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Review paper: Current issues in fish welfare[1]

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Abstract

Human beings may affect the welfare of fish through fisheries, aquaculture and a number of other activities. There is no agreement on just how to weigh the concern for welfare of fish against the human interests involved, but ethical frameworks exist that suggest how this might be approached.

Different definitions of animal welfare focus on an animal's condition, on its subjective experience of that condition and/or on whether it can lead a natural life. These provide different, legitimate, perspectives, but the approach taken in this paper is to focus on welfare as the absence of suffering.

An unresolved and controversial issue in discussions about animal welfare is whether non-human animals exposed to adverse experiences such as physical injury or confinement experience what humans would call suffering. The neocortex, which in humans is an important part of the neural mechanism that generates the subjective experience of suffering, is lacking in fish and non-mammalian animals, and it has been argued that its absence in fish indicates that fish cannot suffer. However, a strong alternative view is that complex animals with sophisticated behaviour, such as fish, probably have the capacity for suffering, though this may be different in degree and kind from the human experience of this state.

Recent empirical studies support this view and show that painful stimuli are, at least, strongly aversive to fish. Consequently, injury or experience of other harmful conditions is a cause for concern in terms of welfare of individual fish. There is also growing evidence that fish can experience fear-like states and that they avoid situations in which they have experienced adverse conditions.

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Human activities that potentially compromise fish welfare include anthropogenic changes to the environment, commercial fisheries, recreational angling, aquaculture, ornamental fish keeping and scientific research. The resulting harm to fish welfare is a cost that must be minimised and weighed against the benefits of the activity concerned.

Wild fish naturally experience a variety of adverse conditions, from attack by predators or conspecifics to starvation or exposure to poor environmental conditions. This does not make it acceptable for humans to impose such conditions on fish, but it does suggest that fish will have mechanisms to cope with these conditions and reminds us that pain responses are in some cases adaptive (for example, suppressing feeding when injured).

In common with all vertebrates, fish respond to environmental challenges with a series of adaptive neuro-endocrine adjustments that are collectively termed the stress response. These in turn induce reversible metabolic and behavioural changes that make the fish better able to overcome or avoid the challenge and are undoubtedly beneficial, in the short-term at least.

In contrast, prolonged activation of the stress response is damaging and leads to immuno-suppression, reduced growth and reproductive dysfunction. Indicators associated with the response to chronic stress (physiological endpoints, disease status and behaviour) provide a potential source of information on the welfare status of a fish. The most reliable assessment of well-being will be obtained by examining a range of informative measures and statistical techniques are available that enable several such measures to be combined objectively.

A growing body of evidence tells us that many human activities can harm fish welfare, but that the effects depend on the species and life history stage concerned and are also context-dependent. For example, in aquaculture, adverse effects related to stocking density may be eliminated if good water quality is maintained. At low densities, bad water quality may be less likely to arise whereas social interactions may cause greater welfare problems.

A number of key differences between fish and birds and mammals have important implications for their welfare. Fish do not need to fuel a high body temperature, so the effects of food deprivation on welfare are not so marked. For species that live naturally in large shoals, low rather than high densities may be harmful. On the other hand, fish are in intimate contact with their environment through the huge surface area of their gills, so they are vulnerable to poor water quality and water borne pollutants.

Extrapolation between taxa is dangerous and general frameworks for ensuring welfare in other vertebrate animals need to be modified before they can be usefully applied to fish.

The scientific study of fish welfare is at an early stage compared with work on other vertebrates and a great deal of what we need to know is yet to be discovered. However, it is clearly the case that fish, though different from birds and mammals, are sophisticated animals, far removed from unfeeling creatures with a 15 second memory of popular misconception. A heightened appreciation of these points

in those who exploit fish and in those who seek to protect them would go a long way towards improving fish welfare.

Key words: Fish, welfare, stress, pain, fisheries, aquaculture, ornamental fish.

Introduction

The aim of this review, which arose from a briefing paper prepared for the Fisheries Society of the British Isles (http://www.le.ac.uk/biology/fsbi/briefing.html), is to give a broad overview of current understanding on a number of issues relating to fish welfare, an area of increasing public concern. The term "fish" includes animals of very different taxonomic status and in this review we mostly consider teleost fish, since these have been the subject of almost all recent research into fish welfare. A broad approach necessarily precludes in-depth, exhaustive coverage of all the relevant issues, but many of these issues have been the subject of recent published reviews and we cite these in the relevant sections. We briefly address what welfare means, why it matters and how welfare science relates to the philosophical discipline of ethics, before considering human activities that may compromise fish welfare and how welfare might be measured. We concentrate on the impact of human activity on welfare at the level of individuals, as opposed to populations, species or ecosystems and address the experiences of living animals (up to and including the point of slaughter) and not the question of whether it is right to kill animals.

To discuss animal welfare objectively, we need a definition and this is not easy to produce because the concept is complex and the word is used in a number of different ways (Dawkins, 1998; Appleby, 1999). Most definitions fall into one of three broad categories (Duncan & Fraser, 1997; Fraser *et al*., 1997), none of which is right or wrong from a scientific point of view; rather they express different ideals about what we should be concerned about in our dealings with animals:

Feelings-based definitions are set in terms of subjective mental states. Here, the requirement for good welfare is that the animal should feel well, being free from negative experiences such as pain or fear and having access to positive experiences, such as companionship in the case of social species. This use of the term welfare obviously depends on the animal concerned having conscious subjective experiences and our ability to interpret such experiences, controversial points (Dawkins, 1998) that are discussed below.
Function-based definitions centre on an animal's ability to adapt to its present environment. Here good welfare requires that the animal be in good health with its biological systems (and particularly those involved

in coping with challenges to stasis) functioning appropriately and not being forced to respond beyond their capacity. This definition is based on things that are relatively easy to observe and measure.

Nature-based definitions arise from the view that each species of animal has an inherent biological nature that it must express. Here good welfare requires that the animal is able to lead a natural life and express its natural behaviour. This approach, which reflects a view that what is natural, is inherently good, focuses on something we can measure, namely what animals do in the wild and in captivity.

Because suffering, health problems and impairment of natural behaviour often accompany each other, in many cases these three approaches will reach the same conclusions. Chickens (*Gallus domesticus*) are strongly motivated to build nests (as opposed to having access to a completed nest) and will work hard for the opportunity to build (Hughes *et al*., 1989); arguably then, nest-building reflects a behavioural need that must be met if the chicken's welfare is not to be compromised. However, in some cases different conclusions about whether welfare is compromised will follow from the different definitions. For example, much behaviour of wild animals is shown in response to adverse conditions (as when fleeing from a predator), but it is hard to argue that feelings of suffering will occur if these responses are not evoked. In other cases, animals may be highly motivated to perform an action independent of its consequences. Their welfare may be compromised if they are deprived of the opportunity to do so, but this is not necessarily the case and it may be difficult to decide whether the different approaches lead to the same conclusion. For example, wild Atlantic salmon (*Salmo salar*) migrate long distances at sea. If this happens because fish leave an area when the local food supply is poor and stop swimming when they find food, there is no reason to believe that farmed salmon will be frustrated when they are prevented from migrating, provided they have plenty of food. If they are simply motivated to swim, then swimming in large circles may be sufficient to avoid such frustration. On the other hand, if they have an instinctive drive to move to new areas regardless of food supply, confinement in cages might well lead to suffering, even though fish are able to swim continuously.

It is, therefore, important to state clearly what definition of animal welfare is being used (Appleby & Sandøe, 2002). In this article, we adopt a feelings-based approach that focuses on animal suffering that is on more-or-less intense unpleasant mental or physical states felt by the animal. One important complicating factor is that the occurrence of unpleasant states does not by itself imply suffering. Such states are an unavoidable part of normal animal life and often serve as signals or behavioural prompts that help the animals satisfy their biological needs. Sometimes, negative experiences are compensated for by corresponding positive experiences, so suffering may be defined as prolonged experience of unpleasant mental states.

Science, ethics and welfare

Humans may affect the welfare of fish in many ways, through fisheries, aquaculture, sports fishing, scientific research or the keeping of fish as a hobby activity, all of which have associated benefits (see Section 8). There is therefore every reason to seek a better empirical understanding of fish welfare and to give careful thought to how we should weigh the welfare of fish against the interests of humans when these are in conflict. Their disciplinary training gives biologists a special role to play in the first of these aims; but not in the second, which is the job of the moral philosopher/ethicist. To put it another way, biologists may be able to tell us whether the welfare of fishes is compromised by a certain human activity and even perhaps by how much, but normally they have neither the expertise needed for nor the responsibility of deciding whether that human activity is justified. However, welfare biology and the ethical analyses of animal use share the goal of elucidating the relationship between humans and other animals (Fraser, 1999). We spell out very briefly here some frameworks that ethicists, typically scholars with a background in philosophy, have developed to guide clear thinking on the complex moral issues of whether and when humans have the right to make use of animals for food production, sports and hobbies (e.g. Rollin, 1993; Sandøe *et al.*, 1997; Heeger & Brom, 2001). It should be noted that, like the biologist, the ethicist does not have the right to decide what is right or wrong; rather their expertise allows them to deliver thoughts that may be relevant when we try to think clearly about these issues.

