



An HSUS Report: Fish and Pain Perception

Stephanie Yue, Ph.D.*

Abstract

In several arenas—legislative, academic, corporate, advocacy, and scientific—the welfare of fish has increasingly attracted attention due in part to the expansion of the aquaculture industry, as well as the growing understanding that many handling methods, management systems, and slaughter practices can induce pain and therefore reduce animal welfare. Unlike other animals raised for human consumption, however, general consensus has not always afforded fish the presupposition that they are, in fact, capable of feeling pain. The typical arguments in support of or against attributing pain capacity to fish revolve around their neuroanatomical development, behavioral and cognitive complexity, physiology, and anatomy. After reviewing the current scientific evidence and exploring the many arguments, it is irrefutably substantiated that fish are capable of experiencing pain.

Introduction

Aquaculture, as defined by the National Oceanic and Atmospheric Administration (NOAA) of the U.S. Department of Commerce, is “the propagation and rearing of aquatic organisms in controlled or selected environments for any commercial, recreational or public purpose.”¹ Described as the fastest-growing food production sector in the world, aquaculture’s growth is expected to continue.² Indeed, simply to satisfy current worldwide fish consumption, the Food and Agriculture Organization of the United Nations predicted in 2006 that worldwide aquaculture production must nearly double in the next 25 years.³ In the last two decades, the aquaculture industry[†] has expanded approximately 8% per year, and it is expected that the number of farmed fish will continue to rise,⁴ perhaps surpassing the number of wild-caught animals from the world’s fisheries.

Domestically, fish are the second most commonly farmed animal, following chickens raised for meat.⁵ According to the U.S. Department of Agriculture’s Census of Aquaculture completed in 2005, nearly 1.3 billion fish were raised that year for human consumption, with the industry dominated by five species: catfish (83.4% of cultured “food fish” by numbers), trout (11.9%), tilapia (2.8%), bass (1.3%), and salmon (0.5%),⁶ totaling approximately 325.4 million kg (717.5 million lbs) as reported by NOAA’s National Marine Fisheries Service.⁷

Given the scale and growth of the U.S. and global aquaculture industries, increasing concern for the treatment of farmed fish has resulted in extensive scientific review of fish welfare and stress,^{8,9,10,11,12,13,14,15,16,17,18,19,20} as well as debates on pain and consciousness in fish.^{21,22,23,24,25,26,27,28}

* Dr. Yue received her Ph.D. in 2005 from the University of Guelph and serves as a consulting farm animal welfare scientist for the Humane Society of the United States and a post-doctoral fellow at the University of Guelph, where she is involved in teaching and graduate program development with its Animal Behaviour and Welfare Group.

† For more information, see “An HSUS Report: The Welfare of Animals in the Aquaculture Industry” at www.hsus.org/farm/resources/research/welfare/welfare_aquaculture.html.

The Function of Pain

Pain is an evolutionary adaptation that helps individuals survive, providing a signal that gives animals the opportunity to remove themselves from damaging situations, thereby increasing their chances of passing on their genetic makeup to future generations.²⁹ Negative experiences incentivize avoiding similar future occurrences to prevent further damage. Teleologically, pain has both survival and adaptive value.^{30,31}

An extremely rare human disorder, congenital insensitivity to pain, highlights the protective benefits of pain. Sufferers experience severe tissue damage, bone fractures, and joint deformities, among other injuries, as a result of sustaining and/or not avoiding physically damaging activities and behaviors.³²

Evolutionary evidence suggests no radical discontinuity between humans and other vertebrate animals,³³ and, as such, a trait like pain perception is not likely to suddenly disappear for one particular taxonomic class. A comparison of empirical data from human and non-human animals has shown that non-human animals begin to exhibit escape behavior at approximately the same stimuli intensity that human subjects first report pain.³⁴ Animal scientists have argued that the pain system should be viewed as an old evolutionary trait, not a recent one.^{35,36} All emotions, including the negative emotional experience of pain, may originate from the most phylogenetically ancient part of the brain—which is reptilian—indicating fish should also have the ability to feel pain.³⁷ Pain perception in fish makes Darwinian and biological sense.

Pain and Nociception

According to the International Association for the Study of Pain (IASP), publisher of the scientific journal *PAIN*, pain is defined as “[a]n unpleasant sensory and emotional experience associated with actual or potential tissue damage, or described in terms of such damage.”³⁸ IASP cautions that the “inability to communicate verbally does not negate the possibility that an individual is experiencing pain and is in need of appropriate pain-relieving treatment” and notes that “[p]ain is always subjective” and “is that experience we associate with actual or potential tissue damage. It is unquestionably a sensation in a part or parts of the body, but it is also always unpleasant and therefore also an emotional experience.”³⁹ In contrast, “[a]ctivity induced in the nociceptor and nociceptive pathways by a noxious stimulus is not pain, which is always a psychological state, even though we may well appreciate that pain most often has a proximate physical cause.”⁴⁰

Simply put, pain is a negative sensory and mental experience, an emotional feeling of distress, suffering, or agony, whereas nociception is the physical, unconscious response to noxious stimuli that results in a behavioral or physiological change.⁴¹ Consider the following example: If one were given local anesthesia before a dentist extracted a tooth, one’s nociceptors—nerve fibers that produce the sensation of pain when they are stimulated by tissue-damaging or noxious stimuli—would respond to the tissue damage, yet the feeling of pain would be blocked. Physiologically, one’s body would respond (e.g., inflammation), but pain would not be experienced until the anesthesia dissipated.

In humans, the conscious, negative experience is an intrinsic component of pain.⁴² In fish, however, some scientists and laypersons have questioned whether it is reasonable to assume that pain can explain some of the avoidance responses by fish to various noxious stimuli, such as being hooked, netted, electrically shocked, clubbed, cut, or mutilated. That is, debate has arisen, and research undertaken, to examine the capability of fish to feel pain.

The Neuroanatomical Argument

In an interview with Gord Ellis, fishing editor of *Ontario Out of Doors Magazine*, University of Wyoming Professor of Zoology and Physiology James D. Rose reportedly said:

It's generally agreed upon among scientists who study pain that the actual experience of pain is a psychological thing and that it's completely separate from the behavioural reactions.... The key issue is the distinction between nociception and pain. A person who is anaesthetized in an operating room, or has had a bad head injury, will respond physically to external stimulation, but he or she will not feel pain. Anyone who has seen a chicken with its head cut off will know that, while its body can respond to stimuli, it cannot be feeling pain.... Some fish species certainly do have nociceptive neurones similar to those found in a human. However, this means only that these animals are capable of sensing noxious stimuli; it provides no evidence for the psychological experience of pain.⁴³

In 2002, Rose published "The Neurobehavioral Nature of Fishes and the Question of Awareness and Pain,"⁴⁴ a literature survey conducted at the behest of the American Fisheries Society.⁴⁵ In his paper, Rose argues that fish cannot feel pain because they do not possess the neocortex, a neuroanatomical structure that, in humans, is associated with conscious awareness. As fish do not possess a neocortex, he concludes that avoidance and pain-like behaviors exhibited by fish are mere unconscious, reflexive responses, akin to the automatic, knee-jerk response humans perform when tapped on the knee. Further, neocortically damaged humans have no consciousness, yet noxious stimulation applied to the faces of these impaired patients can evoke facial grimaces and flinches reminiscent of a person in pain, though the patients are unaware of their own reflexive responses. Similarly, Rose contends that when a fish darts away from an electric shock or the sharp teeth of a predator, for example, that avoidance behavior is not caused by pain, but rather is a behavioral response to negative stimulation—a reflexive, unconscious display of pain-like behavior.⁴⁶

