Anthropomorphism and 'mental welfare' of fishes

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ABSTRACT: Anthropomorphism, the use of human characteristics as a foundation for interpreting behavior and mental capacities of animals, is a bias undermining our understanding of other species, especially species as evolutionarily distant from humans as fishes. Anthropomorphism is not justified by allusions to evolutionary continuity among vertebrates, because no living vertebrate was ever a descendant of humans, so none could have inherited human traits. Nonetheless, it has recently been claimed that fishes are capable of conscious experiences of pain and emotional feelings and that mental welfare is an important issue for fishes. This paper shows that the evidence supporting claims for experiences of pain or conscious emotions by fishes is conceptually and methodologically flawed. In addition, the paper shows that the natural history and behavior of diverse fish species is inconsistent with a presumption of human-like awareness. This behavioral evidence is in accord with neurobiological observations showing that fishes are very different from us and are unlikely to have a capacity for awareness of pain or emotional feelings that meaningfully resemble our own. The factors that are detrimental to fish welfare have been well delineated by valid, objective indicators of physiological and behavioral well-being. This knowledge should guide welfare decisions. An empirical and non-anthropomorphic examination of diverse fishes and their adaptations should be the foundation for welfare decisions that would be truly beneficial to fishes and humans alike.

KEY WORDS: Pain · Nociception · Feelings · Emotion · Evolutionary continuity · Consciousness · Construct validity

ANTHROPOMORPHISM UNDERMINES UNDERSTANDING OF FISHES

Some have argued that fishes have human-like feelings and mental states and that these alleged mental capacities should dictate decisions about fish welfare. This paper's thesis is that fishes are psychologically very different from humans and that an accurate understanding of the nature and welfare needs of diverse fishes requires abandonment of anthropomorphism, the human-centered viewpoint. Many of the points developed here would apply, to some extent, in considerations of animals besides fishes.

We know little with certainty about the minds of others

A fact of life is that we know only our own personal experiences. Our beliefs about experiences of others are always a conjecture, which is encouraged by the apparently innate human psychological trait of 'theory of mind.' This theory of mind causes us to interpret statements and actions of others as reflecting thoughts and feelings we would have in comparable circumstances (Siegal & Varley 2002, Povinelli 2004). Even though we are all members of the same species, we can be deceived by others or we can be simply mistaken concerning the mental states of other humans. In comparison, how confidently could we interpret the possible feelings of an orca as it kills a minke whale by ramming and asphyxiation (Ford et al. 2005)? Is it justified to conclude that the orca is callously delighting in killing the whale, or should we be more cautious and allow for the likelihood that our interpretations might not apply well to the orca? The difficulty of making appropriate decisions concerning the mental states of a very different animal, especially a taxon as diverse and evolutionarily distant from us as fishes, is profoundly greater. Welfare decisions concerning such different species should be predicated on a thorough and accurate examination of the natural behavior and life history

of each species. It would be inappropriate and likely erroneous to make welfare judgments on the basis of how I would feel in a particular situation if I were a fish.

Considerations of the welfare of an individual fish seem very hypothetical and academic when the normal existence of fishes is examined. The lifestyle of billions of individual fishes is one of predation, involving perpetual eating of fishes by other fishes and by many other vertebrate or invertebrate predators. In addition to this, disease is commonplace, as are threats from adverse changes in habitat. Most fishes do not survive to reproductive maturity, but the reproductive adaptations of fishes compensate for this. Individual survival is obviously not as relevant as the transmission of a species' genotype.

The difference between life and death in the world of fishes is often decided in milliseconds. It is instructive to watch a group of bonefish scouring the bottom of a Bahamian flat for invertebrate prey as a shark cruises nearby. The feeding bonefish do not appear to be influenced by the shark's presence, despite the fact that an explosive attack could occur at any time. Instead, they are competing with each other for food. Are the bonefish worried and perpetually in terror? Or are they simply aroused, vigilant, and poised to escape a suddenly looming marine or aerial attacker? Boredom or daydreaming would not be states conducive to bonefish survival. Does it make sense to suppose that these human experiences might exist in a bonefish?

Applied anthropomorphism

Human-centered thinking is a prejudice, a bias, a distorting lens between the affected individual and an objective perspective that is essential to accurately understand other organisms, especially fishes. The problem of anthropomorphism in the study of animal behavior and mental functioning has waxed and waned historically, but it is very evident at the present time (Wynne 2004a,b). In a compelling critique of the resurgent anthropomorphism in animal behavior and behavioral ecology research, Kennedy (1992) argued that anthropomorphism is a fundamental human affliction, difficult to escape, but which undermines our efforts to understand animals. More recent books by Macphail (1998), Budiansky (1998), and Wynne (2004b) also demonstrate how the abandonment of parsimonious, objective explanations of behavior and a tendency to humanize interpretations of animal cognition and behavior are commonly wrong as well as misleading. Over time, there has tended to be a corrective influence in behavioral science, in which some of the most extravagant claims, like a capacity for true language ability in dolphins or apes, is eventually challenged on grounds of the evidence and its interpretation (Macphail 1998, Donald 2001, Wynne 2004b, Terrace & Metcalfe 2005).

To be sure, there have been defenses of anthropomorphism by its practitioners, such as de Wall's argument that resistance to anthropomorphism could constitute 'anthropodenial' in which science might fail to recognize legitimate instances of human-like mental processes in animals (see Wynne 2004a). While there might be some heuristic value in generalizing from humans in studies of species like primates, which have a relatively close evolutionary relatedness to us, anthropomorphic thinking must be done with caution, use of non-teleological language (Kennedy 1992), and full recognition that the animal in question is not a human.

A rather different approach is what Burghardt called 'critical anthropomorphism' (Morton et al. 1990). In contrast to extreme anthropomorphism, in which animals are personified and treated as humans, or misplaced empathy, in which animals' unique natures and adaptations, such as tolerance of heat or cold, are unrecognized, critical anthropomorphism is supposed to be based on an objective understanding of a given animal. Critical anthropomorphism '...requires a willingness to incorporate objective knowledge of an animal's natural history, nervous system, domestication.... It also incorporates the ethological view that animals are adapted to a wide range of environments by evolution...' (Morton et al. 1990, p. 19). The objective evidence regarding the responsiveness of the animal to potentially detrimental conditions is also recognized to be a foundation for understanding the animal in question. In matters of welfare, though, it seems that some people cling to anthropomorphic beliefs because they feel that giving up these beliefs would relegate animals to a lesser status or undermine humane treatment. However, proponents of critical anthropomorphism argue that using knowledge of an animal's species-typical biology, ethology, and psychology will produce improved treatment. How well this unfolds depends greatly on how accurately we actually understand these variables, especially the most elusive: the species' psychology. I will argue for an approach similar to critical anthropomorphism in evaluating the issue of mental welfare in fishes. In contrast, I will maintain that using human traits as a framework for understanding the mentality of animals, particularly those as remotely related to us as fishes, always puts the evolutionary cart before the horse.

Does learning by fishes show that they are conscious?