Thinking clearly is not always the fashion when it comes to animal issues. Often feelings without much thought seem to prevail and this has its problems. The first problem of being led by one's feelings rather than approaching matters through ethical theory is simply that people's feelings about animal use are often unstable or ambivalent and so cannot be relied upon as a rational guide. This immediately leads to a second problem, namely that ambivalence encourages double standards that are both morally objectionable and logically indefensible. The third problem is perhaps the most serious. It is clear that, at present, we are engaged in the West in an increasingly serious debate about the rights and wrongs of animal use. As long as they merely press their intuitively held beliefs, people on either side of the debate about making use of fish as a resource will not be able to communicate effectively. These beliefs are often sincere and strongly held, but they can be extremely difficult to understand and highly resistant to change. The ideal of meaningful and transparent discussion leading to mutual understanding is attainable, however, because people's gut feelings about matters are very often based on underlying ethical assumptions and theories, which are more susceptible to rational assessment than the individual beliefs to which they give rise. The suggestion we wish to make here, then, is that if lay people and scientists are willing to think a little about fundamental ethical theory, they will have a much greater prospect of communicating with one another effectively, articulating their convictions in a coherent manner, and perhaps even reaching a compromise upon which all can agree.

Moral philosophers distinguish a number of types of ethical theory, and in principle any of these might underlie a person's views about animal use by humans. Here we will discuss three prominent theoretical positions: contractarianism, utilitarianism and rights views. These have been selected because they have direct and obvious implications for the ongoing debate over animal use.

Contractarianism

Why should we act morally? This is a central question in moral philosophy, and one to which the contractarian gives a straightforward answer: one should act morally because it is in one's self-interest to do so. The outlook underlying contractarianism is egoism. According to the egoist, when one is obliged to show consideration for other people this is really for one's own sake. In general, by respecting the rules of morality one contributes to the maintenance of a society that is essential to one's own welfare. The moral rules are thus those that best serve the self-interest of all members of the society. Contractarian morality is confined to those individuals who can 'contract in' to the moral community, so it is important to define who these members are. On this topic, Narveson (1983) writes: "On the contract view of morality, morality is a sort of agreement among rational, independent, self-interested persons, persons who have something to gain from entering into such an agreement…"

A major feature of this view of morality is that it explains why we have it and who is party to it. We have it for reasons of long-term self-interest, and parties to it include all and only those who have *both* of the following characteristics: 1) they stand to gain by subscribing to it, at least in the long run, compared with not doing so, and 2) they are *capable* of entering into (and keeping) an agreement… Given these requirements, it will be clear why animals do not have rights, for there are evident shortcomings on both scores. On the one hand, humans have nothing generally to gain by voluntarily refraining from (for instance) killing animals or 'treating them as mere means'. On the other, animals cannot generally make agreements with us anyway, even if we wanted to have them do so…"

On this view there is clearly a morally relevant difference between ones relationship to other human beings and ones relation to animals. We are dependent on the respect and cooperation of other people. If we treat our fellow humans badly, they will respond by treating us badly. By contrast, the animal community will not strike back if, let us say, we use some of its members to hunt or fish for the fun of it. From an egoistic point of view we need only treat the animals well enough for them to be fit for our own purposes. In any case, as Narveson points out, non-human animals cannot enter into a contract, or agreement, governing future conduct, so they cannot join the moral community.

For the contractarian, since neither animal suffering nor the killing of animals is an ethical problem *per se*, any kind of animal use is in itself ethically acceptable. The lack of standing of animals in the moral community does not necessarily mean that the way animals are treated is irrelevant from the contractarian point of view: if people *like* animals, for example, and dislike the practice of their being used in this or that way, animal use can become an ethical issue, because it is in a person's interests to get what he or she likes. Nevertheless the contractarian view of animals is highly anthropocentric, since any rights to protection animals have will always be dependent on human concern. Inevitably, we tend to like some types of animal more than others and are more troubled by the suffering of our favourite sorts of animal. Hence, levels of protection will differ across different varieties of animal.

The contractarian view accords with certain attitudes to animal treatment that are prevalent in our society. Thus it serves to explain why legislation, allegedly for the protection of animals, usually protects the animals that matter most to humans, such as cats and dogs. Contractarianism can, however, seem inadequate. Can it really be correct to hold that causing animals to suffer, even for a trivial reason, or for no particular reason, is morally straightforward as long as no human being is bothered by the relevant conduct? Many would want to insist that it is immoral as such to cause another to suffer for little or no reason, whether one's victim is a human being or an animal. An ethical theory that captures this insistence is utilitarianism.

Typically people have less strong feelings about fish and therefore fish are less well protected than other kinds of animals. According to this approach, one might have legitimate concern for the welfare of fish in an ornamental tank, since the pleasure one gets from them might be reduced if the were in a poor state of welfare. Fish biologists might have a concern for the welfare of their subjects, since poor welfare may well equate to poor science. In both cases we need to be able to recognise and measure good versus poor welfare.

Utilitarianism

According to the utilitarian, the interests of every individual affected by an action count morally and deserve equal consideration. In utilitarian writings the notion of an interest is usually defined in terms of "the capacity for suffering and/or enjoyment or happiness" (Singer, 1989). Thus individuals have an interest in acts that will enhance their enjoyment or reduce their suffering. From this it follows, of course, that all sentient beings, human and non-human, have interests. And since for the utilitarian all interests count morally and deserve equal consideration, this implies that the impact of one's actions on all sentient creatures, including animals, is a matter of moral concern. Thus Singer (1989) writes: "Many philosophers have proposed the principle of equal consideration of interests, in some form or other, as a basic moral principle; but … not many of them have recognized that this principle applies to members of other species as well as to our own. …If a being suffers, there can be no moral justification for refusing to take that suffering

into consideration. No matter what the nature of the being, the principle of equality requires that its suffering be counted equally with the like suffering — in so far as rough comparisons can be made — of any other being."

For the utilitarian, then, ethical decisions require us to strike the most favourable balance of benefits and costs for all the sentient individuals affected by what we do. Doing the right thing, according to the utilitarian, is not only a matter of doing what is optimal. It is also essential to do something rather than nothing: if something can be done to increase well-being, we have a duty to do it. This utilitarian duty to act always to bring about improvements has important consequences for society. In contemporary Western society we have a general tendency to give ourselves priority over animals. A utilitarian will regard this tendency as essentially wrong. However, the anthropocentric outlook is obviously well established, and in view of this it may well be that, for the time being at least, any attempt to ensure that sentient animals are accorded the same status as human beings is bound to fail. It may be that the best thing a utilitarian can do is to secure higher levels of animal welfare within the current system. It may here be relevant to mention that the Journal of Fish Biology requires its authors to refer to the Association for the Study of Animal Behaviour's Guidelines for the Use of Animals in Research (2001), which are firmly based in such a semi-utilitarian approach.

The overwhelming majority of domestic animals are kept for food production. Most are kept under restrictive conditions in which basic behavioural or physiological needs are thwarted. Laying hens, for example, are commonly kept in battery cages where they cannot perform strongly motivated nesting behaviour before egg laying and where the restriction of their movement results in bone brittleness and a high incidence of broken bones. Farmed fish too are kept at high densities. Whether or not their physiological and behavioural needs are thwarted is so far not clear (see section 6). Naturally, such costs must be weighed against the benefit, to human beings, of access to cheap meat and eggs. But given that the average citizen in the developed world consumes far more protein than is physiologically necessary, and often more animal fat than is healthy, low-cost meat cannot be considered a vital human interest.

What all utilitarians agree on, however, is the methodological precept that ethical decisions concerning animal use require us to balance the harm we do to the affected animals against the benefits we derive for humans and other animals. Interestingly, this very precept (i.e. the notion that we can work out what is ethical by trading off one set of interests against another) has been attacked by some moral philosophers. The allegation is that such trade-offs violate the rights of the individuals whose interests are in the moral balance. To get clearer about this, we need to turn to rights theories.

Rights views

There is an obvious sense in which, in focusing on overall improvements in welfare, the utilitarian treats sentient beings as mere instruments. The utilitarian believes that it is ethically justifiable to sacrifice the welfare of one individual where this sacrifice is outweighed by connected gains in welfare. Rights theorists object to this, holding that it is always unacceptable to treat a sentient being merely as a means to obtain a goal. Historically, rights theory is associated with the eighteenth-century German philosopher, Immanuel Kant. In Kant's view, human beings have "an intrinsic worth, i.e. dignity" and should therefore be treated "always as an end and never as a means only". Clearly this view is at variance with the utilitarian's willingness to sacrifice one individual's welfare where this leads overall to welfare gains. Kant himself confined the right to be treated as an end to human beings, but later rights theorists, such as the American philosopher Tom Regan (1989), have argued that the principle of dignity should be extended to animals. Thus "…attempts to limit its scope to humans only can be shown to be rationally defective. Animals, it is true, lack many of the abilities humans possess. They can't read, do higher mathematics, build a bookcase, or make *baba ghanoush*. Neither can many human beings, however, and yet we don't (and shouldn't) say that they (these humans) therefore have less inherent value, less of a right to be treated with respect, than do others. It is the *similarities* between those human beings who most clearly, most non-controversially have such value (the people reading this, for example), and not our differences that matter most. The really crucial, basic similarity is simply this: we are each of us the experiencing subject of a life, a conscious creature having an individual welfare that has importance to us whatever our usefulness to others. We want and prefer things, believe and feel things, recall and expect things. All these dimensions of our life, including our pleasure and pain, our enjoyment and suffering, our satisfaction and frustration, our continued existence or our untimely death — all make a difference to the quality of our life as lived, as experienced, by us as individuals. As the same is true of those animals that concern us (the ones that are eaten and trapped, for example), they too must be viewed as the experiencing subjects of a life, with inherent value of their own."

