491 *Etica & Politica / Ethics & Politics*, XXI, 2019, 2, pp. 491-516
ISSN: 1825-5167

IS 'HISTORY' REPEATING ITSELF? THE CASE OF FISH AND ARTHROPODS' SENTIENCE AND WELFARE

BARBARA DE MORI
Padua University, Italy
Department of Comparative Biomedicine and Food Science
barbara.demori@unipd.it

SIMONA NORMANDO
Padua University, Italy
Department of Comparative Biomedicine and Food Science
simona.normando@unipd.it

ABSTRACT
Animal welfare is an important concern in modern society. The most common ethical underpinning of animal welfare is the concept of sentience. However, there is no agreement yet on the definition of sentience and on which features are essential for a species to be classified as sentient. Unsurprisingly, hot debates flare up periodically about whether a certain species could be considered as sentient and thus on whether its welfare should be granted. In the present paper, we outline the repetitive tendency of such debates, using fish and arthropods as an example. Up to now, these debates tend to end with the vast majority of researchers either recognising sentience in the target species or advising the use of the precautionary principle and thus tentatively act as if the species is sentient in order to take decisions regarding its welfare status. The debate then usually moves to a species progressively less similar to humans and the cycle of the 'sliding scale' begins anew. In view of this tendency, we discuss whether it would be advisable to reject the idea of a sliding scale when welfare relevant decisions are at stake.

KEYWORDS
Fish, invertebrate, animal sentience, ethics, animal welfare.

INTRODUCTION

Animal welfare is at the centre of growing concern in society today and has received much scientific and ethical interest in the last decades, generating an interdisciplinary approach to it [1]. Although there is disagreement on whether access to

[1] See Håstein, Scarfe and Lund, 2005; Fraser, 2008.

welfare should be linked to consciousness or just sentience[2], the most common ethical underpinning of animal welfare is based on the concept of sentience. If there are scientific evidences supporting that an animal is sentient, it deserves ethical consideration[3] and its welfare can be impaired.

Of course, this link between ethics and animal welfare depends on how sentience is conceived. Different definitions of sentience imply different moral considerations for different animals. The absence of a universally agreed upon definition of sentience and of consciousness and of the differences between the two, does not help in this matter[4]. In this paper, we will refer mainly to sentience, deeming it outside the scope of the argumentation to discuss in depth the relationship between it and higher 'degrees' of consciousness[5].

Unsurprisingly, hot debates flare up periodically about whether a certain species could be considered as sentient and thus on whether we have any obligations to grant it a life worth living. In a recursive trend, reminiscent of one of the social behaviour themes Rosnow identifies in Gianbattista Vico's writings[6], most of the sentience debates tend to develop through a similar pattern. They tend to go from unawareness regarding the issue, trough hot scientific and ethics debates, to a final stage in which there is a near consensus on the matter, and up to now usually sentience has been recognised. Of course, even in this final stage, some authors irreducibly disagreeing could still be found, and the implementation of equal welfare consideration in practice can still need time even if sentience has been agreed upon. The debate then tends to move on to concern a non-human animal type progressively less similar to human being, regarding which the cycle begins anew.

In more or less recent times, such a debate has concerned even mammals and human infants, also deemed until recently to have only reflective responses due to nociception[7]. However, the repetitive pattern of sentience debates is becoming more and more evident in recent times when debates are not so far apart in time. A good example is the recent controversy concerning arthropods (e.g., insects, crustaceans, arachnids)[8], which closely resembles the not so temporally distant one concerning fish[9] and is undermined by the same controversies[10].

[2] See Dawkins, 2017.

[3] As defined in Bovenkerk and Meijboom, 2012.

[4] See, for example, Yue Cottee, 2012.

[5] At least since the Cambridge Declaration (see Panksepp *et al.*, 2012) it seems there is a general agreement about the idea that feelings that are involved in the perception of pain, suffering and pleasure need not necessarily be referred to as the presence of a higher/access consciousness, which is able to elaborate a notion of self. Notwithstanding, the controversy still remain. See below for some hints.

[6] See Rosnow, 1978.

[7] See Bellieni, 2012.

[8] See, for example, Broom, 2013; Carruthers, 2007; Horvath *et al.*, 2013; Mason 2011; Perry and Baciadonna, 2017.

[9] See, for example Sneddon *et al.*, 2018.

[10] See, for example, Porcher, 2018.

1. SENTIENCE AND ANIMAL WELFARE: THE CASE OF FISH AND ARTHROPODS

Researchers in animal welfare science have made it progressively evident that animal welfare strongly depends on how an animal *feels* and responds to its living conditions[11]: sentience appears to be the step from which to start studying animal welfare. For the animals traditionally admitted in the realm of sentience, animal welfare has been investigated ad a *state* of the individual animal[12], and to determine it, it has been investigated not only its functional and physiological responses, but also its ethological and cognitive responses. In this sense, the observation of the animal's subjective needs has turned out to be not only a professional demand, but also a moral one, giving the animal an inherent value and telling us how it perceives its living conditions from its perspective[13]. As an expression of good science and social responsibility, in 2009 the Farm Animal Welfare Council (FAWC), the most important international organization for an independent research on animal welfare, proposed to define animal welfare as a 'life worth living' for the animals[14]. Echoing ethical reflections on animals' dignity and inherent value[15], this definition shifts the focus of scientific research from measuring external parameters and the environment in which animals live to the animals themselves, using animals' indicators to evaluate their living conditions[16]. Animals have become subjects *of their life*, as Tom Regan has already stated in animal ethics in the Eighties[17], and animal welfare science and research need to focus directly on individual animals in order to evaluate their responses in terms of welfare. To be the subject of its own life for an animal it means that its life may be better or worse *to it*, regardless of the objective and external measurements and judgements we can formulate.