Recently, a straw man argument has been used to try to elevate the status of fishes. For example, it has been

asserted by Laland et al. (2003, p. 3) that new evidence showing learning by fishes proves that they have more than an '... 'infamous 3 second memory.' Now they are regarded as steeped in social intelligence, pursuing Machiavellian strategies of manipulation, punishment and reconciliation...' In contrast to this statement, extensive evidence showing that fishes can learn and have durable memories has existed for many years (reviewed in Macphail 1982). Therefore, no informed person would believe such a misconception about their memory. However, learning ability in fishes is no basis for a revolution in how we view a fish's place in the natural world or our place relative to fish. Regarding this tendency toward trans-species egalitarianism, Donald (2001, p. 114) has said: 'We can all become relativists… simply by redefining 'intelligence' so that the term becomes meaningless. This achieves nothing and fools no one. Intelligence or cognitive capacity is one thing. Adaptability to an environment is something else altogether. Sometimes adaptability demands intelligence. Most of the time it doesn't, which is fortunate indeed, for most species.' Actually, complex behavior has long been recognized in many invertebrates. While using anthropomorphically loaded terms like 'Machiavellian' may seem to promote the status of fishes, attempting to humanize them ultimately retards understanding of their real natures. Liberating us from simplistic misconceptions of fishes is good, but anthropomorphism of this type explains nothing and 'risks bringing back the dirty bathwater as we rescue the baby' (Wynne 2004a, p. 606).

As Macphail (1998) explained, associative, procedural learning is the fundamental form evident throughout the animal kingdom, but this type of learning is unconscious, even in humans. Invertebrates, most of which have nervous systems without any real brain-like organization, are capable of robust procedural learning, but that is not a reason for equating them with dogs and cats. Additional modes of learning in the domain of explicit (consciously-mediated) learning and memory have apparently appeared relatively recently in the evolution of humans and possibly great apes and some other mammals (Macphail 1998, Hampton 2005). Some have argued that certain birds have explicit memory, but several, less revolutionary alternative explanations for these results exist (Schwartz 2005) and such claims are far from accepted by mainstream investigators of learning, memory, and consciousness (Donald 2001, Hampton 2005). Reports that fishes are capable of complex learning (Laland et al. 2003) are being used to support a further claim that they are conscious and thereby capable of feeling pain and suffering (Huntingford et al. 2006). There are significant problems with this argument. First, although the learning of fishes is highly adaptive, occurs in a wide variety of contexts, and takes forms resembling learning by land vertebrates, assertions that this learning is of the explicit variety are unconvincing. Second, consciousness is thought to be necessary for explicit learning and memory, but it does not follow that a capacity for explicit learning and memory proves that all functional requirements for experiencing pain or suffering, a very different neuropsychological domain, are present.

Anthropomorphism is a problem specific to mentalistic interpretations of fish and other animals

It seems much easier to respect the physical and physiological characteristics of a fish as a foundation for welfare decisions than its psychological traits, whatever those might be. Someone in charge of managing captive fishes in a large aquarium exhibit would logically design feeding practices, water quality parameters, species composition, space, lighting, and cover on the basis of the best objective information about the species in question. Why, then, would someone responsible for the welfare of fishes resort to a human-centered point of view in issues such as pain, suffering, and emotional distress? The species-typical traits of fishes do not stop and become human-like or mammal-like at some 'psychological' level that is miraculously different from their other behavioral and physiological attributes. Fishes are different from us because their brains are very different from ours (Rose 2002). There is no human-like creature hidden in a fish brain. Furthermore, a fish brain is not a miniature human or mammal brain, but is very different in critical respects, especially at the level of the cerebral hemispheres (Rose 2002).

Anthropomorphism lacks construct validity

The terms we use to describe human experiences are not valid or suitable for fishes. Words like fear or pain were devised by humans to describe human experiences. We do not assume that a barracuda might feel some kind of 'blood lust' that would motivate its lethal assault on a school of baitfish and that it would (or should) feel 'guilt' afterward. Do we believe that spawning salmon are 'in love'? If it is alleged that fish can feel fear, suffering, or happiness, for instance, it should be made explicit what is meant by these terms. Is it really implied that the hypothetical state in a fish is actually very similar to the human understanding of what the words mean? What objective evidence validates this conjecture? Unfortunately, as we will see, these questions are not being answered by those who

propose that fishes have human-like psychological experiences.

One of the most standard and vital practices in science is operationism, the requirement that the words used to identify variables in a scientific study be defined in objectively identifiable ways, especially ways that permit quantification. Thus, one might define a measure of 'stress' by quantifying plasma cortisol levels or 'fear' by immobility. In the former case, we would also require the use of a well-validated cortisol assay. However, before one can conclude that the operational definition of stress or fear really reflects our conception of these terms, we must establish that these variables have construct validity, that is, that they actually mean what we imply that they mean (Trochim 2001). When the variable being measured is a direct expression of the phenomenon of interest (e.g. elevated cortisol and stress), the problem of validity is not so difficult. In contrast, mental states and psychological processes are very problematic. The observable variable cannot be taken to actually reflect the psychological variable unless the operationally defined variable is shown to have validity, i.e. it actually measures the construct of interest (Trochim 2001). This technical requirement is a standard concern in psychology but appears to be less appreciated in fish welfare discussions. In many recent publications and media statements, mentalistic terms have been used to describe the psychological properties of fishes without regard for the matter of construct validity. A recent paper authored by the Fisheries Society of the British Isles (FSBI 2002) states that mental suffering is a 'welfare domain' for fishes, and asserts that 'conditions that produce unacceptable levels of anxiety, fear, distress, boredom, sickness, pain, thirst, hunger and so on should be minimized in fish as in other vertebrates, but we know little about such states in fish or how to recognize them' (p. 18). Constructs like fear, pain, and boredom are difficult to validate. Just because they appear to have face validity, that they have a surface resemblance to the thing we want to understand, it cannot be presumed that we all know or agree as to what these words mean. It is essential to show that a measure actually equates with the construct of interest. As discussed below, the research alleging to show pain, fear, or other mental states in fishes (Sneddon 2003, Sneddon et al. 2003a,b, Yue et al. 2004) does not adequately address the essential matter of construct validity.

Welfare implications of anthropomorphism

If one is really interested in understanding the welfare needs of fishes, that purpose is best served by avoiding extreme anthropomorphism and adopting a scrupulously open, empirical point of view focusing on the nature, adaptations, and diversity of these organisms. Contrary to the perspective that the welfare of animals is fostered by *a priori* assumptions that they must be similar to us, I would argue that a more parsimonious and objective approach is more likely to lead us to valid understanding. An anthropomorphic viewpoint is not appropriate for deciding the physical needs of fishes, such as water quality or diet, and, likewise, there is no justification for being anthropomorphic about their 'psychological' needs. The potential costs of anthropomorphism are misguided beliefs and mistaken policies, but there is no risk in being unbiased and objective. If fishes are in fact very like us, this will be discovered too, but with greater certainty.

NOCICEPTION IS NOT PAIN AND EMOTIONS ARE NOT FEELINGS

Protective reactions to noxious stimuli are a universal characteristic of animal life. These reactions occur in the simplest life forms like amoebas, which have no nervous system but will move away from potentially injurious chemical or mechanical stimuli. Many invertebrates, like starfish, have no brain, only sensory receptors connected through a nerve ring to contractile cells that cause movements in response to noxious stimuli. Thus, protective reactions do not require a complex nervous system and occur in animals that are incapable of conscious awareness. Even exceedingly complex protective reactions, like immune responses, can occur wholly unconsciously.