While Rose was not the first to introduce the idea of fish insentience due to a structural brain difference,⁴⁷ his 2002 paper was widely received and is currently a frequently cited reference used by those arguing against the concept of fish pain. In contrast, however, research scientists have presented counterarguments to the neuroanatomical debate, revealing fundamental flaws in Rose's reasoning.^{48,49,50}

Rose's comparison of normal, healthy, fish brain anatomy to a pathological, vegetative state in humans is logically and scientifically unsound, and his assertion that the neocortex is the sole means by which pain can be experienced suggests that it is the seat of consciousness. However, a cursory review of the neurobiology of consciousness^{51,52,53,54} shows both the complexity of the phenomenon of consciousness and that conscious phenomena, such as pain, are not restricted to any one location in the brain.⁵⁵ Additionally, the neocortex is unique to mammals. Were the presence of a large, considerably developed neocortex the requirement for experiencing pain, as Rose suggests, his theory would eliminate birds, amphibians, other non-mammalian animals, and even some mammals from having the capacity of feeling pain,⁵⁶ which is unfounded.^{57,58,59}

An international consortium funded in part by the National Institutes of Health published a report in the February 2005 issue of *Nature Reviews Neuroscience* that found that the "brains of birds appear to be more similar to those of mammals than previously thought.... Previous opinion held that the malleable behavior of mammals required the higher-order neocortex found in mammals. But collected genetic, behavioral, and molecular evidence shows that, although the structures are organized differently, areas of the avian brain perform functions similar to those of the mammalian neocortex, which is responsible for performing sensory information processing."⁶⁰ Similarly, scientific studies have shown that although fish do not possess the exact brain structures that humans do, their brains are both homologous (derived from a common ancestor) and functionally analogous (functioning in a like manner) to the mammalian brain.^{61,62} For example, in teleost fish, the lateral and medial pallia are proposed to be homologous to the mammalian hippocampus (the brain region primarily responsible for memory) and amygdala (a region in forebrain and part of the limbic system involved in the production of emotional responses like fear), respectively.^{63,64,65,66} Studies have found that lesions to the fish lateral pallium result in significant deficits in learning and memory, while lesions to the medial pallium disrupt avoidance learning and fear conditioning, evidence that fish possess functionally analogous brain structures to more derived vertebrate mammals.⁶⁷ Findings also indicate that some fish forebrains have functionally distinct regions and that these are homologous to some major mammalian brain structures.⁶⁸ The brains of many fishes undergo a developmentally different process from the mammalian brain in that the mammalian neural tube, the embryological structure from which the brain and spinal cord develop,⁶⁹ folds in on itself, while the teleost fish

neural tube folds outward.⁷⁰ This difference in neurological development means that in comparison to the mammalian brain, the major fish forebrain structures develop in reverse order.⁷¹ Irrespective of the placement of many of the main structures in the fish brain, their existence, most importantly, has been confirmed.

Through a variety of scientific techniques, researchers have found many similarities in neuroanatomical structure between fish and land-based vertebrates, from gross regional structures to finer neuronal structures,⁷² and neurobiological evidence proposes that there is strong structural conservation throughout evolution.⁷³ Dunlop and Laming extended the idea of investigating brain structures and examined the central nervous system. Recordings were taken from the spinal cord, cerebellum, tectum, and telencephalon of goldfish and trout after the animals were exposed to various stimuli, including noxious pin-prods and heated prods, as well as such neutral sensory stimuli as being stroked with a paint brush. Neuronal responses were elicited in each of these regions of the central nervous system, and, as responses were detected from the spinal cord up to the telencephalon, the scientists determined the existence of an ascending nociceptive pathway. Indeed, responses confined to the dorsal root ganglion, would suggest simple reflexive nociception. However, activity in the higher brain centers, such as the telencephalon, suggest the ability of pain perception.⁷⁴ The researchers propose that the fish telencephalon may therefore be a center for processing pain information, as the neocortex does in mammals. As a primary question regarding pain perception is whether nociceptive responses are simply reflexive responses, this finding provides evidence of the awareness of pain, not merely an unconscious, physical reaction.

The Physiological Argument

Historically, lack of information pertaining to pain perception in fish, coupled with the few early studies that attempted to investigate nociception in some lesser-derived fish species, suggested that the aquatic animals did not have nociceptors and therefore were unable to experience pain.⁷⁵ This supported the belief that the concept of fish pain was both speculative and subjective.⁷⁶

The interest in fish welfare has resulted in an expansion in fish pain research. Neville Gregory,[‡] professor at the University of London's Royal Veterinary College,⁷⁷ helped spawn the scientific inquiry into developing what he considered to be the criteria for the assessment of pain in fish:

1. to establish whether fish have the neurotransmitter, neuron types, and brain structures known to convey information about pain in mammals;
2. to expose fish to what humans would consider painful stimuli, evaluate their responses, and then determine whether these pain-like responses can be suppressed with analgesic drugs that, in turn, can be suppressed by analgesic blockers; and
3. to investigate whether fish can learn to associate aversive stimuli with neutral conditioned cues and whether the animals would then respond with appropriate avoidance behavior when exposed only to those cues, providing evidence that fish are capable of anticipation and that avoidance responses are less likely to be governed by reflexive mechanisms stimulated only by the presence of the negative stimulus itself.⁷⁸

With respect to the first criterion, Sneddon *et al.*'s ground-breaking study on fish pain revealed that fish do indeed possess nociceptors capable of detecting tissue-damaging stimuli such as mechanical pressure (e.g., physical force), excessive temperature (e.g., hot prod), and chemical irritation (e.g., acetic acid). (See Figure 1 below.[§]) This study not only discovered the physical location of the nociceptors on the rainbow trout's head, but also that the nociceptive nerves have some identical properties to those described in the pain system of more derived vertebrate animals. Fish nociceptors, similar to those in mammals, are linked to two categories of nerve

[‡] Dr. Gregory also serves as chair in Animal Welfare Physiology jointly supported by the Royal Veterinary College and the Biotechnology and Biological Sciences Research Council, and has authored more than 290 scientific papers

[§] Reprinted with permission. Sneddon LU, Braithwaite VA, and Gentle MJ. 2003. Do fishes have nociceptors? Evidence for the evolution of a vertebrate sensory system. *Proceedings of the Royal Society of London* 270(1520): 1117.