What to do, then, regarding animals about whom there is no consensus on their status as sentient beings? In past times, this question has justified the *a priori* exclusion of some categories of animals, for example fish, from being granted the same animal welfare status of other species. The debate on whether it was ethically and scientifically legitimate to include fish in the realm of sentience flared in the first decade of the 21st century. At present, most scientists/academics either acknowledge fish sentience or state that there is enough evidence to say that some fish may be

[11] See, for instance, Duncan, 1993, 2016; for a general overview on animal welfare research see Fraser, 2008, 2009.

[12] See Broom, 1991.

[13] See Stamp Dawkins, 1980; 1990.

[14] See FAWC, 2009.

[15] See, for instance, Van de Veer, 1983; Regan, 1983.

[16] On the development of animal indicators as a tool to assess animal welfare, e.g., Whay et al., 2003.

[17] See Regan, 1983.

sentient and thus justify the use of the precautionary principle[18]. Also the majority of the general public now tends to deem fish as sentient beings[19], and hot debates, such as that sparked by Key's denial of fish ability to feel pain, still flare up[20].

The main objection to fish sentience has always been that fish lack the neocortex, a six layered type of cortex present only in mammals, which is involved in human capacity for conscious awareness[21]. A similar, stronger, objections stands for arthropods, which have a simpler nervous system, consisting of less neurons, located in several distributed ganglia, which is deemed likely to limit advanced information processing[22]. However, there is no known minimum brain size requirement for the emotional experience of pain[23], and convergent evolution (i.e., the fact that in different species different structures evolve for the same function) is well accepted[24]. Moreover, both fish and arthropods present nervous system differentiation[25].

Analogies between fish/arthropods and mammals can be found also at other levels. A neuro-endocrine stress response analogous to that in mammals, resulting in the liberation of adrenaline and noradrenaline and of cortisol, is found in teleost fish[26] and it is influenced by stressor predictability as is in other animals[27]. A stress hormone, called the Crustacean Hyperglycaemic Hormone (CHH), converting glycogen into glucose and causing increased lactate concentration, as corticosteroids do in vertebrates, has been found in decapods[28]. A rapid rise in glucose and lactate in response to tissue damage, analogous to the vertebrate stress response was found in the edible crab (*Cancer pagurus*)[29].

[18] See, for instance, EFSA, 2009; Braithwaite et al., 2013; Bshary & Brow, 2014; Bshari, Gingins & Vail, 2014; Smith, 2014; Brown, 2015; Feinberg & Mallat, 2016; Seber, 2016; Lucon-Xiccato & Bisazza, 2017; Vila Pouca & Brown, 2017; Woodruff, 2017; Demin et al., 2018; Graham, von Keyserlingk & Franks, 2018a,b; Knutsson and Munthe, 2018; Sneddon et al 2018; Colson *et al.*, 2019.

[19] See, for instance, Santiago Rucinque, Oliveira Souza &.Maiolino Molento, 2017. However, disagreement remains (e.g., Rose et al., 2014; Key, 2015, 2016; Rose, 2016).

[20] See Key 2016.

[21] See Rose, 2002.

[22] See Bullock et al., 1977.

[23] See Adamo, 2016a.

[24] See Yue Cottee, 2012; Edelman, 2016; Jones, 2016.

[25] For fish, regarding lateralization, dopaminergic connections and pallium specialized areas: Bisazza, Pignatti & Vallortigara, 1997; Portavella, Vargas, Torres & Salas, 2002; Broglio et al., 2005, Portavella and Vargas, 2005; Vargas, Bingman, Portavella, López, 2006; De Santi, Sovrano, Bisazza & Vallortigara, 2001; Karenina, Giljov & Malashichev, 2013, O'Connell, Fontenot, & Hofmann, 2011. For arthropods, regarding the specialized high-order associative functions of the mushroom bodies in the supraesophageal ganglia: Strausfeld, 2002; Avarguès-Weber and Giurfa, 2013; Giurfa, 2013.

[26] See Sumpter, 1997; Brydges, Boulcott, Ellis, Braithwaite, 2009.

[27] See Galhardo, Vital, Oliveira, 2011a.

[28] See Lüschen *et al.*, 1993.

[29] See Elwood, 2012.

Nociception and Pain in fish and arthropods

What seems immediately obvious is that, if we are scientifically justified in applying the notion of sentience and, consequently, of welfare also to fishes, our moral obligation to the protection and promotion of their welfare applies first and foremost to the thorny question regarding their ability to experience *pain* and *suffering*. As famously stated by Jeremy Bentham, "the matter is not 'Can they reason? Can they talk?' rather 'Can they suffer?"[30].

