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Lynne U. Sneddon
University of Liverpool

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Pain Perception in Fish: Evidence and Implications for the Use of Fish

Lynne U. Sneddon
University of Liverpool

ABSTRACT

Pain assessment in fish is particularly challenging due to their evolutionary distance from humans, their lack of audible vocalization, and apparently expressionless demeanour. However, there are criteria that can be used to gauge whether pain perception occurs using carefully executed scientific approaches. Here, the standards for pain in fish are discussed and can be considered in three ways: neural detection and processing of pain; adverse responses to pain; and consciously experiencing pain. Many procedures that we subject fish to cause tissue damage and may give rise to the sensation of pain. Fish are popular as pets, in animal exhibits, and as experimental models, but are also cultured or caught for food. There is little legislation for the protection of fish welfare. Many countries are now exploring the welfare cost to fish, and current practices may need to be reviewed with respect to the current evidence for fish perceiving pain.

Proving the existence of pain perception in an animal is inherently difficult. Humans can relate their internal experiences to one another through language, but without this, pain assessment is problematic as it requires knowledge of how someone else 'feels'. Therefore, understanding what an animal experiences is particularly challenging. However, by drawing up a number of standards, and with insightful experimentation, it is possible to obtain meaningful conclusions upon the capacity for pain perception and indeed how important the experience is to the animal. Amongst vertebrates, fish evoke the most opposition when discussing the capacity for pain due to their evolutionary distance from humans and the composition of their central nervous system. However, the opinions against condense into a semantic argument that if the pain is not identical to that experienced by humans then it is not pain *per se* and just a reflex response. This suggests that any pain or damage endured by an animal is unimportant as there is no suffering or discomfort involved. The majority of animal scientists disagree with this notion since pain must have evolved throughout the vertebrate groups in a similar way to all other sensory systems. Therefore, it is likely that animals do experience pain when injured and that this event will have a negative impact on their internal state. Here, the standards for fish perceiving pain are discussed and can be summarized in three parts: the possession of the neural apparatus to detect and process pain; adverse behavioural and physiological responses *in vivo* to a painful stimulus; and whether the individual has a conscious experience of pain. If fish do indeed suffer or experience discomfort as a result of tissue damage, then the way in which we use fish may need to be reviewed. Fish are popular as pets, used in animal exhibits, and as experimental models, but are also cultured or caught for food. Many practices during these procedures result in injury to the fish yet there is little legislation for the protection of fish from harm. Although many countries are now examining the welfare cost to fish in various scenarios, current practices may need to be revised in light of current evidence for fish perceiving pain.

1. The Debate

1.1 Defining Human Pain

According to the International Association of the Study of Pain (IASP), which is a predominately clinical organization aimed at understanding and treating human pain, the definition of pain has two aspects (IASP, 1979). The first is the sensation of pain via sensory afferent nerves that convey the information to the relevant parts of the spinal cord and brain. Therefore, possessing the correct neural apparatus to detect pain and process it is a requirement of experiencing the sensation. The second requirement is to have an associated emotional response or negative affective state that equates to feelings of discomfort and suffering. This state may impair subsequent behaviour, may elicit novel protective or guarding behaviours, and will usually motivate the individual to seek pain relief. Therefore, this aspect results in a change in behaviour which is normally accompanied by physiological modifications such as the release of stress hormones, cardiovascular responses, inflammation, and so on that enable the individual to act in such a way so as to preserve oneself and prevent further damage. In its purest form pain can be thought of as a strong motivational drive with its primary function being to alert the individual to the danger of injury and to subsequently protect any damaged tissue in order to promote healing. The negative affective component reinforces the avoidance of the situation in the future via learning mechanisms but also serves to impel the conserving changes in behaviour. Thus, the IASP definition provides a number of measurable parameters that can be applied to animal studies. Do animals have the neural apparatus to detect pain stimuli? Do they show adverse changes in behaviour and physiology to a potentially painful event? Do they seek to alleviate the pain they are in?

1.2 Defining Animal Pain

Most definitions of animal pain avoid or omit discussing the negative affective component of pain simply because it is problematic to measure. Knowing exactly how another human 'feels' is impossible unless they tell you. So rather than measuring the direct internal experience of an animal, the definitions of animal pain mainly concentrate on what is actually quantifiable. These definitions focus on either a statement of what a potentially painful event may result in (Zimmerman, 1986) or propose a number of criteria that an animal must fulfil to be capable of pain perception (Sneddon, 2004; 2009; Bateson, 1991). In broad terms, animals should have the apparatus to detect and process pain; pain should result in adverse changes in behaviour and physiology; analgesics (painkillers) should reduce these responses; and the animal should learn to avoid the stimulus that caused pain. These outcomes are sensibly drawn from human responses to pain. However, one should be cautious regarding this extrapolation since animals have motivational drivers that may affect their pain-related responses. For example, prey animals are unlikely to engage in behaviours that may draw the attention of predators and so may not exhibit behavioural responses to a painful event (Flecknell *et al.*, 2007).