fiber that arise as free nerve endings in the skin and differ in diameter and information transmission speed. The A-delta fibers, small in diameter and myelinated, are associated with immediate or “pricking” pain, whereas the even smaller, unmyelinated C fibers are associated with dull, aching, or chronic pain. In the rainbow trout, out of the four different types of nerve fibers, A-delta and C fibers act as nociceptors: A-delta fibers comprise about 25% and are more abundant than C fibers, which comprise approximately 4%. In contrast, C fibers can compose up to 50% of all fiber types in mammals.^{79,80} This proportional difference in the presence of A-delta compared with C fibers between fish and mammals is of unclear significance, but may be merely a reflection of evolutionary divergence. Nonetheless, a nociceptive system similar to the mammalian system has been found to exist in fish. Thus, fish such as trout possess the necessary neuroanatomy and neurophysiology to transduce and process information that would be regarded as painful in humans.⁸¹

Chervova *et al* addressed Gregory’s second criterion in research studies conducted more than a decade ago. The scientists found that fish demonstrated strong aversive tail-flick responses to electric shock, fin pinching, and needle pricking, and that their pain-like response decreased in strength with increasing dosages of opioids and analgesics.^{82,83} With respect to reversing the effects of opioid drugs, studies have shown that the delivery of naloxone, an opioid receptor blocker, reverses the analgesic effect of morphine in different species of fish.^{84,85} Likewise, exogenous analgesic compounds like morphine has been shown to increase pain tolerance in fish who are subjected to painful stimuli.^{86,87} These results are consistent with the fact that opioid receptors and endogenous opioids are found in the spinal cords and brains of fish.⁸⁸

Numerous scientific studies have fulfilled the third and final criterion outlined by Gregory, determining that fish are capable of learning avoidance tasks. Many types of fish species can learn quickly to associate neutral stimuli with aversive stimuli and consequently use these cues to anticipate and therefore avoid the negative stimuli completely.^{89,90,91,92}

It is well-established that fish experience chemical and physiological stress responses in a manner similar to mammals. Fish produce the same stress hormones and release them within a similar physiological pathway.^{93,94} Like mammals, fish show a generalized stress reaction that can be categorized into its primary, secondary, and tertiary responses. The primary response consists of neuroendocrine responses, which include the rapid release of stress hormones such as adrenaline and cortisol. These stress hormones can then activate metabolic pathways in the secondary response phase, which can alter blood chemistry and hematology (e.g., changes in blood glucose concentration). The tertiary response reflects changes in the whole animal; examples include negative effects such as lowered immune function and decreased growth and reproductive capacity.⁹⁵ This general physiological stress response is almost identical to that found in the mammalian system.⁹⁶

Indeed, non-human animals, with their similar underlying physiology, have been used in psychopharmacological studies investigating emotional states and predicated upon the assumption that the animals used are sentient individuals able to experience feelings like pain, anxiety, and fear, similarly to human beings.⁹⁷ Studies of broiler chickens suffering from leg problems have shown that they will preferentially choose diets laden with analgesics,⁹⁸ indicating that the birds were attempting to alleviate their leg pain, and studies of rats have shown that they will self-administer psychostimulant drugs like amphetamine, cocaine, morphine, and heroin after having experienced them before.^{99,100,101,102,103} Similarly, fish have been used in studies that

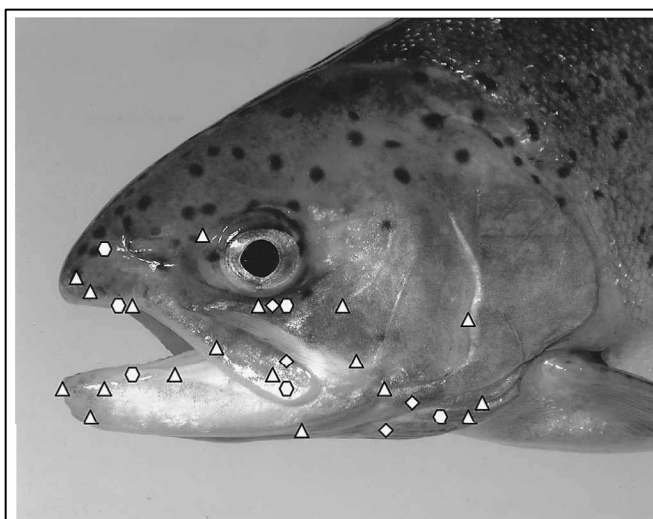


Figure 1. Position of polymodal mechanoreceptors or nociceptors, mechanothermal receptors and mechanochemical receptors on the head and face of the rainbow trout, *Oncorhynchus mykiss* (triangles, polymodal nociceptor; diamonds, mechanothermal nociceptor; hexagons, mechanochemical receptor).

investigate the hedonic effects of addictive drugs. Having similar dopaminergic pathways to mammals, research has shown that fish will seek out the effects of cocaine after initial exposure to the drug.¹⁰⁴

In fish, as in mammals, dopaminergic cell bodies and Substance P terminals are found in the nervous system.^{105,106,107} Substance P is a peptide neurotransmitter that modulates pain sensitivity by activating the neurokinin-1 (NK-1) receptor, which is expressed by groups of neurons throughout the central nervous system. The Substance P peptide is produced by small-diameter sensory pain fibers and is released into the dorsal horn of the spinal cord following noxious peripheral stimulation, promoting an increased sensitivity to pain.¹⁰⁸ Substance P, which is associated with pain transmission, has been found in the central nervous system of fish, with the highest concentrations found in the hypothalamus and forebrain.¹⁰⁹ The similar pain pathways and biochemical mediation of nociception are in many ways similar to those of land-based vertebrates, suggesting the capability of pain perception.¹¹⁰ As such, it follows that fish show pain responses in nociceptive behavioral tests much as mammals do. The convincing body of physiological evidence shows that fish do have the ability for subjective experiences such as pain.

The Behavioral Argument

Traditionally, fish have been viewed by some as simplistic animals¹¹¹—unintelligent and with a limited behavioral repertoire and severely compromised memory—leading to the discounting of their ability to feel pain. In reality, however, fish are neither behaviorally deficient nor cognitively impaired. Fish do not have the ability to make facial expressions and, relative to mammalian animals, have a limited ability for postural changes and vocalizations. Therefore they do not exhibit familiar mammalian responses such as screaming, crying, whimpering, flattening their ears, tucking their tails between their legs, or raising their hackles when threatened. Fish react to threatening or stressful stimuli in more subtle ways such as color changes,^{112,113,114} alterations to their level of movement by swimming rapidly or becoming immobile,^{115,116} and water column utilization by swimming in the upper, middle, or bottom depths of the water.^{117,118} Cautioned Michael Stoskopf, Professor of Aquatics, Wildlife, and Zoologic Medicine and of Molecular and Environmental Toxicology at North Carolina University, “It would be an unjustified error to assume that fish do not perceive pain in these situations merely because their responses do not match those traditionally seen in mammals subjected to chronic pain....”¹¹⁹ Indeed, even a cursory scientific literature search reveals an abundance of data devoted to behavioral and cognitive study of fish.^{120,121,122}