The third of the well-known Five freedoms, which constituted a landmark in the animal welfare scientific literature until recently[31], explicitly underlined that to promote the welfare of animals the 'freedom from pain and suffering' is crucial, as is the 'freedom to express normal behaviour and to have pleasurable experiences'. In general, pain, though very well investigated, is still a very difficult topic to be understood, both from the phylogenetic point of view and in accordance to its 'evolutionary' aims. Is an objective evaluation of it even possible? Though it may seem easy to interpret it according to the survival of the individual being, the impact of its chronic symptoms are not easy to interpret, and so are the ways of occurrence in the different animal species. Furthermore, pain may be of different kinds: it may be acute or chronic, mild or severe, but most of all it is a *subjective* experience, which can be shown on both sensorial and emotional grounds, and consequently needs to be investigated not only from a neurophysiological standpoint, but also a behavioural one.

Thus, if today, in the light of the development of research, we might refer to pain as an unpleasant experience, not only sensorial but also emotional, we must look at the issue of suffering in order to complete its meaning and its importance[32]. With reference to the emotional sphere, what pain as a subjective experience can cause, is *in primis* a suffering condition (which, however, can emerge independently of pain), as well as a psychological disease condition, whose chronicity may change according to the variation in both internal and external conditions.

From an ethical point of view, the scenario gets even more complicated: if welfare mainly concerns the way an animal feels, the state of suffering and feeling pain (but also pleasure) determines, on the emotional ground, a qualitatively relevant change in its life condition, i.e. in the subjective quality of individual existence. Therefore, if we recognize that an animal with an even slight perception of pain and pleasure is the *subject of its own life*, its subjectivity acquires a crucial importance in demanding it to be considered. The main interest of animals capable of feeling pleasure and

[30] Bentham, 1907, p. 312.

[31] The *Five Freedoms* is the official definition of Animal Welfare that was offered in 1979 by FAWC, the Farm Animal Welfare Council, the same Institution that in 2009 has defined welfare as "a life worth living". Cfr. Farm Animal Welfare Council, 1979.

[32] Pain is currently defined as an unpleasant sensory and emotional experience associated with actual or potential tissue damage. Cfr. IASP 1979.

pain, seems to be that of not feeling pain and suffering, and to experience pleasure instead[33].

The argument here does not evidently require us to deal with issues that are harder to consider, such as those concerning their supposed – or not – belonging to the moral community, the recognition of rights for them, their having (or not having) consciousness, and so on. Rather, the appeal is directed to our obligation to respect and provide them for a life worth living. As stated in 2010 by C. Whates, President of the FAWC, paraphrasing Bentham, "*'The question is not just, "Do they suffer?" nor, "Are their needs met?" but rather, "Do they have a life worth living?" '*"[34]. It becomes crucial, therefore, from both a scientific and ethical point of view, to understand their perspective and to acquire an access, even indirectly, to their subjective experiences.

The presence of functional nociception mechanisms and pathways and of the related behavioural responses is generally recognised to both fish and arthropods[35]. More debated is whether fish and arthropods feel pain, especially the emotional component of it. Already in 2003, Sneddon, Braithwaite and Gentle, however, supported the hypothesis that fish could also have pain perception, as a negative mental state[36]. They found irritants injected trout showed reduced neophobia when exposed to a novel object compared to controls injected with saline, whereas a third group of trout, also acetic acid-injected, but then also administered morphine, acted more similar to controls. The authors interpreted their findings as suggesting that fish had pain perception because higher order behaviour patterns, such as attention, were changed by the administration of the noxious stimulus[37]. Other studies supporting the ability of teleost fish to feel pain were performed in the following years, mostly using the fear induced avoidance learning paradigm[38]. This paradigm consists in training fish to form classical associations between neutral stimuli and negative (unconditioned) experiences (usually either being electric-shocked or being netted) and then measure their avoidance of the conditioned stimulus in absence of the negative one to which it had been associated. Fish also showed modulation of their avoidance response to have access to a resource[39]. Such modulation was influenced by a cost/benefit ratio[40], using food as the resource and varying both food

[33] See Boissy *et al.*, 2007.

[34] Whates, 2010, p. 469.

[35] See for fish: Dunlop and Lamig, 2005; Taylor et al 2017; Nordgreen et al., 2007; Sneddon, Braithwaite and Gentle, 2003a; Braithwaite, 2010; Sneddon, 2002; Roques et al. 2012; for arthropods: Johnson & Carder, 2012 Lozada et al. 1988; Walters, 2018.

[36] See Sneddon, Braithwaite and Gentle, 2003b.

[37] See Braithwaite, 2010, p 51.

[38] See Yue *et al.*, 2004; Dunlop, Millsopp, and Laming, 2006; Milsopp and Laming, 2008; Millot *et al.*, 2014.

[39] See Dunlop, Millsopp, and Laming, 2006.