The animal pain parameters are easily measurable, and one can determine whether an animal has the correct apparatus; demonstrates alterations in behaviour and physiology during possible pain that may suggest discomfort rather than simple reflex responses; determine the effects of administering analgesics; and whether the animal is motivated to avoid that stimulus in the future. Collectively this evidence can be interpreted in light of clinical and animal studies which lead the researcher to a sensible conclusion regarding the capacity that animal has for pain perception. More insightful studies have attempted to quantify the importance of the pain to the animal by using distraction techniques (Ashley *et al.*, 2009) or by determining whether the animal will self-administer analgesics, concluding that the animal will do this to reduce the pain thereby improving how it 'feels' (Pham *et al.*, 2010). Although emotion is not included in most of the animal pain definitions, it is by inference included in the evaluation of the

behavioural evidence such that prolonged, negative changes in behavior do indeed reflect a detrimental change in the animal's experience at that time.

1.3 The Conflict Over Animal Pain

The main opposition for animals experiencing pain can be summarized as an argument over the semantic definition of human pain. Many reviewers conclude that if the pain an animal experiences is not identical to the pain humans have then it should not be called pain *per se* (Rose, 2002; Iwama, 2007). It is simply nociception, the detection and reflex response to a noxious, potentially painful stimulus. These noxious stimuli are extremes of temperature, mechanical pressure, and chemicals that excite the nerve endings of nociceptors (specialized receptors). This oppositional stance is particularly strong in the case of fish mainly due to differences in brain structure. The fish brain has far fewer neurons and has a simply structured cortex (forebrain) compared with the highly developed neocortex of primates and humans. Some authors suggest that only humans and primates are, therefore, capable of the conscious experience of pain due to possessing the neocortex. This precludes other mammals such as dogs, cats, rodents, birds, reptiles, and amphibians from experiencing pain yet there is a plethora of scientific studies providing evidence to the contrary (ILAR, 2009). Fish are capable of complex behaviours even with a relatively small brain, including the recognition of profitable prey and danger in the form of predatory threat; identifying conspecifics to choose suitable mates and discrimination of related individuals from non-kin; learning novel adaptive behaviours from others through social learning; learning to avoid aversive stimuli and the recall of complex navigation routes (Brown *et al.*, 2011). These all involve learning and memory mechanisms upon which fish make behavioural decisions that improve their survivorship. Fish also modulate their behavioural decisions based upon previous experience and engage in complicated inter- and intra-specific relationships including cooperation and reciprocation (Alfieri and Dugatkin, 2011). Fish engaging in cooperative relationships can act selfishly to manipulate others (Bshary, 2011). Therefore, fish have a complicated behavioural repertoire that has evolved to maintain them within the constraints of a life history and ecology that is very different to human life.

Rather than considering fish to be incapable of pain because they have a different brain structure to humans, authors have proposed that the pain experience may simply be in a rudimentary form compared with human pain (Bekoff and Sherman, 2004; Sneddon, 2009). Therefore, fish do experience pain but it's more primitive in nature. Of course, proving this is problematic since getting into the fish mind and knowing how it feels is not currently possible. However, evidence from scientific studies is growing with respect to pain perception in fish as detailed below. Arguments regarding the neocortex also state this is where humans 'think' about the pain and where we make decisions about the intensity and how we control our responses to it. For example, a child may fall down and openly cry, whereas an adult may be too embarrassed or realize the injury is only slight and so does not respond in an overt way. If animals, including fish, do not have this ability to think about the pain or control it, then this means it is worse and will always be an intense experience. This needs to be considered when determining the welfare of animals. There are also other definitions of human pain, such as the idea that there need to be connections between the thalamus and other brain regions (including the cortex), and these have been characterized in fish (Rink and Wullimann, 2004). Finally, humans with an intact neocortex and thalamocortical connections cannot feel pain if they have congenital insensitivity to pain with anhidrosis due to mutations in the NTRK1 gene (Lee *et al.*, 2009). Therefore, this gene would seem to be the key to experiencing pain, and many studies have identified this gene in fish (Zfin, 2010; Catania *et al.*, 2007; Germana *et al.*, 2002; 2004; Vecino *et al.*, 1998). Overall, then, in this review fish are considered as candidates for experiencing pain, and the scientific evidence as laid out against the standards set out below will be discussed.

