding in *C. nigrofasciatum*, and to fish in general. A better understanding of the mechanisms involved, including retention and reversibility of this learning, undoubtedly requires further specific research which has not been carried out in fish.

In a study with the maternal mouthbrooding cichlid species *Oreochromis niloticus* and *Oreochromis esculentus*, Russock (1999) extended previous work with *O. mossambicus*. All fry were removed from the mother's mouth as eggs and hatched artificially and were then tested for their responsiveness or preferential behaviour to maternal models. A significant decrease in responsiveness was observed in both species, although at different times for each one, evidence for the existence of a sensitive period being found in both species. Previous experience with maternal models subsequently evoked a preferential response towards such models. According to the author, filial bond formation in these species appears to be characterised by predispositions for maternally specific visual characteristics, which require appropriate experience for their maintenance and for the induction of preferences. The phenomenon presents a similar developmental pattern to that shown by other animal species, including song learning and imprinting in birds and filial following in substrate spawning cichlid fish. However, the stimulus specificity necessary to induce these preferences was not systematically examined and would be a worthwhile avenue of future research.

Learning of parental and sibling characteristics from conspecifics or heterospecifics is an aspect of early behavioural development in many fish species. It has been demonstrated, for example, in studies dealing with affiliative behaviour and species recognition, though the effects of the early learning on such later responses have rarely been discussed within the framework of research on imprinting. Although the findings of such studies do not necessarily prove that imprinting is involved, imprinting-like phenomena may play a fundamental role in determining the response to parents and companions. Warburton and Lees (1996) reared guppies *Poecilia reticulata*, with swordtails, *Xiphophorus helleri*, by placing guppy fry (within 4 h post-hatching) with swordtail fry of the same size and age. Trials took place before the fish had developed secondary sexual characteristics. In a binary choice test, guppies preferred to associate with both familiar and unfamiliar swordtails over unfamiliar unrelated conspecifics. These abilities to learn to recognise conspecifics and heterospecifics suggested the formation of a flexible template based on the phenotypic traits of companions in early life, even if they are fish distinct from the subject individual.

In the cross-fostering experiment with the two Lake Victoria cichlid species mentioned above, male assortative aggression behaviour was also tested to assess the effects of early experience with the phenotype of siblings (Verzijden *et al.*, 2008). Results showed that male aggression biases (in these territorial species for mating) are affected by early experience with siblings. Males directed their aggressive acts on the basis of the composition of the brood in which they had raised (*i.e.* at males with a phenotype similar to the males with which they had grown up), thus indicating a learning component mediating male rival recognition, as well as the direction of male aggression.

Other studies showing the importance of early learning in later social recognition have been conducted with zebrafish, *Danio rerio*. Although zebrafish show no parental care of their eggs and larvae, they form shoals in the wild (Engeszer *et al.*, 2007a). In an interspecific experiment in which wild-type *D. rerio* were cross-reared with pearl danios, *D. albolineatus*, it was found that *D. rerio* spent less time with conspecifics than did controls (McCann & Carlson, 1982). Similarly, Engeszer *et al.* (2004) used wild type and pigment mutant *nacre* individuals (which lack melanophore stripes) and experimental treatments that included cross-reared fish with the alternative phenotype prior to hatching. When fish developed adult pigment patterns, they were subjected to a binary choice test between wild type and nacre stimulus shoals. Fish were able to discriminate between conspecific shoals having different pigment pattern phenotypes. Cross-reared wild type fish preferred to joint nacre mutants and vice versa, suggesting that early social experience during development played a determining role in the acquisition of social preference. This early social learning as to the visual traits of companions could thus have substantial behavioural consequences. Interestingly, a further study also with zebrafish showed the existence of a developmental period of time during which individuals acquire a visually mediated shoaling preference (Engeszer *et al.*, 2007b). Once the acquisition of colour shoaling preference was established, it remained stable even after changing the social environment of fish (*i.e.* exposure to conspecifics with other visual phenotypes for one month) (Engeszer *et al.*, 2007b).