[40] See Millsopp and Lamig, 2008.

deprivation levels and shock intensities, supporting the idea that shock avoidance in fish is not purely a reflex action, but an elastic response subjected to trade-off phenomenon[41]. In 2012, Martins and co-authors, revising the cited evidence, could state that it suggested that fish respond to stimuli in manners that indicate that they are likely to find and perceive them as unpleasant, thus showing the capacity of experiencing negative affective statuses, such as pain and fear.

Evidence of nociceptive sensitization and pain-like states in arthropods have been also accumulating[42]. Already in 1988, Denti and co-authors trained crabs (*Chasmagnathus granulatus)* with a paradigm similar to that used to induce inhibitory avoidance in vertebrates, finding that crabs learned to avoid entering a light compartment in which they had previously been shocked, and retained learning for at least for 3 hours[43]. Perrot-Minnot and colleagues induced an anxiety-like state (expressed through increased sheltering behaviour in the absence of predation risk) in *Gammarus fossarum* using electric shocks[44]. Increasing the number of electric shocks increased also refuges' use and delayed behavioural recovery. The effect was mitigated by pre-treatment with a metabotropic glutamate receptor group II/III agonist. Elwood and Appel found that the response of hermit crabs (*Pagurus bernhardus)* to a noxious stimulation was not solely reflexive in nature (i.e., due to nociception) [45]. The crabs' responses were traded off against other motivational requirements (retaining a preferred shell), and the experience resulted in future avoidance of the situation, suggesting the experience was remembered and had a negative connotation attached to it.

2. THE DEFINITION OF SENTIENCE AND THE CASE OF FISH AND ARTHROPODS

Even in the light of such evidence, for a long time, a *scientific ideology* [46] has characterized the way in which science evaluated subjective experiences in animals, denying evidence of pain, suffering and pleasure, and of any form of consciousness, or at least stating that mental states could not be scientifically investigated in animals[47]. In 2012, a group of neuroscientists signed the well known *Cambridge Declaration on Consciousness*, unmistakably declaring that "convergent evidence indi-

[41] See Dunlop *et al.*, 2006.
[42] See Walters, 2018.
[43] See Denti, Dimant and Maldonado, 1988.
[44] See Perrot-Minnot, Banchetry and Cézilly, 2017.
[45] See Elwood, Appel, 2009.
[46] See Rollin, 1989.
[47] See Dawkins, 2015.

cates that non-human animals have the neuroanatomical, neurochemical, and neurophysiological substrates of conscious states along with the capacity to exhibit intentional behaviors"[48].

Researchers, like Ian Duncan or Marian Stamp Dawkins among others, starting at least from the Eighties, devoted their studies to developing ways to access animals' subjective states. They developed tools for 'asking questions to animals' interpreting behavioural responses to painful and pleasurable experiences from the animals' point of view. These tools included preference tests or consumer demand studies, thus progressively providing indirect access to their inner states[49]. Recent qualitative behavioural assessments have enhanced these researches by attempting to consider the animal *as a whole* and not only for isolated behavioural responses[50].

All these researches highlight the importance of considering animals in accordance to the Cambridge Declaration: the idea of an *automata* animal, as it was attributed to René Descartes (emblem of the scientific revolution of the Seventeenth century) more and more has set the pace towards the Darwinian revolution. However, to decide what animals are sentient seems to depend on the definition of sentience that is adopted: to what extent is it necessary to refer to awareness or consciousness to understand sentience, in order to explain pain, suffering and pleasure in animals?

It seems clear that, in the presence of a central nervous system, as well as of the development of the thalamo-cortical system of a certain kind, and of ways of transmitting feelings and emotions similar to ours, we are in some way forced to recognize similarities in the ways in which pain, suffering and pleasure are perceived. As Voltaire vigorously stated during the Eighteenth century, addressing the mechanist, "you discover in it the same organs of feeling that are in you. Answer me, oh mechanist, has hence nature arranged all the feeling springs inside it for it not to feel?"[51]. But what about animals that are not equipped in the same way?

It is undeniable that the debate around the issue of an animal's capacity of perceiving pain, suffering and pleasure has frequently been affected by the resorting to an ambiguous theory of consciousness. The difficulties concerning the definition of animal consciousness have given rise to a literature which is often characterized by prejudices. Starting at least with J. Griffin in the Seventies[52], the development of studies concerning animal cognition helped clarify such a complex issue, but the problem of having a 'practical' definition of sentience and consciousness, able of dealing with specific issues of welfare remained unsolved.

[48] See Panksepp *et al.*, 2012.
[49] See Duncan and Dawkins, 1983.
[50] See Wemesfelder, 2001.
[51] Voltaire, 1968, p. 108.
[52] See Griffin, 1976.

Different ways to approach the problem have been developed[53]. One way has been to accept the idea that consciousness is, basically, 'a living aid', an extremely important 'adaptation phylogenetically acquired in the course of evolution'[54]. Doing so, it is not hard to share the assumption that the degrees of consciousness we can attribute to animals differ from species to species, and that the feelings that are involved in the perception of pain, suffering and pleasure need not necessarily be referred to as the presence of a higher consciousness which is able to elaborate a notion of self [55]. By consciousness it is sufficient to denote the subjective and interior states of an individual in regards to feelings, emotions and attitudes, thus referring to various degrees of mental complexity to which various ways of pain, suffering and pleasure perceptions correspond.