What implications does the rights view have for animal use? Obviously, the answer to this question will depend on whether we are prepared to go along with Regan and ascribe rights to animals. If we refuse to take this step, rights theory will have little to tell us about animal use. However if we allow that animals possess intrinsic dignity and have rights various things will follow. To begin with, the balancing of human benefits against animal suffering that has been central in our discussion so far becomes to some extent a background issue. No benefit can justify disrespect for the rights of an individual, human or animal.

Categorical abolitionism of this sort probably goes further in its attempt to limit the utilitarian trade-offs than most of us would consider necessary. After all, weighing costs against benefits and seeking what is best overall, in private decisions is part of our daily life. We expect others (for example, employers and

government bodies) to do the same. In all this, we accept that we are not treated, and do not treat others, purely as ends. On the other hand, most people would presumably allow that certain rights are sacrosanct, and that there are limits to the extent to which an individual can be sacrificed for an overall benefit. Only (what we might call) a *moderate* rights view is likely to command widespread acceptance.

How would such a moderate view apply to animal use? The detail would depend on what rights we take to be fundamental. The right to life (or more accurately, the right not to be killed) is often regarded as basic. Curiously, however, this does not appear to be a basic right that people would ascribe to animals: after all, most of us happily eat animals that have been killed just for this purpose. Something like a right to protection from suffering, or significant suffering, seems to be much more promising. We might agree that all animals should be protected from suffering if this involves intense or prolonged pain or distress that the animal cannot control. Fish biologists have a part to play in this debate, since they can help to develop husbandry practices that do not infringe the rights of fish, on this moderated rights view.

An assumption underlying the previous discussion is, of course, that fish are sentient beings. This matters both for the utilitarian, for whom the ability to suffer and feel pleasure is the key criterion of moral consideration and for the adherents of the rights view, who would typically claim that only sentient beings can be bearers of rights. However, this assumption is not uncontroversial especially in the case of non-mammalian animals, as will become clear in the next section.

Welfare, suffering and the perception of pain and fear in fish

In the light of the definition of welfare used here (based on absence of suffering), a major unresolved issue is whether and to what extent an animal can feel pain and experience other forms of suffering. Do events that compromise health or interfere with natural behaviour generate the mental state of suffering? In this context, suffering can be defined as conscious experience (i.e. based on awareness of internal and external stimuli, Chandroo *et al*., 2004a) of something as very unpleasant (Dawkins, 1998). If non-human animals have no capacity for suffering, then arguably it does not matter that animals are exposed to such events (Bermond, 1997). A plant may be dying, but as it has no nervous system to generate mental experiences the possibility that it might be suffering does not arise. This question can arise for any group of animals, including invertebrates and larval fish, but we concentrate here on whether adult fish are capable of suffering and we approach this by considering the controversial issue of whether they experience physical damage as pain (Rose, 2002). To anticipate, our view and that of several other commentators (Chandroo *et al*., 2004a,b) is that adult fish probably do experience some of the adverse states that humans associate with pain and emotional distress, even if they do not have the capacity for self awareness necessary for conscious suffering

in the full human sense (Braithwaite & Huntingford, 2004). On this basis, if fish are injured or exposed to other harmful conditions, this is a cause for concern not just in terms of responsible stewardship of fish populations (Rose, 2002), but also in terms of the welfare of individuals.

People arguing on either side of this debate have used a number of kinds of evidence, none of them entirely satisfactory. Thus it has been argued that the longer the life span of a given species of animal and the more sophisticated its general behaviour, the greater its need for complex mental processes similar to those that in humans generate the conscious experience of suffering. In this context, therefore, it is relevant that the longest-living vertebrates are found among the fishes and that fish behaviour is rich, complicated and far from stereotyped. For example, we know that some species form mental representations of their environment and use these for quite complex feats of navigation (Reese, 1989; Rodriguez *et al*., 1994). Also, many fish live in social groups and some can recognise individual companions (e.g. Swaney *et al.*, 2001). Fish can remember negative experiences. For example, paradise fish (*Macropodus opercularis*) avoid places where they have experienced a single attack by a predator and continue to do so for many months (Czanyi & Doka, 1993) and carp (*Cyprinus carpio*) learn to avoid bait for up to three years after they have been hooked just once (Beukema, 1970). Several fish species are capable of learning complex spatial relationships and forming mental maps (Odling_Smee & Braithwaite, 2003) using an homologous forebrain structure to that responsible for spatial memory in birds and mammals (Broglio *et al*., 2003); some are capable of forming hierarchical associations about order or sequence of spatial information (Burt de Perera, 2004). Furthermore, techniques used by experimental psychologists have demonstrated that different types of information, such as the timing of an event or the experience of a noxious stimulus, are processed in different areas of the forebrain, yet somehow these experiences can be integrated, and enable the fish to generate appropriate avoidance responses (Portavella *et al*., 2004; Yue *et al*., 2004). Thus, while animals could show these kinds of associative learning without necessarily having conscious awareness (Rose, 2002), clearly experiences such as exposure to a predator or tissue damage can be strongly aversive for a fish. And in fact, current literature on fish cognition indicates that several fish species are capable of learning and integrating multiple pieces of information that require more complex processes than associative learning (e.g. Braithwaite, 2006; Sovrano & Bisazza, 2003). Thus, we conclude that where there is evidence of fish species with sophisticated cognitive and behavioural processes, the experience of suffering may be a real possibility.

On the specific point of whether fish experience physical injury as pain, it is helpful to consider current knowledge of pain perception pathways in mammals. In this context, the sensory structures that detect harmful (or noxious) stimuli are called *nociceptors* rather than pain receptors, to stress the fact that detecting and responding to noxious stimuli is not necessarily the same as feeling pain (Broom, 1998). What do we know of these systems in fishes? As far as the possession of receptors that detect harmful stimuli is

concerned, more primitive fish such as lampreys (*Petromyzon marinus*) have free nerve endings in the skin that respond physiologically to mechanical pressure and heat, but behavioural reactions associated with nociception were not recorded (Matthews & Wickelgren, 1978). It is also difficult to determine whether the mechanoreceptors in lamprey are truly nociceptive-specific or simply pressure-specific (Christenson *et al*., 1988). In at least one teleost fish (the rainbow trout, *Oncorhynchus mykiss*), however, anatomical and electrophysiological examination of the trigeminal nerve (which is known to convey pain information from the head and mouth in terrestrial vertebrates) has identified two types of nociceptor, A-delta and C fibres (Sneddon, 2002; Sneddon *et al*., 2003a).

In terms of the anatomy that generates the conscious experience of pain in humans, the brain of a fish is clearly far smaller relative to body size (some 300 times smaller by volume) and simpler in structure than that of a human (Kotrschal *et al*., 1998). In particular, the forebrain, or telencephalon, is relatively undeveloped compared with humans and fish lack cortical structures such as the neocortex, part of the brain with a key role in the subjective experience of pain in humans (Rose, 2002). However, there may be a greater degree of homology between the forebrain of fish and mammals (e.g. Broglio *et al*., 2003; Portavella *et al*., 2004) and even if this is not the case, we know that the same job can be done by different parts of the brain in different kinds of animals. For example, the brain of cephalopods is built on an entirely different plan from that of vertebrates, yet it generates highly complex behaviour (Hanlon & Messenger, 1996). Likewise, visual stimuli are processed by part of the cerebral cortex in mammals, but in birds some visual information is processed extensively by the midbrain optic tectum (Shimizu & Karten, 1993). It is not impossible that parts of the brain other than the cerebral cortex have evolved the capacity for generating negative emotional states/suffering in non-mammalian vertebrates.

Jawed fish are known to produce some of the natural opiates that modulate nociception in mammals (Substance P, enkephalins and □-endorphins, Rodriguez *et al*., 1993; Zaccone *et al*., 1994; Balm & Pottinger, 1995). This does not necessarily mean that these substances serve the same function in fish as they do in mammals, although the behavioural response of goldfish to analgesics is similar to that of a rat (*Rattus norvegicus*, Ehrensing *et al*., 1982). In mammals opiates act at neural levels below the neocortex (Rose, 2002), but this does not preclude their having a pain-suppressing effect. In support of this point, recent behavioural experiments have demonstrated effects of noxious stimulations around the mouth of rainbow trout (Sneddon *et al*., 2003a). In contrast to control treatments, fish administered with a weak acetic acid solution or bee venom showed dramatic and prolonged increases in opercular beat rate and suspension of feeding. In addition, the trout given the noxious stimulation were observed to rest on the substrate, rocking from side to side. Trout treated with acetic acid were also observed rubbing their snouts on the base and walls of the test tank. Similar studies have also shown that the adverse behaviour of fish under noxious

stimulation can be mitigated if an analgesic (morphine) is administered (Sneddon *et al*., 2003b). Taken together, these findings suggest that fish have the sense organs and the sensory processing systems required to perceive harmful stimuli and, probably, the central nervous systems necessary to experience at least some of the adverse states that we associate with pain in mammals. Hence our working position that adult fish have the capacity to perceive painful stimuli and that these are, at least, strongly aversive.

