

Fish and welfare: do fish have the capacity for pain perception and suffering?

VA Braithwaite* and FA Huntingford†

* Ashworth Laboratories, School of Biological Sciences, King's Buildings, University of Edinburgh, Edinburgh EH9 3JT, UK

† Institute of Biomedical and Life Sciences, Graham Kerr Building, University of Glasgow, Glasgow G12 8QQ, UK

* Contact for correspondence and requests for reprints: V.Braithwaite@ed.ac.uk

Abstract

Humans interact with fish in a number of ways and the question of whether fish have the capacity to perceive pain and to suffer has recently attracted considerable attention in both scientific and public fora. Only very recently have neuroanatomical studies revealed that teleost fish possess similar pain-processing receptors to higher vertebrates. Research has also shown that fish neurophysiology and behaviour are altered in response to noxious stimulation. In the light of this evidence, and in combination with work illustrating the cognitive capacities of fish, it seems appropriate to respond to a recently published critique (Rose 2002) in which it is argued that it is not possible for fish to experience fear or pain and that, therefore, they cannot suffer. Whilst we agree with the author that fish are unlikely to perceive pain in the same way that humans do, we believe that currently available evidence indicates that fish have the capacity for pain perception and suffering. As such, it would seem timely to reflect on the implications of fish pain and suffering, and to consider what steps can be taken to ensure the welfare of the fish that we exploit.

Keywords: animal welfare, awareness, fish, pain, stress, suffering

Introduction

Considerable advances have been made in terms of defining the welfare requirements of higher vertebrates such as birds and mammals (eg Dawkins 1998; Mendl 2001; Sørensen *et al* 2001). In contrast, we know considerably less about the welfare requirements of fish. Yet humans interact with fish in a number of ways: they are fished and farmed for consumption, they are used for biological and medical research, and they provide an opportunity for sport and hobbies. Therefore, it is perhaps timely that we start to address the issue of fish welfare and, in particular, of whether or not fish have the capacity for suffering. Some work has already begun to address such issues; for example, a document on fish welfare was recently commissioned and published by the Fisheries Society of the British Isles (FSBI 2002). Additionally, the Canadian Council on Animal Care is currently drawing up guidelines on the care and use of fish in research, teaching and testing (see Griffin & Gauthier 2004, pp 181–186, this issue).

These documents and a number of other studies indicate that we should be concerned about fish welfare. For example, there is considerable evidence that fish, as with most organisms, do not respond well to prolonged periods of stress: chronic exposure to aversive conditions can generate stress-induced changes in the immune system making fish more vulnerable to disease (Pickering & Pottinger 1989). Recent research has also shown that the physiological effects of stress in fish are comparable to those in higher

vertebrates (Wedemeyer *et al* 1990; Barton & Iwama 1991; Wendelaar Bonga 1997). Furthermore, neuroanatomical approaches have now revealed that teleost fish possess the same types of pain-processing fibre as higher vertebrates (Sneddon 2002). What is currently unclear, however, is whether fish have an awareness of stress and pain — in other words, whether or not they have the capacity to experience pain and suffering. There would, therefore, appear to be a number of grounds for the consideration of fish welfare, but there is also the need at this early stage for more scientific research to identify appropriate welfare criteria. For example, what do fish require in terms of resources, and what opportunities do they need to behave in ways that are important to them? These are questions that have been asked of a number of higher vertebrate animals (Mendl 2001), but to date they have not been asked of fish.

