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REVIEWS

Ecology and welfare of aquatic animals in wild capture fisheries

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Abstract The expansion of commercial aquaculture production has raised awareness of issues relating to the welfare of aquatic animals. The "Five Freedoms" approach to animal welfare was originally devised for farmed terrestrial animals, and has been applied in some countries to aquatic animals reared in aquaculture due to several commonalities inherent within food production systems. There are now moves towards assessing and addressing aquatic animal welfare issues that may arise in wild capture fisheries. However, all "five freedoms" are regularly contradicted in the natural environment, meaning this concept is inappropriate when considering the welfare of aquatic animals in their natural environments. The feelings-based approach to welfare relies on a suffering centered view that, when applied to the natural aquatic environment, requires use of value judgements, cannot encompass scientific uncertainty regarding awareness in fish, elasmobranchs and invertebrates (despite their unquestioned welfare needs), and cannot resolve the welfare conundrums posed by predator–prey interactions or anthropocentrically mediated environmental degradation. For these reasons, the feelings-based approach to welfare is inadequate, inappropriate and must be rejected if applied to aquatic animals in wild capture fisheries, because it demonstrably ignores empirical evidence and several realities apparent within the natural aquatic environment. Furthermore, application of the feelings-based approach is counterproductive as it can alienate key fisheries stakeholders, many of whom are working to address environmental issues of critical importance to the welfare, management and conservation of aquatic animal populations in their natural environment. In contrast, the function-based and nature-based approaches for defining animal welfare appear appropriate for application to the broad range of welfare issues (including emerging environmental issues such as endocrine disruption) that affect aquatic animals in their natural environment, without the need to selectively ignore groups such as elasmobranchs and invertebrates. We consider that the welfare needs of aquatic animals are inextricably entwined with the need for conservation of their populations, communities and their environment, an approach that is entirely consistent with the concept of ecosystem-based management.

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Introduction

Animal welfare science is a burgeoning field that draws on all branches of biology, particularly behavioural ecology and neuroscience (Dawkins 2006). Human interaction with aquatic animals (particularly fish, crustaceans and molluscs) has continued to escalate in recent years, particularly in the field of aquaculture, where considerable attention has been focussed on several issues relating to the welfare of aquatic animals in production systems (Hastein et al. 2005; Ashley 2007). Global aquaculture production has increased from around 1 million tonnes in 1950, to around 52 million tons in 2006 (FAO 2009). In 2008, aquatic animals provided more than 2.9 billion people with at least 15 percent of their average per capita animal protein intake, a slight decrease from the peak of 16% in 1996 (FAO 2009). Aquaculture continues to be the fastest growing animal food-producing sector, with per capita supply from the industry increasing from 0.7 kg in 1970 to 7.8 kg in 2006, an average annual growth rate of 6.9 percent. Indeed, aquaculture appears set to overtake capture fisheries as a source of food fish in the near future (FAO 2009).

The proliferation of commercial aquaculture has raised awareness of issues related to the welfare of the animals raised within these artificial production systems (Hastein et al. 2005; Ashley 2007). Commercial aquaculture usually requires control of the entire lifecycle of the cultured animal, from broodstock maturation, to spawning, larval rearing, and growout of juveniles to market size at stocking densities that usually exceed those the animals naturally experience in the wild. Consequently, most attention towards aquatic animal welfare in aquaculture has been focussed on several features intrinsic to aquaculture production, including stress and welfare aspects of husbandry, transport, disease management, harvest and slaughter (Poli et al. 2005; Hastein et al. 2005; EFSA 2009).

The proliferation of information related to the welfare of aquacultured animals has been followed by increasing interest in the welfare of aquatic animals in other areas, including ornamental industries and wild capture fisheries (Hastein et al. 2005; Davie and Kopf 2006). To some extent, this is a logical progression, given that many of the aquatic animals used in ornamental industries are now produced in aquaculture facilities, as are large numbers of fish and shellfish that are now released into the wild as part of stock enhancement initiatives (Blankenship and Leber 1995; Lorenzen et al. 2010). The development of live markets for wild caught teleosts and crustaceans that utilise extended periods of transport and holding of live animals in captivity prior to their slaughter in restaurants (e.g. Lee and Sadovy 1998) has also bought welfare issues in wild capture fisheries to greater prominence.

The issue of welfare of aquatic animals in wild capture fisheries is somewhat problematic because, unlike food production systems, the natural aquatic environment is a food chain. Predation is the largest source of mortality of fishes (Bailey and Duffy-Anderson 2001) and in the wild many millions of aquatic animals die every day from predation, mostly in what humans would consider to be the most inhumane circumstances (such as being cut in half, skewered or eaten and digested whole while still alive). Large numbers of wild aquatic animals also perish in natural and anthropogenically induced fish kills (e.g. Gaughan et al. 2000; Whittington et al. 2008; Hobbs and McDonald 2010; La and Cooke 2011). The natural existence of fishes in the wild seems very harsh from the anthropomorphic human perspective, but fishes are well adapted to this harsh lifestyle (Rose 2007) and indeed these interactions are fundamental components of natural selection and evolution (Lima 2002). This all suggests that welfare concepts that are developed for terrestrial and aquatic animals reared their entire lives in closed production systems are likely to have limited relevance for wild aquatic animals living within their natural environment. This certainly does not mean that concepts of welfare are not applicable to wild aquatic animals, but suggests that welfare arrangements originally devised for domestic terrestrial animals and cultured aquatic animals are unlikely to be directly relevant to wild capture fisheries.

In recent times, advocacy by animal liberationists, animal rights activists and some non-government animal welfare organisations has shifted to scrutinize fishing (arguments discussed in Cooke and Sneddon 2006; Arlinghaus et al. 2007a, 2009), even to the extent of publishing public position statements relating to aquatic animal welfare issues in wild capture fisheries (e.g. Mood 2010). These documents generally advocate broad restriction or even cessation of certain fisheries practices based on largely anthropomorphic assessments of awareness and "pain perception" in fishes as well as invertebrates such as decapod crustaceans, and cephalopod molluscs (Mood 2010). As noted by other authors (e.g. Iwama 2007), the motivations of such advocacy groups are outside the scope of the present paper, as is an in-depth discussion of the various ethical and philosophical issues surrounding fishing, which are covered elsewhere (Arlinghaus and Schwab, in press; Arlinghaus et al., in press). Instead, we will provide a science-based assessment of the various issues related to aquatic animal welfare in the natural environments utilized by wild capture fisheries, which requires avoidance of anthropomorphism (Hastein et al. 2005; Arlinghaus et al. 2007a, 2009; Rose 2007).

Some authors (e.g. Mood 2010) have asserted that "there is increased scientific acceptance that fish are able to feel fear, pain and distress". However, empirical science is unable to prove that fish are capable of awareness (Volpato et al. 2007), meaning that the scientific debate as to whether fishes can feel "pain" and "fear" is by no means settled, and will not be in the foreseeable future (Chandroo et al. 2004a, b; Stevens 2009). Furthermore, different species of teleosts display significant variation in their responses to noxious stimuli (Newby and Stevens 2008; Reilly et al. 2008), while elasmobranchs are widely considered to be unable to detect injurious stimuli due to the relative lack of unmyelinated nerve fibers, and their lack of typical polymodal nociceptive neurons (Goadby 1959; Snow et al. 1993; Smith and Lewin 2009). This situation has been complicated by recent scientific literature that has allowed observations of aversion behaviour in response to noxious stimuli applied to fish (Sneddon 2003; Sneddon et al. 2003; Sneddon 2009) and even invertebrates (Barr et al. 2008; Appel and Elwood 2009a, b; Elwood and Appel 2009; Elwood et al. 2009) to be interpreted as evidence that fish and some invertebrates may "perceive pain" in a manner comparable to that experienced by "higher" vertebrates (EFSA 2009), and even humans. This is despite the fact that many of these interpretations amount to "no more than value judgements" (Chandroo et al. 2004b, page 291) delivered by some authors (Sneddon 2003; Sneddon et al. 2003; Barr et al. 2008; Appel and Elwood 2009a, b; Elwood and Appel 2009; Elwood et al. 2009) based on limited data from experiments that often have significant methodological limitations (Rose 2003, 2007; Chandroo et al. 2004b; Newby and Stevens 2008; Stevens 2009). It is also apparent that some researchers have ignored the need to consider the fundamental difference between the relatively simple process of describing responses to nociception, and the very complex process of demonstrating the existence of the psychological and emotional experience of pain (Rose 2007). It is very important to differentiate between nociception and pain, because the latter depends on conscious awareness and always encompasses a felt emotional component, and the International Association for the Study of Pain (IASP) stresses that nociceptor activation is itself not pain (Smith and Lewin 2009).

With this background of scientific uncertainty regarding the issue of pain in aquatic animals, and faced with a need to better define an official position to ensure acceptable welfare outcomes for aquacultured animals, government authorities in several jurisdictions have made certain assumptions, that usually use a "precautionary ethical principle" (Volpato et al. 2007) which in effect gives fishes and even some invertebrates "the benefit of the doubt" (Sneddon 2006; Lund et al. 2007; Mather and Anderson 2007; EFSA 2009). For example in the UK the Committee on Recognition and Alleviation of Pain in Laboratory Animals stated "*although there is a general agreement that pain is an aversive experience experienced by mammals and probably all vertebrates, the committee assumes in this report that all vertebrates are capable of experiencing pain*" (UK National Research Council 2009). Unfortunately, this assumption is scientifically inaccurate (i.e. false), a fact that highlights how value judgements and incorrect assumptions have become entrenched even at high levels of decision making on these issues, when the scientific evidence for "lower" vertebrates is either absent, or at most equivocal, in the case of teleosts (Rose 2007; Stevens 2009) and invertebrates (Barr et al. 2008; Appel and Elwood 2009b), or directly contradictory, in the case of elasmobranchs (Goadby 1959; Snow et al. 1993; Rose 2007; Smith and Lewin 2009). In effect, "benefit of the doubt" in this field of research has meant that because scientific proof that fishes or invertebrates can "feel pain" is lacking, it has become obligatory to assume that they can.