One of the most important advances in the scientific study of pain (Rose 2002) is the realization that pain is a purely conscious experience and separate from behavioral and physiological reactions to injury. According to the Society for the Scientific Study of Pain (Price 1999, Rose 2002), pain has a sensory-perceptual aspect and an emotional-feeling aspect. The perceptual part tells us that we have been injured, like the first sensation when you hit your thumb with a hammer. The emotional-feeling part is separate, as the suffering that follows after we first become aware of hitting our thumb. In contrast to pain, nociception is the non-conscious processing of noxious stimuli. Injury-detecting sensory receptors are called nociptors, not pain receptors, because pain is a conscious experience due to processing by higher-order cortical regions in our brain and is not simply due to nociptor activation (Rose 2002). Accordingly, pain is not an invariable result of nociptor activation. Nociception includes behavioral and physiological responses that range from simple limb withdrawal reflexes to more complex behaviors like vocalizing, grimacing, and

avoiding the noxious stimulus. Thus, given these complex behaviors, it is incorrect to define pain as being any response more than a 'simple reflex,' as Sneddon et al. (2003a) and Sneddon (2003) have done in recent studies of rainbow trout. In addition, part of an organism's defense against nociceptive stimuli is an ability to learn to avoid situations where nociceptive stimuli have occurred. However, as explained above, this kind of learning is non-conscious procedural learning, which is why it is present even in primitive invertebrates. Therefore, evidence of an earthworm or a fish learning to avoid nociceptive stimuli is not evidence that they experience pain.

Emotion is to feelings as nociception is to pain

Extensive recent research on emotions has revealed a relationship between emotions and feelings comparable to that between nociception and pain (Rose 2002). This idea was put forth by LeDoux (1996) and more fully articulated by Berridge & Winkielman (2003) and Damasio (2005). In this way of understanding affective responses, emotions are identified as the fundamental unconscious visceral, behavioral, hormonal, and neural responses to positive and aversive stimuli or situations, including learned reactions to these stimuli. Emotions are autonomous and functional in their own right, but they also provide the pre-conscious, raw material for the experience of feelings, which arise through further processing at a conscious level by higher cortical regions (Fig. 1), essentially the same regions that underlie the conscious experience of suffering in pain. This use of the terms emotion and feeling has not attained the standardized practice that nociception and pain have. However, understanding the nociception-pain and emotion-feeling distinction is the key to comprehending the difference between fishes and humans in their capacities for experiencing pain or conscious suffering.

Fish 'pain' and the Schiavo case

A failure to understand the nociception-pain and emotion-feeling distinction was a principal factor contributing to the confusion and contentiousness of the recent case of Theresa (Terri) Schiavo (Thogmartin 2005). In 1990, Mrs. Schiavo collapsed and experienced a period of anoxia which caused extensive, irreversible damage to her cerebral cortex. Examining neurologists agreed that she was unconscious in a persistent vegetative state, which, due to its long duration, was irreversible. For a period of years her husband fought a legal battle to have the feeding tube removed

from his wife. This effort was resisted by her parents and eventually many others, including politicians and government officials. A factor contributing to this controversy was a series of video recordings of Mrs. Schiavo, which showed her to be awake, quite reactive to noxious stimuli, and seeming to exhibit emotional behaviors. People unaware of the dissociation between wakefulness and consciousness as well as the capacity of an unconscious, decorticate human to exhibit such behaviors, were convinced that she must be aware and capable of experiencing pain, suffering, and other feelings. These individuals stated that Mrs. Schiavo's behaviors were consciously mediated because they were more than 'simple reflexes,' an argument we shall revisit. Eventually, the medical evidence led to a court decision permitting removal of the feeding tube, and Mrs. Schiavo died of dehydration. A subsequent autopsy confirmed that her cerebral cortex had massively degenerated, a fact consistent with the diagnosis of unconsciousness (Thogmartin 2005).

The Schiavo case applies directly to contentions that fishes feel pain (or other emotional feelings) in that the responses of fish, which do not have the cerebral structures essential for conscious awareness of pain or feelings, can exhibit a wide range of normal behaviors with their cerebral hemispheres removed (reviewed in Rose 2002). These behaviors include learning to avoid noxious stimuli, feeding, spawning, and other social interactions. Thus, these behaviors of fishes, like the reactions of Mrs. Schiavo, are examples of unconscious nociception and emotion and other processes that are mediated by subcortical brain and spinal structures (Berridge & Winkielman 2003, Damasio 2005). In fishes, however, a far more complete range of behavior is present without the cerebral hemispheres. That is, while a human is a more cerebral cortex-dependent organism, a fish is a far more brainstem-dependent organism (Rose 2002). It is possible to propose that fishes have other brain structures that could perform the same functions as the human cerebral cortex, but the burden of proof for such a proposal is on the individual making it. There are no undedicated regions in a fish brain that could take on the task of generating consciousness. The fish brainstem, for example, is fully devoted to functions similar to those of the mammalian brainstem (Rose 2002).

CLAIMS FOR FISH PAIN, FEAR, AND SUFFERING ARE PREDICATED ON ANTHROPOMORPHIC THINKING AND LACK CONSTRUCT VALIDITY

A series of papers by Sneddon and associates (Sneddon 2003, Sneddon et al. 2003a,b) have been put forth by these authors as evidence for conscious pain and

fear experienced by rainbow trout and other fishes. The evidence and interpretations presented by these authors are flawed in many critical respects.
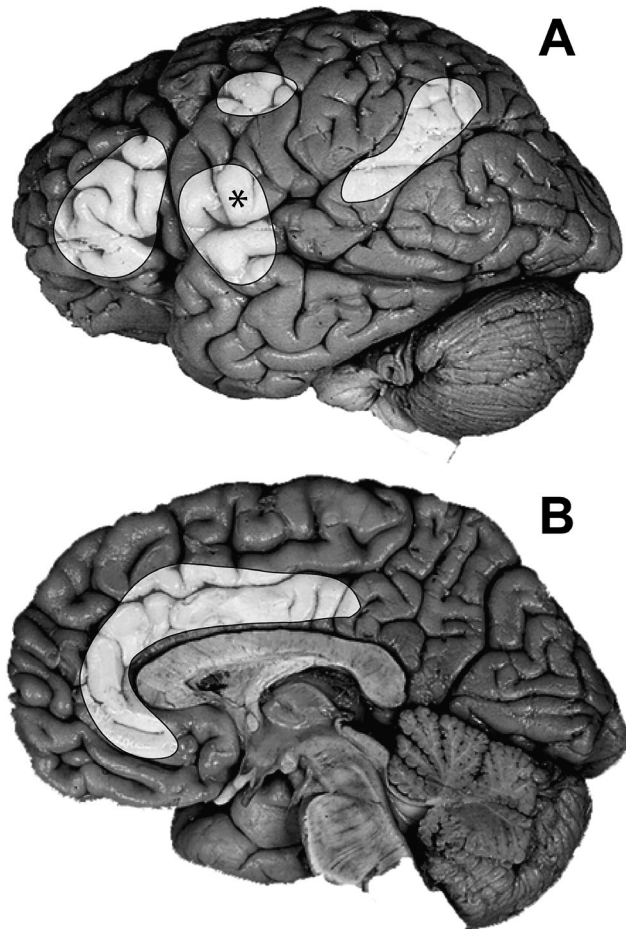

Fig. 1. Pain systems in the human brain. Modern human brain imaging techniques like functional magnetic resonance imaging and positron emission tomography have yielded a wealth of information about the brain regions that are responsible for pain. These imaging studies have repeatedly shown the highlighted neocortical areas depicted in (A) and (B) to be activated specifically during the reported experience of pain. Diverse evidence, in addition to these imaging studies, has led pain investigators to conclude that these are the brain structures that generate the pain experience (reviewed in Rose 2002). Fishes have no brain structures that are comparable to these neocortical regions nor do they have a 'substitute' brain system for pain. The region designated by the asterisk in (A) includes a deep cortical zone, the insula, which is not visible in this view of the brain surface. (B) The midline of the brain, with a region of the cingulate gyrus highlighted. The cingulate gyrus is a structural variant of the neocortex that is part of the collective ensemble of the mammalian neocortex. Recent research (e.g. Rose 2002, Damasio 2005) has shown that a virtually identical system of brain structures is responsible for human feelings, i.e. the conscious aspect of preconscious emotional reactions. See text for further explanation. Original brain image supplied courtesy of J. Sundsten, University of Washington

A highly publicized example of a claim for pain experience by rainbow trout was a paper by Sneddon et al. (2003a) describing nociceptors, but neither it nor its sequel (Sneddon 2003) actually provided any proof that fish can experience pain or can suffer. The most serious problem with these papers is that the authors' definitions of pain and nociception were invalid. The behaviors used as an indication of pain were not distinguished from purely unconscious nociceptive responses. Furthermore, in order to prove that a fish experiences pain, it is necessary to show that a fish has consciousness. Without consciousness, there is no pain in a fish, a human, or any other organism. None of the fish behaviors in the Sneddon et al. (2003a,b) papers require or prove the involvement of consciousness.