The necessity for measures to protect the welfare of fish has recently been questioned in a detailed and timely review by James Rose (2002). Rose puts forward the argument that fish cannot experience pain and suffering because they lack certain brain structures required for the conscious perception of pain in humans. He argues that the psychological experience of pain requires the presence of a highly developed neocortex, in particular the frontal lobe cortex. Rose therefore concludes that the conscious perception of suffering is restricted to humans and higher primates because appropriately developed neocortical structures are found only in these animals. This is an extreme stance that finds

little support among others working on animal pain (eg Broom 1991; Bateson 1991; Gentle 1992; Molony *et al* 2002). Rose acknowledges that fish can generate robust neuroendocrine and physiological stress responses to noxious stimuli, but suggests that these are entirely non-conscious reactions similar to those generated by non-noxious stimuli. In other words, according to Rose, a fish that responds to an electric shock with an altered heart rate and with erratic, darting swimming behaviour (Verheijen & Bulwalda 1998) is no different from a male fish commencing a vigorous courtship display in response to the presence of a female (Rowland 1994).

Rose goes on to suggest that fish behaviour is largely generated by structures within the brainstem and that the relatively small cerebral hemispheres of fish act only to modulate behaviour. Although he recognises the diversity of specialisations that various fish brains exhibit, he describes fish behaviour as highly stereotyped and invariant within a species. He also discusses the capacity of fish for associative learning but he does not believe that such learning requires any form of conscious awareness.

In essence, Rose puts forward the case that without a well-developed neocortex a fish cannot have conscious awareness and therefore does not have the capacity for the emotional experiences of pain and suffering. We do not agree with this logic. For example, comparisons of avian and mammalian visual systems clearly illustrate how different taxonomic groups can perceive and process the same type of information but through different pathways and neural structures (Shimizu & Karten 1993). Extrapolating this analogy, the ability to suffer and perceive an emotional experience associated with pain may not be solely restricted to the pre-frontal cortex of humans and higher primates; other animals may process similar information in different ways. Just as the taxon-based approach to visual perception is more informative than a comparative approach, it may be the case that identifying taxon-specific capacities for pain perception and suffering is more useful than drawing on the comparative examples used by Rose (2002).

Rose (2002) takes the viewpoint that pain is both a sensory and an emotional experience and that nociception cannot result in pain unless the neural activity associated with it is consciously perceived. This definition of pain and suffering suggests that no organism other than a human or higher primate has the capacity to consciously suffer. There appear to be two ways of countering this argument. The first, which has been adopted by a number of researchers working in the field of animal welfare, is to advocate that pain should be considered without an emotional element and that a distinction should be drawn between human pain and animal pain (eg Bateson 1991). The second is to consider the cognitive abilities of the animal and to determine through empirical research what capacity the animal has for suffering. This approach has the advantage of determining whether or not an animal has the capacity for pain perception and other responses that are associated with suffering, regardless of the underlying neuroanatomy which is clearly different in many vertebrate taxonomic groups.

Our aim in this review is to examine whether there is sufficient evidence to conclude that fish have the capacity for pain perception and suffering. To do this we review recent work investigating the capacity of trout for pain perception. We then consider how cognitive capacities can be assessed and review current literature to examine what is already known about the cognitive capacities of fish.

Are fish capable of perceiving noxious stimuli?

Recent neuroanatomical and neurophysiological research has determined that teleost fish, such as the trout, possess 'nociceptors', specialised receptors that exclusively respond to noxious stimuli. Earlier work by Whitear (1971) identified free nerve endings in the skin tissue of teleost fish that were considered to be possible candidates for nociceptors. Surprisingly, however, it is only recently that the presence of nociceptors in teleost fish has been confirmed (Sneddon 2002; Sneddon *et al* 2003). In higher vertebrates there are two classes of nociceptive nerves: 1) A delta fibres, which are slow conducting, small myelinated fibres, and 2) C fibres, which are slower conducting, smaller and unmyelinated (Wall & Melzack 2000). Both of these classes of fibre have now been found in the trout trigeminal nerve, which is the main nerve innervating the face and head of vertebrates (Sneddon 2002). In birds and mammals, trigeminal A delta and C fibres convey both somatosensory and nociceptive information to the brain (Wall & Melzack 2000). Electrophysiological recordings made from afferent cell bodies in the trigeminal ganglion of trout showed that receptors isolated on the head and face were able to detect noxious stimuli such as mechanical pressure, temperature and chemical stimuli, thus confirming the presence of nociceptors (Sneddon *et al* 2003). Taken together, these results indicate that fish possess the necessary neuroanatomy and neurophysiology to perceive and process information about stimuli that would be regarded as painful by humans.