Another approach has been that of focusing on sentience alone as something specific and different from consciousness, and linking welfare to it as its essential component[56]. Dawkins takes it further by arguing that we should leave the problem aside and focus on a consciousness-free definition of animal welfare instead: "Animal welfare can be defined objectively in terms of animal health and what animals want". Such a definition, from her point of view, is "practical enough to point out what factual scientific information is needed in any given case"[57].

The debate is far from resolved[58], but regardless of that, what is important is to recognize a special dignity – and, as a consequence, admit a moral obligation – to the living entities being *capable* (independently of the degree of such a *capacity*) of perceiving pain and pleasure, and of having memory of pleasurable or painful experiences. Which features are essential for a species to be classified as *capable* of perceiving pain and pleasure, and eventually of having memory of pleasurable or painful experiences? If sentience is deemed to correspond to phenomenal consciousness (i.e., awareness of feelings)[59], there could be some disagreement on, for example, whether the ability of forming mental representation and of thinking about one own actions are relevant features for it. Braithwaite in her milestone book about fish pain, listed three feature as the most cited for being essential for sentience[60]: the ability to experience mental states (i.e., sensations and emotions), the ability to form mental representations, and the ability of thinking about one own actions. Interestingly enough, although some pioneer advocated insect sentience already in 1987[61],

[53] As already stated, for the purpose and extent of this paper, this question will only be touched on and not discussed in depth.

[54] See Morton 2000.

[55] See Panksepp 2005.

[56] See Duncan 2016.

[57] Dawkins, 2016, p. 1.

[58] See, for example, Broom, 2014; Birch, 2017.

[59] See Dawkins, 2015.

[60] See Braithwaite, 2010.

[61] See Lokwood, 1987.

investigation of all these features in fish and arthropods peaked from the last years of the 20th century.

2.1 Mental states (i.e., sensations and emotions) in fish and arthropods

It has been noted that emotions are likely to have evolved in fish for the same function as in other vertebrates[62], and behavioural variables routinely employed to investigate subjective mental states in other vertebrates have been successfully demonstrated in fish[63]. The results of the already mentioned studies using fear induced avoidance learning or showing the fish ability to use 'trade-offs'[64] together to the existence of limbic structure analogues in the fish brain together with dopaminergic connections[65] further bear on this topic. Fish have also been shown to have preferences[66], motivational states[67], appraise relevant aspects of the environment[68], and show play behavior[69] and social modulation of welfare challenges' consequences[70]. Interestingly, Yue, Duncan and Moccia successfully supported the presence of the negative emotion "fear" in the rainbow trout using the conditioned-suppression paradigm, an approach commonly used to assess levels of anxiety or fear in other vertebrates[71]. This procedural paradigm consists of the suppression, by means of a fear-evoking, conditioned stimulus, of a stable and repetitive operant behaviour that is maintained by positive reinforcement. Emotion-like states have been studied also in bees and other insects. Perry and colleagues[72] found out that pre-test sucrose affected a dopamine-modulated response of bumblebees to an ambiguous cue to reward as well as a response to a simulated attack[73]. Authors reliably controlled for confounding so that the finding are suggestive of sucrose inducing a positive mental state in the bees, which altered subsequent responses. Gibson and colleagues[74] found that flies' (*Drosophila*) defensive responses to moving overhead translational stimuli (i.e., "shadows") were not purely reflexive, but had characteristics which suggested they expressed underlying emotion states (scalable responses, persistency, delay in resuming previous activities proportional to number of negative

[62] See Kittilsen, 2013.
[63] See Yue Cottee, 2012.
[64] See Yue, Moccia and Duncan, 2006; Milsopp and Laming, 2008.
[65] See O'Connell, Fontenot, Hofmann, 2011.
[66] See, for instance, Kistler *et al.*, 2012; Sullivan, Lawrence and Blache, 2016)
[67] See Galhardo *et al.*, 2011b.
[68] See Galhardo et al., 2011a.
[69] See Burghardt, 2013.
[70] See White et al 2017.
[71] See Duncan and Moccia, 2008.
[72] See Perry *et al.*, 2016.
[73] See Plowright, 2017.
[74] See Gibson *et al.*, 2015)

stimuli), suggesting a graded decaying internal defensive state, possibly analogous to fear in mammals.