In the behavioral experiments by Sneddon et al. (2003a), large volumes of bee venom, acetic acid solution, or saline were injected into the jaws of rainbow trout. These volumes of liquid were equivalent to injecting more than 100 ml of venom or acid solution into the lip of a human. However, despite the large injections of venom or acid, manipulations that would cause severe pain to a human, the trout actually showed remarkably little effect. Their activity level was not changed, they did not hide under a shelter in the tank, and they fed spontaneously in less than 3 h. Furthermore, fish that received no injection at all or fish that received a saline injection did not feed, on average, for 1 h and 20 min. Thus, a large saline injection (which would have been very painful to a human) produced no more effect than handling alone.

These outcomes contradict allegations that the trout were in pain. First, sustained pain should have triggered an endocrine stress response, initiated by brain release of corticotrophin-releasing factor (crf), which causes locomotor activation in vertebrates, including increased swimming in salmonids (Lowry & Moore 2006). No change in swimming occurred. Second, suppression of feeding is regarded as a cardinal effect of stressful or noxious stimuli in fishes (Iwama et al. 1997, Huntingford et al. 2006) and is also an effect of stress-related crf release (Bernier 2006). The comparatively rapid initiation of feeding (relative to uninjected or vehicle-injected trout) is inconsistent with a presumption that the trout were suffering from pain, particularly if the effect of the acid persists for 5 to 6 h (Sneddon et al. 2003b). Third, while acid and venom-injected fish showed an infrequent rocking behavior (about once every 2 to 3 min), there is no reason to believe that it was more than an unconscious effect on balance, rather than an indication of 'pain.' Fourth, it was reported that acid-injected fish sometimes 'rubbed' their mouths against the gravel, but the venom-injected fish did not. The authors concluded that mouth rubbing was due to pain. If so, why did the

venom-injected fish, that were also supposed to be in pain, not perform this behavior? If mouth rubbing were really due to pain or even nociception, any method for producing nociception should produce this behavior. This interpretation of mouth rubbing is a clear violation of construct validity, an essential standard in the measurement of psychological variables. Furthermore, these authors interpreted the longer time to resume feeding by the venom or acid-injected trout as representing avoidance of mouth stimulation. If so, why did the trout rub their mouths on gravel to reduce pain? These interpretations are clearly contradictory as well as non-validated. In short, the mouth rubbing, feeding suppression, and rocking put forth as behavioral assays for pain lack essential validation or even logically consistent interpretation.

One of the few effects actually produced by the acid or venom injections was an elevated opercular beat rate. This response could have resulted from various physiological effects of the acid or venom, especially gill irritation due to leakage from the injection site. However, even if increased opercular beat rate was due to nociceptive stimulation of the mouth, this non-consciously-controlled movement proves nothing about conscious pain.

When it is considered that the acid and venom injections would presumably have produced a large scale and sustained nociceptor activation (Sneddon 2003, Sneddon et al. 2003a), it is remarkable that the injections had so little effect. Rather than proving a capacity for pain, these results suggest resilience to oral trauma by the trout.

The description of the mouth rubbing behavior by Sneddon et al. (2003a) was reminiscent of a behavior I observed in a study on rainbow trout with whirling disease (Rose et al. 2000). We determined that the characteristic circular swimming and several other aberrant behaviors were due to abnormal development of the skull and vertebrae, causing a marked compression of the brainstem and spinal cord. One of the abnormal behaviors was swimming with the mouth in contact with the bottom of the aquarium. This behavior, similar to the 'mouth rubbing' behavior reported by Sneddon et al. (2003a) was frequent, but not as conspicuous as the other behaviors, so it was not reported. Had we been inclined toward anthropomorphic interpretations in the whirling disease study, we might have said that whirling behavior occurred because the fish were frightened, and swimming with the mouth in contact with the bottom of the tank could have been an effort to keep a low profile and reduce visibility while fleeing. However, we proposed a more parsimonious interpretation that was consistent with the known neural control of locomotion and posture in fishes.

In a subsequent paper, Sneddon (2003) reported that mouth rubbing behavior after an oral acid injection was reduced by morphine and concluded this to be proof that mouth rubbing was an indication of pain. As I explained in an earlier paper (Rose 2002), opiates exert their effects mainly at the spinal cord and brainstem, on non-conscious levels of function. Therefore, morphine effects on responses to noxious stimuli can occur entirely through actions on nociception (or other kinds of unconscious neurobehavioral functioning) and constitute no evidence that the trout were feeling pain. Also, opiates have diverse effects on the nervous system in addition to reducing nociceptive signaling (Strand 1999), so there is no certainty that the morphine effect was even specific to nociception.

Sneddon et al. (2003b) have tried to bolster their claims for fish pain by stating that the 'anomalous' behaviors produced by acid or venom injections satisfy the criteria for 'animal pain.' The problem with this assertion is that their criteria for animal pain are based on invalid and outdated conceptions of pain and its neural basis. Their criteria were (Sneddon et al. 2003b, p. 438): '(1) to show that the animal has the same apparatus to detect a noxious stimulus that humans have, (2) to demonstrate that a noxious event has adverse behavioral and physiologic effects, (3) the animal should learn to avoid this noxious stimulus, and (4) the behavioral impairments during a noxious event should not be simple reflexes.' However, these criteria are contradicted by extensive evidence that was presented earlier (Rose 2002). The first criterion requires only the presence of nociceptors, which by themselves are insufficient for experiencing pain. The conscious experience of pain requires an adequately developed forebrain neocortex, which fishes do not have (Northcutt & Kaas 1995, Rose 2002). The second criterion is invalid because physiological and behavioral responses to noxious stimuli are fully possible and (even in humans), regularly executed without awareness. Thus, they are not evidence of pain awareness. Criterion 3 is invalid because avoidance learning involves only unconscious associative learning and thus fails to prove the existence of consciousness, an essential requirement for pain (Macphail 1998, Rose 2002). This problem also negates claims for demonstration of fear in rainbow trout where associative conditioning was also used (Sneddon et al. 2003b, Yue et al. 2004). The fourth criterion is also unacceptable for several reasons. A 'simple reflex' was not defined or distinguished from a complex reflex. Furthermore, evidence from decorticate humans (e.g. the discussion of the Schiavo case above) as well as from humans with sleep disturbances demonstrates that we are fully capable of highly complex, seemingly goal-directed behavior while unconscious. Eating, climbing, driving, sexual assaults,

homicides, and other complex behaviors can occur during states of unconsciousness in humans (Plazzi et al. 2005, Ebrahim 2006). Consequently, it is well-established that very complex behaviors that are more than 'simple reflexes' can be performed unconsciously.