In one such study, pain perception in goldfish and rainbow trout was investigated by using flexible learning ability. Researchers used spatially cued behavioral responses of the fish to noxious stimuli. Individual fish were placed into a test tank, and, whenever an animal swam into a particular region of the tank, electric shocks of low or high intensities were administered to the skin where nociceptors are known to be located. In response to the electric shocks, both species of fish showed escape and avoidance behaviors, such as becoming immobile and erratic, high-speed “panic” swimming, and eventually learned to avoid the electrified areas. The scientists found that this escape and avoidance behavior changed significantly when a conspecific, a fish of the same species, was put into the tank with them. Rather than avoiding the zone where low-shock intensity was delivered, rainbow trout elected to stay in the electrified area for the opportunity to be near a conspecific. In contrast, goldfish were unwilling to spend time either in the low- or high-electrical stimulating zones in order to be near a conspecific, despite having spent a significant amount of time in these zones during periods of non-stimulation. The researchers explained this difference in behavior as illustrating the difference in social habits of the two species: Goldfish are not truly social animals, whereas trout may have a need for shoaling (swimming in a synchronous group), particularly during threatening situations. The findings of this study show that painful shock avoidance in fish is not purely a reflex response; fish have purposeful control over their own behavior.¹²³

The behavioral component of Sneddon *et al.*'s nociceptor study also suggests that the trout's behavioral responses to noxious stimulation are modulated by higher cognitive function. The researchers designed a feeding experiment to quantify the animals' level of motivation to eat after undergoing presumably painful treatments.¹²⁴ Motivational states are often considered to be affective states (those that describe an animal's mental state or mood),¹²⁵ and changes in emotional state result in changes in cognitive processing and

behavior.^{126,127} To investigate how pain affects motivational states, the scientists put trout in tanks containing a food-dispensing apparatus. Before the experiment began, fish were trained to swim to the dispenser to retrieve food pellets upon a light cue. Once fish had learned this task, they were divided into four groups: The fish in one group received no treatment, those in the second group had their mouths injected with saline, the third had their lips injected with acetic acid solution, and the animals in the fourth group were given bee venom. Acetic acid solution and bee venom are known to cause inflammation and irritation in mammals, and constituted the noxious treatments. When given the chance to feed upon light cue again, the trout treated with the noxious stimuli showed significantly prolonged suppression to regain feeding behavior compared to the control groups. The researchers also noticed dramatically increased opercula beat rates (gill or ventilation rates), which indicated physiological stress.¹²⁸ Abnormal behaviors were observed as well. Fish in the two noxiously treated groups rocked from side to side on their pectoral fins while resting on substrate, indicating a negative emotional response or discomfort.^{129,130} Fish whose lips were treated with acetic acid were also observed rubbing their snouts against tank walls and bottom substrate. These behaviors were not seen in the two control groups. The researchers interpreted these results as a reflection of not only underlying changes in physiology, but also the demonstration of the experience of pain.¹³¹

In another behavioral study, Sneddon *et al.* investigated the interaction of avoidance behavior and fear to better understand the phenomenon of pain perception in fish. It is known that trout are typically neophobic, showing fearful avoidance behavior towards novel objects, and either stay away from or require a significant amount of time to approach an unknown object. Sneddon *et al.* investigated the trout's attentional state by placing a novel object, in this case a brightly colored plastic object, into the holding tanks and comparing the avoidance responses of control fish who had been injected in the snout with innocuous saline and test fish who had been injected in the snout with noxious acetic acid. While the control group avoided the novel object, thereby behaving as expected given trout's neophobia, the test fish treated with the noxious acid spent more time closer to the plastic object. The researchers explained this difference in behavior as an impairment of attentional state or avoidance behavior by the test fish due to their distractions caused by the experience of noxious stimulation, or pain.¹³²

This theory begged the question as to what would happen if the fish were given an analgesic. The researchers were able to show that the attentional deficit was reversed with intramuscular injection of morphine sulfate, a pain reliever. That is, once the test fish who had been injected with noxious acetic acid received an analgesic, both the control and test groups demonstrated comparable levels of avoidance behavior towards the novel object. Sneddon's team suggested that the provision of analgesia reduced pain, which therefore reinstated attention and fear toward the novel object and thereby diminished the impairment of the avoidance response in the test fish.¹³³ Very similar results have been seen in the human scientific literature, as it is known that pain can interfere with cognitive tasks. For example, patients suffering from painful fibromyalgia can suffer from concentration and memory deficits.¹³⁴ Sneddon *et al.* concluded that their results, along with the growing body of literature in fish welfare, provide sufficient evidence to show the fulfillment of criteria for animal pain, at a minimum with regard to rainbow trout.¹³⁵

Conclusion

On the basis of scientific evidence, fish have the capacity for experiencing and feeling pain. In a review of fish nociception and pain, Sneddon followed a set of pain criteria developed by Patrick Bateson, emeritus professor of ethology at the University of Cambridge and president of the Zoological Society of London,¹³⁶ and successfully determined multiple scientific examples from fish data that fulfilled each requirement,^{137,138,139} similar to the way in which Gregory's criteria for pain have been addressed.¹⁴⁰

Indeed, the typical arguments against fish pain perception are easily refutable. For some time, a challenge in understanding non-human animals' emotions and behaviors was steeped in our inability to communicate verbally with them, thereby making the lack of common language a primary barrier. However, behavioral tests have allowed animals to express their perceptions, preferences, aversions, and prioritization of desires. This enables conscious experiences to be accessible for scientific investigation.¹⁴¹ Said Marion Stamp Dawkins,

Professor of Animal Behavior at the University of Oxford and Vice-Principal of Somerville College, behavioral tests allow animals to “vote with their feet”¹⁴² or, in this case, with their fins.

Ample behavioral, physiological, neurobiological, and pharmacological evidence exists to support the thesis that fish are capable of suffering from pain.^{143,144} Posited Gregory, “The appropriate question appears not to be *do fish feel pain?* but rather, *what types of pain do fish experience?*”¹⁴⁵

¹ National Oceanic and Atmospheric Administration Office of Sustainable Fisheries. 1998. NOAA’s Aquaculture Policy. http://aquaculture.noaa.gov/pdf/17_noaaAqpolicy.pdf. Accessed September 4, 2008.

² Håstein T. 2004. Animal welfare issues relating to aquaculture. In: Proceedings of the global conference on animal welfare: an OIE initiative, Paris, February 23-25 (Luxembourg: Office for Official Publications of the European Communities, pp. 219-31).

³ Food and Agriculture Organization of the United Nations. 2006. Nearly half of all fish eaten today farmed, not caught. FAO Newsroom, September. www.fao.org/newsroom/en/news/2006/1000383/index.html. Accessed September 4, 2008.

⁴ Food and Agriculture Organization of the United Nations. 2006. Nearly half of all fish eaten today farmed, not caught. FAO Newsroom, September. www.fao.org/newsroom/en/news/2006/1000383/index.html. Accessed September 4, 2008.

⁵ Food and Agriculture Organization of the United Nations. 2008. FAOSTAT. <http://faostat.fao.org/>. Accessed September 4, 2008.

⁶ U.S. Department of Agriculture National Agricultural Statistics Service. 2006. Census of aquaculture (2005). 2002 Census of Agriculture Volume 3: Special Studies, Part 2.

⁷ National Oceanic and Atmospheric Administration National Marine Fisheries Service. 2007. U.S. aquaculture production in 2005. FishWatch: U.S. Seafood Facts. www.nmfs.noaa.gov/fishwatch/images/aquaculture_production_exp.gif. Accessed September 4, 2008.