2.2 Mental representations

Already in 1990, fish had been found to have the ability to differentiate between a cooperative and a non-cooperative partner fish, adjusting their behaviour accordingly[75]. In 1999, Mizukami and co-authors[76], designed a study to investigate whether goldfish could make abstract mental representation, pairing a food reward to a situation in which no food was visible and vice versa. The author reasoned that in this paradoxical setting, the fish needed to make the conceptualisation food=no food and vice versa in order to solve the task successfully. The fish succeeded in solving the task, choosing the compartment in which there was no visible food over the one in which they could see it. In the same year, Topál and Csányi used a conditioned fear paradigm and showed interactive learning in paradise fish, which appeared able to associate two temporally distinct, uncorrelated events (shock and view of an unfamiliar potentially predator fish) to construct a mental representation of a 'potentially dangerous predator' and acted accordingly[77]. Grosenick Clement and Fernald[78] showed that fish (*Astatotilapia burtoni*) had the ability of for transitive inference in social contexts, making inferences about the relative rank of two other fish that had never been paired before, based on the fact that one of them had won and the other had lost when paired with the same other fish. The authors' interpretation of the findings was that the fish had formed an abstract representation of the hierarchy among the other individuals. Fish have also shown to have the ability for quantity discrimination[79]. However, the most frequently cited examples of mental representations in animals are spatial maps[80]. Fish have been shown to be able of spatial orientation and to use it to approach places where appetitive stimuli have been found and avoid those where aversive stimuli have occurred[81]. As far as arthropods are concerned, bees have well known spatial orientation abilities[82] and studies on social transmission of spatial orientation in bees were at the basis of Karl von Frisch's Nobel Prize already in 1973. Using an elegant experiment, in which a group of displaced bees were anesthetised for several hours in order to induce a shift in the sun compass, Chesemann and colleagues[83] gave further support to the already

[75] See Milinski, Kullin and Kettler, 1990.

[76] See Mizukami et al., 1999.

[77] See Topál and Csányi, 1999.

[78] See Grosenick Clement and Fernald, 2007.

[79] See Stancher *et al.*, 2013; DeLong *et al.*, 2017.

[80] See Braithwaite, 2010.

[81] See Broglio, Rodriguez and Salas, 2003; Lee *et al.*, 2012.

[82] See Menzel *et al.*, 2006.

[83] See Chesemann et al., 2014

extensive evidence for the use of a metric cognitive map in bees, ruling out the sun-referenced home-vector alternative hypothesis. From the point of view of the present paper, about the tendency of some sort of debate to repeat itself with different animal species, it is interesting to note that the authors write that "half a century ago, the claim that any non-human animal had a cognitive map was deeply controversial [...] Now that it is well established by behavioural and neurobiological evidence that rodents have a metric cognitive map, the question of whether insects do is a frontier question"[84]. Abstract representation in bees is not limited to maps[85]. Bees have been found to learn abstract concepts such as sameness/difference, above/below, right/left and combinations of above/below or right/left with sameness/difference[86]. Bees were also successful in discriminating both face-like and non-face-like stimuli and categorized appropriately novel stimuli into these two classes using configural information[87].

2.3 The ability of thinking about one own actions in fish and arthropods

Bshary Horner, Ait-el-Djoudi and Frickle described non-random cooperative hunting (an ability deemed to have high cognitive requirements), including the use of signals, between grouper fish (*Plectropomus pessuliferus)* and a giant moray eel (*Gymnothorax javanicus)* to hunt prey which has found refuge in holes in the reef to which the grouper had no access to[88]. Their finding support the idea that fish were likely to be able to think abstractly about their actions[89].

One way to investigate the ability to think about one own actions is assessing metacognition. Metacognition can be defined as the knowledge of one's internal representations (i.e., the knowing to know) and is investigated by paradigms, which evaluate whether animals perform introspective evaluation of their knowledge before engaging or not in a difficult task, behaviourally "asking" the animal to report on its own degree of confidence in its behaviour[90]. Already in 2013, Perry and Barron, in a carefully controlled study, found out that honeybees displayed metacognitive-like processes, selectively avoiding (i.e., "opting-out") difficult tasks (i.e., ones for which they lacked the information allowing them to successful solve a discrimination)[91]. They were also able to transfer the concept of opting out to a novel task.

[84] *Ivi*, p. 8949.
[85] As reviewed by Avarguès-Weber and Giurfa, 2013.
[86] See Giurfa et al. 2001; Muszynski and Couvillon, 2015.
[87] See Avarguès-Weber et al., 2010.
[88] See Bshary Horner, Ait-el-Djoudi and Frickle, 2006.
[89] See Braithwaite, 2010.
[90] See Giurfa, 2015.
[91] See Perry and Barron, 2013; Giurfa, 2015.

Notwithstanding, as the scientific evidence that fish express behaviour suggestive of their experiencing affective states using mental representations and possibly thinking about their actions was accumulating[92], a new challenge arose.

3. THE ARTIFICIAL INTELLIGENCE (AI) CONTROVERSY AND THE LIMITS OF SENTIENCE AS A CRITERION FOR MORAL CONSIDERATION

Artificial Intelligence (AI) studies have developed rapidly in recent years. They showed that AI have modifiable pain systems, can show complex learning and motivational responses to nociception without having (as far as we know) the related subjective experience that are usually inferred from the former[93]. Some robots even have circuits mimicking emotions by altering their responsiveness to inputs and thus produce context dependent behaviour[94]. As a consequence, Adamo stated that presence of the aforementioned abilities in fish could not be used to infer sentience in these animals[95]. The debate is increasing. However, AI is programmed by people, for example using a programming code telling the AI to express a series of responses leading to the termination of a certain situation the AI is programmed to detect. Even programs composed of artificial neural networks, which have been shown to be able to learn to play games by experience alone, without explicitly feeding them a program code of the rules/strategies to follow, still depend on some initial programming to function. Inert matter does not become AI without human intervention. So, the question become the following: if AI are programmed (more or less directly) to function in a way that causes them to show the behavioural correlates of mental states, how are fish programmed/induced to behave in a way suggestive of pain perception, fear and other mental states? In an evolutionary perspective, emotions/mental states are thought to have an adaptive function and to have evolved to aid in decision-making and thus motivating behaviour that is advantageous in terms of fitness[96]. In a sense, if we still want to use the analogy with AI, and simplifying things for sake of clarity, emotions/mental states are exactly the programming sequence/code/language that give a (flexible) instruction to animals on how to behave in a certain situation. It is therefore not surprising that, together studies on patterns of neural activities using modern precision techniques[97], the understanding