BIOLOGICAL CONTINUITY AND BACKWARD EVOLUTION

One putative justification for anthropomorphic thinking about brain and mental functions in fishes is that it is consistent with Darwinian evolution to assume that if we have certain mental properties, like feelings of fear or pain, that other species should have such attributes as well. This is not valid evolutionary reasoning. Organisms that share a common ancestor could reasonably be expected to share an ancestral trait, but humans were never ancestors to fishes, so using a human mental capacity like pain or diverse, conscious feelings as a starting point for conjectures about possible psychological attributes of fishes is a backward evolutionary thinking and makes no biological sense. It is more reasonable to identify characters that were present in the common ancestor that might be transmitted to the divergent, descended types (i.e. humans and fishes). However, because the organism that was a common ancestor to humans as well as modern fishes was probably a long extinct, early gnathostome (Long 1995), we know virtually nothing with certainty about its behavior or psychological attributes.

Could there be an 'alternative mechanism' for pain in fishes?

It might be argued that a human-like psychological capacity, such as pain, is so basic to survival that it could have been present in a common ancestor, or should have appeared through parallel evolution (Chandroo et al. 2004), but there is no compelling evidence that either scenario happened. For example, no sharks or rays studied to date have nociceptors (reviewed in Rose 2002), much less a brain capable of pain experience, and they evolved after early gnathostomes (Long 1995).

It is easy to propose that a fish brain might have a capacity for experiencing pain. However, it is a very different matter to prove such a proposal. Showing that some neurons in the cerebrum of a fish respond to nociceptive stimuli, whether by electrophysiological recording (Dunlop & Laming 2005), magnetic resonance imaging, or any other method, is not evidence for pain or for a capacity for pain in a fish brain, because nociceptive responses can occur in the brain

(even under anesthesia) without concurrent pain (see Rose 2002). At least 2 fundamental lines of evidence must be presented in order to make a preliminary case for pain experience by fishes or any other animal. The first and most essential is to provide valid evidence that behavioral responses to nociceptive stimuli actually depend on consciousness. This remains to be done. Second, brain systems of adequate structural and functional expansion and differentiation must exist to permit specialized and separate processing of pain and consciousness from other domains of brain activity. Fish brains are not equipped to perform such operations. Fishes have a pallium, a primitive form of cortex that lacks the structural complexity, diversity of neuron types, overall size, and functional diversification present in the human neocortex (reviewed in Rose 2002). Furthermore, although diverse types of sensory information reach the fish pallium, this information is highly convergent, i.e. it is condensed into a relatively small space, which in many species, like rainbow trout, is dominated by the sense of smell (Folgueira et al. 2004a,b). Consequently, the functionally specialized cortical modules required for processing of pain, feelings, language, or other conscious processes are not present in the fish brain.

The most empirically supportable as well as parsimonious view is to argue, as some of the most prominent investigators of pain and feelings (e.g. LeDoux 1996, Craig 2002, Damasio 2005) have done, that processes like nociception and emotion are probably ancient attributes of animals, and that they have evolutionary continuity. However, pain and feelings, conscious extrapolations of nociception and emotion, evolved much more recently and depended on development of a sufficiently complex cerebrum (Fig. 1) with regions that provide for a remapping of nociception and emotion-related subcortical activity onto a structurally and functionally differentiated, consciousness-supporting cortical system (Craig 2002, Damasio 2005).

Welfare implications of the distinction between pain and feeling versus nociception and emotion

The evidence presented in the preceding 3 sections supports the argument that fishes are incapable of conscious pain or feelings. However, conditions that are noxious, if sufficiently intense or sustained, are likely to cause disturbed homeostasis, which could be expressed through disrupted behavior as well as pathological endocrine, autonomic, or immunological regulation. These disturbances would be mediated through unconscious processes in the brain. However, the need to avoid or reduce exposure of fishes to conditions that provoke these homeostatic disturbances is

not necessarily different from the need that would prevail if fishes experienced pain and feelings. Thus, generally speaking, the same consideration should be given to the vulnerabilities and reactivity of fishes regardless of whether they are assumed to have conscious awareness. This has been the position expressed in the Guidelines for the Use of Fishes in Research put forth by the American Fisheries Society (Nickum et al. 2004). This issue will be revisited below. There are some situations, of course, where

there are very differing practical implications of concluding that fishes are incapable, as opposed to capable, of conscious pain or feelings. The issue of humane slaughter in commercial fishing is one such case. Here, since the fish will be killed, the unconscious, relatively short-term disruption of homeostasis is not so much of an issue, whereas pain and conscious suffering of fish held and being killed could be a significant welfare matter (van de Vis et al. 2003). According to the evidence presented here and earlier
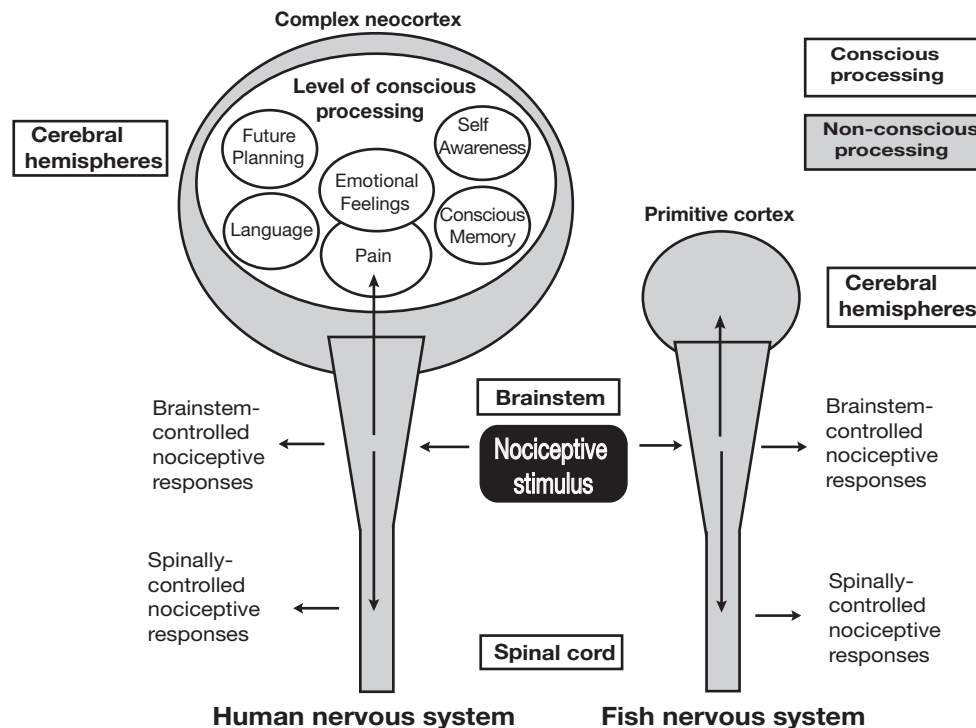