Likewise, results with a strong early-learned component as regards colour pattern preferences were found by Spence and Smith (2007), also using zebrafish, *Danio rerio*. Three related species which differed in colour pattern were cross-reared and fish were tested for shoaling preference before reaching sexual maturity. Once more, colour patterns learned in early development affected shoaling preferences. Individuals preferred to associate with shoals of the colour pattern they had bee exposed to in early life, the preference being stronger when the patterns were more distinct. Although Moretz *et al.* (2007) found no clear evidence for sensitive periods in determining social preferences in zebrafish and Kozak and Boughman (2008) showed that preferences can be learned through social experience in a species pair of sticklebacks, in general these studies show that experiences gained during early development – an imprinting-like phenomenon – can shape many behavioural patterns and have a strong influence in forming some association preferences.

The examples described above also provide evidence that it is possible to alter the behaviour and preferences of fish by manipulating the social environment of rearing. Early experience with visual signals (*e.g.* pigments, body patterns) strongly influences future social preferences and behaviour, and since mating is more likely to take place with others in the same social unit, such visual cues can aid correct conspecific identification (*i.e.* right or wrong species for reproduction) and, as a result, the choice of future social consorts. Deficits or alterations in social interactions and preferences in hatchery reared fish and in polyculture systems arising from the abnormal social environment in which they are reared could easily contribute to poor survival of individuals, although much more research is needed in this respect.

Although imprinting initially referred to learning the visual characteristics of the imprinting object, subsequent experimental studies indicated that auditory and chemical stimuli can facilitate, or provide a medium for, such visual imprinting. For example, olfactory cues are used in brood care in parent-offspring communication in cichlids and other fish families; thus chemical imprinting may occur in addition to or instead of visual cues (Verzijden and ten Cate, 2007). In fact, Gerlach *et al.* (2008) were recently able to demonstrate that zebrafish (*Danio rerio*) can recognise kin from non-kin and develop a preference towards related individuals, shown later on in life, which is based on a learned olfactory imprinting process. Individuals were subjected to an olfactory choice test and it was found that olfactory imprinting (*i.e.* preference for kin odours) was shown by fish that had been exposed as larvae to odour cues of kin individuals on day 6 post-fertilisation. Thus, the imprinting time window (sensitive period) related to kin recognition occurs on day 6 post-fertilisation in a developmental period of approximately 24 hours. Larvae exposed to kin odours before or after, but not on day 6 post-fertilisation did not recognise kin. Likewise, cross-fostered larvae exposed to non-kin odour during such a sensitive period did not result in imprinting on the odour cues of unrelated individuals; nor did isolated larvae imprint on their own chemical cues. According to the authors, it appears that zebrafish learn the olfactory template for later kin recognition in a period after hatching when larvae still shows limited mobility, possibly coinciding with the period before dispersion from the spawning ground and mixing with non-kin larvae.

The concept of chemical imprinting might also be applicable, for example, to the chemical stimulation provided by the particular odour of the natal stream. In some fish species, individuals return to the precise stream in which they were hatched, apparently because hatchlings imprint on the particular odour of a specific stream, a process known as chemical (or olfactory) imprinting. This learning process takes place during a sensitive period of development and is reminiscent of filial imprinting (Dittman & Quinn, 1996). Although it is beyond the scope of this study to provide an exhaustive account of the ever-increasing literature dealing with this kind of imprinting, the subject is discussed briefly in the following section.

5. Chemical Imprinting

Migrations to natal sites are widespread among fish species (*e.g.* Quinn & Dittman, 1992). However, chemical imprinting has been more intensively investigated in experiments with fish that exhibit a long-range migratory behaviour, such as those of the family Salmonidae (salmon, trout and charr species) (*e.g.* Dittman & Quinn, 1996). Depending on the species, juvenile salmon remain for a variable period of time in their natal freshwater stream before transforming to ocean life and descending to the sea as smolts. They then spend 1-4 years feeding and growing in the marine environment. Some species roam thousands of kilometres in the ocean to return at maturity to the continent, entering rivers and swimming upstream to reach their natal stream to spawn. Adults usually die in these streams after breeding, with only a few species surviving to spawn again. The guiding mechanisms of this migratory spawning journey in the ocean that allows salmon to go back to the streams where they hatched are not yet clearly established.