[92] See Chandroo, Duncan and Moccia, 2004.
[93] See Adamo, 2016a,b, 2018.
[94] See Adamo, 2016.
[95] See Adamo, 2018.
[96] See Kittilsen, 2013; Perrot-Minnot et al, 2017.
[97] See Adamo, 2018; Storm *et al.*, 2017.

of the evolutionary role of mental states and emotions in various kinds of animals is advocated as the way to give a final answer to the question of sentience[98].

However, apart from the AI controversy, other, more or less obvious, factors should be considered. First, sentience, being an inner feature is an elusive entity, so it is unlikely (even impossible) that any scientific study can give absolute certainty or proof/evidence of its existence, even in other humans[99]. Considering the existence of such ultimate evidence as a requirement for granting some kind of animals welfare-oriented protection is not even scientifically correct. It is straightforward that we should allow fish and arthropods, or even other kind of beings, to be considered sentient if they show the same behavioural and physiological correlates for sentience that had been accepted as supporting that other kind of animals (e.g., mammals) had it. Therefore, and as said by many[100] if there is "sufficiently qualified uncertainty"[101] regarding a species' sentience, or its ability to be affected by the quality of its life, it should be enough to consider that species as worth be granting moral status and welfare protection under a "precautionary principle".

Second, often sentience (in the form of its correlates) is denied to a species only because the issue has not been investigated properly. When appropriate carefully controlled experiments are performed, often animals, even the ones deemed to be "less cognitively developed", show responses that support the hypothesis that they are likely to have the requirements that the scientific world has established to be indicative of sentience. In this regard, it is important that scientific evidence be examined to rule out methodological weaknesses[102] or confounding variables[103], for example regarding the possibility that a supposed pessimistic bias in bees was indeed only a mechanical effect on octopamine levels. The latter is usually done in reference to the Lloyd Morgan's canon, saying that in no case may we interpret an action as the outcome of the exercise of a higher psychical faculty, if it can be interpreted as the outcome of the exercise of one which stands lower in the psychological scale[104]. In the context of the animal sentience debates, Lloyd's canon is often invoked to deny animals "higher" mental abilities (i.e., those linked to sentience) when findings could be explained by "lower" ones. However, this often-misinterpreted canon[105], does not say that one can rule out the existence of a "higher" mental faculty when findings can be explained as the outcome of a "lower one", but just that one cannot say that that animal has such higher faculty. As many authors support[106],

[98] See Kittilsen, 2013.
[99] See, for example, Wadiwel, 2016; Woodruff, 2017; Birch 2017.
[100] See Birch, 2017.
[101] Knutsson and Munthe, 2017, p. 214.
[102] See, Diggles, 2018 for crustacean.
[103] See, for instance, Giurfa,2013; Bateson *et al.*, 2011.
[104] See Morgan, 1903.
[105] See Thomas, 2001.
[106] See, for instance, Edelman and Seith, 2009.

"absence of evidence" does not need to be, and should not be accepted to be, "evidence of absence" in regard to animal sentience. If a person absentmindedly touches a hot iron, and immediately retracts his/her hand, we can easily explain the response in terms of a nociceptive reflexive response (i.e., a "lower" faculty than pain perception), but we cannot use this finding to support that humans do not have pain perception. What is ridiculously straightforward in humans tends not to be applied when "lower" animals are concerned.

Third, do "less sentient" animals always suffer less? Another approach to deny "lower animals" access to the moral protection granted to "higher animals" in the face of their fulfilling the requirements of sentience is advocating a difference "not in kind", but "in degree" of sentience between animal species, and using it to justify different treatment. This approach is also used in the 3R Tenet[107], where substituting animals that are deemed to have lower degree of sentience to ones with a higher ones whenever possible, constitutes a requirement, in terms of 'replacement', for acceptability of a scientific research[108]. Does a "lower degree" of sentience actually mean that that animal suffers less? Paradoxically it could be the opposite, at least in some situations. If today a human should endure a day of hardship, he/she can think about the abstract idea of a better tomorrow, make plans to reach it and have hopes about it. Even just thinking about better days can be a form of distraction. If the present is all a given animal is able to feel, perceive and think about, would not a harsh present be worse for him/her than for a human who can escape it at least in his/her thoughts? One would say that the inability to have hopes, or even just thoughts of something different from a dreadful eternal present is likely to make the harsh situation even harder, not easier, for the "less sentient" animal. In this situation, under an Unequal Interests Model of Degrees of Moral Status the experiential well-being of the "less sentient" being becomes more morally relevant than the analogous situation in a "higher sentient" one[109].