⁸ Fisheries Society of the British Isles. 2002. Fish welfare. Briefing Paper 2. Fisheries Society of the British Isles, Granta Information Systems. www.fsbi.org.uk/docs/brief-welfare-refs.pdf. Accessed September 4, 2008.

⁹ Huntingford FA, Adams C, Braithwaite VA, et al. 2006. Current issues in fish welfare. *Journal of Fish Biology* 68(2):332-72.

¹⁰ Conte FS. 2004. Stress and the welfare of cultured fish. *Applied Animal Behaviour Science* 86(3-4):205-23.

¹¹ Schwedler TE and Johnson SK. 2000. Animal welfare issues: responsible care and health maintenance of fish in commercial aquaculture. U.S. Department of Agriculture Animal Welfare Information Center Bulletin, Winter 1999/2000. www.nal.usda.gov/awic/newsletters/v10n3/10n3schw.htm. Accessed September 4, 2008.

¹² Wedemeyer GA. 1997. Effects of rearing conditions on the health and physiological quality of fish in intensive culture. In: Iwama GK, Pickering AD, Sumpter JP, and Schreck CB (eds.), *Fish Stress and Health in Aquaculture: Society for Experimental Biology Seminar Series 62* (Cambridge, U.K.: Cambridge University Press, pp. 35-71).

¹³ Håstein T. 2004. Animal welfare issues relating to aquaculture. In: Proceedings of the global conference on animal welfare: an OIE initiative, Paris, February 23-25 (Luxembourg: Office for Official Publications of the European Communities, pp. 219-31).

¹⁴ Håstein T, Scarfe AD, and Lund VL. 2005. Science-based assessment of welfare: aquatic animals. *Revue Scientifique et Technique (International Office of Epizootics)* 24(2):529-47.

¹⁵ Ashley PJ. 2007. Fish welfare: current issues in aquaculture. *Applied Animal Behaviour Science* 104:199-235.

¹⁶ Damsgård B, Juell JE, and Braastad BO. 2006. Welfare in farmed fish. *Fiskeriforskning*, Report 5/2006. www.fiskeriforskning.no/content/download/1226258/2566567/file/Rapport+05-2006+Welfare+in+farmed+fish.pdf. Accessed September 4, 2008.

¹⁷ Schreck CB, Olla BL, and Davis MW. 1997. Behavioral responses to stress. In: Iwama GK, Pickering AD, Sumpter JP, and Schreck CB (eds.), *Fish Stress and Health in Aquaculture: Society for Experimental Biology Seminar Series 62* (Cambridge, U.K.: Cambridge University Press, pp. 145-70).

¹⁸ Pickering AD. 1998. Stress responses of farmed fish. In: Black KD and Pickering AD (eds.), *Biology of Farmed Fish* (Sheffield, U.K.: Sheffield Academic Press, pp. 222-55).

-
- ¹⁹ Pottinger TG and Pickering AD. 1997. Genetic basis to the stress response: selective breeding for stress-tolerant fish. In: Iwama GK, Pickering AD, Sumpter JP, and Schreck CB (eds.), *Fish Stress and Health in Aquaculture: Society for Experimental Biology Seminar Series 62* (Cambridge, U.K.: Cambridge University Press, pp. 171-93).
- ²⁰ Barton BA and Iwama GK. 1991. Physiological changes in fish from stress in aquaculture with emphasis on the response and effects of corticosteroids. *Annual Review of Fish Diseases* 1:3-26.
- ²¹ Sneddon LU, Braithwaite VA, and Gentle MJ. 2003. Do fishes have nociceptors? Evidence for the evolution of a vertebrate sensory system. *Proceedings of the Royal Society of London. Series B, Biological Sciences* 270:1115-21.
- ²² Broom DM. 2001. Evolution of pain. In: Soulsby ELJ and Morton D (eds.), *Pain: Its Nature and Management in Man and Animals* (London, U.K.: Royal Society of Medicine Press, pp. 17-25).
- ²³ Rose JD. 2002. The neurobehavioral nature of fishes and the question of awareness and pain. *Reviews in Fisheries Science* 10(1):1-38.
- ²⁴ Chandroo KP, Duncan IJH, and Moccia RD. 2004. Can fish suffer?: perspectives on sentience, pain, fear and stress. *Applied Animal Behaviour Science* 86(3-4):225-50.
- ²⁵ Chandroo KP, Yue S, and Moccia RD. 2004. An evaluation of current perspectives on consciousness and pain in fishes. *Fish and Fisheries* 5:281-95.
- ²⁶ Braithwaite VA and Boulcott P. 2007. Pain perception, aversion and fear in fish. *Diseases of Aquatic Organisms* 75:131-8.
- ²⁷ Rose JD. 2007. Anthropomorphism and 'mental welfare' of fishes. *Diseases of Aquatic Organisms* 75:139-54.
- ²⁸ Bshary R, Wickler W, and Fricke H. 2002. Fish cognition: a primate's eye view. *Animal Cognition* 5:1-13.
- ²⁹ Bateson P. 1991. Assessment of pain in animals. *Animal Behaviour* 42:827-39.
- ³⁰ Broom DM. 2001. Evolution of pain. In: Soulsby ELJ and Morton D (eds.), *Pain: Its Nature and Management in Man and Animals* (London, U.K.: Royal Society of Medicine Press, pp. 17-25).
- ³¹ Acerbi A and Parisi D. 2007. The evolution of pain. In: Costa FAE, Rocha LM, Costa E, Harvey I, and Coutinho A (eds.), *Advances in Artificial Life. Proceedings of the 9th European Conference on Artificial Life (ECAL 2007)* (Berlin, Germany: Springer, pp. 816-24).
- ³² Rosemberg S, Marie SKN, and Kliemann S. 1994. Congenital insensitivity to pain with anhidrosis (hereditary sensory and autonomic neuropathy type IV). *Pediatric Neurology* 11(1):50-6.
- ³³ Harrison P. 1991. Do animals feel pain? *Philosophy* 66(255):25-40.
- ³⁴ Erickson HH. 2005. Animal pain. *Journal of Applied Physiology* 56:1135-6.
- ³⁵ Dawkins MS. 2000. Animal minds and animal emotions. *American Zoologist* 40:883-8.
- ³⁶ Broom DM. 2001. Evolution of pain. In: Soulsby ELJ and Morton D (eds.), *Pain: Its Nature and Management in Man and Animals* (London, U.K.: Royal Society of Medicine Press, pp. 17-25).
- ³⁷ Sohlberg S, Mejdell C, Ranheim B, and Soli NE. 2004. [Opinions about feeling pain by fish, true or nonsense? A literature review]. *Norsk Veterinærtidsskrift* 116:429-38.
- ³⁸ International Association for the Study of Pain. 2008. IASP pain terminology. www.iasp-pain.org/AM/Template.cfm?Section=Home&template=/CM/HTMLDisplay.cfm&ContentID=3088#Pain. Accessed September 4, 2008.
- ³⁹ International Association for the Study of Pain. 2008. IASP pain terminology. www.iasp-pain.org/AM/Template.cfm?Section=Home&template=/CM/HTMLDisplay.cfm&ContentID=3088#Pain. Accessed September 4, 2008.
- ⁴⁰ International Association for the Study of Pain. 2008. IASP pain terminology. www.iasp-pain.org/AM/Template.cfm?Section=Home&template=/CM/HTMLDisplay.cfm&ContentID=3088#Pain. Accessed September 4, 2008.
- ⁴¹ Robertson SA. 2002. What is pain? *Journal of the American Veterinary Medical Association* 221(2):202-5.
- ⁴² Rose JD. 2002. The neurobehavioral nature of fishes and the question of awareness and pain. *Reviews in Fisheries Science* 10:1-38.
- ⁴³ Ellis G. Do fish feel pain? www.gordellis.com/articles/other_03.htm. Accessed September 4, 2008.
- ⁴⁴ Rose JD. 2002. The neurobehavioral nature of fishes and the question of awareness and pain. *Reviews in Fisheries Science* 10:1-38.
- ⁴⁵ Ellis G. Do fish feel pain? www.gordellis.com/articles/other_03.htm. Accessed September 4, 2008.