2. The Evidence

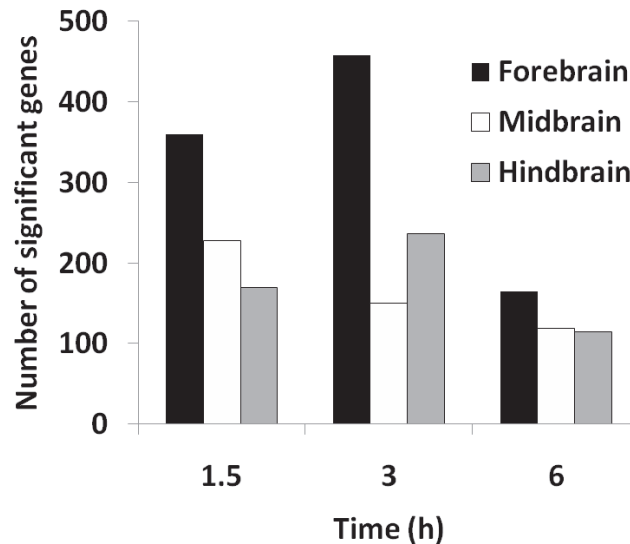
As previously mentioned, definitions of animal pain propose three main standards. Firstly animals should have the neural apparatus—the sensory system—to detect, process, and react to noxious stimuli. Secondly, their responses to a potentially painful event should reflect an aversive experience. Thirdly, the behavioural responses of the animal may reflect an internal dimension or negative affective component such that the animal ‘feels’ pain or is conscious of the fact it is in pain. Recent scientific studies have sought to produce evidence for the existence of pain in fish. Fish are currently the third most popular pet behind cats and dogs (Iwama, 2007), and are also the third most popular experimental model in the UK after rats and mice (APC, UK). Fish are an important source of protein, with over half a million tonnes of fish produced by aquaculture in Europe (FEAP) annually and approximately 73 million tonnes of fish caught in marine waters globally (FAO, 2006). Therefore, our use of fish needs careful consideration if we conclude that they may be able to experience some form of pain.

2.1 The Neural Apparatus for Pain

In order to detect noxious, potentially injurious stimuli, animals must possess nociceptors which are free nerve endings that usually preferentially detect such stimuli. These are of two fibre types; small diameter, myelinated A-delta fibres and smaller, unmyelinated C fibres (Figure 1: colour plate). Neuroanatomical and electrophysiological studies have identified nociceptors in common carp (Figure 1; Roques *et al.*, 2010) and rainbow trout (Ashley *et al.*, 2007; 2006; Sneddon, 2003b; 2002; Sneddon *et al.*, 2003a). These nociceptors are strikingly similar in their electrophysiological properties to those found in mammals, and they respond to noxious heat, mechanical pressure, and noxious chemicals such as acid and bee venom. After detection, the sensory information from these nociceptors must be conveyed to the spinal cord and brain. Pathways from the periphery, the body and face, have been traced in fish, and again the spinal (body) and trigeminal (face) pathways are comparable with those in mammals (review in Sneddon, 2004). Connections within the brain should convey the information from these incoming pathways to cortical areas via the thalamus and these connections have been characterized in the zebrafish brain (Rink and Wullimann, 2004). Therefore, the neural apparatus to detect pain is evident in teleost (bony) fish. However, studies have questioned whether these connections exist in cartilaginous fish (sharks, skates, and rays; Snow *et al.*, 1993).

Opinions against fish perceiving pain have stated that these responses are merely nociceptive reflexes and are restricted to the hindbrain or spinal cord (Rose, 2002; Iwama, 2007). Recent scientific studies refute this. Recordings made of the brain, including the forebrain and midbrain, which are important in human pain processing (Derbyshire, 2010), have shown there is electrophysiological activity in both of these areas in goldfish and rainbow trout during painful stimulation that differs from neutral stimuli (Dunlop and Laming, 2005). Gene chip or microarray to measure global gene expression in the forebrain, midbrain, and hindbrain of common carp and rainbow trout also demonstrated that the molecular responses to painful stimulation were different to non-noxious treatment and that the forebrain was most affected (Figure 2; Reilly *et al.*, 2008b). Genes were identified that are involved in initial pain responses in mammals, and those involved in recovery were upregulated after six hours when the fish were exhibiting recovery (Figure 2). Imaging techniques have also demonstrated that the forebrain and midbrain of common carp (Figure 3: colour plate) are differentially activated using functional magnetic resonance imaging (fMRI), which is commonly used in human studies to identify the important sites of conscious pain processing (Borsook *et al.*, 2010; Valet *et al.*, 2010). Therefore, ‘higher’ brain areas are activated at the molecular, physiological, and functional levels in fish experiencing a potentially painful event. This gives much weight to the proposal that fish experience some form of pain rather than a nociceptive reflex.

Figure 2. Fold-change values for treatment compared to control expression values in common carp. Normalized expression values in control and treatment were compared with a one-way ANOVA for each time point and brain region. The number of genes differentially regulated ($p < 0.05$) in each of the groups is plotted (adapted from Reilly *et al.*, 2008b).