It is unfortunate that decision makers in the field of aquatic animal welfare in laboratories and aquaculture have essentially chosen expedience over science, especially given that scientific uncertainty relating to the presence or absence of awareness and pain perception in teleosts, elasmobranchs and aquatic invertebrates does not exclude the need to consider their welfare (Hastein et al. 2005; Iwama 2007; Rose 2007; Arlinghaus et al. 2007a, 2009; EFSA 2009). The functional, science based concept of good welfare relates to the aquatic animal being in good health, with its biological system functioning within normal ranges and not being forced to respond to stressors beyond its normal capacity (see Huntingford et al. 2006; Arlinghaus et al. 2007a; Iwama 2007). This definition can be applied to all human interactions with aquatic animals whether they be in the laboratory, in an aquaculture production system, or in the wild, irrespective of whether they are considered sentient or not (Rose 2007; Arlinghaus et al. 2007a, 2009). Here we review literature relevant to the assessment of the welfare of aquatic animals in their natural environment. We present evidence from the literature, empirical field data and observations of the ecology of a range of aquatic animals in the wild to challenge the concept that feelings-based welfare guidelines adopted using "the benefit of the doubt" to address urgent welfare issues in aquaculture production systems are adequate and appropriate for application to populations of wild aquatic animals and the fisheries that target them. This review is presented so that this issue can be better understood and so the information can ultimately be used to better inform scientific, public and political decisions regarding the welfare of aquatic animals in their natural environments.

Concepts of welfare in aquatic animals

Most definitions of animal welfare fall into one of three broad categories (feelings, function or nature based), which in some countries (particularly in Europe) are encompassed to a greater or lesser extent within frameworks such as the "Five Freedoms" (FAWC 1979; FSBI 2002). This section will explore how suitable these concepts are for application to the specific question of welfare of aquatic animals living in their natural environment.

The "Five Freedoms" approach

There have been various attempts to define welfare in aquatic animals in recent times, most frequently in relation to their existence in aquaculture production systems (Ashley 2007; EFSA 2009), but also in relation to wild capture fisheries (Huntingford et al. 2006; Arlinghaus et al. 2007a, 2009; Mood 2010). Ashley (2007) and EFSA (2009) stated that welfare, as defined in a terrestrial farm animal context, is often expressed in what is known as the "Five Freedoms", as proposed by the UK Farm Animal Welfare Council (FAWC 1979). These included:

1. Freedom from Hunger and Thirst—by ready access to fresh water and a diet to maintain full health and vigour;
2. Freedom from Discomfort—by providing an appropriate environment including shelter and a comfortable resting area;
3. Freedom from Pain, Injury or Disease—by prevention or rapid diagnosis and treatment;
4. Freedom to Express Normal Behaviour—by providing sufficient space, proper facilities and company of the animal's own kind;
5. Freedom from Fear and Distress—by ensuring conditions and treatment which avoid mental suffering.

This feelings-based (defined in more detail below) concept of animal welfare refers to the state of an individual (EFSA 2009), however, it is assumed that when welfare needs of individuals in a population are met, then welfare of the population can be considered to be good (EFSA 2009). When these concepts of welfare originally devised for farmed terrestrial animals are examined in the context of aquatic animals in their natural environment, it is apparent that the "five freedoms" are rarely, if ever, experienced by wild aquatic animals. This is mainly due to natural processes such as predation, which is required if the predator is to fulfill principle 1, but in doing so this also requires other aquatic animals (prey) to endure experiences that would presumably contradict principles 2, 3 and 5. Natural environmental fluctuations often result in contradiction of principles 1 and 2, while the natural process of parasitism also requires aquatic animals to endure conditions that presumably would contradict principles 2, 3 and often 4 (Lester 1971; Giles 1983; Seppala et al. 2004, 2008; Barber 2007). We will also discuss in later sections how some anthropogenic changes to natural aquatic ecosystems have invalidated the underlying "five freedoms" assumption that if the welfare needs of individuals are met, then welfare of the population can be considered to be good.

The "five freedoms" based approach has been adopted by some government authorities in relation to aquaculture welfare (EFSA 2009) as well as welfare biologists who are active in determining welfare standards for laboratory use of animals (UK National Research Council 2009). Veterinarians have also worked closely with development of these standards, suggesting that a veterinary approach to aquatic animal welfare ultimately leads to adoption of a feelings-based approach to welfare issues in aquaculture, and sometimes even in wild capture fisheries (Hastein et al. 2005; Davie and Kopf 2006; EFSA 2009). This may be due to veterinarians being traditionally trained to use the "five freedoms" approach to welfare through their disciplines focus on addressing welfare issues for terrestrial vertebrates such as birds and mammals, especially in production systems. In practice in aquaculture, huge efforts are expended to avoid predation (usually through regular grading to reduce cannibalism) and veterinarians are well aware of the constant need for biosecurity and optimal husbandry to prevent disease outbreaks, because both are economically damaging to the farmer, as well as being considered detrimental to aquatic animal welfare in intensive production systems (Hastein et al. 2005; Barber 2007; Bergh 2007). However, both predation and parasitism are completely natural occurrences in the wild and indeed, both are fundamental components of healthy aquatic ecosystems (Casini et al. 2008; Mikheev 2009) as they contribute to natural selection and evolution. We are cognizant of this fact, and wish to point out that a much broader range of issues have the potential to impact aquatic animal welfare in their natural environment. We contend that the "five freedoms" concept of welfare was never intended by its originators to be applied to wild aquatic animals. Because the "five freedoms" are regularly contradicted by several natural processes fundamental to aquatic ecosystem function, we consider the concept to be inappropriate for this application and it should not be applied to welfare issues relating to populations of aquatic animals living in their natural environment.

The "feelings-based" approach

The feelings-based (or suffering centred) approach to assessing aquatic animal welfare is based on a definition of welfare that revolves around the absence of suffering (Huntingford et al. 2006). This approach has essentially been defined in terrestrial farm animals within the "five freedoms" discussed previously. An extension of the feelings-based approach to aquatic animal welfare has been proposed in which it is suggested that welfare needs should be guided by the wants and preferences of the aquatic animal (Volpato et al. 2007; Volpato 2009). Huntingford et al. (2006) acknowledged that several definitions of animal welfare exist, and also acknowledged that wild fish naturally experience a variety of adverse conditions, from attack by predators or conspecifics to starvation, or exposure to poor environmental conditions. They then stated this does not make it acceptable for humans to impose such conditions on fish (Huntingford et al. 2006), even though anthropogenic impacts on natural aquatic ecosystems have unavoidably resulted in exposure of wild fish to poor environmental conditions throughout the developed world (discussed in more detail below). Animal rights and animal liberation derivations of the feelings-based approach to welfare also exist (Arlinghaus et al. 2007a, 2009), which if left to their logical conclusion, ultimately lead some authors to reject the legitimacy of historically acceptable activities such as aquarium keeping and fishing (Volpato 2009).

Because the feelings-based approach is centred upon avoidance of pain and suffering, the question of awareness and whether an animal is capable of feeling pain (and hence can suffer) becomes important to this definition of welfare (Huntingford et al. 2006). However, for aquatic animals, this then brings another question, that relates to "which animals require protection?" (e.g. Broom 2007; Lund et al. 2007). At this point it is interesting to note that Huntingford et al. (2006), Broom (2007), Lund et al. (2007), Braithwaite and Boulcott (2007) and many others (e.g. EFSA 2009) who have advocated use of the feelings-based approach to aquatic animal welfare appear to have explicitly avoided discussing the question of welfare of elasmobranchs. This is probably because the feelings/suffering centred definition of welfare these authors use requires them to reject any need for welfare of elasmobranchs, due to the fact that elasmobranchs appear unable to detect injurious stimuli (and hence are unlikely to be able to "suffer") due to the relative lack of unmyelinated nerve fibers, and their lack of nociceptive neurons (Snow et al. 1993; Smith and Lewin 2009). In contrast, the function-based and nature-based approaches to welfare (see below) are inclusive of elasmobranchs, and indeed all other aquatic animals.

The feelings-based approach to welfare of aquatic animals has several flaws that become increasingly apparent when considering its application to the various taxonomic groups that occur in the natural aquatic environment. Firstly, the feelings-based approach relies on assessment of people's feelings about animal use as well as value judgements on what the animals themselves are feeling (Chandroo et al. 2004b; Huntingford et al. 2006). However, human feelings are often unstable or ambivalent and so cannot be relied upon as a rational guide (Huntingford et al. 2006), and of course, it is impossible to determine what aquatic animals are feeling (Volpato et al. 2007; Rose 2007). Secondly, the feelings-based approach is not based upon the reality of aquatic trophic ecology. The feelings-based approach advocates that aquatic animal welfare should be guided by the wants and preferences of those animals (Volpato et al. 2007; Volpato 2009), however, it is readily apparent by their predator avoidance behaviour that fish in the wild do not prefer to be eaten by other fishes. Nevertheless, natural predation remains the largest source of mortality in aquatic environments (Bailey and Duffy-Anderson 2001), demonstrating that the feelings-based approach does not reflect the reality of the predatory nature of the natural aquatic environment—it cannot resolve the conundrum posed if the welfare needs of a piscivorous predator are satisfied by violating the welfare needs of a baitfish. Thirdly, as discussed in more detail later, the feelings-based approach does not encompass the many (often insidious) effects environmental degradation has on the welfare of aquatic organisms in their natural environments. Finally, any definition of welfare that cannot encompass the question of welfare of elasmobranchs and invertebrates must be either inadequate, or simply invalid for aquatic animals, as elasmobranchs and invertebrates are important components of natural aquatic ecosystems deserving of significant welfare consideration (Garcia et al. 2008). Science does not ignore reality, but simply seeks to explain it, hence the feelings-based approach to aquatic animal welfare promoted by Huntingford et al. (2006), Sneddon (2006), Braithwaite and Boulcott (2007), Volpato et al. (2007), Volpato (2009) and others must be rejected by science if it is applied to aquatic animals in the wild, because on several counts it demonstrably ignores reality within the natural aquatic environment.