Fig. 2. Summary of how injury-related (nociceptive) stimuli are processed by the human and fish nervous systems (Rose 2002). The diagrams are based on 2 major properties of the central nervous systems in humans and fishes: (1) a relative similarity between the structure and function of the spinal cord and brainstem for processing nociceptive stimuli, and (2) profound differences at the level of the cerebral hemispheres that are responsible for the capacity of humans, but not fishes, to consciously experience pain. The neocortex of humans contains a level of conscious processing that includes specialized systems for our most complex experiences and abilities, including language, planning for the future, self awareness, pain, and emotional feelings. On the other hand, much of our brain activity, including all of that below the level of the neocortex, occurs non-consciously despite having great complexity. Nervous system regions that operate non-consciously are shaded in gray in the diagrams. Activation of the spinal cord by nociceptors initiates nociceptive responses, a complex, coordinated array of non-conscious protective reactions. In addition, this nociceptive activity is transmitted to the brainstem, where the non-conscious nociceptive responses include brainstem-controlled reactions, like facial grimacing, avoidance responses, and autonomic reactions. Ultimately, the nociceptive activity is transmitted to the cerebral cortex. There, in a fully conscious human, this nociceptive activity activates a separate level of processing in neocortical structures that potentially, but not always, leads to the experience of pain. In fishes, rather similar processing of nociceptive information probably occurs at the spinal cord and brainstem due to the general similarity in the organization of these levels in humans and fishes. However, this depiction does not apply to sharks or rays, which have not been found to have nociceptors. Nociceptive stimuli contacting the body, fins, or tail would be processed in the spinal cord and the nociceptive response could be an escape response. Nociceptive stimuli impinging on the face or mouth would be processed by the brainstem, and the nociceptive responses could include head, mouth, and opercular movements in addition to escape. Because fishes have only a primitive type of cortex, the pallium, they do not have the brain systems necessary for producing the experiences of pain and suffering, which depend on our large and complex neocortex. As explained in the text, a similar functional organization applies to unconscious emotional reactions to provocative stimuli and to conscious feelings of these emotions. The former would be regulated by spinal, brainstem, and other non-conscious levels of brain processing, whereas the latter would arise due to operation of specialized modules within the neocortex. These modules largely overlap with the regions that generate pain experience (see Fig. 1). In fishes, because the cortical modules are absent, only the unconscious emotional reactions are generated

(Rose 2002), however, any policies or socio-political agendas predicated specifically on the assumption that fishes are capable of conscious suffering would be unfounded, even though I would argue that a case still exists for respectful handling, including slaughter, of such fish.

WHAT IF FISHES WERE CAPABLE OF SOME KIND OF CONSCIOUS AWARENESS?

Although it is extremely unlikely that fishes could have consciousness or a capacity for pain or suffering meaningfully resembling what we know, it is revealing to consider, for the sake of argument, what kind of consciousness a fish might have if it were capable of awareness. This question was posed by Dennett (1996). Although Dennett argued that consciousness is likely to be a very recent evolutionary phenomenon (presumably excluding fishes), he proposed that the issue of whether a particular type of animal has consciousness could be addressed by a careful study of its behavior and adaptations to pose the question: how would a fish behave if it were conscious? Of course, this is a fundamentally anthropomorphic exercise, but it is highly instructive.

Evidence from the biology and behavior of fishes contradicts the idea that fishes feel pain or suffer in a human or mammal-like way

The normal existence of fishes seems very harsh from the anthropomorphic, human perspective. Nevertheless, fishes are well adapted to this harsh lifestyle. The eating habits of fishes, in particular, tell us a great deal about them. Fishes regularly consume things that would be very painful for us to eat: urchins, crabs, coral, barnacles, hard shellfish, stingrays, needlefish, and countless species of fishes with spiny, rigid, or venomous fin rays. Often, species-specific types of oral handling by the predator reduce injury, and predators show preferences for prey that are more easily ingested (Helfman et al. 1997). Nonetheless, these fishes still frequently eat injurious prey, and it is common for predatory fishes to be found with numerous spines from marine catfish, urchins, or stingrays embedded in their mouths and throats (Smith 1953, Heemstra & Heemstra 2004). Even herbivorous and omnivorous fishes swallow inedible materials like stones and sand and expel them from the mouth or through gill rakers or ingest and excrete them. These eating habits of fishes are inconsistent with the assertion that they are troubled by pain or respond to nociceptive stimuli as we or other mammals would.

The diverse, sometimes extreme, habitats of fishes necessitate very different reactivity to environmental stimulation. Water temperature, pressure, and pH are among the most extremely variable environmental parameters normally encountered by fishes. In the deepest oceanic locales, at depths of several thousand meters, temperature is near freezing and pressures exceed hundreds of kilograms per square centimeter. Exposed to such conditions, humans would likely experience excruciating pain. Eventually, nociceptors would become nonfunctional. Obviously, nociception, if it operates under these conditions, would have to have very different properties in pelagic fishes than in humans. The extreme diversity of environments normally occupied by fishes makes it clear that there is much to be learned about nociception in fishes, including the probability that it is very different and that 'nociceptors' may serve somewhat different functions than in humans and other mammals.

The diverse habits and adaptations of fishes also challenge simplistic anthropomorphic speculations about psychological capabilities besides pain, such as a capacity for boredom (FSBI 2002). Would a parasitic male anglerfish get bored living in extreme depths and constant darkness while permanently fused to a female by his mouthparts? What of the many lie-in-wait predators, like flatfishes, that must be constantly vigilant in order to successfully capture passing prey, which themselves must be constantly vigilant to avoid capture?

The behavior of fishes in angling contexts contradicts the idea that they could be suffering from pain

Angling is one of the most contentious current issues regarding fish welfare. It is also a source of valuable, objective information regarding the responsiveness of fishes to potentially nociceptive stimuli. Fishes react vigorously when hooked, and these reactions are anthropomorphically interpreted as being due to pain. However, are the actual behavioral reactions of a hooked fish what you would expect if a human (or a dog or cat) were hooked and retrieved in the manner of an angler landing a fish? Consider the following points.

(1) Sharks and rays have no sensory receptors for detecting injurious stimuli, but these fishes, like bony fishes, react to hooking with flight and struggling. Although there is evidence that some, perhaps many, teleost fishes have nociceptors (Whitear 1971, Sneddon et al. 2003a, Dunlop & Laming 2005), studies of a number of shark and ray species have not found evidence of nociceptors (reviewed in Rose 2002). Sharks are, in the words of the marine ichthyologist J. L. B. Smith (1953), 'notoriously indifferent to wounds.' The species found not to have nociceptors by Snow et al. (1993),

including the blacktip reef shark *Caracharinus melanopterus*, big shovelnose *Rhinobatus* sp., and stingrays *Himantura* spp., are known by anglers to be extremely strong fighters when hooked (pers. obs. and B. Diggles pers. comm.), a response that is impossible to explain as being due to pain or for that matter, nociception.

(2) A teleost fish's reactions to being hooked are not readily explained as a human-like reaction to 'pain.' Does the rapid swimming and leaping by a hooked teleost depend on nociceptive stimuli from the hook? Usually, a hooked fish swims strongly away from the fisherman, instead of giving ground, sometimes to the point of breaking the angler's line. In so doing, the fish is swimming toward the source of noxious stimulation, the hook in the mouth, thereby intensifying the stimulus. The exact opposite is the human response to an embedded fishhook or other injury, i.e. to attempt to diminish further noxious stimulation. It is also opposite the reaction of a mammal to noxious stimulation, such as a rat in the 'demand curve' test used to assess the aversiveness of a stimulus (Dawkins 1980). In this test, a mammal will act to diminish, not increase, aversive stimulation. In addition, many game fish, classified as such because of their strong, sustained swimming when hooked, are predators that repeatedly eat noxious prey, which may leave spines embedded in their mouths and throats (Smith 1953, Heemstra & Heemstra 2004). If the strong swimming of these fishes when hooked represents an attempt to flee from a painful stimulus, they should also be expected to avoid eating things that injure their own mouths. The behavior of these predators is inconsistent with a high degree of reactivity to nociceptive stimuli, much less pain.