2.2 Adverse Behavioural and Physiological Responses

Behavioural responses are one of the first observable signs that an animal is reacting to a stimulus (Hawkins, 2002; Sneddon, 2009). Human behavioural reactions to pain are very much dependent on the type of pain experienced. For example, with a sprained ankle an individual may limp, with abdominal pain the individual may lie down, whereas with a moderate headache there may be no obvious changes in behaviour. Equally, in animals there is no universal indicator that can be used. Each type of pain must be assessed for each species of animal, since prey animals may respond very differently to predatory species as discussed previously (Hawkins, 2002). However, there are objective measures such as cardiovascular responses that can be quantified along with changes in behaviour including the suspension of normal behaviour such as feeding, activity, or social interactions (Sneddon, 2003a; Flecknell *et al.*, 2007; Ashley *et al.*, 2009; Reilly *et al.*, 2008a; Sneddon *et al.*, 2003b,a). When responding to pain, an animal should not simply show a reflex withdrawal response but should exhibit prolonged adverse changes in behaviour indicative of discomfort or possible suffering. As seen in humans, performance on other tasks should be impaired if pain is the predominating event (Buhle and Wager, 2010). Therefore, studies on fish have sought to understand what responses fish demonstrate during potentially painful stimulation and to comprehend whether pain is indeed important to the fish.

Responses from rainbow trout, common carp, goldfish, Nile tilapia, and zebrafish provide evidence for protracted responses following a painful event (Roques *et al.*, 2010; Dunlop *et al.*, 2006; Millsopp and Laming, 2008; Ashley *et al.*, 2009; Reilly *et al.*, 2008a; Sneddon, 2003a; Sneddon *et al.*, 2003b). These responses include anomalous behaviours such as rubbing of the injection site where noxious chemicals were administered; avoidance of the area where an electric shock was given; reduction in swimming and general activity; suspension of feeding behaviour; and the inability to respond appropriately to other external cues such as novel objects, avoiding light, and predatory cues (Figures 4A & 6). In trout, these responses are ameliorated by the administration of an analgesic, morphine (Sneddon, 2003a). These reactions occur for up to 6 hours post noxious stimulation and subside as the fish appear to recover, and

have not been identified in non-noxious treated fish nor in studies on stress. In some of these studies on nociception and pain, concurrent changes in physiology were also apparent, such as a dramatic rise in gill ventilation rate of rainbow trout, zebrafish, and goldfish (Reilly *et al.*, 2008a; Sneddon, 2003a; Sneddon *et al.*, 2003b,a; Newby *et al.*, 2009); increased cortisol in trout (Ashley *et al.*, 2009); and exocytosis of mucus in gill cells of the Nile tilapia (Figure 4B; Roques *et al.*, 2010). All of these physiological parameters indicate a stress response over and above the responses to handling stress, anaesthesia, and sham treatment. However, in common carp there were no changes in ventilation rate or swimming, and in Nile tilapia swimming activity actually increased after removal of tail tissue. This demonstrates that the responses to pain in these teleost fish are quite specific to each species, which necessarily precludes the development of a collective set of indicators (Table 1). Therefore, given that fish are one of the most diverse vertebrate groups, future research should explore the reactions of many more species against a variety of pain stimuli.

Figure 4. A. Dark/light preference of Nile tilapia under normal conditions (Control), after handling, and after the tail has been fin clipped. Compared to control, untreated fish, a fin clip induces a larger shift in preference than the handling stress alone ($*p<0.05$). B. Quantification of the mucus cells frequency in gills of Nile tilapia under normal conditions (Control), after handling, and after the tail has been fin clipped. There was a significant decrease in mucus-filled mucus cells in the gill filaments 1h after fin clipping ($*p<0.05$). In the accompanying handled group, this decrease was not observed (adapted from Roques *et al.*, 2010).