The "function-based" approach

In contrast to the feelings-based approach, the function-based approach to aquatic animal welfare focuses on the concept that good welfare requires that the aquatic animal is 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 (Huntingford et al. 2006; Iwama 2007; Rose 2007; Arlinghaus et al. 2007a, 2009). This definition can be based on behavioural, physiological, neurological, pathological and cellular criteria that are within the normal range for that organism, in full recognition that these criteria may vary temporally as well as ontogenetically (Iwama 2007). These criteria are relatively easy to observe and amenable to measurement in a scientific manner (Huntingford et al. 2006; Arlinghaus et al. 2009). A valid definition of a stressed state representing reduced welfare is the state when these conditions extend beyond the organism's normal range for some biologically significant period of time (Iwama 2007).

The function based approach relies on factual science (Arlinghaus et al. 2007a, 2009). It does not depend upon concepts of awareness and resolution of the scientific debate on which aquatic animals may or may not experience feelings such as "pain", "suffering" and "fear". Because of this, the function based approach to welfare is inclusive of elasmobranchs and invertebrates (Iwama 2007) as well as teleosts, despite the fact that the questions of perception of pain and fear in all three groups has not and cannot be solved by empirical science, and hence will not be resolved in the foreseeable future (Chandroo et al. 2004a; Iwama 2007; Volpato 2009; Rose 2007). The function based approach can also be used to encompass environmental issues, including emerging anthropogenically derived welfare issues such as endocrine disruption (Blazer et al. 2007; Kidd et al. 2007; LeBlanc 2007; Tillitt et al. 2010; Sarria et al. 2011), that cannot be addressed using feelings or suffering centred approaches, because individual animals affected by endocrine disruption do not necessarily "suffer" in a conventional sense, even though the entire population may collapse as a result (Kidd et al. 2007; Cotton and Wedekind 2008). The function based approach is also known as a pragmatic alternative, because unlike the feelings-based approach, function based welfare outcomes can be measured and assessed within a factual and logical framework that can be supported by empirical science (Poli et al. 2005; Arlinghaus et al. 2007a, 2009).

To summarise, the function-based approach is a scientifically defensible approach for assessing aquatic animal welfare that encompasses all types of aquatic animals (including elasmobranchs and invertebrates). This approach is applicable to all types of welfare issues (including emerging issues such as endocrine disruption) that may affect all types of aquatic animals in their natural environment, while remaining consistent with empirical evidence of ecosystem processes in that environment. Because of its suitability for this application, the function-based approach will be used throughout the remainder of this paper when discussing concepts relating to welfare of aquatic animals in wild capture fisheries.

The "nature-based" definition

A third definition of welfare that is sometimes applied to captive animals arises from the view that each species of animal has an inherent biological nature that it must express (FSBI 2002; Huntingford et al. 2006). For this definition, good welfare requires that the animal is able to lead a natural life and express its natural behaviour. As might be expected, the nature based definition is useful when discussing the welfare of aquatic animals in their natural environment. For example, it appears applicable in situations of environmental degradation where anthropogenic processes such as river regulation (e.g. construction of dams, alterations of water levels and flows) and habitat modification (e.g. draining of wetlands) prevent aquatic animals from completing key aspects of their normal life history (e.g. spawning migrations or recruitment of larvae and juveniles to nursery areas). The nature-based definition of welfare would also encompass situations where water pollution causes significant functional changes to the cellular and physiological systems of aquatic animals to the detriment of aquatic animal health, potentially resulting in changes to reproductive morphology and behaviour that mean the animals can no longer lead a normal reproductive life (Blazer et al. 2007; Kidd et al. 2007; LeBlanc 2007; Cotton and Wedekind 2008; Tillitt et al. 2010). For these reasons, the nature-based approach has broad utility when discussing welfare issues of aquatic animals in wild capture fisheries, and hence will be used in conjunction with the function-based approach when discussing these issues throughout the remainder of this document.

Ecological aspects of the natural environment of relevance to aquatic animal welfare

Predation

Aquatic environments are food chains with several trophic levels that almost invariably incorporate phytoplankton, zooplankton, zooplanktivorous and/or herbivorous and/or omnivorous fishes and shellfish, and higher predators (McCann et al. 1998). Within these food chains, huge numbers of aquatic animals die each day from predation (Bailey and Duffy-Anderson 2001), usually in circumstances humans would consider most inhumane, but the predation process is natural and integral to the functioning of healthy ecosystems. The lives of the majority of aquatic animals end by being eaten alive. Birds and marine mammals consume significant volumes of fishes (Bailey and Duffy-Anderson 2001); however, the majority of fishes are eaten by other fishes (Scharf et al. 2000; Juanes et al. 2002). Suction feeding, which is the most common feeding mode amongst predatory teleosts, is a hydrodynamic process involving rapid inhalation of whole prey into the predators mouth (Lauder and Shaffer 1993; Ferry-Graham and Lauder 2001). Ram feeding is commonly used by pelagic piscivores and involves the rapid movement of the predator towards the prey resulting in a physical strike that uses inertia to capture and/or disable and dismember the prey animal (Scharf et al. 1998; Porter and Motta 2004). Bite feeding is used by some predators to pluck less elusive prey from surfaces and from within confined areas (Mehta and Wainwright 2007). Elasmobranchs may use suction, ram or bite feeding methods, depending on the life history of the species and the prey type being consumed (Wilga et al. 2007). In nearly all cases, death of the captured prey occurs during or after further oral manipulation via cutting or crushing in the oesophagus, or swallowing whole (Porter and Motta 2004) followed by asphyxiation and digestion inside the predators stomach. Other modes of feeding include filter feeding of plankton, which is the main feeding method used by molluscs. Ram filter feeding of zooplankton also occurs in some teleosts and elasmobranchs under certain circumstances (Sazima 1998), while most crustaceans are deposit feeders and scavengers. Teleosts and elasmobranchs regularly consume unpalatable and injurious prey, such as sea urchins, crabs, coral, barnacles, hard shellfish, stingrays, needlefish, and various species of fishes with spiny, rigid, or venomous fin rays (Smith 1953; Heemstra and Heemstra 2004; Rose 2007).

Piscivorous fishes are often cannibalistic, particularly as larvae (Huss et al. 2010) and juveniles, however adult fish also regularly consume their progeny (filial cannibalism, see Smith and Reay 1991; Manica 2007). Cannibalism of siblings occurs both within and between year classes of teleosts (Smith and Reay 1991), while some elasmobranchs display a particular form of sibling cannibalism, which due to their ovoviviparous nature, allows cannibalism of eggs (oophagy) and siblings in utero (Gilmore 1993). It is interesting to note that predation may promote filial cannibalism even in terrestrial vertebrates such as reptiles (Huang 2008), demonstrating how important predation is for shaping the structure and function of ecological communities in the natural environment. The domination of pristine coral reefs (arguably some of the healthiest aquatic environments remaining on the planet) by apex predators (Friedlander and DeMartini 2002) suggests that predation is intrinsically linked to environmental health in the natural aquatic environment. However, the complexity that predation brings to concepts of aquatic animal welfare in the natural environment are many, and can be demonstrated through examples such as the rotenone treatment of Lake Davis, USA to remove introduced northern pike (*Esox lucius*) (see Johnson et al. 2009), and the government sponsored predator removal fishery targeting the native northern pike minnow (*Ptychochelius oregonensis*), that threatens viability of endangered salmonids in the Columbia and Snake Rivers, USA (Friesen and Ward 1999; Schilt 2007).

Mass mortalities

Large numbers of aquatic animals die each year in natural and anthropogenically mediated mass mortality events, such as algal blooms (Hallegraeff 1993; Landsberg 2002). During algal blooms, disease and mortality of aquatic animals can result from either abrasion or clogging of gills by high numbers of algal cells in the water, anoxia due to high biological oxygen demand at night and/or chemical oxygen demand when algal cells break down, or when algae produce extracellular chemical compounds that are toxic to fish and shellfish (algal toxins) (Brusle 1995; Landsberg 2002). Mobile species such as teleosts and elasmobranchs tend to actively avoid algal blooms but those affected by toxins may swim erratically and exhibit signs of respiratory distress, while crustaceans may even crawl out of the water in their attempts to escape asphyxiation (Defur et al. 1990). While some algal blooms are undoubtedly natural events that arise from suitable combinations of oceanographic, physiochemical and meteorological conditions, there is increasing evidence that anthropogenic pollution in the form of eutrophication from sewage outfalls and urban/agricultural runoff, oil spills, nutrient enrichment from aquaculture, and transfer of noxious algal species via ballast water are responsible for promoting algal blooms at increasing frequencies in the natural environment (Hallegraeff 1993; Heil et al. 2001). Reductions in the biomass of suspension feeding organisms such as bivalve molluscs may also play a lesser role in explaining the increasing frequency of algal blooms (Boesch et al. 2001; Newell 2004).