Cost and benefits of human interactions with fishes

Table 1 outlines a number of human activities that may potentially compromise the welfare of individual fish and so cause the harm against which any benefits must be weighed. The word "potentially" is used deliberately because at this point we wish to simply identify areas of possible concern. Harmful effects on welfare can be indirect, as when humans inadvertently alter natural habitats or expose fish to harmful chemicals, or direct, for example through commercial fisheries, through sports fisheries, through intensive production, through keeping fish as pets or in public aquaria or through scientific research. This review does not aim to make judgements about what is acceptable and what is unacceptable, but instead seeks to identify potentially harmful effects of human activities on fish welfare, as far as possible on the basis of documented evidence.

Table 1. Some human activities that could potentially compromise fish welfare

ACTIVITY	EXAMPLES OF POTENTIAL EFFECTS ON WELFARE
Environmental Degradation	• Reduced availability of natural food. • Introduction of exotic species into existing fish communities. • Habitat modification, creating (e.g.) sub-optimal hydrological regimes. • Loss of or displacement from natural habitats. • Reduced population densities (or crowding) and abnormal social experiences. • Disturbance through tourism. • Acute and chronic exposure to pollutants and litter.
Commercial and	• Injury during trawling.

sports fisheries	• Tagging/fin clipping during stock assessment. • In both, tissue damage, physical exhaustion and severe oxygen deficit during capture. • In both, pain and stress during slaughter. • In angling, pain and stress in tethered fish when live bait is used. • In angling, release of reared fish inappropriately equipped for survival in the wild. • In angling, stocked fish introduced to lakes may be denied the opportunity to migrate.
Aquaculture	• High densities in simple and constraining conditions, both in normal rearing conditions and for husbandry. • Poor water quality. • Aggressive interactions, which can cause damage and constrain access to food. • Food deprivation (e.g. during disease treatment and before harvest). • Handling and removal from water during routine husbandry procedures • Unnatural light-dark regimes, to control breeding. • Handling, constraint and, sometimes, low oxygen levels during transportation. • Permanent adverse physical states and possibly increased levels of aggressiveness due to selection for fast growth. • Increased exposure to predators, attracted to fish farms or used to grade out smaller fish (in extensive tilapia aquaculture). • Transmission of disease between wild and farmed stocks.

	• Crowding, handling, removal from water and pain during slaughter.
Keeping ornamental fish and display fish in public aquaria	• For ornamental fish, capture by sub-lethal poisoning. • For ornamental fish, permanent adverse physical states due to selective breeding. • For ornamental fish, release or escape of exotic species • Inappropriate temperatures, poor water quality and physical constraint during transport. • Confined space and poor water quality once housed. • Inappropriate physical conditions. • Inappropriate social conditions, with shoaling fish at low densities and predators with prey. • Inappropriate diets.
Scientific research	• Genetic-modification induced for scientific research may have detrimental effects on welfare. • Fish used in the laboratory for experimental purposes are often confined and may be exposed to a range of deliberately-imposed adverse physical, physiological and behavioural states. • Fisheries research often involves electrofishing, tagging, fin clipping or otherwise marking fish, which potentially cause pain and injury. • And in both cases, handling during research procedures may cause injury.

Having said that, it is worth stressing the benefits that humans derive from such activities. An estimated 150 million people worldwide rely on fisheries, aquaculture and associated activities for their livelihoods, with 38 million directly engaged in fishing, and 10 million in aquaculture as of 2002 (FAO 2004). Many of those engaged in fishing live in the world's poorest countries and remain landless – hence fisheries are the only means of support for whole communities. Aquaculture is making an increasing contribution as fisheries production from 3.9% of the total in 1970 to 31.9% in 2003. This has been the result of increased aquaculture production against a backdrop of declining wild stocks. Between 1993 and 2003 there was an average annual increase of 9.4% in aquaculture production, with 42.3 million tonnes of aquatic animals produced in 2003 with an estimated farm-gate value of US$61.0 billion (Lowther, 2005). Total world trade of fish and fisheries products was US$58.2 billion (export value) in 2002 (FAO 2004) greater than that of rice, coffee, sugar and tea combined (World Bank 2005). The total value of fish exports worldwide was $58 billion in 2002, greater than that of rice, coffee, sugar and tea combined (World Bank, 2005). Sports fisheries and ornamental fish keeping are major recreational activities. For example, in England and Wales there are an estimated 2.9 million freshwater anglers, equating to approximately 3.5% of the population. Of these, 2.3 million are coarse (non-salmonid) anglers making an average of 43 trips per year (National Rivers Authority, 1995). In 2001 there were 34.1 million anglers in the USA or approximately 1 in 6 of the population over 16 years of age, these people spent an estimated US$34.6 billion on fishing, this is direct expenditure excluding employment and ancillary industries associated with fishing (U.S. Department of the Interior, Fish and Wildlife Service 2001). Ornamental fish are the third most common pet after dogs and cats, 35 to 40 million entering the US per annum, with a retail value of the fish and accessories ranged between 189 and 305 million US$ (e.g. Mintel, 1991). Whether or not any of these activities do indeed harm fish is considered later, in Section 7.

Natural threats to wild fish

It is not self-evident that natural is necessarily good in any general sense. Additionally, in nature fish regularly make adaptive trade-offs between different needs. For example, like other animals they accept heavy costs in order to reproduce, in terms for example of physical injury and serious depletion of nutrient reserves/impairment of body condition; these are all conditions that we would regard as evidence of impaired welfare. This poses a problem when considering welfare, since what is natural conflicts with what is good in terms of physical condition, and there may be no real situation where all aspects of welfare are ideal. There is a moral difference between deviation from an optimal state that is caused by natural events and suffering caused by human activity (especially when fish have no choice of environment). Arguably, the term "welfare" is not relevant to adverse experiences that are not anthropogenic; even so, an understanding of the

natural threats encountered by wild fish and how frequently these occur (Table 2) can help to clarify our thoughts on fish welfare. Wild fish experience injury, poor environmental conditions and stressful events due to encounters with potential predators and fish of the same species, restricted food supplies, parasitic infection and disease and natural environmental change. One implication is that fish are likely to have mechanisms for dealing with the adverse conditions that they encounter naturally and that these will respond (up to certain limits) during their interactions with humans. Following from this, such natural responses might provide a means of assessing fish welfare.

Table 2. Natural threats to the welfare of wild fish

STRESSOR	COMMENT AND SELECTED EXAMPLES
Predators	• Predation rates can be very high. e.g. Excluding predators reduces mortality by 26% in wrasse (Shima, 2002). • Unsuccessful predatory attacks may cause wounding and an increased risk of disease. e.g. 30% of wild sticklebacks (*Gasterosteus aculeatus*) showed injuries due to failed predatory attacks (Reimchen, 1994). • The threat of predation may suppress feeding and may cause fish to forage sub-optimally (Hart, 1997).
Conspecifics	• Many species live naturally in groups of the same species, which provide protection against predators. Obligate shoaling fish separated from companions will strive to join a shoal (Pitcher and Parrish, 1993). • In many other species (or in shoaling species under particular circumstances) conspecifics fight over resources and this can cause physical damage and depletion of energy reserves (Neat *et al.*, 1998). Many mature wild Atlantic salmon parr have wounds from attacks by larger fish (Garcia de Leaniz, 1990). Losers may be deprived of resources and/or exposed to chronic social stress (Abbott & Dill, 1989, Alanara, 1997).

Food availability and body condition	• Wild fish often experience periods of food deprivation (Dutil & Lambert, 2000), though many species have flexible metabolic systems to cope with periods of prolonged food deprivation (O'Connor *et al.*, 2000). • Growth rates in fish held captive with excess food consistently and markedly exceed those achieved by fish in the wild (e.g. in *Cynolebias viarius* – Errea & Danulat, 2001). • Lipid deposition rates and mineral content of body tissues may also differ between wild and captive reared fish (e.g. for sea bass, Orban *et al.*, 2002). • At least 50% of larvae of the common Japanese goby *Rhinogobius brunneus* die through starvation prior to obtaining their first food (Iguchi & Mizuno, 1999).
Extensive migration	• Daily vertical migration by pelagic fishes results in slower growth (Lima, 1998). • Energy reserves in spawning salmon can be reduced by more than 90% following upriver migration (e.g. Jonsson *et al*., 1991).
Parasites and Disease	• In the wild most fish carry a parasite burden that impairs their health (Margolis *et al*., 1982). High gill parasite loads in fish from the Salton Sea, • California caused gill damage, depressed respiration and osmoregulation and juvenile mortality in several species (Kuperman *et al.*, 2001). • In Orange roughy *Hopostethus atlanticus* from New Zealand, parasite loading was negatively correlated with growth (Gauldie & Jones, 2000).
Suboptimal environmental conditions	• Most environmental variables fluctuate naturally, so wild fish will experience conditions that deviate from optimal for the species concerned, and that may be near to or beyond their limits of tolerance. • Fish can avoid or adapt to sub-optimal environmental conditions

(at an energetic cost), but exposure to conditions beyond their limit of tolerance is, by definition, lethal.