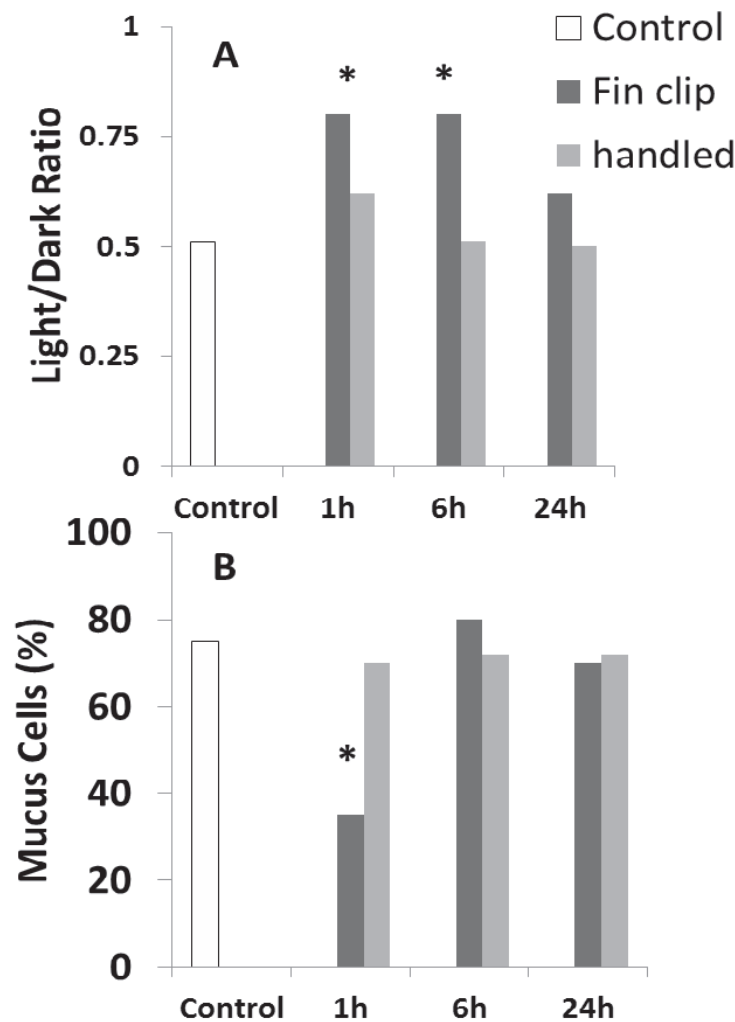


Table 1. Behavioural and physiological measures of responses to a potentially painful event in a number of fish species (↑ = increase; ↓ = decrease; ↔ = no change; √ = performance of novel anomalous behaviours; NM = not measured and omitted from methods; adapted from Reilly *et al.*, 2008a; Roques *et al.*, 2010).

Fish Species	Swimming	Ventilation Rate	Feeding	Plasma Cortisol	Light Preference	Changes in Gill Physiology	Anomalous Behaviours
Rainbow trout	↓	↑	↓	↑	NM	NM	√
Common carp	↔	↔	↓	NM	NM	NM	√
Zebrafish	↓	↑	↓	NM	NM	NM	√
Nile tilapia	↑	NM	NM	↔	↑	↑	NM

To understand if the experience of pain is important to the fish, studies have employed various strategies to investigate whether diversion tactics or competing motivational drivers influence the responses to pain. Goldfish and rainbow trout learn to avoid an area where they are given an electric shock (Dunlop *et al.*, 2006). If the intensity of the electric shock increases, the goldfish profoundly reduce the number of entries and time spent in this shock zone (Figure 5A,B). However, by starving the goldfish they will re-enter the area after three days if food is provided there, thereby trading off satiating their hunger with the risk of experiencing the electric shock (Millsopp and Laming, 2008). Goldfish experiencing three days of deprivation increased the number of entries and time spent in this shock area (Figure 5C,D) but simultaneously performed more tail flips and escape reactions possibly due to the anticipation of being shocked. Thus, when the fish were motivated by hunger, they were willing to endure the electric shock to obtain food. If pain was unimportant, then the fish would have re-entered this zone immediately.

Fear tests, such as novel object presentation, gauge how neophobic an animal is since they will normally react to a strange object by avoiding it. Fear is obviously a strong stimulus that may be more competitive for an animal's attention than pain. Rainbow trout normally avoid novel objects, but when experiencing pain their neophobia is absent (Sneddon *et al.*, 2003b). These fish spent approximately 33% of the time very close to the novel object. In contrast, normal fish spent less than 5% in close proximity. When given morphine, fish experiencing pain avoided the object, demonstrating that removal of the pain via analgesia resulted in a normal neophobic response. Similarly, rainbow trout experiencing pain do not respond appropriately to predator cues (Ashley *et al.*, 2009; Figure 6). Normal fish engage in escape attempts and increased use of cover. Noxiously stimulated fish do not try to escape and actually reduce refuge use when presented with a predator cue. Together these results suggest that pain is an important state for fish since pain responses were not affected by fear or the risk of predation.

2.3 Are Fish Conscious?

Proving any animal is conscious is a real challenge. However, one of the key criteria is self-recognition. Most studies on humans and mammals use mirror tests where the individual recognizes themselves (Thunken *et al.*, 2009). Studies on fish using such an approach have not been successful simply because the life history and biology of fish had not been considered. Fish live in an aquatic world where smells and olfaction are of paramount importance. Therefore, findings on a study in a cichlid fish demonstrated

clearly that individuals recognized their own odour and preferred this over the odour of other fish irrespective of familiarity of that individual or whether they were related (Thunken *et al.*, 2009). Again consciousness is likely to have evolved throughout the animal groups and, therefore, the fish's capacity may be more primitive compared with human consciousness and is likely to be on a phylogenetic sliding scale (Bekoff and Sherman, 2004).