Many aquatic animals are stressed or killed by asphyxiation due to hypoxia as a result of local coastal and oceanographic processes with or without eutrophication (Loesch 1960; May 1973; Pihl et al. 1991), exposure to anoxic water during water body stratification or lake turnover processes (Stanley and Nixon 1992), and high water temperatures (Hobbs and McDonald 2010). Most water breathing aquatic animals are well adapted to cope with oxygen fluctuations within a certain range, but beyond the lower limit they are not able to physiologically acclimatize further (Wells 2009). The late Holocene global warming trend in combination with anthropogenic eutrophication are likely to combine to increase the frequency of kills of aquatic animals due to the increased occurrence of hypoxia (Long and Seitz 2009; Pena et al. 2010), especially in areas with high water temperatures (Hobbs and McDonald 2010).

Disease is a significant factor that often regulates populations of aquatic animals in the wild, with epizootics altering not only host population dynamics, but also habitat and ecosystem function (Harvell et al. 1999; Daszak et al. 2000; Burreson et al. 2000; Ward and Lafferty 2004). Virtually all wild aquatic animals are host to one or more disease agents or parasites (Kinne 1984), however, the host/parasite relationship is usually well balanced (Snieszko 1974, Fig. 1) such that mass mortalities of the host seldom occur in the wild under normal circumstances. The host/parasite relationship can become unbalanced when hosts are exposed to novel exotic or recently

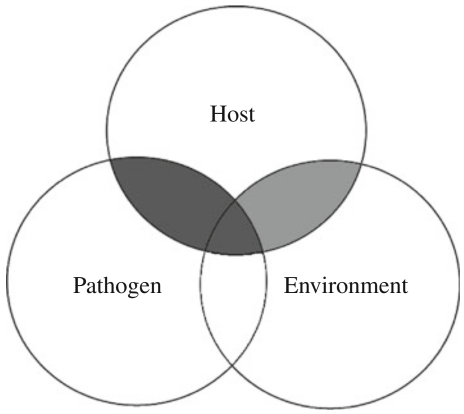

Fig. 1 The balance and interactions between a pathogen, its host and the environment. Stress and disease (*shaded areas*) occurs when a host is exposed to a novel or exotic pathogen, or if the host becomes immunosuppressed by adverse environmental conditions. Stress and disease can also occur in periods of poor environmental quality, even in the absence of pathogens (*lighter shading*). Concept based on Snieszko (1974)

introduced disease agents (Burreson et al. 2000) and/or when hosts are exposed to sub-optimal environmental conditions, chemicals and xenobiotics (Couch and Courtney 1977; Fisher et al. 1999; Thorne and Thomas 2008), and/or become immunosuppressed (Peters and Raftos 2003)—these are the usual prerequisites required for epizootics of wild aquatic animals to occur (Snieszko 1974). Aquatic biosecurity is indeed a very important issue, and science-based structures exist at national and international levels to minimize biosecurity risks posed by translocation of exotic pests and diseases via national and international trade (e.g. OIE 2010).

As an example of the importance of biosecurity for aquatic animal welfare, two of the worlds largest kills of marine organisms occurred in Australia, where disease caused by a novel herpesvirus caused mass mortalities of up to 75% of the population of pilchards (*Sardinops sagax neopilchardus*) throughout the 6,000 km range of the species in Australian coastal waters in 1995 and again in 1998/1999 (Gaughan et al. 2000; Whittington et al. 2008). It was estimated that over 28,000 tonnes of pilchards died in the 1998/1999 kill in Western Australian waters alone, which equates to approximately 800 million individuals based on an average weight of 35 g each (Gaughan et al. 2000). Western Australia comprises only part of the entire fishery (Gaughan et al. 2000), hence it is likely that several billion individuals were killed throughout the entire range of each disease outbreak. Infection of the gill epithelium by the herpesvirus resulted in severe inflammation, epithelial hypertrophy, and hyperplasia (Whittington et al. 1997). Affected fish died of asphyxiation around 3–4 days after initial infection, as evidenced by blood gas results that indicated hypoxaemia (low oxygen) and hypercapnea (high carbon dioxide) (Whittington et al. 1997). Observations of affected pilchards showed no unusual behavioural changes of fish in the school, unless they were chased, at which time affected fish would leave the school, begin swimming in an unco-ordinated manner, and would die within a few minutes (Whittington et al. 1997; Diggles, personal observations of underwater video). The massive extent of the pilchard kills resulted in significant, but largely unquantified, ecological effects for birds, fishes, and other predators that usually consumed pilchards (Gaughan et al. 2000). Exposure of a naïve population to an exotic herpesvirus carried by imported frozen pilchards used as aquaculture feed is considered to be the cause of both these events (Hine and MacDiarmid 1997; Gaughan 2002; Murray et al. 2003; Whittington et al. 2008).

Anthropogenic pollutants

As well as contributing to fish kills associated with hypoxia and algal blooms (see above), a broad range of anthropogenic pollutants are responsible for a wide range of stressors that can cause behavioural changes, disease and mortality (and hence have welfare implications) in populations of aquatic animals (Couch and Courtney 1977; Overstreet 1988; Sindermann 1996; Fisher et al. 1999; Scott and Sloman 2004). Anthropogenic waterborne pollutants include wastewater, stormwater and non-point source pollution, nutrients, silt/sediment, metals, acid mine drainage, persistent organic pollutants, pharmaceuticals, detergents, endocrine disruptors, pesticides and herbicides, petroleum hydrocarbons, and nanomaterials (Harmon 2009). Pollution is particularly problematic in freshwater rivers and estuaries, especially in regions where natural environmental flows are low or sporadic, but it also impairs ecosystem function in coastal regions. Accumulation of floating plastics in mid-ocean regions is also now occurring, with potential adverse effects on aquatic animal and ecosystem health (Boerger et al. 2010). Effects of anthropogenic pollutants on aquatic animals can be overt, as in the case of mortality of aquatic animals during oil spills (Chasse 1978), or insidious, as in the case of behavioural changes (Scott and Sloman 2004) and emerging problems such as endocrine disruption. Endocrine disruption can result from contamination of groundwater, rivers and other water bodies with pesticides and herbicides (Tillitt et al. 2010), or from exposure of aquatic animals to xenoestrogens commonly found in municipal stormwater or sewage, that can result in sublethal or lethal toxicity (Laufer et al. 2005; Sarria et al. 2011) or even population collapse through recruitment failure (Kidd et al. 2007; Cotton and Wedekind 2008). Mortalities of eggs, larvae and other planktonic stages of aquatic animals due to pollution (Bailey et al. 2000; Palma et al. 2009; Partridge and Michael 2010), or even from efforts to clean up pollution (Wilson 1977; Schein et al. 2009), are also insidious as they usually go unrecognized due to natural variability in recruitment, except perhaps in specific circumstances such as one-off pollution events that affect discrete populations (Thorne and Thomas 2008) or failure of larval settlement resulting in long term declines of natural spatfall in the culture of shellfish (Phelps and Mihursky 1986; His et al. 1999).

Aquatic animals in their natural environment are exposed to mixtures of anthropogenic chemicals, usually at very low concentrations. However, recent advances in endocrinology and toxicology have demonstrated that adverse effects of some chemicals may be non-monotonic and therefore not directly dose dependent (Meyers et al. 2009), meaning that exposures to low chemical concentrations are not necessarily benign. There is also increasing realization in the field of mixture toxicology that the customary chemical-by chemical approach to environmental chemical risk assessment is too simplistic, resulting in underestimation of the risk of chemicals to the environment and aquatic animals (Belden et al. 2007; Altenburger and Greco 2009; Kortenkamp et al. 2009; Sarria et al. 2011). It appears that concentration addition (adding up the concentrations of the various chemicals) provides a conservative but broadly applicable model for estimating environmental effects due to chemical interactions (Belden et al. 2007; Kortenkamp et al. 2009). However, chemical mixtures have also been reported to present risks to conservation of endangered salmonids through synergistic effects (Laetz et al. 2009). While welfare issues related to pollution have been recognised for some time (Montgomery and Needleman 1997), clearly this new information has significant and far reaching consequences in relation to the health and welfare of aquatic animals in the wild, particularly for the highly sensitive larval stages of many aquatic organisms, as well as the health of organisms at other trophic levels within their receiving environments (Kirby and Miller 2005; Jones 2005; Reyes et al. 2007; Lewis et al. 2009; Magnusson et al. 2010).

Increasing levels of noise in aquatic ecosystems is another form of anthropogenic pollution that is gaining increased research attention (Popper 2003; Popper and Hastings 2009; Slabbekoorn et al. 2010). Sources of noise pollution include pile driving, shipping, military activities, sonar and seismic surveys. Deleterious effects of loud noise can include stress, behavioural changes such as avoidance of feeding and spawning grounds (especially during seismic surveys), hearing damage, injury and even death, with eggs and larvae being particularly vulnerable (Popper and Hastings 2009). More subtle impacts resulting from reduction of the ability of fish to hear biologically relevant sounds could also include interference with critical functions such as acoustic communication, predator avoidance, prey detection, and learning (Slabbekoorn et al. 2010). Because of this, increasing noise pollution in aquatic systems must be considered a welfare concern under both the function-based and nature-based definitions.

Accidental and deliberate introductions of non indigenous species has been considered by some authors as a form of chronic biopollution (Olenin et al. 2007). Non-indigenous species introductions can be particularly problematic in the aquatic environment as introduced species are often impossible to eradicate and can quickly become embedded in aquatic food chains (Harvey and Kareiva 2005), causing significant and largely irreversible changes to the natural functioning of aquatic ecosystems. There are many instances where well planned and managed introductions (e.g. introduction of sportfish as part of fisheries enhancement programs) have resulted in significant socioeconomic benefits with few negative environmental impacts. However, accidental introductions (as well as illegal or poorly planned deliberate introductions) of non-indigenous species can cause enormous environmental damage (Johnson et al. 2009) and represent significant threats to the welfare of native aquatic animals under the nature-based definition.