-
- ⁴⁶ Rose JD. 2002. The neurobehavioral nature of fishes and the question of awareness and pain. *Reviews in Fisheries Science* 10:1-38.
- ⁴⁷ LaChat MR. 1996. An argument in defense of fishing. *Fisheries* 21(7):20-1.
- ⁴⁸ Chandroo KP, Duncan IJH, and Moccia RD. 2004. Can fish suffer?: perspectives on sentience, pain, fear and stress. *Applied Animal Behaviour Science* 86(3-4):225-50.
- ⁴⁹ Chandroo KP, Yue S, and Moccia RD. 2004. An evaluation of current perspectives on consciousness and pain in fishes. *Fish and Fisheries* 5:281-95.
- ⁵⁰ Huntingford FA, Adams C, Braithwaite VA, et al. 2006. Current issues in fish welfare. *Journal of Fish Biology* 68:332-72.
- ⁵¹ Damasio AR. 1999. *The Feeling of What Happens: Body and Emotion in the Making of Consciousness* (New York, NY: Harcourt Brace & Company).
- ⁵² Searle JR. 2000. Consciousness. *Annual Review of Neuroscience* 23:557-78.
- ⁵³ Zeman A. 2001. Consciousness. *Brain* 124(7):1263-89.
- ⁵⁴ Seth AK, Baars BJ, and Edelman DB. 2005. Criteria for consciousness in humans and other mammals. *Consciousness and Cognition* 14:119-39.
- ⁵⁵ Brooks J and Tracey I. 2005. From nociception to pain perception: imaging the spinal and supraspinal pathways. *Journal of Anatomy* 207:19-33.
- ⁵⁶ Cooke SJ and Sneddon LU. 2007. Animal welfare perspectives on recreational angling. *Applied Animal Behaviour Science* 104:176-98.
- ⁵⁷ Gentle MJ. 1992. Pain in birds. *Animal Welfare* 1:235-47.
- ⁵⁸ Machin KL. 2001. Fish, amphibian, and reptile analgesia. *The Veterinary Clinics of North America. Exotic Animal Practice* 4:19-33.
- ⁵⁹ Stevens CW. 2004. Opioid research in amphibians: an alternative pain model yielding insights on the evolution of opioid receptors. *Brain Research Reviews* 46:204-15.
- ⁶⁰ Medical News Today. 2005. Birds' brains more similar to those of mammals than previously thought. *MedicalNewsToday.com*, February 8. www.medicalnewstoday.com/articles/19719.php. Accessed September 4, 2008.
- ⁶¹ Portavella M and Vargas JP. 2005. Emotional and spatial learning in goldfish is dependent on different telencephalic pallial systems. *European Journal of Neuroscience* 21:2800-6.
- ⁶² Salas C, Broglio C, Durán E, et al. 2006. Neuropsychology of learning and memory in teleost fish. *Zebrafish* 3(2):157-71.
- ⁶³ Portavella M and Vargas JP. 2005. Emotional and spatial learning in goldfish is dependent on different telencephalic pallial systems. *European Journal of Neuroscience* 21:2800-6.
- ⁶⁴ Shrager Y, Bayley PJ, Bontempi B, Hopkins RO, and Squire LR. 2007. Spatial memory and the human hippocampus. *Proceedings of the National Academy of Sciences of the United States of America* 104:2961-6.
- ⁶⁵ Davis M. 1992. The role of the amygdala in fear and anxiety. *Annual Review of Neuroscience* 15:353-75.
- ⁶⁶ LeDoux JE. 1996. *The Emotional Brain: The Mysterious Underpinnings of Emotional Life* (New York, NY: Simon & Schuster).
- ⁶⁷ Broglio C, Gómez A, Durán E, et al. 2005. Hallmarks of a common forebrain vertebrate plan: specialized pallial areas for spatial, temporal and emotional memory in actinopterygian fish. *Brain Research Bulletin* 66:277-81.
- ⁶⁸ Butler AB. 2000. Topography and topology of the teleost telencephalon: a paradox resolved. *Neuroscience Letters* 293:95-8.
- ⁶⁹ 1996. *The Bantam Medical Dictionary: Second Revised Edition* (New York, NY: Bantam Books).
- ⁷⁰ Rodríguez F, Broglio C, Durán E, Gómez A, and Salas C. 2006. Neural mechanisms of learning in teleost fish. In: Brown C, Laland K, and Krause J (eds.), *Fish Cognition and Behavior* (Oxford, U.K.: Blackwell Publishing Ltd., pp. 243-77).
- ⁷¹ Rodríguez F, Broglio C, Durán E, Gómez A, and Salas C. 2006. Neural mechanisms of learning in teleost fish. In: Brown C, Laland K, and Krause J (eds.), *Fish Cognition and Behavior* (Oxford, U.K.: Blackwell Publishing Ltd., pp. 243-77).
- ⁷² Echteler SM and Saidel WM. 1981. Forebrain connections in the goldfish support telencephalic homologies with land vertebrates. *Science* 212(4495):683-5.