Figure 5. (A) Mean number (+SE) of entries and (B) duration (+SE) of time spent in a feeding/electric shock zone in goldfish after the application of an electric shock at 1, 5, and 20 volts. (C) Mean number (+SE) of entries and (D) duration (+SE) of time spent in the feeding/electric zone in goldfish after 0 and 3 days food deprivation (modified from Millsopp and Laming, 2008, by permission from Elsevier).

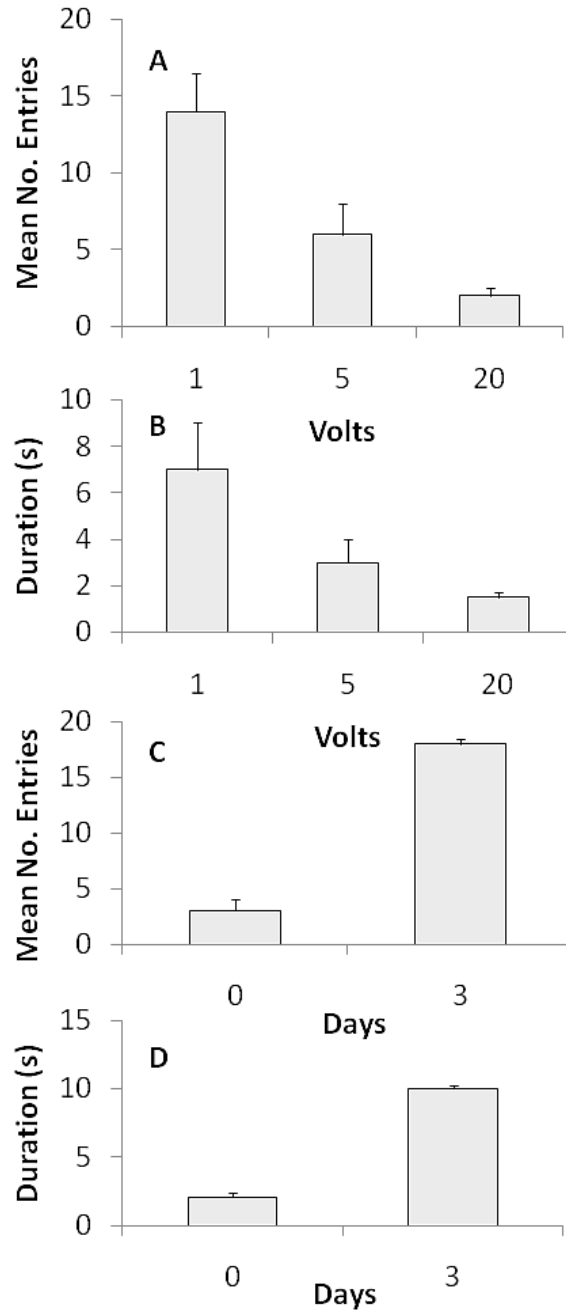


Figure 6. The mean percentage change in refuge use and escape behavior in rainbow trout that were injected subcutaneously with saline as a control or acetic acid as a pain stimulus (adapted from Ashley *et al.*, 2009).

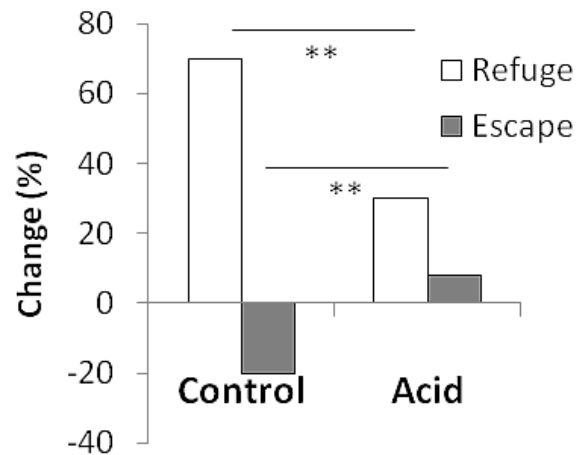
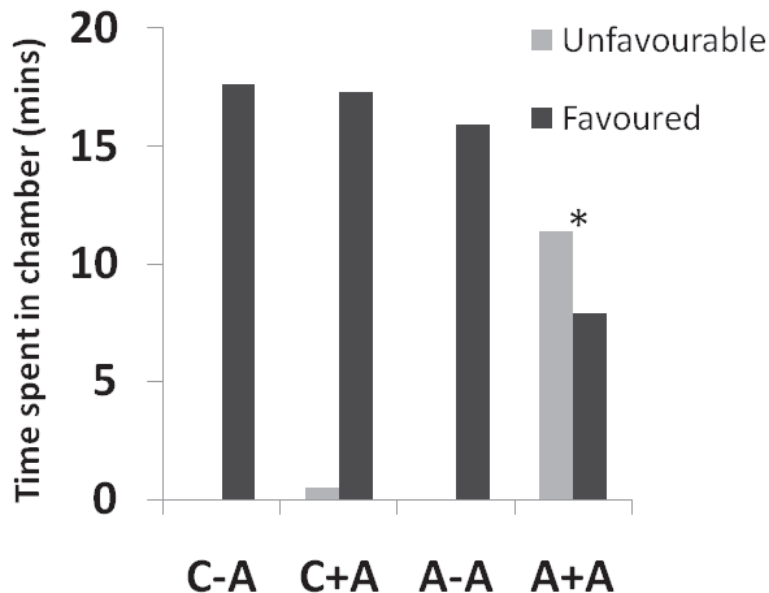