(3) A fish may be hooked twice in rapid succession. Many anglers have hooked a given fish within minutes of hooking it before. The proof that this fish was previously hooked is usually that the angler's fly or lure is still in its mouth after having been broken free in the initial hooking (Smith 1953, Behnke 2004). Especially compelling findings come from a study on the Yellowstone River within Yellowstone National Park (Schill et al. 1986), where a wild cutthroat trout in study sections of the river had been caught and released an average of nearly 10 times in a 42 d period. In addition, the investigators caught 1 marked trout 4 times within 24 h and 2 others twice within 2 h. Many other examples of rapid re-catching of previously hooked and landed fish have been documented for freshwater and marine species despite the extremely low *a priori* probability of such an event where fish are free to move in open water. The Suntag Database in Australia records cases of freshwater and marine fishes caught by anglers and then tagged and released. Of 27 260 fish recorded in this way, 313 were recaught on the same day, includ-ing 6 fish recaught in 10 min or less (B. Sawynok pers. comm.).

In experimental studies, some fish apparently learned to avoid certain lures or baits more readily than others (Beukema 1970, Hackney & Linkous 1978, Raat 1985, Burkett et al. 1986), but, within a study population of a single species, individual fish showed great differences in the degree to which having been caught affected their probability of recapture.

The evidence cited above for rapid recapture of fish by anglers is important because suppression of feeding is widely regarded as an indicator of a fish's reaction to stress-producing or aversive stimuli (Iwama et al. 1997, Schreck et al. 1997, Huntingford et al. 2006). It would appear that the nociceptive stimuli and other aspects of being caught by an angler are frequently not sufficiently noxious to suppress feeding or disrupt behavior for long. These observations are also consistent with the utility of catch-and-release fishing as a management technique, which depends on the fact that previously caught fish not only survive, but can be caught again without a detrimental effect on the health, behavior, or reproduction of the population.

Does fear explain the behavior of a hooked fish?

The evidence presented above contradicts the idea that pain, or even nociception causes the behavior of hooked fishes. How well would conscious feelings of fear account for these behaviors? Not well. Fishes show flight responses to certain types of stimuli, such as the rapid approach of a predator. The initial escape response to a sudden stimulus like a predator's attack or a hookset is typically so rapid (tens of milliseconds, Eaton et al. 1988) that it does not permit any possible conscious fear-like processes that would require time-consuming, higher level activity in the brain (Esslen et al. 2004, Damasio 2005). Of course, hooked fishes sometimes swim to the cover of structure, much as they would if making a response to a predator or other 'alarming' stimulus. These responses appear to be like fear but as in the case of pain and nociception, it is critical to use terminology validly. A qualified terminology, such as 'flight behavior' or 'fear-like behavior' would be appropriate because it is consistent with the likelihood that fishes have unconscious emotions, as emotions are defined above, and because we know so little about the nature of hypothetical, but unconscious, 'fear-like' states in fishes.

Biotelemetry and catch-and-release angling

Certainly nociceptive signaling might have detrimental effects in its own right, even if it were only

unconsciously processed. However, diverse evidence from biotelemetry demonstrates that fishes are commonly not very adversely affected by physical insults that would be painful and debilitating to humans. A recent review of biotelemetry techniques (Bridger & Booth 2003) considered the effects of these procedures on the health and well-being of fishes. The effects of biotelemetry procedures are complex, of course, but several consistent patterns were evident. Following transmitter placement, diverse species typically showed good survival and remarkably little behavioral impairment, including a capacity for spawning migrations. The detectable immediate effects of transmitter placement, including endocrine stress responses, were typically moderate and brief, 24 h or less. Predation is a major threat to fishes after transmitter placement, but predation risk seems to depend greatly on how a fish is handled at the time of transmitter placement as opposed to the presence of the transmitter per se. For example, it is important to give the fish adequate time to regain normal spontaneous activity and full responsiveness to the environment before being released (Cooke & Philipp 2004).

From an anthropomorphic perspective, imagine having a transmitter the size of a beer bottle attached by sutures through your back, surgically implanted in your peritoneal cavity, or inserted orally into your stomach. Then, after one of these procedures, you were put into an environment as challenging and dangerous as ones normally occupied by free-ranging fishes. If fishes were debilitated by pain or discomfort to the degree that would surely occur in a human, the kind of functioning exhibited by transmitter-bearing fishes would be surprising rather than the norm.

Studies of catch-and-release fishing also provide useful insights into the real world of fishes. Whereas these studies tend to focus on mortality, they are of interest because they provide evidence as to whether hypothetical pain and suffering from being hooked and landed could be inherently detrimental to fishes. A meta-analysis of catch-and-release mortality by Taylor & White (1992) and an experimental study by Schisler & Bergersen (1996) showed that survival depended virtually entirely on physical injury or stresses such as time out of water. Under optimal conditions such as flies with barbless hooks, survival was as high as 97.4%. Once again, the Yellowstone River study is especially informative, because, in spite of being caught and released many times in 6 wk in a predator-rich environment, cutthroat trout mortality was estimated at 0.3%. From a practical perspective, outcomes of catch-and-release studies leave no major amount of unexplained variation in survival aside from identifiable physical factors. If psychological distress or physiological stress caused by pain and suffering due to being caught were a significant factor in their well-being, mortality would not be so obviously explained by 'non-psychological' variables. Vulnerability to predation or injury from environmental hazards like strong currents would be particularly important threats to survival if the neurobehavioral functioning of a fish were compromised by psychological distress due to being caught and handled (Cooke & Philipp 2004).

Why do fishes swim away when hooked?

The foregoing evidence is consistent with the interpretation that pain, nociception, or conscious fear cannot explain the behavior of a hooked fish. Instead, this behavior is best understood as an innate pattern of responses, principally the startle response and swimming, which are elicited by diverse stimuli, not just those that would activate nociceptors. Startle and swimming responses are controlled by lower levels of the nervous system, which allows these responses to be generated very rapidly, a necessity for the survival of fishes. Intervention of consciousness would likely slow the response time and be highly detrimental to the effectiveness of predatory and anti-predator behaviors.

Sensory stimuli that elicit escape responses are diverse but typically abrupt, such as a looming visual stimulus, a sudden pulse of vibration, or sudden mechanical stimulus on the head or body (Grillner et al. 1998, Bosch et al. 2001, Ritter et al. 2001, Rossignol et al. 2006). These stimuli rapidly activate brainstem neurons, which excite spinal cord neurons that generate a rapid tail thrust. Activation of sustained swimming is produced by a network of spinal cord neurons known as the swimming pattern generator, which is regulated by neurons in the lower brainstem, that control the onset, offset, and speed of swimming (Grillner et al. 1998, Ritter et al. 2001, Rossignol et al. 2006).

Our understanding of the control of startle and swimming in fishes shows that reactions to hooking and retrieving by an angler can be explained without the involvement of nociception, much less conscious pain or fear. Hooking a fish in the mouth activates non-nociceptive as well as nociceptive sensory receptors, which, like many abrupt, non-nociceptive stimuli, generate a rapid signal to brainstem neurons that triggers a tail flick escape response and swimming. Sustained tension on the hook activates the spinal swimming generator much like visual stimuli from pursuit by an aquatic predator would (relevant neurobehavioral mechanisms reviewed in Grillner et al. 1998 and Rossignol et al. 2006). Thus, stimulation by the hook need not involve nociceptors to evoke escape and swimming. Instead, these reactions are explained by

known effects of non-nociceptive stimuli on brainstem and spinal circuits controlling swimming, which also accounts for the behavior of hooked sharks (lacking nociceptors).