Related to these studies, a number of behavioural experiments were also undertaken to investigate changes in behaviour as a consequence of noxious stimulation (Sneddon *et al* 2003). Trout treated with noxious chemical stimuli (acetic acid or bee venom) showed a prolonged decreased motivation to feed and a dramatically increased opercula beat rate in comparison to identically handled saline-treated controls. Fish that were recovering from noxious stimulation also exhibited anomalous behaviours such as rocking whilst resting on the substrate. Furthermore, some fish were observed rubbing their snouts, the site where the noxious stimulus had been administered, on the walls and substrate of the tank.

In an extension of these behavioural investigations, fear responses were investigated in fish that had experienced a noxious stimulus (Sneddon *et al* in press). Since trout generally show considerable fear of novel objects, fear was quantified as the amount of time a fish spent avoiding a novel object that had been temporarily placed in its tank. Sneddon and colleagues (in press) observed that the fear response was reduced in fish that had experienced a noxious stimulus, but that this reduction in fear was reversed with

the application of an analgesic (morphine). These results suggest that the attention of a fish currently responding to nociceptive stimulation is preoccupied and, consequently, the ability of the fish to generate a normal fear response is decreased. These new results support the earlier observations of Ehrensing and colleagues (1982) who found that the intracranial application of morphine to goldfish decreased their response to electric shock. Subsequent application of opiate antagonists reversed this effect. Although compelling, the approach by Ehrensing and his colleagues (1982) was criticised because the application of morphine might be expected to reduce reactions to a stimulus regardless of whether it was associated with pain or not. The approach of Sneddon and colleagues (in press) tackles this criticism because in this case the effect of the morphine was to revive the novel object avoidance behaviour in the fish.

The fact that fish have the same types of nociceptor as higher vertebrates (A delta and C fibres), that these respond to noxious stimulation, and that the motivation and general behaviour of fish are adversely affected by such stimulation, would appear to provide compelling evidence that fish can perceive and react to noxious stimuli. Whether this is evidence that fish have the capacity to experience pain and suffering is a much harder question to answer, however, because to determine this we need to understand the cognitive capacities of fish.

Assessing the cognitive capacities of non-human animals

Advances in the last decade have revealed several surprising findings in terms of the cognitive abilities of a range of different vertebrates. Experiments have directly addressed whether or not animals other than humans have any form of self-awareness or consciousness, and in several cases the results have shown animal minds to be far more versatile and complex than was originally believed. Such approaches are therefore providing a greater insight into the psychological capacities of animals (Balda *et al* 1998; Shettleworth 1998).

Here we highlight empirical examples that illustrate the complex cognitive capabilities of three different non-human vertebrates. Firstly, Harding and colleagues (2001) ingeniously developed a method of quantifying the mental state of rats by measuring how positively or negatively they respond in an operant paradigm. By getting rats to discriminate between different types of auditory tone, the researchers found that rats coming from social group housing were more likely to generalise between a sample tone and a similar but different tone, than were rats from a socially deprived environment. In this way, the mental state of the test rats could be categorised as either optimistic or pessimistic (Harding & Mendl 2001; Harding *et al* 2001). Secondly, work with food-storing birds has shown that corvids have the capacity to learn to understand the intentions of their conspecifics (Emery & Clayton 2001). Here, birds that have experienced pilfering another bird's store will not store food in the presence of other birds. This is not the case for birds that are naive with respect to the possibility

of pilfering. These observations indicate that birds with a knowledge of pilfering are able to attribute this ability to other birds. Mental attribution, however, has previously been thought to be unique to humans (Heyes 1998). Thirdly, recent work by Hampton (2001) has demonstrated that rhesus macaques can be trained to indicate their perception of whether they have a good or poor memory of an event. Again, through an elegant operant paradigm, macaques were able to indicate their ability to accurately solve a task. Hampton suggests that to be able to do this the animal must have a conscious awareness of its memory ability.