How fish respond to natural threats to their welfare

Stress responses in fish

Much of our understanding of how fish respond to adverse conditions comes from the extensive literature on the biology of stress. In common with all vertebrates, fish possess a suite of adaptive behavioural and physiological strategies that have evolved to cope with destabilising challenges, or stressors. Although there are some differences in detail arising from the contrast between the aquatic and terrestrial environment and from minor differences between the endocrine systems of fish and higher vertebrates, overall the stress responses of fish equate closely to those of other animals (Barton, 1997; Wendelaar Bonga, 1997). This parity extends to the behavioural elements of the stress response. Recent work with salmonid fish has shown that the integrated behavioural and physiological mechanisms that comprise the distinct "coping strategies" believed to be present in mammals (Koolhaas *et al*., 1999; Wingfield, 2003; Huntingford & Adams, 2005) are also evident in fish, with heritable reactive and proactive traits demonstrated in rainbow trout (Øverli et al., 2005).

Behavioural responses to stress

Behavioural responses are an animal's first line of defence against adverse environmental change, predators, and social conflict, often being triggered by the same stimuli that initiate a physiological stress response. As noted above, it is becoming clear that in fish, as in other animals, individual's exhibit distinct behavioural strategies when faced with potentially threatening circumstances, and the type of behavioural response initiated, and the magnitude of the neuroendocrine response to the stressor, can be individual traits (Schjolden *et al*., 2005). The range of behavioural responses exhibited by fish to deal with stressors of varying magnitude is diverse. Altered patterns of swimming (changes in speed and direction) are shown in response to many stressors (e.g. Juell & Fosseidengen, 2004). After an attack by another fish of the same species, fish may flee and hide or take up a submissive posture, often with altered body colour (*e.g*. O'Connor *et al*., 2000; Sutor & Huntingford, 2003). When attacked by a predator, fish may respond by shoaling (Pitcher & Parrish, 1993), freezing (e.g. Goodey & Liley, 1985) or taking shelter (e.g. Brown & Warburton, 1999) and may change colour in this context as well (Endler 1986). Feeding may be suppressed following an encounter with a predator, or inefficient feeding strategies may be adopted (Hart, 1993) and fish may avoid areas in which they have been attacked (Lima, 1998). Specific adaptive behaviour patterns are

observed in response to parasitic disease (Furevik *et al.*, 1993) and to tissue damage (for example, carp that are hooked in the mouth show rapid darting, spitting and shaking of the head (Verheijen & Buwalda, 1988) and rainbow trout injected with acetic acid in their lips rub their snouts against the substratum (Sneddon *et al*., 2003).

Acute physiological stress responses

The neuroendocrine stress response in fish is virtually identical to that of mammals (Wendelaar Bonga, 1997) and is mediated by the hypothalamic-pituitary-interrenal (HPI) axis. Perception of a stressor by the fish initiates a rapid, neurally-stimulated release of catecholamines (adrenaline/epinephrine and noradrenaline/norepinephrine; Perry & Bernier, 1999) from the chromaffin tissue, homologous to the mammalian adrenal medulla. This is accompanied by release of corticotropin-releasing hormone (CRH) from the hypothalamus which in turn promotes the release of corticotrophin (adrenocorticotrophic hormone, ACTH) by the pituitary and subsequent synthesis and secretion of cortisol from by the interrenal tissue, the homologue of the mammalian adrenal cortex (Sumpter, 1997; Okawara et al., 1992; Weld et al. 1987). Cortisol concentrations return to pre-stress levels within hours of exposure to a brief stressor (Pickering & Pottinger 1989; Waring *et al*., 1992), but elevated cortisol levels generally persist during continuous, chronic stress (Pottinger & Moran, 1993; Pottinger *et al*., 1994). If a repeated stressor is not inherently damaging, acclimation, or habituation, can occur (Pickering & Pottinger, 1985). The neuroendocrine stress response is responsible for coordinating and stimulating adaptive adjustments to respiratory and metabolic function and is endocrinologically more complex than indicated by this brief overview.

Chronic physiological stress response

Where *fish* cannot escape a stressor, or where the stressful stimulus is episodic or intermittent, prolonged activation of the stress response has deleterious consequences. These include loss of appetite, impaired growth and muscle wasting, immunosuppression and suppressed reproduction. Clearly, observing such changes provides strong indications that the well-being of the fish has been significantly compromised. Many of the adaptive elements of the acute response described above affect energy intake and increase energy utilisation, so prolonged activation of the HPI axis is likely to reduce growth indirectly through a negative effect on energy balance. In addition, secretion of growth hormone is reduced in fish during periods of stress (Pickering *et al*., 1991; Farbridge & Leatherland, 1992), so there are also direct effects on the mechanisms that control growth. Poor growth has also been reported in wild fish as a result of environmental stressors such as altered pH (e.g. Puste & Das, 2001), reduced dissolved oxygen (Kramer, 1987) and salinity (Brett, 1979). Since growth and reproduction are functionally linked (Thorpe et al., 1998),

stress-induced impairment of growth may indirectly interfere with maturation. Additionally, reproductive activity is suppressed directly during periods of stress, via a wide range of mechanisms (Pottinger, 1999).

In teleost fish, defence against disease is mainly based on a non-specific immune system that does not depend on prior disease challenge. The main components are chemicals in the body fluids that destroy or inactivate invading organisms and circulating and tissue-dwelling phagocytes that engulf or destroy invading organisms. The specific immune system, which has a memory component that can adapt to different invading organisms (e.g. Press, 1998) is less well developed than in birds and mammals, comprising circulating lymphocytes responsible for antibody production and phagocytic cells, which have an additional role in presenting antigens to the specific immune system. Chronic stress has a generally immunosuppressive effect in fish, mediated in particular by the actions of cortisol (Weyts *et al*., 1999), and increased mortality due to fungal and bacterial pathogens (e.g. Pickering & Pottinger, 1989; Plumb, 1994) is the common outcome.

Functional considerations

The stress response has evolved to assist the survival of the animal under demanding conditions in the natural environment. However, natural stressors tend to be brief and/or avoidable. In contrast those stressors that are imposed upon fish by anthropogenic agents may be unavoidable and prolonged or repetitive. Under such circumstances, chronic or repeated activation of behavioural and physiological stress responses is maladaptive and potentially harmful. Ideally, indicators of welfare should signal problems in advance and allow intervention before this state has been reached.

Assessing fish welfare

Ways of measuring fish welfare.

Based on knowledge of the natural responses of fish to adverse conditions, the physiological, health and/or behavioural status of individual fish have been used as indicators of compromised welfare, though the link between components of the stress response and welfare is not simple.

Stress responses represent an animal's natural reaction to challenging conditions and these are often used as indicators of impaired welfare, so studies of physiological stress feature prominently in welfare research. However, it is important to recognise that physiological stress is not synonymous with suffering (Dawkins, 1998). There is no particular reason to suggest that the temporary physiological activation that prepares fish for activity is detrimental to welfare and in some contexts short-term stress responses (for example, in

anticipation of feeding) may well be beneficial (Moberg, 1999). Indirect effects such as suppressed reproduction may well be adaptive responses to poor conditions in the wild, but even so it seems reasonable to assume that in captive fish they indicate exposure to chronic, unavoidable stress, which may have compromised welfare. Thus although the concept of stress does not fully capture the complexities of animal welfare, monitoring stress responses may give us an important part of the picture. In particular, where several components of the stress response (including up-regulation of particular genes, Ribas *et al*., 2004) are all influenced in a similar way by the same condition, this suggests that there is cause for concern about the welfare of the fish involved.

The link between health and welfare is also complex. If an individual fish shows disease symptoms, it seems reasonable to infer that it is in a poor state of welfare, as a direct result of the disease. However, the converse is not necessarily true since the welfare of a healthy fish may be compromised, for example through inappropriate social environments. In addition, because stress can suppress immune function and increase risk of infection, a high incidence of disease and mortality in a population may indicate that there is an underlying problem with the fish's environment. It would be overly simplistic to assume that disease is invariably the result of poor living conditions or that the occurrence of disease inevitably implies that the problem is due to human mismanagement. Even fish experiencing optimal conditions may suffer from disease and serious epidemics occur in populations of wild fish (e.g. Epizootic Ulcerative Syndrome, Lillie & Roberts, 1997).

Behavioural studies have been important in welfare research for a number of reasons. Since altered behaviour is an early and easily observed response to adverse conditions, specific responses to natural stressors (such as 'freezing' in the presence of a predator or rubbing to remove ectoparasites) can be used as an indicator of impaired welfare. Likewise, since animals pay attention to those stimuli that are currently important for fitness, changes in attentional state can be used to highlight welfare problems. For example, trout exhibit strong avoidance responses when exposed to a novel object (Sundstrom *et al*., 2004). Such responses are suppressed if the fish has been exposed to a noxious stimulus, but not in fish treated with some form of analgesic. The fact that exposure to noxious stimuli interferes with the normal neophobic responses suggests that fish give a high priority to such stimuli (Sneddon *et al*., 2003b). Additionally, since animals may suffer if prevented from performing their full behavioural repertoire, behavioural deficits have been used to identify conditions that compromise welfare (Mench & Mason, 1997). Behavioural techniques such as choice tests that give insights into the priorities that animals place on different options have proved valuable in welfare research on birds and mammals, even though the underlying assumption that animals choose what is good for them is not always valid (Dawkins 1998, 2004). Choice tests have often been used on fish, though the aim is not usually related to fish welfare; for example, fish may be required to chose

between different temperatures (Bevelhimer, 1996), between schools of different composition (Metcalfe & Thomson, 1995) or between water with different concentrations of potentially lethal pollutants (Giattina & Garton, 1983). There is clearly scope for more work along these lines directly aimed at identifying conditions that promote good welfare in fish.