Figure 7. The median time spent in a preferred, favoured chamber compared with an unfavourable chamber in a maze test using zebrafish. The fish were either injected with saline as a non-noxious control (C) or acid (painful treatment) in the absence (-A) or presence (+A) of analgesia in the unfavourable chamber. Acid injected fish spent more time in the unfavourable chamber when analgesia was present ($*p < 0.001$; Sneddon *et al.*, unpublished data).



The crucial issue in the debate regarding fish perceiving pain is whether they are conscious of it and whether they 'know' they are in pain. Studies on other animals have shown that rodents self-administer analgesics, preferring to drink analgesic dosed water or eat dosed food when presented with a choice (Pham *et al.*, 2010). This represents an attempt on the animal's part to reduce the pain it is in, thereby providing convincing evidence that its internal mental state is one of discomfort. The problem with fish is that they suspend feeding behavior during painful stimulation until they have recovered (Reilly *et al.*, 2008a; Sneddon, 2003a; Sneddon *et al.*, 2003a). In order to circumvent this problem, an experiment was

designed to understand if fish were willing to endure unfavourable conditions to gain access to pain relief. Zebrafish were placed in a maze where they could choose one of two chambers. One chamber was barren and the other chamber was enriched with gravel, a plant, and through the transparent rear of the chamber a group of zebrafish provided social enrichment. Zebrafish displayed a clear preference for the enriched chamber for at least six consecutive tests. At this point the zebrafish were injected with saline, a non-noxious control, or a noxious chemical and placed in the maze. In half of these trials, an analgesic was placed into the barren, unfavourable chamber. Those fish experiencing pain lost their preference for the enriched chamber and were willing to spend more time in the barren, unfavourable area only if analgesia was present (Figure 7). This demonstrates that the fish were willing to pay the cost of being in an unpreferred environment to obtain analgesia, and thus it can be inferred that these fish must have obtained some reward possibly in terms of pain relief such that the pain was reduced. Future research should employ more insightful tactics to try and improve our understanding of how important the pain experience is and how aware fish are of this potentially detrimental internal state.

3. Concerns for the Use of Fish

If it is accepted that fish experience some form of pain, humans as moral beings should ethically seek to reduce, minimize, and alleviate that pain. The numbers of fish that are caught in commercial fisheries are astounding, with an estimated one trillion each year (<http://fishcount.org.uk/>). If we consider the welfare of the individual and the ways in which fish are caught often leading to tissue damage possibly giving rise to pain, the potential for impaired fish welfare during capture outweighs the number of mammals used in intensive farming. Wild caught fish are subject to capture methods (Table 2) that could be refined by reducing the numbers caught to improve sustainability of fish populations but also reduce the amount of fish caught for oil or for producing fish farm food and avoiding the use of fish as live bait. More humane methods of slaughter should be developed where fish are killed very quickly, and the time of capture could also be shortened by improving fishing gear technology. All of these factors would result in reducing the detrimental effects upon the fish.

Aquaculture also has a number of welfare concerns such as holding fish in high stocking densities leading to aggression and high transmission of necrotic diseases; vaccination where fish are handled and suffer mortality; transporting them in confined containers leading to stress; food deprivation; and injurious slaughter practices (Ashley, 2007; Table 2). Consequently, fish may suffer injury prior to death and hence may experience pain. The implementation of improved practices such as lower stocking density will result in increasing costs to the consumer. Knowledge from investigations into improved procedures is vital to inform the development of better procedures to minimize any adverse impact upon the farmed fish.

Fish are also used as companion animals and for recreational sport where there are few regulations and generally any member of the public can purchase a pet fish or engage in the sport of angling. Angling involves the catch and release of fish for sport or personal enjoyment (in contrast to catch and kill where the fish is caught to be eaten). During capture fish are hooked (causing tissue injury), removed from the water (causing suffocation), and then released. This practice elicits a stress response (Arlinghaus *et al.*, 2007; 2009) as well as impaired behaviour after release (e.g. Cooke and Philipp, 2004; Danylchuk *et al.*, 2007). If poor welfare ensues, such as pain, fear, and physiological stress, then it would seem appropriate to review this in light of the consequences. Germany has answered this moral question by restricting the capture of fish for food purposes only. If there is a benefit to humans when fish are used as food then perhaps this is justified, however, catch and release may need careful moral and ethical consideration. Many angling organizations and scientists have made recommendations to improve the welfare of caught fish (e.g. freshwater anglers, Australia, in Cooke and Sneddon, 2007; Norwegian Food Safety Agency, 2010; Table 2).