These different examples show that animals other than humans and higher primates do have the capacity for self-awareness and for some forms of mental representation. Being able to generate mental representations or being self-aware is not, therefore, as proposed by Rose (2002), unique to the well-developed brains of humans and higher primates. The field of animal cognition is thus providing a more detailed understanding of the cognitive capacities of animal brains.

The cognitive capacities of fish

Although few studies have investigated the cognitive capacities of fish, there is growing evidence that fish can form mental representations (eg Rodriguez *et al* 1994) and that several fish species have the capacity for complex, flexible learning and memory (Odling-Smee & Braithwaite 2003b). Very recently, the journal *Fish and Fisheries* devoted a whole issue to fish learning (Laland *et al* 2003). The papers in this volume clearly demonstrate the similarities between fish and other vertebrates in terms of their learning processes. Together this body of work suggests that, like the birds and mammals mentioned in the examples above, fish may have the capacity to generate mental representations of events. Using Rose's (2002) own logic, if fish have the capacity for mental representation then we should consider that they may also have the capacity to experience suffering.

The behavioural repertoires and learning and memory abilities of fish, far from being stereotyped and invariant (Rose 2002), have now been shown to be flexible not just between species but in some cases between different populations of the same species (Braithwaite 1998; Laland *et al* 2003). For example, fish have been shown to be capable of recognising and remembering individual conspecifics, and they can ascribe competitive abilities to these individuals (Metcalf & Thomson 1995; Griffiths 2003). Furthermore, learning has also been shown to play a key role in anti-predator behaviour by allowing fish to adjust their responses in line with their experiences within a particular environment (Kelley & Magurran 2003). Fish are also flexible in the types of orientation information that they learn and remember (Girvan & Braithwaite 1998; Odling-Smee & Braithwaite 2003a).

Rose (2002) does present evidence that a number of fish species are capable of associative learning and he lists a number of behaviours that are generated by associative learning processes. Such forms of learning, sometimes referred to as 'implicit learning', do not require conscious

awareness, and this is true in humans as well as in other animals (Macphail 1998). Rose also uses examples from studies in which the forebrains of fish are removed, to argue that most fish behaviours are controlled by brainstem and spinal cord functions (Overmeir & Hollis 1983; Overmeir & Papini 1986). For example, it has been demonstrated that fish can still feed and can learn simple associations even in the absence of their forebrain (Rooney & Laming 1988; Laming & McKinney 1990; Salas *et al* 1996). However, this approach is limited in what it can tell us because teleost fish that have intact forebrains are capable of complex learning and behaviour, such as associating events with times and places (Reebs 1999) and learning to avoid sites that they perceive to be dangerous (Huntingford & Wright 1989; Kelley & Magurran 2003).

One of the most informative areas of fish cognition to be investigated is spatial learning. For example, several fish species can generate internal map-like representations (Rodríguez *et al* 1994; Braithwaite 1998; Odling-Smee & Braithwaite 2003b), which provide them with the ability to make short-cuts or to select between alternative routes to reach a goal without having to rely on a specific sequence of locations or landmarks. Perhaps one of the most impressive illustrations of the use of an internal map comes from the work of Aronson (1951, 1971) who observed the escape responses of rock-pool gobiid fish. Aronson showed that fish learn the local topography at high tide so that when they are trapped in one rock-pool at low tide they can accurately jump and escape into another pool if they are threatened. Only fish that are given the opportunity to learn the topography at high tide are successful in locating the position of rock-pools for their escape.