Habitat alteration and degradation

Habitat alteration and loss is one of the most significant processes adversely affecting aquatic animal welfare in their natural environments. Natural perturbations from storms and floods can result in large losses of aquatic habitat, but these are temporary insults from which healthy ecosystems can at least partially recover (Preen et al. 1995; Campbell and McKenzie 2004; Gardner et al. 2005). Floods can also be beneficial to fish in allowing access to habitats not normally or only intermittently available to them, and by facilitating migrations that are otherwise prevented by man-made structures (e.g. weirs). However, many anthropogenic changes to aquatic animal habitat result in permanent alteration and loss of habitat and irreversible changes to aquatic ecosystem functions (Boesch 2006). Some of the most obvious anthropogenic issues relate to modification, regulation or diversion of river flows through construction of dams and weirs, which can act as impassable barriers that prevent aquatic animals from completing key aspects of their normal life history, such as spawning migrations (Rosenberg et al. 1997; Schilt 2007; Poff and Zimmerman 2010). Dams and weirs also eliminate natural spawning cues and spawning habitat through alteration of natural water levels, water temperatures and river flows (Gehrke et al. 1995; Haxton and Findlay 2008; Murchie et al. 2008). Although there have been some attempts to restore connectivity via dam removal (Bednarek 2001), use of fishways (Roscoe and Hinch 2010) and development of flow regimes for regulated rivers that are more natural (Poff et al. 1997), many of these approaches have failed. Fish interacting with hydropower facilities can also be injured or killed by impingement on screens or entrainment in turbines, a topic that also has welfare considerations (Schilt 2007). Abstraction of water for irrigation and drinking supply can cause huge environmental problems, and in some instances, entire river systems have become overallocated (Garrick et al. 2009), resulting in complete loss of environmental flows, and even replacement of environmental flows under drought conditions with water from anthropogenic inputs such as stormwater and effluent from sewage outfalls (Bailey et al. 2000). Channelization of rivers is another common form of fisheries habitat alteration in agricultural, urban and industrial areas. Usually this involves straightening and stabilization of river banks with rocks or concrete, dredging of sediments, use of levee banks for flood mitigation and removal of snags and woody debris in order to improve navigability (Boesch 2006; Makiguchi et al. 2008). All of these processes decrease access of aquatic animals to suitable living, spawning and nursery habitat, resulting in significant loss of recruitment capacity and biodiversity (Mauney and Harp 1979; Rochette et al. 2010), both of which must be considered welfare concerns under the nature-based definition.

In estuaries and inshore regions, destruction of nursery habitat through draining of wetlands, removal of mangroves and degradation of coral reefs, biogenic reefs and seagrasses through reduced water quality (sedimentation/eutrophication/herbicides and other chemicals in stormwater and agricultural/urban runoff), are significant forms of habitat alteration that directly influence recruitment success for larvae and juveniles of a wide variety of aquatic animals (Boesch et al. 2001; Jones et al. 2004; Kirby and Miller 2005; McMahon et al. 2005; Jones 2005; Gardner et al. 2005; Coral Disease Working Group 2008; Lewis et al. 2009). Again, all of these processes affect the physiology and recruitment capacity of aquatic organisms, as well as alter ecosystem function and energy flow, and hence they must be considered welfare concerns under both the function-based and nature-based definitions.

Ecology and welfare of aquatic animals in aquaculture

Aquaculture by definition requires removal of aquatic animals from their natural food chains in order to culture them under controlled conditions typical of a production system (Stickney 2000). In an aquaculture production system, the aquatic animals do not occupy ecological niches or trophic positions in a food chain, they simply become stock that are fed and which normally do not contribute to recruitment for future generations of the population. Under these conditions, each individual animal becomes valuable as a commodity, just as in other production systems for birds (e.g. chickens) and mammals (e.g. sheep, cattle, pigs).

The aquaculturist is usually responsible for every aspect that underpins the survival of the animals they are rearing, including spawning of broodstock, rearing eggs and larvae, weaning, feed intake, nutrition, and all aspects of environmental quality (water quality, tank size, shape and stocking density), husbandry related issues such as grading and tank cleaning, as well as transport, harvesting and slaughter (Stickney 2000). Underpinning all of these activities in commercial aquaculture is the need to keep costs down in order to maximize profit (or at least, to avoid making a loss). Because economic pressures often may conflict with conditions that optimize welfare of cultured aquatic animals, there is a need for stringent guidelines to ensure the welfare requirements of aquatic animals in commercial aquaculture are met (Hastein et al. 2005; Ashley 2007).

In commercial production systems, ethical decisions influencing aquatic animal welfare outcomes have been encouraged through codes of practice, or even enforced through legislation that regulates certain aspects of aquaculture production. The next question in aquaculture welfare usually then relates to "which animals need to be protected" (e.g. Broom 2007; Lund et al. 2007). This position implies that some aquatic animals need greater protection from human influences than others, which is a characteristic of the feelings-based approach. Proponents of this school of thought suggest that for aquatic animals, fish, decapod crustaceans and cephalopod molluscs should be given greater welfare consideration so that human actions in production systems do not cause their welfare to become poor (Broom 2007; Mather and Anderson 2007). Because aquatic animals in aquaculture systems do not occupy ecological niches or trophic positions in a larger food chain, the feelings-based approach is likely to provide acceptable welfare outcomes for most (but not necessarily all), types of aquatic animals reared within aquaculture production systems. Nevertheless, a function-based approach to measuring welfare based on behavioural, physiological, neurological, pathological and cellular criteria is still commonly used to ensure these are within the normal range for the aquacultured organisms, and environmental parameters such as water quality are optimised to reduce stress and disease (Fig. 1) in the interests of production efficiency and product quality as well as aquatic animal welfare (Wilkinson et al. 2008).

Welfare of wild aquatic animals in relation to capture fisheries

While natural predation is generally the greatest source of mortality of aquatic animals in their natural environment, fishing is also a significant source of mortality (Bailey and Duffy-Anderson 2001), and indeed fishing mortality may approach or even exceed natural mortality in some overfished populations (Coggins et al. 2007). While mortality due to natural predation and anthropogenic environmental degradation is usually highest during larval and juvenile stages, fishing mortality tends to increase with increasing body size (Bailey and Duffy-Anderson 2001). Wild capture fisheries (commercial and subsistence) landed around 92 million tones of fish and shellfish in 2006, with around 10 million tonnes originating from inland capture fisheries, and 82 million tonnes from marine capture fisheries (FAO 2009). The estimated first sale value of global capture fisheries was US $91.2 billion (FAO 2009). World capture fisheries production has been relatively stable in the last decade (with the exception of fluctuations driven by catches of anchoveta in the Southeast Pacific due to El Niño Southern Oscillation), with China, Peru and the United States remaining the highest producing countries (FAO 2009).

Recreational fishing in developed countries is fundamentally different to commercial fishing in that the primary reason for participation is leisure, although this does not preclude the catch being taken for domestic consumption (Cooke and Cowx 2004). Cooke and Cowx (2004) estimated that recreational fishing contributes to around 12% of the global fish harvest, with around 47 billion fish caught (killed or released) annually by recreational fishers, with around 36% of that number being harvested. This indicates that recreational anglers tend to release a significant proportion of the fish they catch and indeed this is often the case not only where fisheries management regulations require release of undersized, oversized or protected species, but also from selectively choosing the fish they harvest and voluntary catch and release fishing (Arlinghaus et al. 2007b). The proportion of fish taken by recreational anglers varies in different fisheries, and depending on target species, and may equal or exceed the commercial catch in some areas (Coleman et al. 2004).

The need for effective fisheries management

Fisheries harvest is a form of predator/prey activity (Yodzis 1994, Hoekstra and van den Bergh 2005) and hence is similar in many ways to natural processes that constantly occur in the aquatic environment. However it is different from natural predation in that humans are very efficient top level predators that can greatly influence functioning of aquatic food webs (Casini et al. 2008). As recently as the late nineteenth century, some prominent scientists considered that fishing activities had little significant impact on marine fisheries (Huxley 1884), although it was already evident at that time that certain freshwater fisheries with limited productivity could be overfished (Arlinghaus et al. 2007b). However, the massive increases in human population and technology in the 135 years since Huxley's speech (developments that could not have been foreseen by late nineteenth century scientists), have increased fishing power exponentially (Hart and Reynolds 2002). The rate of technological advance began with the motorization of fishing fleets in the late nineteenth and early twentieth centuries (Valdermarsen 2001). Throughout the twentieth century, rapidly increasing population growth and advancing technology driven by military needs resulted in many innovations in fishing gear, aeronautics, electronics, computers, radar and acoustic techniques, earth orbiting satellites, GPS and remote sensing technology, all of which have been directed towards the capture of fish (Valdermarsen 2001). Because of this vast increase in fishing power, fishing in today's world almost invariably requires strict management if overfishing is to be avoided (Hart and Reynolds 2002).

Fisheries management as a scientific discipline has developed to control fishing effort and landings in order to reduce overfishing and maintain sustainable fisheries which minimize their adverse effects on the long term viability of exploited populations of fish and other animals within aquatic food webs (Hart and Reynolds 2002). There is no doubt that overfishing can adversely affect fish populations and ecosystems, however, suggestions by some scientists that overfishing alone has caused massive environmental changes (Jackson et al. 2001) are greatly overstated (Boesch et al. 2001). Overfishing has either followed on from habitat degradation and pollution (Thorne and Thomas 2008), or both processes have proceeded simultaneously (Boesch et al. 2001), and thus all have contributed to degradation of the aquatic environment. Indeed, habitat degradation and pollution are primarily responsible for significant ongoing reductions in fisheries productivity in many parts of the world where pollution and/or human development has occurred (Thorne and Thomas 2008; Rochette et al. 2010). Fishing may not be the primary agent contributing to reductions in fish stocks or environmental degradation in many instances (Rochette et al. 2010), but its management is still a critical component of ecosystem based management which is being increasingly adopted in our attempts to protect and restore aquatic animal populations in degraded systems (Boesch 2006; Thorne and Thomas 2008).