Integrating different measures of welfare

Because there are so many potential signs of impaired welfare, the most reliable assessment of well-being will be obtained by examining a range of informative measures. This raises the question of how such a battery of measures can be combined objectively to give an overall impression of welfare, and there are various methods of multivariate analysis that might be used in this context. For example, Principal Components Analysis was used to integrate four commonly used measures of fish welfare reflecting different functional systems (condition of body and fins and plasma concentrations of glucose and cortisol) into a single welfare score for farmed Atlantic salmon (Turnbull *et al*., 2004). As well as reflecting coherence within the data, this score was consistent with the evaluation of welfare by experienced farmers and was significantly negatively related to, among other things, stocking density and cage position. In a related study using experimental tanks, a similar multivariate score was used to relate welfare to disturbance (among other factors), welfare being best in more frequently disturbed tanks. Behavioural studies suggested that this counter-intuitive result arose because aggression during feeding was suppressed by human disturbance (Adams *et al*., in prep.).

Sensitive and easily applied welfare indicators for fish

Data on fish physiology, biochemistry and behaviour are informative, but collecting them is time consuming, technically complex and involves handling or killing fish in order to collect blood or other tissue. Non-invasive methods exist, such as measuring cortisol levels in the water in which fish have lived (Ellis *et al*., 2004) or in their faeces (Oliveira *et al*., 1999, Turner *et al*., 2003), but these sometimes lack the precision of direct measurements made on individual fish. Such intensive work is necessary in scientific research, but is impractical for everyday use, in pet shops or on working fish farms, for example. What is needed for practical management of welfare here is a set of simple, non-intrusive signs or danger signals that can be used easily without complicated laboratory analysis. A number of possible welfare indicators can and have been used to assess the welfare of individual fish (Table 3). Some of these are based on assessments of health that can be used on dead fish (see Tierney & Farrell, 2004), but others are based on behaviour and production. These are well known to people with a practical interest in fish welfare, such as owners of ornamental fish and responsible fish farm workers, as the study by Turnbull *et al*. (2004) cited above showed.

How well these signs work in any given case will depend on the species concerned (for example, eye colour may be a good indicator of social stress in salmon, but not in sticklebacks), on circumstances (for example, depleted energy reserves might be cause for concern in an immature salmon, but not in one that has just bred) and also on individual status (failure to feed may be a sign of poor welfare in a juvenile salmon in the summer, but not necessarily in the winter when they may show adaptive natural anorexia). The potential for using the full range of available indicators will vary with the context in which fish welfare is to be assessed; fish farmers may have to rely on a few signs, but people keeping ornamental fish are well placed to use many of them, on all their fish. In addition, on farms, sick or damaged fish may be more conspicuous than those in good condition, so it is important to develop sampling protocols that give an accurate picture of the welfare status of the whole population.

How human activities affect fish welfare

The scientific study of fish welfare lags behind that of the welfare of other vertebrates (reflecting the pressure of public concern), but there is still an extensive literature on the subject, using several of the welfare indicators outlined above. It is beyond the scope of this review to provide an exhaustive account of this literature, but in this section we comment briefly on the subject, using just a few examples and concentrating on the areas of potential concern identified in Table 1.

Table 3. Possible easily-measured indices of welfare and examples of their use. We list only those based on direct observations of fish rather than the systems in which they are held.

POSSIBLE INDEX	EXAMPLES
Changes in colour	Stress-induced changes in skin or eye colour (which have a complex neural and hormonal background) have been reported in a number of fish species, including ornamental species (Etscheidt & Manz, 1992) and so could be a sign of exposure to adverse events. E.g. eye colour as an index of social stress/subordinate status in salmonids (O'Connor et al. 2000; Sutor & Huntingford, 2003).
Changes in ventilation rate:	A high oxygen demand is reflected by rapid irrigation of the gills. The rate of opercular beats is therefore increased by stress and can be counted automatically or by eye. This, together with a visual

	assessment of gill status, is used as a sign of incipient problems in ornamental fish (Etscheidt & Manz, 1992) and ventilation rate has been used to monitor exposure to pollutants (Handy & Depledge, 1999).
Changes in swimming and other behaviour patterns	Fish may respond to unfavourable conditions by changing swimming speed and space use (Morton, 1990; Etscheidt & Manz, 1992; Kristiansen *et al*., 2004). Abnormal swimming has been used as a sign of poor welfare in farmed fish (Holm *et al*., 1998). Behavioural responses to adverse conditions (or lack of responsiveness to specific stimuli) are signs of both general and specific trouble (Morton, 1990). These include excessive activity or immobility (Etscheidt & Manz, 1992), body positions that protect injured fins, escape attempts and rubbing to dislodge ectoparasites (Furevik *et al*., 1993).
Reduced food intake	There are many reasons why a fish might not eat, but the fact that feeding is suppressed by acute and chronic stress means that an unexpected loss of appetite is a sign of potentially impaired welfare.
Loss of condition	Fish change shape and/or lose weight for many reasons, but because reduced feeding and mobilisation of reserves are secondary stress responses, where fish are regularly weighed and measured, or where body shape can be assessed by eye (for example by the visibility of the vertebrae, Escheidt & Manz, 1992) loss of condition can indicate possibly impaired welfare.
Slow growth	Growth rates in fish are flexible and naturally variable, but provided we have an estimate of expected growth prolonged low rates of growth may be indicative of chronic stress. Thus where fish are regularly weighed or where size can be assessed by eye (or by underwater camera) slow growth can be used as a possible sign of trouble.
Morphological abnormalities	Because adverse conditions can interfere with normal development, the occurrence of morphological abnormalities can be used as an indicator of poor larval rearing conditions (Boglione *et al*., 2001; Cahu *et al*., 2003), although whether this represents problem for welfare depends on the degree of sentience of the larvae concerned.

Injury, including fin damage	Injury may be a direct consequence of an adverse event, in which case, a high frequency of such injuries is a sign of poor welfare. For example, dorsal fin injury in salmonids is often caused by attacks from conspecifics (Turnbull *et al*., 1998) and scales that are dislodged with blood visible rather than lying flat, are a sign of poor welfare in ornamental fish (Etscheidt & Manz, 1992). In addition, because immune responses can be suppressed by cortisol, slow recovery from injury (or a high incidence of injury) may be a sign of generally poor conditions. As well as acute damage, healed injuries may result in long-term abnormalities (e.g. in salmon healed fin injuries may cause permanently short fins) that potentially compromise performance and welfare.
Disease states	Since the causes of most aquatic diseases are complex and dependent on environmental conditions, the presence of disease can indicate an underlying problem with the environment or management. Increased incidence of disease in any population of fish should be treated as a warning that there may be other underlying problems. However, interpreting the welfare implications of an observed disease requires a detailed understanding of the natural history of the disease. In some cases, diseases are not sufficiently well understood to interpret their implications for welfare. Even records of treatment can be difficult to interpret since they may either indicate that the owner is responding appropriately to disease outbreaks or the fish are being exposed to a predictable endemic disease.
Reduced reproductive performance:	For many farmed species, reproduction is prevented or avoided in growing stock. Where this is not the case, for example, in brood stock or in ornamental fish, because chronic stress impairs reproductive function, failure of adult fish to breed or to display normal patterns of reproductive development when feed, light and temperature regimes are appropriate is a possible sign of poor welfare.

Environmental degradation

As far as environmental degradation is concerned, this is clearly a cause of poor welfare in very large numbers of fish (Montgomery & Needleman, 1997). Heavy metals cause extensive gill damage in acidic water, but are non-toxic in hard, alkaline water. (see Wedermeyer, 1997). We now know that heavy tourism can cause detectable stress response of reef fish (Oliveira *et al*., 1999). Pollution of water bodies as a result of direct or indirect input of industrial emissions and effluents is widespread through natural fish habitats and can severely affect fish welfare. To give just a few examples, reduced growth rates in fish has been reported in response to low pH (Puste & Das, 2001) and reduced dissolved oxygen (Kramer, 1987). Eutrophication can impair growth of fish even when food is available in excess, but at the same time remedial measures to reduce impacts of human activities may also have adverse effects on fish. For example, following policy-induced reductions in phosphorus input and subsequent 'oligotrophication' of the waters, growth rates were reduced in largemouth bass in a well established fishery, due to reduced primary productivity with consequences further up the food chain (Maceina & Bayne, 2001).

Commercial and sports fisheries

The welfare of fish caught by commercial fisheries (still the largest area of human-fish interactions) is also a cause for serious concern. Fish are harmed by capture (e.g. cortisol levels increase in sea bream captured by trammel net and many fish are mortally injured, Chopin & Arimoto, 1995) and slaughter methods (especially asphyxia) are highly stressful (Poli *et al*., 2002). In addition, non-target species captured as by-catch are often injured or killed (Pronovi *et al*., 2001). A growing scientific literature has shown that several aspects of sports fisheries have negative effects on fish welfare; some of these studies are shown in Table 4. Compared to aquaculture very few studies have addressed fish welfare in commercial fisheries.

Table 4. Examples of scientific studies of the impact of various aspects of angling on fish welfare.