Such complex cognitive capacities are evident even though teleost fish have a relatively simple brain and nervous system (Kotraschal *et al* 1998). Yet, despite this simplicity, teleost fish represent the most abundant and diverse group of vertebrates to have evolved and radiated into a wide range of niches (Nelson 1994). In association with this divergence, fish brains and their nervous systems, in particular their sensory systems, have also diverged and become specialised (Kotraschal *et al* 1998). Although there are considerable differences between the brains of teleost fish and other vertebrates, recent research suggests that there are some similarities. For example, Broglio and colleagues (2003) have clearly identified an area of the teleost fish forebrain, the lateral pallium, as analogous to the avian and mammalian hippocampus — the brain area associated with long-term memory and spatial relationships. It is likely that further detailed work on fish brain organisation and behaviour may well yield other interesting commonalities between fish and other vertebrates.

In summary, as illustrated in the various examples above, despite their relatively simple nervous systems, teleost fish are capable of complex, flexible behaviours and of forming mental representations. One implication of such findings is that we need to establish how fish cognitive capacities are disrupted when we interact with fish. This may, therefore, represent a good starting point for studies of fish welfare.

Conclusions and animal welfare implications

We conclude that, despite the relatively simple structure and small size of the teleost brain and nervous system, teleost fish certainly produce complex behaviour and are probably capable of cognition. It is clear that teleost fish do not possess a neocortex, nor do they have the well-developed prefrontal cortical lobes that are believed to be the seat of human consciousness (Macphail 1998). Fish do, however, have the capacity for simple mental representations and as such they may have the potential to suffer.

The increasing rate at which humans now interact with and manage different types of fish population indicates that an interest in fish welfare is both timely and necessary. In particular, the increasing reliance of humans on farmed fish is increasing the demands placed on the aquaculture industry. To meet these demands the industry needs to expand and fish farmers will be required to intensify fish production. Welfare in fish is a novel concept. Recent suggestions that fish cannot experience pain or suffering do not appear to be supported by the current literature. The evidence we review strongly suggests that fish do have the capacity to experience pain and fear, albeit of a taxon-specific kind, and that fish therefore deserve appropriate welfare and husbandry considerations that will minimise their potential suffering.

Fish welfare is a new field that needs to be developed by increasing our understanding of how fish cognition is altered when fish interact with humans, what fish require in terms of resources, and what maintains their health. We therefore suggest that there is an urgent need for the development of appropriate fish welfare guidelines.

Acknowledgements

Many of the ideas we report here were developed in discussion with Colin Adams, Mike Gentle, Sunil Kadri, Vince Molony, Tom Pottinger, Lynne Sneddon and Jimmy Turnball. We also thank Culum Brown and Sean Nee for their comments and suggestions.

References

- Aronson L R** 1951 Orientation and jumping in the Gobiid fish *Bathygobius soporator*. *American Museum Novitates* 1486: 1-22
- Aronson L R** 1971 Further studies on orientation and jumping behaviour in the Gobiid fish *Bathygobius soporator*. *Annals of the New York Academy of Science* 188: 378-392
- Balda R P, Kamil A C and Pepperberg I M** 1998 *Animal Cognition in Nature*. Academic Press: San Diego, USA
- Barton B A and Iwama G K** 1991 Physiological changes in fish from stress in aquaculture with emphasis on the response and effects of corticosteroids. *Annual Review of Fish Disease* 1: 3-26
- Bateson P** 1991 Assessment of pain in animals. *Animal Behaviour* 42: 827-839
- Braithwaite V A** 1998 Spatial memory, landmark use and orientation in fish. In: Healy SD (ed) *Spatial Representations in Animals* pp 86-102. Oxford University Press: Oxford, UK
- Broglio C, Rodríguez F and Salas C** 2003 Spatial cognition and its neural basis in teleost fishes. *Fish and Fisheries* 4: 247-255
- Broom D M** 1991 Animal welfare: concepts and measurements. *Journal of Animal Science* 69: 4167-4175