Clearly then, using the nature-based definition of welfare, proper and effective fisheries management is a fundamental prerequisite for ensuring the welfare and viability of aquatic animal populations targeted by fisheries within their natural environments. Fisheries management thus forms one part of a broader ecosystem based approach that must also encompass management of environmental degradation and prevention/control of exotic pests and diseases (Fig. 2). The importance of fisheries management in this relationship is increased wherever fisheries management is rudimentary or non-existent, such as in many developing countries (Allen et al. 2005).

Emerging concern regarding welfare of aquatic animals in capture fisheries

While huge amounts of effort are often expended on fisheries management in order to maintain sustainable fisheries (at least in most developed countries), the topic of aquatic animal welfare in wild catch fisheries has historically received little attention. This has now changed. While perceived welfare issues associated with commercial and recreational fishing activities

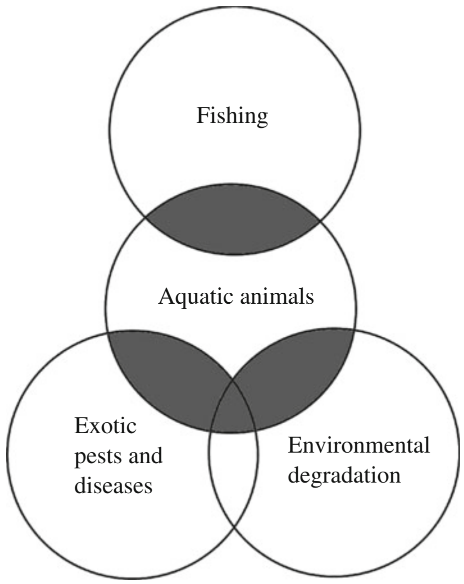

Fig. 2 Schematic representation of the ecosystem based approach to environmental management, illustrating where factors such as environmental degradation, fishing and exotic pests and diseases influence the welfare of aquatic animals (*shaded areas*). The degree of overlap and interactions of the various factors influencing aquatic animal welfare can vary depending on many factors

have probably always accompanied the history of fishing in some cultures (Arlinghaus and Schwab, in press), advocacy from interest groups in Western societies demanding improvement of the welfare of teleosts in wild capture fisheries continues to increase (e.g. Mood 2010). However, the absence of this perceived need in many Eastern cultures, and throughout the developing world, suggests the advocacy expressed by the likes of Mood (2010) may be due to increased affluence in Western societies in conjunction with isolation of humans in post-industrialized societies from their dependence on the natural world (Louve 2005; Arlinghaus et al. 2007b; Arlinghaus and Schwab, in press; Arlinghaus et al. in press).

Welfare of individuals versus populations

Some authors consider a clear distinction should be made between conservation of aquatic animal populations and the welfare needs of individual animals (Davie and Kopf 2006). Davie and Kopf (2006) stated that “Conservation is related to welfare but stands separate in that a population cannot suffer welfare compromise, something which an animal, alone, must endure”. However, the suffering centered (feelings-based) approach adopted by Davie and Kopf (2006) is inherently inadequate, because they overlook the broad range of factors influencing the welfare of populations and even entire communities of aquatic animals in their natural environments. Empirical evidence shows that populations and communities of aquatic animals can (and frequently do) experience compromised welfare in their natural environment (see previous sections for examples). Furthermore, the evolution of behaviours such as terminal spawning (semelparity) in some taxa, such as salmonids (Crespi and Teo 2002) and cephalopods (Rocha et al. 2001) demonstrate that natural processes in aquatic ecosystems favour survival of the population, even to the detriment of the survival of some individuals. Indeed, this is a fundamental process driving natural selection. This suggests that the welfare needs of wild aquatic animals are inextricably entwined with the need for conservation of their populations and their environment, which is the very basis of the ecosystem based management approach (Boesch 2006).

Welfare standards will need to be applicable to populations of all types of wild aquatic animals within all trophic levels of the ecosystem if a true ecosystem-based management approach is to be adopted. Welfare standards will also need to be applicable to emerging environmental issues such as endocrine disruption, which does not necessarily cause suffering to individual animals, but has potentially massive ramifications for fisheries management and conservation of aquatic animals at the population and ecosystem community level (Cotton and Wedekind 2008). These objectives can only be achieved if function-based and nature-based approaches to welfare are adopted, because unlike the feelings-based approach, the former two have the utility to encompass the entire range of aquatic animal welfare issues at all trophic levels in the natural environment.

Welfare issues in commercial fisheries

If it is agreed that function and nature-based approaches have the most utility for addressing aquatic animal welfare issues that may arise in the natural environment, the question then becomes—What fisheries practices are likely to cause welfare issues under these definitions, and how can these activities be mitigated to improve aquatic animal welfare? Clearly, avoidance of overfishing, bycatch and rebuilding of overfished populations is one fundamental prerequisite (FAO 1995). However, an indepth discussion of the various factors influencing fisheries management is beyond the scope of this paper. The answer to other welfare issues will depend on the type of fishing being conducted, the fishing gear used, the environment in which the fishery operates, the fisheries management arrangements controlling that fishery, and probably many other factors as well. Because of these reasons, mitigation of welfare issues that may arise during the fishing process must be closely linked and complementary to the conservation and environmental objectives acting within the management arrangements used for each fishery.

Fishing interaction with aquatic organisms generally begins with the harvest process, hence avoidance of unintended captures (i.e. bycatch, see Hall et al. 2000) is one effective way to improve fish welfare in all fisheries. For commercial fisheries using trawls, nets, traps and longlines, large numbers of teleosts can be captured at the same time, or at least within a very short time period. In commercial fisheries, the period between capture and death of the animal is variable, depending on the fishing technique and gear used, and many other variables such as the target species, water depth, water temperature, market destination and so on. Death of commercially caught teleosts and elasmobranchs usually occurs due to asphyxiation, though barotrauma and crushing may be the most common method of killing for animals taken in deep sea trawls (Davis 2002; B Diggles, personal observation). In some fisheries, chilling in an ice slurry (with or without exsanguination) or clubbing followed by ice slurry is sometimes used, while iki jime (pithing) followed by destruction of the spinal chord then snap freezing is often used for larger high value species such as tunas (Harada 1988). If administered accurately, iki jime can be a humane slaughter process that results in the lowest levels of stress and maximal product quality in slaughtered teleosts and elasmobranchs compared with all other methods of dispatch (Poli et al. 2005). However, this method is not conducive to slaughter of large numbers of fish at one time, as is commonly needed in commercial fisheries. Chemical anaesthetics are not used in wild capture fisheries, possibly because their use by fishers is explicitly illegal in many jurisdictions due to pre-existing fisheries management arrangements prohibiting their possession, and also due to the need to protect consumers from exposure to some chemicals (Marking and Meyer 1985). Their disposal also presents environmental problems, and in any case, there is evidence to suggest that use of some anaesthetics may not result in superior welfare compared with traditional methods such as use of ice slurrys, at least for warmwater species (Blessing et al. 2010). There are little data relating to the use of other methods such as carbon dioxide and electrical stunning, but their use in commercial fisheries is likely to be uncommon or non-existent due to logistical constraints.

Asphyxiation is the usual fate of the majority of fishes captured in commercial fisheries. Asphyxiation is a natural process of mortality for wild aquatic animals under normal conditions when they are consumed by predators, or during adverse environmental conditions such as water hypoxia, hence this may be an acceptable method of slaughter for commercial fishing if a nature-based definition of welfare is used. However, death by asphyxiation is not ideal if a function-based definition of welfare is used for species such as teleosts and elasmobranchs, given that it results in a transient physiologically stressed state prior to death that also reduces product quality due to increased lactic acid buildup from anaerobiosis (Harada 1988; Wilkinson et al. 2008). This suggests that improvements to fish welfare may be achievable if commercial fisheries that usually rely on asphyxiation can move towards other slaughter methods such as use of ice slurrys (with or without exsanguination), cerebral percussion or iki jime, with the added benefit of a likely improvement in product quality (and the promise of increased market price and shelf life as a result) (Harada 1988; Lowe et al. 1993). However, practical application of improved slaughter techniques may be difficult or impossible to apply in some commercial fisheries due to their incompatibility with the fishing environment encountered or even the management arrangements utilized for each fishery, and they may be undesirable in others. For example, many decapod crustaceans, such as crabs and lobsters, can survive for reasonably long periods out of the water if kept moist, due to the rigid structure of their gills and the relative abundance of oxygen in air compared with water. For these reasons, it is relatively easy for commercial fishers to improve product quality by simply delivering decapod crustaceans to markets live. The number of markets accepting live crustaceans and teleosts has increased significantly (Lee and Sadovy 1998; Scales et al. 2007), and the requirements of prolonged captivity, transport and handling of teleosts and crustaceans prior to slaughter in these industries poses potential welfare issues that are essentially identical to those that arise in aquaculture production systems (B. Diggles, personal observations).

Given the large range of fishing techniques, fishing environments, target species, target markets and other variables influencing aquatic animal welfare in commercial fisheries, it is impossible to draw universal conclusions regarding details of what might be best welfare practice for slaughter, except to state that the most logical way to introduce welfare concepts to commercial fishing industries is likely to be through research and development of industry codes of best practice tailored for each individual fishery and its markets. This process is already underway in some parts of the world, such as Australia.