PRACTICE	SOME DEMONSTRATED EFFECTS ON WELFARE
Capture – hooking	Injury and mortality following hooking is common, but primarily associated with deep-hooked fish (DuBois *et al*., 1994; Hulbert & Engstrom-Heg, 198; Muonehke & Childress, 1994).
Capture – playing / landing	Capture of fish of various species by rod and line elicits a stress response of short duration (Gustaveson *et al*., 1991; Pankhurst & Dedual, 1994; Pottinger, 1998). Estradiol levels are suppressed in rainbow trout within 24h of capture by rod and line (Pankhurst &

		Dedual, 1994). Capture and playing in largemouth bass (*Micropterus salmoides*) produces marked increases in heart rate (Cooke *et al*., 2004).
Capture handling	–	Exposure of exercised fish to air can have severe metabolic effects (lactate increase and altered acid-base balance) that may be greater in larger fish (Ferguson *et al*., 1993). Capture and handling suppresses reproductive function in brown trout (Melotti *et al*., 1992).
Retention / constraint / release	/	Retention of fish post-capture in either keep nets or stringers induces physiological stress responses, but recovery following release can be rapid (Pottinger, 1998; Sobchuk & Dawson, 1988). Hooking and handling for release can increase scale damage by 16% (Broadhurst & Barker, 2000), possibly making released fish liable to infection. Behavioural modification can occur following release (Mesa & Schreck, 1988; Olla & Davis, 1989; Cooke & Phillip, 2004)). Livewell confinement increased mortality in walleye and largemouth bass used in live release tournaments (Suski *et al*., 2005).

Aquaculture

Because there is growing public concern for well-being farmed fish, there has been a considerable amount of research into the impact of many aspects aquaculture practice on fish welfare, some of which is reviewed by Conte (2004). More examples are given in Table 5.

Table 5. Examples of scientific studies of the impact of various aspects of aquaculture on fish welfare.

PRACTICE	SOME DEMONSTRATED EFFECTS ON WELFARE
Transportation	Transportation induces physiological stress requiring prolonged recovery (Bandeen & Leatherland, 1997; Barton, 2000; Rouger *et al*., 1998; Iversen *et al*., 1998; Sandodden *et al*., 2001; Chandroo *et al*.,. 2005).

Handling and Netting	Physical disturbance evokes a neuroendocrine stress response in many species of farmed fish (reviewed by Pickering 1998) and reduces disease resistance (Stangeland *et al*., 1996). Handling stress increases vulnerability to whitespot in channel catfish (Davis *et al*., 2002.
Confinement and short-term crowding	Physical confinement in otherwise favourable conditions increases cortisol and glucose levels and alters immunological activity in various species (Garci-Garbi, 1998). Carp (*Cyprinus carpio*) show a mild, physiological stress response to crowding that declined as the fish adapted, but crowded fish are more sensitive to an additional acute stressor (confinement in a net; Ruane *et al*., 2002). Crowding during grading increases cortisol levels for up to 48h in Greenback flounder *Rhombosolea tapirinia*, Gunther (Barnett & Pankhurst, 1998).
Inappropriate densities	High densities may impair welfare in some species (trout and salmon: Ewing & Ewing 1995, sea bass, *Dicentrarchus labrax* L,: Vazzana, 2002, red porgy, *Pagrus pagrus*, Rotllant & Tort, 1997, seabream *Sparus auratus*, Montero *et al*., 1999), but enhance it in others (Arctic charr Jergensen *et al*., 1993). Halibut suffer less injury at high densities (Greaves, 2001) but show more abnormal swimming (Kristiansen & Juell, 2002; Kristiansen *et al*., 2004). The relationship may not be linear (in salmon negative effects begin to kick in at a critical density, Turnbull *et al*., 2004) and density interacts with other factors such as water quality (Ewing & Ewing, 1995; Scott *et al*., 2001;, Ellis *et al*., 2002). Genes coding for heat shock proteins are over-expressed in sea bass held at high densities (Gornati *et al*., 2004). An enolase gene is up-regulated in sea bream held at high densities (Ribas *et al*., 2004).
Enforced social contact	Aggression can cause injury in farmed fish, especially when competition for food is strong (Greaves & Tuene, 2001). Subordinate fish can be prevented from feeding (Cubitt, 2002), grow poorly and are more vulnerable to disease (reviewed by Wedermeyer, 1997).

Water quality deterioration	Many adverse effects of poor water quality have been described, with different variables interacting. E.g. undisturbed salmonids use c 300 mg of oxygen per kg of fish per hour and this can double if the fish are disturbed. For these species, access to aerated water is essential for health (Wedermeyer, 1997). Immunoglobulin levels fall in sea bass held at low oxygen levels (Scapigliati *et al.*, 1999). Poor water quality mediates density effects on welfare in rainbow trout (Ellis *et al*., 2002).
Bright light and photoperiod manipulation	Atlantic salmon avoid bright light at the water surface, except when feeding (Fernö *et al.*,1995; Juell *et al*., 2003). Continuous light is associated with increased growth in several species (e.g. cod: Puvanendran & Brown, 2002)
Food deprivation	Dorsal fin erosion increases during periods of fasting in steelhead trout (Winfree *et al.*, 1998). Plasma glucose increased in Atlantic salmon after 7 days without food, but other welfare indices were unaffected (Bell, 2002). Atlantic salmon deprived of food for longer periods (up to 86 days) lost weight and condition, but this stabilised after 30 days (Einen *et al*., 1998). Farmed Atlantic salmon swim slower and fight less during feeding bouts when fed on demand (Andrews *et al*., 2002).
Disease treatment	Therapeutic treatments themselves may be stressful to fish (e.g. Griffin *et al*., 1999, 2002; Thorburn *et al*., 2001; Yildiz & Pulatsu, 1999; Sorum & Damsgard, 2003).
Unavoidable contact with predators	Brief exposure to a predator causes increased cortisol levels and ventilation rate and suppressed feeding (e.g. Metcalfe *et al*., 1987). Mortality and injury due to attacks by birds and seals can be high among farmed fish (e.g. Carss, 1993).
Slaughter	All slaughter methods are stressful, but some are lees so than others (Robb *et al.*, 2000; Southgate & Wall, 2001). Sea bass killed by chilling in ice water had lower plasma glucose and lactate levels and showed less marked behavioural responses than those killed by other methods, in particular by asphysia in air and electro-stunning (Poli *et al*., 2002; Skjervold *et al*., 2001), see Robb & Kestin, 2002; Lines

	et al., 2003; Van de Vis *et al*., 2003.

Keeping ornamental fish

Various bodies are concerned with ethical issues arising from the keeping of ornamental fish, whether in private homes or in public aquaria. These issues include conservation of species used by the aquarium trade and their habitats as well as the welfare of the individual fish themselves. Table 6 gives examples of some recent scientific of the impact of various practices in ornamental fish keeping on the welfare of individual fish.

Table 6. Examples of scientific studies of the impact of various aspects of ornamental fish keeping on fish welfare.

PRACTICE	SOME DEMONSTRATED EFFECTS ON WELFARE
Capture by sublethal poisons	Marine tropical fish captured by sodium cyanide suffer very high mortality for several weeks after capture (Hignette, 1984). Clove oil is a better alternative (Erdmann, 2002).
Transportation	Mortality during capture of ornamental fish from South America ranges may be as high as 30%. A further 5 to 10% mortality is estimated to occur during transportation and at the holding facilities (Ferraz de Olivera, 1995). During the acclimation period following importation mortalities can be up to 30% (FitzGibbon, 1993). Shipping of zebra fish (*Brachydanio rerio*) by road in oxygenated bags elevated cortisol levels, but recovery is rapid on transfer to aquaria (Pottinger & Calder, 1992).
Constraint in a confined space	See above, under aquaculture.
Handling	See above, under aquaculture.
Inappropriate densities/species combinations	Lack of appropriate social environment (wrong species or inappropriate numbers) is an important cause of poor health in ornamental fish (Etscheidt, 1995).
Poor water quality	81% of ornamental fish are held outside the optimal pH range, 36% at inappropriate temperatures (Etscheidt & Manz, 1992). Poor water quality is the commonest cause of mortality in ornamental

	fish (Schunck, 1980).
Deprivation of social contact	Angelfish transferred singly to a new tank take longer to resume feeding than those transferred in groups of 3 or 5 (Gomez-Laplaza & Morgan, 1993).
Inappropriate food levels	Inappropriate range and types of food can cause poor health in ornamental fish (Etscheidt, 1995). Inappropriate feeding is not usually a direct cause of mortality in ornamental fish, but can be a contributory factor (Schunck, 1980).
Unavoidable contact with predators	In 19% ornamental tanks prey were housed in small tanks in direct contact with predators (Escheidt & Manz, 1992; Foggitt, 1997). See above under aquaculture.
Disease treatment	See above under aquaculture.

Scientific research

Scientific research (including research by welfare scientists) raises various concerns about its impact on welfare of its subjects, which have been the subject of a number of reviews and guidelines (Nickum, 1988; Borski & Hodson, 2003; Jackson, 2003). Such research (including studies of fish) is strongly regulated in many countries to ensure that harm in terms of compromised welfare is outweighed by benefits in terms of enhanced knowledge on important issues (e.g., the UK Animals (Scientific Procedures) Act, 1986), and is not considered further in this review.

What are the welfare issues?

A number of general points emerge from the brief literature review presented in the previous section:

1. ***Some categories of human activity do indeed compromise fish welfare:*** If one accepts disturbed behaviour, chronically elevated cortisol levels, increased incidence of disease and poor growth (for example) as indicators of welfare in fish, then there are many examples of harmful effects of human activities on fish welfare (Table 2).