According to a favoured hypothesis, stream recognition is based on chemical imprinting (Hasler & Scholz, 1983). Apparently, exposure of the young salmon to the smell of its early environment (*i.e.* the home stream) leads to the formation of a chemical memory which is used by the adult to migrate back to the river and hatching site that smell like its home stream. If this is so, the migratory response is imprinted in salmon. The evidence that supports this idea derives from several experiments. For example, Morin *et al.* (1989) exposed fish to a water current containing a natural odorant (the amino acid L-cysteine) during 24 hours. Independent groups received this treatment at various stages during the smoltification phase. Subsequently, fish were placed in a test situation in which the L-cysteine was presented and changes in heart rate were measured as an index of chemical recognition. The heart rate of the fish decreased when exposed to such known stimulus, but the decrease was found to be maximum for fish exposed to the chemical stimulus between day 21 and 28 of the smoltification phase.

The existence of a peak of effectiveness indicates the presence of a sensitive period for the effects of the exposure to a particular odorant. Although the mechanisms underlying olfactory imprinting and homing remain unclear, the sensitive period is frequently linked to this transitional developmental period of smelting, which prepares the stream-dwelling parr for life in the ocean. Some of the morphological, physiological and behavioural changes that take place at this stage are linked to increases in plasma thyroid hormone levels. These increases may in turn affect anatomical changes in the peripheral olfactory system (Lema & Nevitt, 2004). However, the sensitive period for imprinting appears to be more variable than suggested initially. The stage at which salmon become imprinted may depend on the natural history of salmon populations, while chemical imprinting may also occur earlier. Quinn *et al.* (2006) have recently found that this process can occur between the period when the embryos hatch and when they emerge from the gravel as free-swimming fry some months later. These authors also demonstrated the capacity for very fine-scale homing in sockeye salmon populations.

Likewise, recent electrophysiological and behavioural studies indicate that amino acids dissolved in the home stream water constituted possible home stream odour substances for homing in salmon (Shoji *et al.*, 2003), thus supporting the notion of long-term imprinted olfactory memory (the olfactory hypothesis).

Additional support that salmon imprint to site-specific odours is provided by studies showing that salmon can detect, imprint and home to synthetic chemical odorants at very low concentrations (reviewed by Quinn & Dittman, 1992). Direct evidence of the relevance of the olfactory sense in relation to salmon migration comes from experiments in which the salmon's olfactory sense was impaired (Døving

& Stabell, 2003). Treated salmon homed less accurately than untreated controls, whereas intact salmon can discriminate between waters from different streams.

Although evidence clearly indicates that early chemical cues have lasting effects and that chemical imprinting might underlie the migratory behaviour of salmon species, such research is still controversial. The learning process of juveniles in their normal wild life might be more complex than that inferred from the above experiments. What these experiments show is that the olfactory sense of salmon is crucial in the maintenance of their life cycle and that the memory of the home stream is critical to guide them home. Many difficulties remain to be resolved in attempts to apply imprinting theory to the management of populations, but researchers in this field stress that this type of chemical imprinting is a suitable method to use in hatcheries and that the notion of chemical imprinting has many applications in the management of salmonids (*e.g.* by cueing fish to a desired homing location, such as hatchery of origin or a specific water resource). However, a hatchery is an unnatural environment for incubation and rearing and hence for imprinting. This may have detrimental effects on the welfare and behaviour of fish. Salmon reared exclusively in a hatchery may have impaired homing ability or motivation compared to wild fish; the hatchery also affects other behaviour patterns, including exploratory behaviour (Griffith *et al.*, 1999). In the wild, salmon experience constantly changing environmental conditions and a variety of water sources prior to seaward migration. In most hatcheries, however, salmon are reared in a single water source and under uniform conditions (*e.g.* little variation in temperature and water flow) and so do not receive adequate imprinting opportunities. Additionally, the mechanisms by which salmon learn and recognise complex mixtures and sequence of odorant may differ from imprinting on a single (artificial) odorant (Dodson & Bitterman, 1989). The alteration of this process and deprivation of individuals of the opportunity to perform the incredible journey they accomplish in the wild can only have uncertain, possibly detrimental, effects which have not yet been suitably studied.