Welfare issues in traditional and subsistence fisheries

There are large numbers of subsistence and traditional fishing industries around the world, mainly in third world and developing countries. Many of these have characteristics similar to small scale commercial fisheries, though the gear used is often less advanced, and may even include gear normally used in recreational fisheries. For traditional and subsistence fishers, however, concepts of aquatic animal welfare are usually alien, though some cultures do not approve of fishing for purposes other than procurement of food, relating to a concept of "not playing with ones food", which may have some conservation or welfare connotations (Arlinghaus et al. 2007b). In general, however, food security trumps animal welfare when human welfare is suffering due to lack of protein. Furthermore, it is highly likely that many traditional and subsistence fishers would find it logistically impossible, financially prohibitive and/or culturally unacceptable to alter traditional harvest methods and employ slaughter techniques deemed of superior welfare quality by post-industrialized nations.

Welfare issues in recreational harvest fisheries

Recreational fishing will be defined here sensu Arlinghaus et al. (2007b) as fishing that does not generate resources to meet physiological needs essential for human survival (e.g. nutrition) and for which obtaining food or selling fishing products to offset cost is not the primary motivation. In Western cultures, recreational fishing is typically called angling, and is defined as an activity conducted with a hook, line and often rod and reel, during free time (as opposed to working time) (Arlinghaus et al. 2007b). Other forms of recreational fishing include spearfishing, and capture of fish and crustaceans in traps or nets.

Welfare issues related to the angling process generally begin with the hooking of the fish, though in some regions the use of live bait has been identified as a welfare issue by using feelings-based welfare definitions (Arlinghaus and Schwab, in press). However, live baiting using aquatic animals would be acceptable if a nature-based definition of welfare is used, given that huge numbers of aquatic animals within their natural environment are killed every day by predation in a similar manner. On the other hand, it may be considered a welfare issue in at least some circumstances if a function-based approach to welfare is used, as some species of teleost used as live bait are likely to experience physiological stress from being hooked and restrained on the hook and line for any significant period of time (Davie and Kopf 2006). If a function-based approach to this issue is required, more research into the physiological stress associated with live baiting may be warranted, including studies of recovery and survival rates of live baits that are not eaten by predators, but are dehooked and subsequently released.

In most Western countries, recreational fisheries management regulations such as minimum sizes, maximum sizes, bag limits and even total protection of some species require anglers to release all fish that do not meet the management requirements mandated for that jurisdiction. In addition, a large proportion of anglers choose only to harvest a particular or preferred species, or a particular size range of fish, to further limit the fish that they harvest (i.e. selective harvest). Because of this, the majority of fishes captured by recreational anglers are released (Cooke and Cowx 2004). Due to the nature of the capture method, fish typically experience less damage when captured by angling than when caught by most commercial fishing gears such as seines and gill-nets. Therefore, releasing fish in comparatively good condition is more likely in recreational fishing than in most commercial fisheries (Arlinghaus et al. 2007b). There have been many studies of the various factors that influence the anatomical hooking location of teleosts captured by anglers. Hooking location is usually the most important factor influencing survival rates of teleosts captured and released by recreational anglers, with deep hooking resulting in more serious trauma and higher mortality rates (Muoneke and Childress 1994; Cooke and Sneddon 2006). In order to fully realize the potential fisheries management and conservation benefits that can accrue from adhering to fisheries regulations, recreational anglers can reduce the rate of deep hooking through adjustment of hook size and type (e.g. use of larger hooks or circle hooks), and use of artificial lures rather than bait (Muoneke and Childress 1994; Diggles and Ernst 1997; Cooke and Suski 2005). Obviously, reduction in deep hooking can also be expected to result in improved welfare outcomes for angled fish that must be released by regulation (Cooke and Sneddon 2006).

Selection of appropriate tackle, particularly sufficient line strength, can reduce the time taken to capture fish using hook and line gear, which reduces the magnitude of physiological changes due to exercise (Skomal and Chase 2002), and hence is expected to improve the welfare and survival of angled fish (Davie and Kopf 2006). Barbless hooks are easier to remove and therefore result in less air exposure time (Diggles and Ernst 1997), and also reduce tissue damage compared with barbed hooks, thus their use appears consistent with the improved welfare and survival of angled fish (Cooke and Sneddon 2006; Davie and Kopf 2006). Use of knotless landing nets or equipment such as lip grips may reduce physical damage due to scale loss and splitting of fins and hence offer the opportunity for further welfare improvements, provided they are properly used (Barthel et al. 2003; Danylchuk et al. 2008). Indeed, anglers can adopt a wide range of techniques and behavioural practices which can improve survival and welfare outcomes for angled fish that must be released (reviewed by Cooke and Sneddon 2006; Pelletier et al. 2007). Today, many individuals are going even further in their efforts to reduce their fishing related environmental footprint, through avenues such as use of biodegradable lures, sinkers and fishing line (Thyer 2009).

There are also potential welfare issues for those fish that are taken by recreational anglers for harvest. Unlike commercial fishing, teleosts and elasmobranchs caught by recreational angling are typically captured singly or in small numbers at any one time, depending on the number of hooks deployed. This means that recreational anglers are better positioned to ensure that every fish chosen for harvest can be slaughtered quickly using best practice methods for humane killing. While asphyxiation remains commonly used by many anglers, in recent years there has been increased encouragement of the use of other slaughter methods such as ice slurrys (with or without exsanguination), cerebral percussion and iki jime (Recfish Australia 2008; EIFAC 2008). As for commercial fisheries, use of these methods is not only generally considered to be more humane, they have the added benefit of improvement in product quality (Davie and Kopf 2006).

Recreational spearfishing has one clear welfare benefit over virtually all other forms of fishing, that being there is virtually no bycatch. Spearfishers select the animal they wish to take prior to shooting it, which contrasts with recreational angling where there is often bycatch due to anglers having limited control over the species captured (though certain species can be "targeted" quite effectively through use of specific tackle, baits/lures and techniques). In comparison, commercial fishing techniques such as netting, trawling and longlines can have very high levels of bycatch, though methods have been developed to try and reduce this in some fisheries (Broadhurst et al. 2008). However, issues related to the welfare of fishes that are speared but escape from the spear remain, as do those related to humane slaughter of speared fish that are not taken with a "kill shot" (i.e. one that kills the fish immediately by penetrating vital organs or the brain). For the latter, because recreational spearfishers shoot and handle their catch one by one, the same options for humane slaughter as outlined for recreational angling will apply.

Clearly there are many ways that recreational fishers can improve the welfare outcomes for aquatic animals they release or retain during the course of fishing. Indeed, codes of practice that outline acceptable welfare standards for aquatic organisms and encourage utilization of best practice methods relating to virtually every aspect of recreational fishing have been developed and adopted by fishers in some countries (Recfish Australia 2008; EIFAC 2008; Arlinghaus et al. 2010). The use of best practice relating to maintenance of fish in live wells, maximizing survival of released fish as well as encouragement of use of humane killing methods has also been outlined in the NEATFish environmental standard for fishing tournaments that has been developed in Australia (Sawynok et al. 2008) and is available online at www.neatfish.com. Because many basic aspects of the angling process are reasonably standardized in most western countries, anglers in regions where codes of practice are not available can be guided by the contents of the existing codes of practice that have been developed for other jurisdictions (Recfish Australia 2008; EIFAC 2008; Arlinghaus et al. 2010). Nevertheless, due to the enormous range of fishing techniques, environmental variables, target species and management arrangements that comprise recreational fisheries around the globe, fine tuning of welfare standards developed in these existing codes of practice may be needed and, if so, this should be pursued through research and development tailored for the unique situations that arise in each country.

Welfare issues in recreational catch and release fisheries

Voluntary catch and release (as distinct from harvest oriented recreational fishing and mandatory catch and release due to fisheries regulations) is an activity that is virtually unique to the recreational angling sector (Arlinghaus et al. 2007b). Tag and release is a derivation of voluntary catch and release with an additional endpoint of obtaining scientific information about the survival, movements and growth of released fish if they are recaptured at a later date. Catch and release fishing, if properly applied, provides a fishery management answer to potential angling-induced impacts on fish populations by releasing fish, which minimizes the impact of angling on the resource while providing important social and economic benefits to society at the same time (Policansky, 2002, Sutton 2003, Arlinghaus et al. 2007b). This perspective, however, overlooks some cultural, ethical and even legal issues associated with voluntary catch and release in some regions (Arlinghaus 2007, Arlinghaus et al. 2007a, in press). Indeed, in Germany and Switzerland, application of a feelings-based approach to fish welfare has resulted in bans on voluntary catch and release fishing, probably generating an overall reduction in welfare status for individual fish and affected fish populations due to a variety of reasons (Arlinghaus 2007; Arlinghaus et al. 2007a, 2009).

One unique welfare issue related to voluntary catch and release is the temporary retention of teleosts in live wells and display/recovery tanks during fishing tournaments. Several studies have shown that improperly used live wells can expose fish to suboptimal water quality that can result in significant reductions in the physiological fitness of teleosts held in them for extended periods of time (Suski et al. 2006, 2007; White et al. 2008), while live weighins expose the fish to additional handling, prolonged air exposure and fin and scale damage (Dowling et al. 2010). Water quality in display/ recovery tanks used after live weighins in some tournaments can also be suboptimal, and the tanks themselves can be used in multiple tournaments in quick succession in different catchments, presenting an unquantitated biosecurity risk (B Diggles, unpublished observations). The NEATFish environmental standard for fishing tournaments encourages tournament organisers to rethink their tournament format by rewarding tournaments for utilizing best practice, that being immediate release of the fish at the site of capture without use of livewells or live weighins (Sawynok et al. 2008). For tournaments that choose to retain use of live wells, live weighins and display tanks, the NEATFish standard rewards organisers who impose various regulations designed to improve fish welfare in live wells, such as enforcement of minimum tank volumes, insulation of livewell tanks to reduce temperature fluctuations, use of compulsory water circulation, spot checks on water quality, and so on (Sawynok et al. 2008).