2. ***The same factor can have variable effects on fish welfare depending on circumstances:*** Experiments in which the same environmental factor (for example, stocking density) is manipulated often give variable results because different species of fish, and different life history stages of the same species, require different environments for good welfare. Additionally, even within the same species and age group, inherited individual differences in strength of response to a standardised stressor have been reported, for example in

rainbow trout (Pottinger & Carrick, 1999) and in carp (Cyprinus carpio L, Tanck *et al*., 2001). Finally, the complex nature of fish welfare means that the various factors that impact on it may interact. For example, in aquaculture a given stocking density may generate signs of poor welfare under one flow regime (Ellis *et al*., 2002) or level of disturbance (Turnbull *et al*., 2004), but not under other conditions.

3. ***It is therefore not possible to specify conditions that guarantee fish welfare****:* The fact that the effect of varying one factor (such as density) frequently depends on the status of many other factors (such as disturbance and water quality), leads to the important conclusion that, even for a particular species, gender and age of fish, we cannot guarantee the welfare by defining a simple set of husbandry conditions. This in turn emphasises the need for sensitive on-the-spot indicators of welfare, as discussed in section 6.3.

4. ***Fish are different from other vertebrates in ways that have important implications for welfare:*** The effects of human activity on fish welfare are not always what one would predict by extrapolating from birds and mammals. One way to emphasise this point is to consider the influential framework for animal welfare based on the so-called five freedoms (used by the UK Farm Animal Welfare Council) or domains in which welfare may be compromised (Mellor & Stafford, 2001) and how this framework might be applied to fish.

Domain 1. Water and food deprivation, malnutrition. Animals should have ready access to clean water and an appropriate diet in sufficient quantities and with a composition that maintains full health and vigour.

Fish allow their body temperature to fluctuate with that of the environment (i.e. they are ectothermic) and also show striking natural variation in appetite and the evidence suggests that food deprivation is not such a critical aspect of their welfare. Wild fish show marked changes in appetite (some temperature-based and others depending on life history events) that determine the effect of food deprivation on welfare. In the winter juvenile salmon may become naturally anorexic, eating little for weeks (Metcalfe & Huntingford, 1988). These fish will feed when their energy reserves fall to a critical level, but up to this point, low rations would not compromise welfare. On the other hand, maturing salmon show a spontaneous peak in appetite in spring, when nutrient reserves for migration and spawning are accumulated (Kadri *et al.*, 1996) and food deprivation at this point may well compromise welfare. This is not to say that it is acceptable to starve fish for long periods; they certainly have mechanisms that motivate them to feed when their stomachs are empty and their nutritional reserves are low and restricted food may have other effects such as increasing levels of aggression. However, under appropriate circumstances periods of food deprivation may not cause welfare problems and may well mitigate adverse effects of other husbandry activities. The natural diet of wild fish varies markedly between species and as with other vertebrate groups, it is important to ensure that captive fish are given a nutritionally appropriate diet, although in most species we do not know exactly what this should be. The nutritional requirements of established farmed species are well known, the industry has invested substantially in developing appropriate diets and farmed fish no doubt enjoy better nutrition than their wild counterparts. However, for less well established species, there may be nutritional problems. For example, diets lacking in critical micronutrients impair welfare in many species, according to a range of

indicators such as high mortality, morphological abnormalities, poor immune function, abnormal behaviour, poor feeding, impaired sensory function and slow growth (De Silva & Anderson, 1995). As far as water deprivation is concerned, juvenile salmon transferred to seawater too soon in the smolting process can become severely dehydrated, and may die as a consequence (Southgate & Wall, 2001).

Domain 2. Environmental challenge. Animals should have a suitable environment, including shelter and a resting area, whether outdoors or indoors.

Since fish are in intimate contact with their environment through the huge surface of their gills, water quality (in terms of dissolved oxygen, ammonia and pH) and the presence of contaminants (organic and inorganic pollutants) are probably the most critical aspects of the environment for fish welfare and also the best defined. Optimal conditions vary markedly between species. For example, cyprinid fish are very tolerant of low dissolved oxygen levels whereas salmonid fish are not (Wedemeyer, 1996). Within the cichlids, some species are found naturally in waters with a pH as low as 4, whereas others flourish at pH as high as 9 (Lowe-McConnell, 1991; Ross, 2000). The flow characteristics of the fish's natural habitat are also of importance, some species preferring static water, others tolerating or preferring relatively high flow rates. The extent to which the nature of the substratum is important for welfare, particularly in bottom-dwelling species, is not known, but several species have been shown to grow better when shelters are available (e.g. Gwak, 2003). In general, except for the high densities involved, the environment experienced by farmed fish is markedly less complex than that experienced by their wild counterparts. Several behavioural deficits in hatchery-reared fish (for example, inability to handle live prey and impaired anti-predator responses) have been ascribed developmental effects of such deficiencies and various kinds of environmental enrichment have been used to reverse these deficits (reviewed by Huntingford, 2004).

Domain 3. Disease, injury and functional impairment. Disease should be prevented or rapidly diagnosed and treated.

Diseases frequently indicate an underlying environmental problem, so diagnosing and controlling a disease must always take account of the whole system and not consider the fish alone. Diseases of fish are mostly species and system specific and many are poorly understood, but methods of prevention are available for an increasing number (Biering *et al*., 2005; Håstein *et al*., 2005).

Domain 4. Behavioural/interactive restriction. Animals should have sufficient space, proper facilities and where appropriate, the company of the animal's own kind.

Many species form dense schools in the wild and this is important when assessing the welfare of such species if held at high density in captivity, since being held at densities that are too low rather than too high may impair welfare. This is a case where it can be misleading to extrapolate from birds and mammals to fish. As discussed in Section 1, we do not know whether fish such as salmon are motivated to migrate by a particular route (as opposed to finding food or swimming long distances, which they can do in farm cages for example); if this were the case, their behavioural needs might not be met in a sea cage. The concept of

"facilities" may be inappropriate for fish, though some species need shelter or cover, some may require nesting material when breeding, some need tough structures on which to chew (Etscheidt, 1995).

Domain 5. Mental and physical suffering. Conditions that produce unacceptable levels of anxiety, fear, distress, boredom, sickness, pain, thirst, hunger and so on should be minimised.

Domain 5 is critical since it relates adverse experience to emotional response. As discussed in section 2, the subjective experiences of fish are very hard to understand, so it is not easy to identify "conditions that produce unacceptable levels of anxiety… and so on." Most of the cues that are employed to identify distress and fear responses in other vertebrates are simply not accessible for fish - for example, there are no direct parallels for facial or vocal signalling. Greater understanding of cognitive processes in fish is needed before we can make the link between welfare and suffering in this group.

Conclusions

There are more than 30,000 species of teleost fish and we only know a little about conditions that promote welfare for just a few of these, but even so a picture is beginning to emerge (partial and blurred at present) of how various human activities impinge on the welfare of fish and therefore of what might be done to improve matters. This review highlights the need for better knowledge and a fuller understanding of fish welfare. Some of these areas of ignorance concern issues that are fundamental to the whole concept of fish welfare, what it means and how it might be measured. These are listed below:

1. The single most important area of ignorance is a lack of understanding of the mental capabilities of fish and how objectively measurable responses to challenges (physical damage and physiological and behavioural responses) are associated with subjective states of well-being or suffering.
2. After that, given the importance of the concepts of natural being good, for each exploited species, it is important to discover whether there are actions that the fish are highly motivated to perform and that, like nest building in domestic hens, may be described as 'behavioural needs'.
3. We also need to know more about diseases in fish, about the links between stress, immune function and disease states and therefore about the relationship between health and welfare.
4. In practical terms, a better array of welfare indicators (for example, easily observed morphological and behavioural cues) is requires for everyday use in circumstances where time consuming scrutiny of fish using laboratory-based tests is impossible.
5. Other gaps in existing knowledge are also important, but will be somewhat easier to fill because they involve expanding the information already available for some species and in some contexts.
6. A certain amount is known about the effect of angling and aquaculture practices on fish welfare, but there is very little information on the welfare of ornamental fish, especially from capture to point of sale. Questions also remain about conditions within aquaria and ornamental ponds. What are the

effects of being confined in a small, exposed space, of social isolation or of frequent interactions with a predator?

7. As with the welfare of ornamental fish there is very little information on the welfare of fish in the context of commercial fisheries
8. Where both angling and aquaculture are concerned, we know a reasonable amount about welfare of salmonids, but very little about other kinds of fish that are reared commercially or caught by anglers.
9. Even for the well studied species and well documented effects, the exact mechanisms by which the adverse effects come about are unknown. For example, there is plenty of evidence of poor welfare in salmon and trout held at very high densities, but it is not clear whether this is the result of poor water quality, high levels of aggression, simple physical damage or some other process (Ellis et al. 2002). It is important to clarify such issues in order to decide on appropriate remedial measures.

By spelling out current understanding on the welfare of fish, we hope that this review will contribute to debate on the subject. This is a difficult area to review, because many academic disciplines have an interest in it, because complex concepts are involved that are hard to define and because there are large areas of ignorance and, consequently, of disagreement. In this document a pragmatic working position has been taken on a number of important questions (whether fish suffer and whether this matters, for example), recognising that this position may have to be changed in the light of facts that emerge in the future. In spite of these difficulties, a great deal of painstaking research has shown how fish respond to the adverse events that they experience in nature and how these could be used to probe their welfare.

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