-
- ⁷³ Edelman DB, Baars BJ, and Seth AK. 2005. Identifying hallmarks of consciousness in non-mammalian species. *Consciousness and Cognition* 14:169-87.
- ⁷⁴ Dunlop R and Laming P. 2005. Mechanoreceptive and nociceptive responses in the central nervous system of goldfish (*Carassius auratus*) and trout (*Oncorhynchus mykiss*). *The Journal of Pain* 6(9):561-8.
- ⁷⁵ Sneddon LU, Braithwaite VA, and Gentle MJ. 2003. Do fishes have nociceptors? Evidence for the evolution of a vertebrate sensory system. *Proceedings of the Royal Society of London. Series B, Biological Sciences* 270:1115-21.
- ⁷⁶ Chandroo KP, Duncan IJH, and Moccia RD. 2004. Can fish suffer?: perspectives on sentience, pain, fear and stress. *Applied Animal Behaviour Science* 86(3-4):225-50.
- ⁷⁷ Gregory N. 2007. Royal Veterinary College staff home page: Professor Neville Gregory. www.rvc.ac.uk/AboutUs/Staff/ngregory/index.cfm. Accessed September 4, 2008.
- ⁷⁸ Gregory N. 1999. Do fish feel pain? *ANZCCART News* 12(4):1-3.
- ⁷⁹ Sneddon LU. 2003. Trigeminal somatosensory innervation of the head of a teleost fish with particular reference to nociception. *Brain Research* 972:44-52.
- ⁸⁰ Braithwaite VA and Boulcott P. 2007. Pain perception, aversion and fear in fish. *Diseases of Aquatic Organisms* 75:131-8.
- ⁸¹ Braithwaite VA and Boulcott P. 2007. Pain perception, aversion and fear in fish. *Diseases of Aquatic Organisms* 75:131-8.
- ⁸² Chervova LS, Lapshin DN, and Kamenskii AA. 1994. Pain sensitivity of trout and analgesia induced by intranasal administration of dermorphine. *Doklady Biological Sciences* 338:424-5.
- ⁸³ Chervova LS. 1997. Pain sensitivity and behavior of fishes. *Journal of Ichthyology* 37(1):98-102.
- ⁸⁴ Ehrensing RH, Michell GF, and Kastin AJ. 1982. Similar antagonism of morphine analgesia by MIF-1 and naloxone in *Carassius auratus*. *Pharmacology Biochemistry and Behavior* 17:757-61.
- ⁸⁵ Chervova LS and Lapshin DN. 2000. Opioid modulation of pain threshold in fish. *Doklady Biological Sciences* 375:590-1.
- ⁸⁶ Ehrensing RH, Michell GF, and Kastin AJ. 1982. Similar antagonism of morphine analgesia by MIF-1 and naloxone in *Carassius auratus*. *Pharmacology Biochemistry and Behavior* 17:757-61.
- ⁸⁷ Sneddon LU. 2003. The evidence for pain in fish: the use of morphine as an analgesic. *Applied Animal Behaviour Science* 83:153-62.
- ⁸⁸ Sneddon LU. 2004. Evolution of nociception in vertebrates: comparative analysis of lower vertebrates. *Brain Research Reviews* 46:123-30.
- ⁸⁹ Behrend ER and Bitterman ME. 1964. Avoidance-conditioning in the fish: further studies of the CS-US interval. *The American Journal of Psychology* 77(1):15-28.
- ⁹⁰ Gallon RL. 1972. Effects of pretraining with fear and escape conditioning on shuttlebox avoidance acquisition by goldfish. *Psychological Reports* 31:919-24.
- ⁹¹ Piront ML and Schmidt R. 1988. Inhibition of long-term memory formation by anti-ependymin antisera after active shock-avoidance learning in goldfish. *Brain Research* 442:53-62.
- ⁹² Zhuikov AY, Couvillon PA, and Bitterman ME. 1994. Quantitative two-process analysis of avoidance conditioning in goldfish. *Journal of Experimental Psychology* 20(1):32-43.
- ⁹³ Donaldson EM. 1981. The pituitary-interrenal axis as an indicator of stress in fish. In: Pickering AD (ed.), *Stress and Fish*. (London: Academic Press, pp. 11-47).
- ⁹⁴ Mazeaud MM and Mazeaud F. 1981. Adrenergic responses to stress in fish. In: Pickering AD (ed.), *Stress and Fish* (London, U.K.: Academic Press, pp. 49-75).
- ⁹⁵ Iwama GK. 2007. The welfare of fish. *Diseases of Aquatic Organisms* 75:155-8.
- ⁹⁶ Sumpter JP. 1997. The endocrinology of stress. In: Iwama GK, Pickering AD, Sumpter JP, and Schreck CB (eds.), *Fish Stress and Health in Aquaculture* (Cambridge, U.K.: Cambridge University Press, pp. 95-118).
- ⁹⁷ Sherwin CM. 2001. Can invertebrates suffer? Or, how robust is argument-by-analogy? *Animal Welfare* 10:S103-18.
- ⁹⁸ Danbury TC, Weeks CA, Chambers JP, Waterman-Pearson AE, and Kestin SC. 2000. Self-selection of the analgesic drug carprofen by lame broiler chickens. *The Veterinary Record* 146:307-11.
- ⁹⁹ Deminiere JM, Piazza PV, Le Moal M, and Simon H. 1989. Experimental approach to individual vulnerability to psychostimulant addiction. *Neuroscience & Biobehavioral Reviews* 13:141-7.

-
- ¹⁰⁰ Parker LA. 1992. Place conditioning in a three- or four-choice apparatus: role of stimulus novelty in drug-induced place conditioning. *Behavioral Neuroscience* 106(2):294-306.
- ¹⁰¹ Klebaur JE, Bevins RA, Segar TM, and Bardo MT. 2001. Individual differences in behavioral responses to novelty and amphetamine self-administration in male and female rats. *Behavioural Pharmacology* 12(4):267-75.
- ¹⁰² Kearns DN, Weiss SJ, and Panlilio LV. 2002. Conditioned suppression of behavior maintained by cocaine self-administration. *Drug and Alcohol Dependence* 65:253-61.
- ¹⁰³ Lenoir M and Ahmed SH. 2007. Heroin-induced reinstatement is specific to compulsive heroin use and dissociable from heroin reward and sensitization. *Neuropsychopharmacology* 32:616-24.
- ¹⁰⁴ Darland T and Dowling JE. 2001. Behavioral screening for cocaine sensitivity in mutagenized zebrafish. *Proceedings of the National Academy of Sciences of the United States of America* 98(20):11691-6.
- ¹⁰⁵ Hornby PJ, Piekut DT, and Demsky LS. 1987. Localization of immunoreactive tyrosine hydroxylase in the goldfish brain. *The Journal of Comparative Neurology* 261(1):1-14.
- ¹⁰⁶ Sharma SC, Berthoud VM, and Breckwoldt R. 1989. Distribution of substance P-like immunoreactivity in the goldfish brain. *The Journal of Comparative Neurology* 279(1):104-16.
- ¹⁰⁷ Mattioli R, Santangelo EM, Costa ACC, and Vasconcelos L. 1997. Substance P facilitates memory in goldfish in an appetitively motivated learning task. *Behavioural Brain Research* 85:117-20.
- ¹⁰⁸ De Felipe C, Herrero JF, O'Brien JA, et al. 1998. Altered nociception, analgesia and aggression in mice lacking the receptor for substance P. *Nature* 392:394-7.
- ¹⁰⁹ Kestin SC. 1994. Pain and stress in fish. A report prepared for the Royal Society for the Prevention of Cruelty to Animals, citing: Kelly JS. 1979. Report of the panel of enquiry into shooting and angling (1976-1979). Chaired by Lord Medway.
- ¹¹⁰ Chandroo KP, Duncan IJH, and Moccia RD. 2004. Can fish suffer?: perspectives on sentience, pain, fear and stress. *Applied Animal Behaviour Science* 86(3-4):225-50.
- ¹¹¹ Call J. 2002. A fish-eye lens for comparative studies: broadening the scope of animal cognition. *Animal Cognition* 5:15-6.
- ¹¹² O'Connor KI, Metcalfe NB, and Taylor AC. 1999. Does darkening signal submission in territorial contests between juvenile Atlantic salmon, *Salmo salar*? *Animal Behaviour* 58:1269-76.
- ¹¹³ Höglund E, Balm PHM, and Winberg S. 2000. Skin darkening, a potential social signal in subordinate arctic charr (*Salvelinus alpinus*): the regulatory role of brain monoamines and pro-opiomelanocortin-derived peptides. *The Journal of Experimental Biology* 203:1711-21.
- ¹¹⁴ Endo M, Kumahara C, Yoshida T, and Tabata M. 2002. Reduced stress and increased immune responses in Nile tilapia kept under self-feeding conditions. *Fisheries Science* 68:253-7.
- ¹¹⁵ Huntingford FA. 1990. Fear and the suppression of behavioural responses in fish. In: Brain PF, Parmigiani S, Blanchard RJ, and Mainardi D (eds.), *Fear and Defence* (London: Harwood Academic Publishers, pp. 41-67).
- ¹¹⁶ Yue S, Moccia RD, and Duncan IJH. 2004. Investigating fear in domestic rainbow trout, *Oncorhynchus mykiss*, using an avoidance learning task. *Applied Animal Behaviour Science* 87:343-54.
- ¹¹⁷ Sloman KA, Metcalfe NB, Taylor AC, and Gilmour KM. 2001. Plasma cortisol concentrations before and after social stress in rainbow trout and brown trout. *Physiological and Biochemical Zoology* 74(3):383-9.
- ¹¹⁸ Sloman KA, Montpetit CJ, and Gilmour KM. 2002. Modulation of catecholamine release and cortisol secretion by social interactions in the rainbow trout, *Oncorhynchus mykiss*. *General and Comparative Endocrinology* 127:136-46.
- ¹¹⁹ Stoskopf MK. 1994. Pain and analgesia in birds, reptiles, amphibians, and fish. *Investigative Ophthalmology & Visual Science* 35(2):775-80.
- ¹²⁰ Bshary R, Wickler W, and Fricke H. 2002. Fish cognition: a primate's eye view. *Animal Cognition* 5:1-13.
- ¹²¹ Laland KN, Brown C, and Krause J. 2003. Learning in fishes: from three-second memory to culture. *Fish and Fisheries* 4:199-202.
- ¹²² Brown C, Laland K, and Krause J. 2006. *Fish Cognition and Behavior*. Fish and Aquatic Resources Series 11 (Cambridge, U.K.: Blackwell Publishing Ltd.).
- ¹²³ Dunlop R, Millsopp S, and Laming P. 2006. Avoidance learning in goldfish (*Carassius auratus*) and trout (*Oncorhynchus mykiss*) and implications for pain perception. *Applied Animal Behaviour Science* 97:255-71.