- Dawkins M S** 1998 Evolution and animal welfare. *Quarterly Review of Biology* 73: 305-328
- Ehrensing R H, Michell G F and Kastin A J** 1982 Similar antagonism of morphine analgesia by MIF-I and naloxone in *Carassius auratus*. *Pharmacology, Biochemistry and Behaviour* 17: 757-761
- Emery N J and Clayton N S** 2001 Effects of experience and social context on prospective caching strategies by scrub jays. *Nature* 414: 443-446
- FSBI** 2002 *Fish Welfare (Briefing Paper 2)*. Fisheries Society of the British Isles. Granta Information Systems: Cambridge, UK. Available at: <http://www.le.ac.uk/biology/fsbi/briefing.html>
- Gentle M J** 1992 Pain in birds. *Animal Welfare* 1: 235-247
- Girvan J R and Braithwaite V A** 1998 Population differences in spatial learning and memory in threespined sticklebacks. *Proceedings of the Royal Society of London, Series B, Biological Sciences* 265: 913-918
- Griffin G and Gauthier C** 2004 Guidelines development and scientific uncertainty: use of previous case studies to promote efficient production of guidelines on the care and use of fish in research, teaching and testing. In: Kirkwood J K, Roberts E A and Vickery S (eds) *Proceedings of the UFAW International Symposium 'Science in the Service of Animal Welfare', Edinburgh 2003*. *Animal Welfare* 13: S181-S186 (Suppl)
- Griffiths S W** 2003 Learned recognition of conspecifics by fishes. *Fish and Fisheries* 4: 256-268
- Hampton R R** 2001 Rhesus monkeys know when they remember. *Proceedings of the National Academy of Sciences* 98: 5359-5362
- Harding E J and Mendl M** 2001 Is the glass half empty or half full? A novel approach for assessing mental states in laboratory rodents. In: Garner J P, Mench J A and Heekin S P (eds) *Proceedings of the 35th International Congress of the International Society for Applied Ethology* p 64 (Abstract). Centre for Animal Welfare at UC Davis: California, USA
- Harding E J, Mendl M, Nicol C and Paul E S** 2001 Using discrimination training to assess mental states. *Animal Welfare* 10: S240 (Abstract)
- Heyes C M** 1998 Theory of mind in nonhuman primates. *Behavioral and Brain Sciences* 11: 101-148
- Huntingford F A and Wright P J** 1989 How sticklebacks learn to avoid dangerous feeding patches. *Behavioural Processes* 19: 181-189
- Kelley J L and Magurran A E** 2003 Learned predator recognition and antipredator responses in fishes. *Fish and Fisheries* 4: 216-226
- Kotrschal K, van Staaden M J and Huber R** 1998 Fish brains: evolution and environmental relationships. *Reviews in Fish Biology and Fisheries* 8: 373-408
- Laland K N, Brown C and Krause J** 2003 Learning in fishes: from three-second memory to culture. *Fish and Fisheries* 4: 199-202
- Laming P R and McKinney S J** 1990 Habituation in goldfish (*Carassius auratus*) is impaired by increased interstimulus interval, interval variability, and telencephalic ablation. *Behavioral Neuroscience* 194: 869-875
- Macphail E M** 1998 *The Evolution of Consciousness*. Oxford University Press: Oxford, UK
- Mendl M** 2001 Animal husbandry: assessing the welfare state. *Nature* 410: 31-32
- Metcalfe N B and Thomson B C** 1995 Fish recognize and prefer to shoal with poor competitors. *Proceedings of the Royal Society of London, Series B, Biological Sciences* 259: 207-210
- Molony V, Kent J E and Kendrick I J** 2002 Validation of a method for assessment of acute pain in lambs. *Applied Animal Behaviour Science* 76: 215-238
- Nelson J S** 1994 *Fishes of the World*. Wiley and Sons: New York, USA
- Odling-Smee L and Braithwaite V A** 2003a The influence of habitat stability on landmark use during spatial learning in the threespine stickleback. *Animal Behaviour* 65: 701-707