Welfare implications of evidence from the natural history of fishes, angling, and biotelemetry studies

Collectively, the evidence presented above shows that it is unreasonable to assume that pain, or even non-conscious nociception, explains behavioral responses to hooking and retrieving during angling. Secondly, in the real world of fishes, detrimental effects of noxious stimuli or certain traumatic events, especially at the behavioral level, are frequently not apparent, so if pain were experienced by fishes, its importance would have to be minor or at least different from that experienced by humans. A fish with an ability to feel pain and to suffer that is meaningfully like ours would not be recaught by an angler within minutes of release or break away with a hook still embedded in its mouth. Such a fish would not repeatedly eat urchins or stingrays and accumulate embedded venomous spines in its mouth and throat. Such a fish would not be adapted for undergoing prolonged starvation, disease, injury, and exertion prior to reproducing as is typical of Pacific salmon. The empirical evidence supports a view that fishes can be highly reactive to diverse threatening stimuli, but that nociception is likely of lesser significance than other threats. Furthermore, the evidence cited above indicates that fish species may differ from humans and other mammals in their reactivity to noxious stimuli.

If fishes have consciousness, their consciousness must be so different from ours, as deduced from their brains and their behavior, that we have no idea what it would be like. Even those scientists who would include fairly diverse species of vertebrates in the 'consciousness club' would not believe that fishes could have self awareness (Donald 2001, Tulving 2005). The debate about that capacity is centered on whether it is unique to great apes or just humans (Macphail 1998, Donald 2001, Povinelli 2004, Wynne 2004b, Terrace & Metcalfe 2005). This point is of great importance because one of the most critical determinants of suffering from pain is the personal awareness and ownership of the pain (Price 1999). This is why dissociation techniques, in which a person can use mental imagery to separate himself from pain, are effective for reducing suffering (Price 1999). In contrast, without awareness of self, the pain is no one's problem. It is simply there, something to be reduced or avoided if possible, but it is not a 'personal' problem.

Nonetheless, the apparent differences in the reactivity of fishes to nociceptive forms of stimuli in no way diminish their vulnerability to many types of physical threats. Fishes may be robust in some circumstances and fragile in others. Disease, many forms of injury, and extreme exertion are frequently debilitating or lethal to fishes, especially when coupled with unfavorable circumstances like stressful water conditions. Similarly, long-term or repeated exposure to environmental stressors often causes physiological dysfunction, behavioral impairment, or increased disease susceptibility (Schreck et al. 1997), even though the stressors' effects would be non-conscious rather than 'psychological.' Such debilitating variables are well documented (Iwama et al. 1997, Huntingford et al. 2006). However, there are substantial grounds for concluding that 'psychological' factors like pain or suffering are not relevant welfare concerns for fishes.

WHO COMMANDS THE MORAL HIGH GROUND IN THE FISH MENTAL WELFARE DEBATE?

My assessment of the claims for human-like mental capacities of fishes leads me to conclude that those claims lack empirical support and validity. However, these claims are often made with strong convictions. An open and objective discussion of the fish mental welfare issue, which separates sound empirical evidence from ideology, would be in the best interests of both fishes and humans. Fishes are ultimately best served by those who have a valid understanding of them. Current understanding of the psychological nature of fishes hardly warrants the implementation of legislation that would impact humans socially and economically without necessarily benefiting fishes. More caution and critical thinking are in order first.

Aquaculture, commercial fishing, and angling are principal areas addressed by the mental welfare discussion. My view is that using objective information based on clearly validated indices of fish well-being, like reproduction, stress responses, growth, disease resistance, or detrimentally disturbed behavior, without speculations about happiness and boredom or other anthropomorphic conjectures, will readily identify environmental or experiential conditions detrimental to welfare (Iwama et al. 1997, Erickson 2003, Nickum et al. 2004). Furthermore, an objective, non-anthropomorphic examination of the normal behavior and adaptations of diverse species of fish will provide the best guide to species-specific welfare.

The goal here should not to be to make humans feel better about 'humane' (i.e. consistent with human values) treatment of fishes, but to take a pragmatic approach to addressing the actual, objectively evident needs of fishes. In my opinion, the most pressing threats to most fishes are at the habitat and population

levels. If we lose species, or their essential habitats, we have had misplaced priorities. In my home, the semi-arid Rocky Mountains, large-scale commercial aquaculture is not practiced, and commercial fishing is nonexistent. Our fish welfare concerns are focused on the numerous and frequently anthropogenic threats to free-living fishes. These threats include water diversion for a localized but burgeoning human population, global warming, loss of habitat due to poor land use practices and pollution, and introduction of exotic species and diseases. The most effective and often sole forces protecting fishes and their environments here have been anglers' organizations and state agencies funded by fishing license sales and taxes on angling equipment. Efforts of these groups have protected and restored diverse native fishes and preserved the habitats of a multitude of other aquatic and terrestrial species that depend on environments supporting fishes. In contrast, those who seek to discredit angling are undermining the most fundamental welfare needs of large numbers of fishes. If these people were successful in eliminating angling, fishes would become even more of an abstraction to our largely urbanized population and there would be no alternative force coming to their aid with such commitment and financial resources. It would be hypocritical to suggest that anglers working to protect fishes at the habitat level are doing so just out of self interest. All parties involved in the fish welfare issue have some form of self interest at stake. However, self interests that lead to a dissociation of many millions of people from real contact with fishes would ultimately undermine fish welfare on a catastrophic scale.

CONCLUSIONS

Understanding the mental experiences of another human is relatively difficult, but understanding the possible experiences of organisms in a taxon as diverse and evolutionarily distant from us as fishes is much more difficult. Even so, humans are strongly inclined to anthropomorphically generalize our feelings to other organisms, but humanized interpretations of animal cognition and behavior are commonly wrong as well as misleading. The natural lifestyle of fishes is typically harsh by human standards, with extreme environments and perpetual predation, yet thousands of fish species are adapted to these lifestyles. Nonetheless, mental suffering, including experiences like pain, fear, and boredom, has been proposed by some as a 'welfare domain' for fishes. Studies purporting to show pain or fear in fishes have been flawed by invalid definitions of these states and a failure to distinguish unconscious from conscious behaviors. Anthropo-

morphic thinking about fishes would predict that they should behave as though they were conscious and had human-like awareness of fear and pain. However, evidence from natural history, angling, and other sources shows that fishes frequently do not respond to presumably noxious stimuli in ways that would be expected if they had human-like consciousness or sensibilities. Furthermore, substantial contemporary research shows that we must distinguish unconscious nociception from conscious pain and unconscious emotions from conscious feelings. Fishes should be viewed as having nociceptive and emotional responses to noxious or provocative stimuli, although the character of these emotional responses would likely differ from that of humans. In addition, without having the necessary cerebral cortical development (or alternative system), it is extremely improbable that fishes could consciously experience pain or feelings. However, while they may be responsive to noxious stimuli in different ways than humans might expect, reactivity to injurious or provocative stimuli constitutes an important welfare concern for fishes. Stimuli and conditions detrimental to fishes are well documented through objectively validated indices like physiological stress or disturbed reproduction or maladaptive behavior. This is the evidence that should guide welfare considerations. Generally, the consideration given to the vulnerabilities and reactivity of fishes should not depend on whether fishes are assumed to have conscious awareness. However, policy decisions driven by anthropomorphic mentalistic views of fishes are likely to promote misunderstanding and be detrimental to fishes and humans alike.

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