-
- ¹²⁴ Sneddon LU, Braithwaite VA, and Gentle MJ. 2003. Do fishes have nociceptors? Evidence for the evolution of a vertebrate sensory system. *Proceedings of the Royal Society of London. Series B, Biological Sciences* 270:1115-21.
- ¹²⁵ Paul ES, Harding EJ, and Mendl M. 2005. Measuring emotional processes in animals: the utility of a cognitive approach. *Neuroscience and Biobehavioral Reviews* 29:469-91.
- ¹²⁶ Harding EJ, Paul ES, and Mendl M. 2004. Cognitive bias and affective state. *Nature* 427:312.
- ¹²⁷ Paul ES, Harding EJ, and Mendl M. 2005. Measuring emotional processes in animals: the utility of a cognitive approach. *Neuroscience and Biobehavioral Reviews* 29:469-91.
- ¹²⁸ Sneddon LU, Braithwaite VA, and Gentle MJ. 2003. Do fishes have nociceptors? Evidence for the evolution of a vertebrate sensory system. *Proceedings of the Royal Society of London. Series B, Biological Sciences* 270:1115-21.
- ¹²⁹ Uchida K, Kuwada H, and Tsukamoto K. 1993. Tilting behaviour, a fear response to frightening stimuli, as a possible predictive index for stocking effectiveness in the juveniles of red sea bream *Pagrus major*. *Nippon Suisan Gakkaishi* 59(6):991-9.
- ¹³⁰ Sneddon LU, Braithwaite VA, and Gentle MJ. 2003. Do fishes have nociceptors? Evidence for the evolution of a vertebrate sensory system. *Proceedings of the Royal Society of London. Series B, Biological Sciences* 270:1115-21.
- ¹³¹ Sneddon LU, Braithwaite VA, and Gentle MJ. 2003. Do fishes have nociceptors? Evidence for the evolution of a vertebrate sensory system. *Proceedings of the Royal Society of London. Series B, Biological Sciences* 270:1115-21.
- ¹³² Sneddon LU, Braithwaite VA, and Gentle MJ. 2003. Novel object test: examining nociception and fear in the rainbow trout. *The Journal of Pain* 4(8):431-40.
- ¹³³ Sneddon LU, Braithwaite VA, and Gentle MJ. 2003. Novel object test: examining nociception and fear in the rainbow trout. *The Journal of Pain* 4(8):431-40.
- ¹³⁴ Grace GM, Nielson WR, Hopkins M, and Berg MA. 1999. Concentration and memory deficits in patients with fibromyalgia syndrome. *Journal of Clinical and Experimental Neuropsychology* 21(4):477-87.
- ¹³⁵ Sneddon LU, Braithwaite VA, and Gentle MJ. 2003. Novel object test: examining nociception and fear in the rainbow trout. *The Journal of Pain* 4(8):431-40.
- ¹³⁶ Bateson P. 1991. Assessment of pain in animals. *Animal Behaviour* 42:827-39.
- ¹³⁷ Sneddon LU, Braithwaite VA, and Gentle MJ. 2003. Novel object test: examining nociception and fear in the rainbow trout. *The Journal of Pain* 4(8):431-40.
- ¹³⁸ Sneddon LU. 2004. Evolution of nociception in vertebrates: comparative analysis of lower vertebrates. *Brain Research Reviews* 46:123-30.
- ¹³⁹ Sneddon LU. 2004. Evolution of nociception in vertebrates: comparative analysis of lower vertebrates. *Brain Research Reviews* 46:123-30.
- ¹⁴⁰ Gregory N. 1999. Do fish feel pain? *ANZCCART News* 12(4):1-3.
- ¹⁴¹ Wemelsfelder F. 2001. The inside and outside aspects of consciousness: complementary approaches to the study of animal emotion. *Animal Welfare* 10:S129-39.
- ¹⁴² Dawkins MS. 1977. Do hens suffer in battery cages? *Environmental preferences and welfare. Animal Behaviour* 25:1034-46.
- ¹⁴³ Chandroo KP, Duncan IJH, and Moccia RD. 2004. Can fish suffer?: perspectives on sentience, pain, fear and stress. *Applied Animal Behaviour Science* 86(3-4):225-50.
- ¹⁴⁴ Chandroo KP, Yue S, and Moccia RD. 2004. An evaluation of current perspectives on consciousness and pain in fishes. *Fish and Fisheries* 5:281-95.
- ¹⁴⁵ Gregory N. 1999. Can fish experience pain? *Surveillance* 26(3):8-10.

The Humane Society of the United States is the nation's largest animal protection organization—backed by 10 million Americans, or one of every 30. For more than a half-century, The HSUS has been fighting for the protection of all animals through advocacy, education, and hands-on programs. Celebrating animals and confronting cruelty. On the Web at humanesociety.org.