6. Conclusions

This study highlights how fish are affected by their early social environment and that the absence of some natural elements of the environment (parents, chemical cues) which are fundamental to some learning processes at that early developmental stage, may have detrimental effects on behaviour and welfare. In the same way as maternal effects on egg quality can affect behaviour at later stages (Huntingford, 2004), the influence of parents at early stages can affect the behaviour of individuals at juvenile and adult stages. Imprinting is thus supposed to be important in the life of many fish species, including a range of commercial species. Accordingly, much more research is needed on imprinting in fish to establish the kind of implications that its presence or absence may have for later behaviour and whether it is a condition that favours and/or is relevant to their welfare. Disruption or the absence of the imprinting process is usually not taken into consideration in most culture systems, although it can be a potential source of behavioural alterations. The challenge for fish culture and captive breeding programmes is to identify and, if necessary, provide rearing conditions under which natural early learning processes, including imprinting, may take place. It is also important to consider evolved behavioural tendencies when species are considered for culture rearing and restocking. This will help to avoid the imposition of rearing conditions which, inadvertently or not, eliminate the occurrence of normal processes in the early development. The behavioural alterations that can occur in fish reared under these conditions may lead to undesirable consequences (*e.g.* in repopulation programmes). Likewise, little is known about behaviour and stress in fish at early life stages, but individuals with extended parental care may be more vulnerable to parental separation stress. Nonetheless, with the ever-increasing interest in fish welfare and culture, the study of the imprinting process and behaviour of larval fish appears to be an important and fertile field for the future.

7. References

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8. About the Authors

Luis M. Gómez-Laplaza, studied Psychology at the Universidad Complutense of Madrid (Spain), and took his PhD at the School of Biological Sciences of The University of Birmingham in U.K. He is mainly interested in the proximate factors of behaviour and uses freshwater shoaling fish species as model organisms. Many of the questions under his study are related to aspects of social behaviour, since the shoaling behaviour of fish is an excellent experimental system to test many hypotheses. The study of social interactions within a group, such as aggressive behaviour, dominance and hierarchies formation have led him to examine behavioural profiles dependent on social status. Mechanisms underpinning group formation, including the influence of familiarity and social status of the individuals, together with the assessment of cognitive abilities involved in spatio-temporal learning and status recognition represent another of his research lines. He has also carried out studies on the effects of previous experience and experimental manipulation (e.g. separation and social deprivation) on some behaviour patterns of the subjects. Luis M. Gómez-Laplaza is currently lecturing Animal Behaviour at the Department of Psychology, University of Oviedo (Spain) and is member of the editorial board of some Spanish scientific journals.

Pura Gil-Carnicero, received her PhD in Psychology from the Universidad Complutense of Madrid (Spain), and she is currently professor of Developmental Psychology at Psychology Department of Oviedo University, Oviedo (Spain). The general focus of her research is on factors associated with skills construction in human infants. Specifically, her interests have been focused on the social frameworks in which social and spatial knowledge is built through childhood and adolescence, as much in formal education (school) as in non-formal education (family). Also she has been investigating the relationship between marital conflict, parenting and children attachment styles; attachment in adults and gender violence, as well as adult attachment and quality of life in women with breast cancer. She is a Psycho-Pedagogical adviser in Projects on Cooperation for Development (including dialogue construction among communities in Kosovo), financed by AECID (Spanish Agency of International Cooperation for Development), and local government adviser for Animal Welfare issues. At present she is co-organising an International Conference on Farm Animals Welfare, which will be held in Oviedo (Spain), organised and financed by the local government.