Table 2. Selected welfare concerns in the use of fish where tissue damage may occur that potentially could give rise to the sensation of pain. Improvements are suggested to reduce the impact upon fish welfare (adapted from Ashley *et al.*, 2007; Sneddon, 2006; 2009).

Use of Fish	Welfare Concern	Suggested Improvement
Pet trade	<ul style="list-style-type: none"> • Wild caught fish damaged during capture • Transport • Disease and poor water quality 	<ul style="list-style-type: none"> • Captive bred fish species only • Reduce transport times • Training of owners
Aquaculture	<ul style="list-style-type: none"> • High stocking density results in aggressive injuries and transmission of disease • Slaughter 	<ul style="list-style-type: none"> • Reduce stocking densities; consider food delivery to reduce competition; anaesthesia during vaccination to prevent disease • Automating brain destruction using percussive stunning
Angling or recreational catch and release	<ul style="list-style-type: none"> • Injuries during hooking, landing the fish, hook removal, and suffocation in air 	<ul style="list-style-type: none"> • Use barbless hooks that cause less damage; minimize time during capture; keep fish in water as long as possible; quick and efficient removal of hooks; consider euthanasia when mortality is likely
Fisheries	<ul style="list-style-type: none"> • Large numbers of fish damaged when caught • Live bait • Slaughter — fish killed by suffocation or gutted/filletted when alive 	<ul style="list-style-type: none"> • Reduce numbers caught and improve equipment techniques to minimize capture time • Ban the use of live bait • Fish should be killed as quickly and humanely as possible. Consider use of automated percussive equipment as used in fish farms
Experimentation	<ul style="list-style-type: none"> • Pain caused by invasive procedures or exposure to toxicants 	<ul style="list-style-type: none"> • Use of analgesics where appropriate and development of humane endpoints

As pets, there is growing interest in the welfare of ornamental fish that can be purchased in most pet stores. One normally envisages the lonely goldfish in a small fish bowl lacking social and environmental stimulation. These bowls provide insufficient dissolved oxygen for the fish to breath and indeed these have been banned in Rome, Italy (The Times, 2005). There are very few regulations with respect to keeping these animals, and yet if one wanted to use them in experimentation, appropriate training and certification would be required in many countries. Ornamental species caught in the wild deplete natural populations rather than being bred in captivity. The tremendous difference in coming from a spatially complex wild environment to a relatively barren aquarium tank has not been explored. These fish are often transported in relatively small plastic bags for up to 48 hours without aeration or fresh water, resulting in deteriorating conditions (IATA, 2009; Walster, 2008). This can cause mortality (for example, in guppies) due to stress during lengthy transport periods (Lim *et al.*, 2003). Our understanding of the welfare consequences of the ornamental fish trade is in its infancy, and future studies are needed to inform our knowledge of where the problems lie and what can be done to reduce them.

Finally, fish are also used in large numbers in scientific experimentation; however, in contrast to the recreational and commercial use of fish, there are comprehensive guidelines and legislation produced by government bodies of many countries (e.g. EU Directive, 2010). Intensive training and licensing in some countries results in fish experiments being scrutinized in detail to ensure that the welfare of fish is considered, there are a minimum number of animals used, and that there are real scientific outcomes that justify the use of live animals. There is a general consensus that the welfare of animals undergoing experimentation, where stress, fear, and pain may be studied, is strictly controlled and that researchers should consider more humane approaches and use analgesics where appropriate. Unfortunately, in the case of fish, there are few studies exploring analgesia, therefore future investigations should explore the efficacy and correct dose of a variety of analgesic drugs.

4. Conclusion

There is growing scientific evidence to support the case for fish perceiving and experiencing some of the negative affective aspects of pain. It is clear that a painful stimulus does result in adverse changes in behaviour and physiology which may impair the welfare and well-being of fish. Although some authors are opposed to the concept of fish perceiving pain, all commentators state that the welfare of fish is an important issue and that fish should be treated humanely (Rose, 2002; Iwama, 2007). Therefore, our use of fish as pets, in recreational sport, in fisheries, aquaculture, and as experimental groups require careful consideration to minimize any injuries that may give rise to pain, but also to refine our techniques and procedures to reduce any deleterious effects upon fish welfare. The treatment of fish would mostly be considered unacceptable in mammals; therefore, to improve fish welfare this may need a complete change in mindset as to the value of fish as potentially conscious animals.

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