Apart from live wells, from a function-based or nature-based approach to aquatic animal welfare, the issues relating to voluntary catch and release are otherwise identical to those posed by involuntary or mandated catch and release (see previous section). That is, in order to realize the potential fisheries management and conservation benefits that can accrue from releasing fish, recreational anglers should maximize welfare outcomes for voluntarily released fish by selection of appropriate tackle and techniques that reduce the rate of deep hooking, reduce the time taken to capture the fish, result in less air exposure time and physical damage while handling the fish, and so on (Cooke and Sneddon 2006; Pelletier et al. 2007). Again, codes of best practice and angler education are likely to be the most effective way to introduce welfare concepts, minimize the potential drawbacks and maximize the welfare benefits that accrue from voluntary catch and release angling.

Discussion

Humans have always been predators of animals, including fishes, and we never stopped being predators and part of the ancient food chain. Some ecologists realized this long ago, though others have persisted in their attempts to separate humanity from nature (Western 2001). Our self-awareness and ethical sensibility, features not shared with our animal relatives, should make us exercise good judgment and appropriate restraint in our modern predatory activities, but this has not necessarily extended to an ability to solve complex environmental problems. The human population explosion has resulted in many environmental problems that have disrupted the functioning of aquatic ecosystems, posing significant threats to the biodiversity and welfare of aquatic animals in their natural environments.

An enormous range of human activities result in water pollution and habitat change that have significant impacts on the environmental processes that directly influence aquatic animal welfare. Indeed, even non-consumptive ecotourism activities such as recreational boating, whale watching and diving can damage the aquatic environment and stress or change the natural behaviour of the subject animals (Hardiman and Burgin 2010). In fact, all humans contribute to water quality problems such as those related to sewage outfalls, and virtually all land-based anthropogenic developments impact the welfare of wild aquatic animals in some way. Emerging issues such as endocrine disruption pose significant threats to aquatic animal welfare (Salmon and Trout Association 2008; Sarria et al. 2011) and demonstrate that conventional “five freedoms” and feelings-based concepts of welfare are incapable of encompassing the broad range of anthropogenic threats to the welfare of aquatic animals in the wild, not just teleosts, but all animals that comprise the various trophic levels that underpin functioning of entire ecosystems.

There are undoubtedly some welfare issues related to harvest and release of aquatic animals during fishing, but these must be kept in perspective, as they are relatively easy to address through education and codes of best practice. In contrast, the magnitude and nature of the numerous anthropogenically mediated environmental threats to aquatic animal welfare makes them extremely difficult to address. In stark contrast to the esoteric problems relating to the possibility of perception of “suffering”, “pain” and “fear” in invertebrates and “lower” vertebrates, the process of anthropogenic degradation of aquatic environments is very real and global in nature, but its effects on aquatic animal welfare remain largely unseen and unnoticed by the vast majority of the humans who are inflicting these very same insults.

Indeed, the majority of the human population in post industrialized societies are now largely divorced from the reality of their dependence on the natural world (Louve 2005). Most humans care little for aquatic animals, seeing them as simply sources of food found at the supermarket, pets, or natural curiosities they sometimes see in cartoon movies or on television. Because of this, it makes little sense to alienate key stakeholder groups such as commercial and recreational fishers who have a significant (albeit sometimes vested) real life interest in the welfare of the aquatic animals they directly interact with in the natural environment. All aquatic animals in their natural environment have important ecological roles as components of food chains. This suggests we should be concerned with the welfare of not only teleosts, but all aquatic animals (Iwama 2007). For example, zooplankton (composed in part of eggs and larvae of crustaceans, polychaetes, molluscs and teleosts) is a very important lower trophic component of aquatic ecosystems. There is increasing empirical evidence that demonstrates zooplankton can be severely affected by anthropogenic pollutants at environmental concentrations (Gerritsen et al. 1998; Bailey et al. 2000; Palma et al. 2009). Zooplankton are an integral component of the food chain and provide the first forage for nearly all wild fishes and many other aquatic animals. On function-based and nature-based welfare grounds, one can argue that we should be concerned with the welfare of zooplankton—they require protection from anthropogenic pollution in order to better secure the welfare of the higher trophic level organisms that have planktonic components of their lifecycle, and/or rely on plankton for food. But few humans are concerned with the welfare of plankton. However, scientists and angling groups in Australia have recently called for reduced pollution from agrichemical sources, in order to better protect planktonic food organisms as well as habitat and the larval stages of recreationally important fish species (Diggles 2010; Magnusson et al. 2010). This is not an isolated case—recreational fishing groups have also been prominent in their calls to address emerging issues such as endocrine disruption (Salmon and Trout Association 2008), as well as many other environmental problems affecting fish and other aquatic animals of relevance to fisheries (Granek et al. 2008).

The Fisheries Society of the British Isles (FSBI 2002) stated that none of the broad definitions of animal welfare (feelings, function and nature-based definitions) is right or wrong; they simply capture different aspects of what the word welfare means. We agree with this statement in principle, but demonstrate in this paper that some definitions of welfare have shortcomings that mean they should not be applied to all situations. It is clear that the feelings-based approach to welfare that has been widely adopted for laboratory experimentation and aquaculture production systems, has some serious shortcomings in its scientific foundation if it is applied to wild capture fisheries (Rose 2007). The feelings-based approach cannot be applied to all types of aquatic animals, cannot encompass predator prey interactions, nor does it adequately address the many environmental issues threatening the welfare of entire populations of aquatic animals in their natural environment (Fig. 3). Because of this, science must reject application of the feelings-based approach to aquatic animal welfare in the natural aquatic environment.

Nevertheless, in some countries, animal rights-based and feelings-based approaches to fish welfare have been adopted to fisheries, resulting in legislation that has adversely impacted effective fisheries

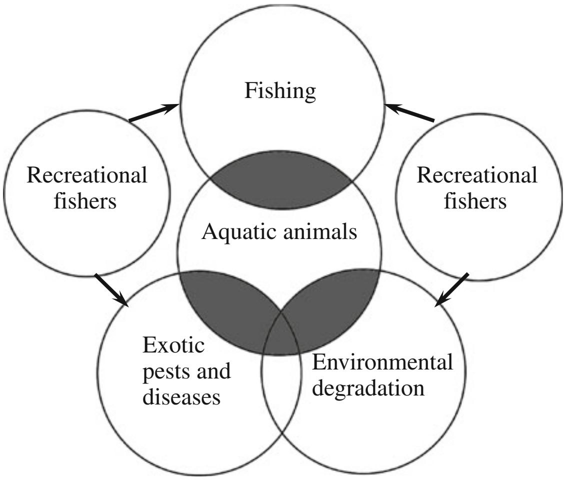

Fig. 3 Schematic representation of the ecosystem based approach to environmental management. The *arrows* indicate where stakeholders such as recreational fishers are active in combating issues such as unsustainable fishing, environmental degradation and exotic pests and diseases that adversely influence the welfare of aquatic animals (*shaded areas*)

management by dictating how recreational fishers can legally interact with fish, to the detriment of not only the individual fish, but also many potentially beneficial social, economic and ecological outcomes (Arlinghaus 2007; Arlinghaus et al. 2007a, 2009). However, recreational fishers provide significant contributions towards addressing a broad suite of anthropogenically derived environmental issues of critical importance to the welfare, management and conservation of aquatic animal populations in their natural environment. These include their support for research, and adoption of research findings that have improved aquatic animal survival (and hence welfare) in capture fisheries (Pepperell 2008), via their surveillance for early detection of incursions of exotic pests and diseases, via their vocal advocacy for improved management of biosecurity, fisheries and the environment (e.g. Salmon and Trout Association 2008), and through their financial support (through license revenue) and active participation in projects to improve water quality and restore aquatic habitats (Bate 2001; Arlinghaus et al. 2007a, 2009, 2010; Granek et al. 2008). This demonstrates that application of the feelings-based approach to welfare issues in wild capture fisheries is counterproductive because it can actually reduce aquatic animal welfare by inhibiting existing environmental initiatives undertaken by key stakeholders in those fisheries.

In contrast, the function-based and nature-based approaches to welfare apply to aquatic animals at all trophic levels within each ecosystem, and can be used to address the many environmental issues threatening the welfare of entire communities of aquatic animals in their natural environment. Given the breadth and magnitude of the anthropogenic insults that affect wild aquatic animals in todays world, it must be concluded that the welfare needs of wild aquatic animals are inextricably entwined with the need for conservation of their populations, communities and their environment as part of an ecosystem based management approach (Boesch 2006). Maximising welfare outcomes for wild aquatic animals starts with maintenance and rehabilitation of water and habitat quality, effective fisheries management (including minimization of bycatch and discards) and limiting anthropogenic spread of pests and diseases (Burreson et al. 2000; Gaughan 2002; OIE 2010), due to the massive influence all these factors have on ecosystem health, disease, and survival of larval, juvenile and adult stages of all aquatic animals. Within an ecosystem based management framework, function-based and nature-based approaches to welfare issues can then be used to direct stakeholder groups such as recreational and commercial fishers to improve specific welfare outcomes for aquatic animals through adoption of codes of best practice that use welfare criteria that are scientifically based. This approach will allow these same stakeholders to maximise the welfare of the aquatic animals they directly interact with, and permit them to continue to expend their time and energies attempting to address the many other pressing environmental issues that threaten the welfare of aquatic animals in todays world.

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