- Odling-Smee L and Braithwaite V A** 2003b The role of learning in fish orientation. *Fish and Fisheries* 4: 235-246
- Overmeir J B and Hollis K** 1983 The teleostan telencephalon and learning. In: Davis R and Northcutt G (eds) *Fish Neurobiology, Volume 2, Higher Brain Functions* pp 265-284. University of Michigan Press: Ann Arbor, Michigan, USA
- Overmeir J B and Papini M R** 1986 Factors modulating the effects of teleost telencephalon ablation on retention, relearning and extinction of instrumental avoidance behaviour. *Behavioral Neuroscience* 100: 190-199
- Pickering A D and Pottinger T G** 1989 Stress response and disease resistance in salmonid fish: effects of chronic elevation of plasma cortisol. *Fish Physiology and Biochemistry* 7: 253-258
- Reebs S G** 1999 Time-place learning based on food but not on predation risk in a fish, the inanga (*Galaxias maculatus*) *Ethology* 105: 361-371
- Rodríguez F, Durán E, Vargas J P, Torres B and Salas C** 1994 Performance of goldfish trained in allocentric and egocentric maze procedures suggest the presence of a cognitive mapping system in fishes. *Animal Learning and Behaviour* 10: 108-114
- Rooney D J and Laming P R** 1988 Effects of telencephalic ablation on habituation of arousal responses within and between daily training sessions in goldfish. *Behavioral and Neural Biology* 49: 83-96
- Rose J D** 2002 The neurobehavioral nature of fishes and the question of awareness and pain. *Reviews in Fisheries Science* 10: 1-38
- Rowland W J** 1994 Proximate determinants of stickleback behaviour: an evolutionary perspective. In: Bell M A and Foster S A (eds) *The Evolutionary Biology of the Threespine Stickleback* pp 297-344. Oxford University Press: Oxford, UK
- Salas C, Broglio C, Rodríguez F, Lopez J C, Portavella M and Torres B** 1996 Telencephalic ablation in goldfish impairs performance in a 'spatial constancy' problem but not in a cued one. *Behavioural Brain Research* 79: 193-200
- Shettleworth S J** 1998 *Cognition, Evolution and Behavior*. Oxford University Press: Oxford, UK
- Shimizu T and Karten H J** 1993 The avian visual system and the evolution of the neocortex. In: Zeigler H P and Bischof H J (eds) *Vision, Brain and Behaviour in Birds* pp 103-114. MIT Press: Massachusetts, USA
- Sneddon L U** 2002 Anatomical and electrophysiological analysis of the trigeminal nerve in a teleost fish, *Oncorhynchus mykiss*. *Neuroscience Letters* 319: 167-171
- Sneddon L U, Braithwaite V A and Gentle M J** 2003 Do fish have nociceptors? Evidence for the evolution of a vertebrate sensory system. *Proceedings of the Royal Society of London, Series B, Biological Sciences* 270: 1115-1121
- Sneddon L U, Braithwaite V A and Gentle M J** Novel object test: examining pain and fear in the rainbow trout. *Journal of Pain*: in press
- Sørensen J T, Sandøe P and Halberg N** 2001 Animal welfare as one among several values to be considered at farm level: the idea of an ethical account for livestock farming. *Acta Agriculturae Scandinavica, Section A, Animal Science* 30: 11-16
- Verheijen F J and Bulwalda R J A** 1988 *Do Pain and Fear Make a Hooked Carp in Play Suffer?* CIP-GEDEVENS Koninklijke Bibliotheek: Den Haag, Utrecht, The Netherlands

Wall P D and Melzack R 2000 *Textbook of Pain, Fourth Edition*. Churchill Livingstone: Edinburgh, UK

Wedemeyer G A, Barton B A and McLeay D J 1990 Stress and acclimation. In: Schreck C B and Moyle P B (eds) *Methods for Fish Biology* pp 451-489. American Fisheries Society: Bethesda,

Maryland, USA

Wendelaar Bonga S E 1997 The stress response in fish. *Physiology Review* 77: 591-625

Whitear M 1971 The free nerve endings in fish epidermis. *Journal of Zoology* 163: 231-236