Fourth, is sentience the limit? What we call sentience is a set of mental abilities that make humans able be deeply affected by situations and to assess whether a set of situations, a life, is "worth living" or not. What if animals, the ones we do not consider sentient, or not sentient enough, have another method, a method we cannot even imagine, to assess whether something is worth living? What if they are as deeply affected by the result of their "detection" method as humans are, when, using sentience, they assess the situation as not worth living? Is this reliance of sentience to grant moral status to animals the ultimate frontier of anthropocentrism?[110]

[107] See, for instance, Fenton, 2012.

[108] See *The European Parliament and the Council Directive 2010/63/EU of 22 September 2010 on the protection of animals used for scientific purposes*.

[109] See De Grazia, 2008.

[110] See Fenton, 2012.

4. CONCLUSION. FISH AND ARTHROPODS' WELFARE AS A MATTER OF OVERRIDING THE SLIDING SCALE AND OF ADOPTING A PRECAUTIONARY PRINCIPLE

As said previously, there is a tendency to repeat the same pattern when sentience is investigated in a species in order to decide whether it should be granted the same welfare concern as others, which have already gone through the process and been recognised as sentient. It is symptomatic that these debates are "progressive", i.e., tend to focus each time on beings which are perceived to be lower on the so called "*scala naturae*" schema, than the ones previously investigated. The "*scala naturae*" is an anthropocentric construct, ranking animals for cognition and sentience, which scientists and general public tend to conform to, but which has no evolutionary/scientific logic[111]. Unsurprisingly, the ranking tends to be influenced by how similar an animal species is to a human being (e.g., primates) and/or how familiar and emotionally important it is to humans (e.g., dogs). As stated, such a scale is reflected in the official norms suggesting replacement in laboratory experiments and in a corresponding view that conceives of moral considerability as a sliding scale[112].

The scientific validity of the "*scala naturae*" has been rejected by the scientific community, because all existing species have had the same success on evolutionary terms. One wonders whether it is time to grant equal moral consideration to all beings for which there is "sufficiently qualified uncertainty"[113] about their ability to be affected, even slightly, by the quality of their life[114]. Thus, we could focus less on debates that give the idea of a search for beings that we could be morally allowed not to protect, and devote more resources on improving the life of the animals we "use" for our purposes. Much avoidable pain and suffering is still caused to animals in human care. Ethical commitment to animal welfare ought to be considered a common and essential objective, aimed at unifying the different perspectives, and urge an ongoing debate around society. The welfare and treatment of the animals we use for our interests need to be conceived with no hesitation as a matter which we are compelled to account for in ethical terms, and not only in scientific, economical or professional ones.

[111] See Morris *et al.*, 2012; Fenton, 2012.

[112] Fenton, 2012; Meijboom and Bovenkerk, 2013.

[113] Knutsson and Munthe, 2017, p. 214.

[114] Of course, in this paper we have focused on a sentientist approach to moral importance and we have investigated the moral importance of animals on the basis of the fact they may be able to have morally relevant negative mental states. As stated by De Grazia, a capacity to feel pain, as it implicates a capacity to be harmed and to fare badly, may not confer high moral status, but it does confer some moral status (see DeGrazia 2008).

ACKNOWLEDGEMENTS

The authors wish to thank Anne McBride for sparking SN's interest in fish sentience and Linda Ferrante for help in locating some of the references.

BIBLIOGRAPHY

Adamo, S. A., 2016a. Do insects feel pain? A question at the intersection of animal behaviour, philosophy and robotics. *Animal Behaviour, 118*, 75-79.

Id., 2016b. Consciousness explained or consciousness redefined? *PNAS,* 113(27), p. 3812.

Id., 2017. The "Precautionary Principle" – A work in progress. *Animal Sentience* 2017.025.

Id., 2018. Sentience, the final frontier. *Animal Sentience* 2018.118

Allen, C., 2013. Fish Cognition and Consciousness. *Journal of Agriculture and Environmental Ethics 26*, 25–39, DOI 10.1007/s10806-011-9364-9

Avarguès-Weber, A, Giurfa, M., 2013. Conceptual learning by miniature brains. *Proceedings of the Royal Society B*, *280*, 20131907.

Avarguès-Weber, A, Portelli, G., Benard, J., Dyer, A., Giurfa, M., 2010. Configural processing enables discrimination and categorization of face-like stimuli in honeybees. *The Journal of Experimental Biology*, *213*, 593-601.

Bateson, M. et al., 2011. Agitated honeybees exhibit pessimistic cognitive biases. Curr. Biol. 21, 1070–1073, as in Giurfa, M. (2013). Cognition with few neurons: higher-order learning in insects. *Trends in Neurosciences*, 36, 285-294.

Bellieni, C. V., 2012. Pain assessment in human fetus and infants. *The AAPS Journal*, 14(3), 456-461.

Bentham J., 1907. *Introduction to the Principles of Morals and Legislation*, Oxford Clarendon Press.

Birch, J., 2017. Animal sentience and the precautionary principle. Animal Sentience 2017.017

Bisazza, A., Pignatti, R. & Vallortigara, G. 1997. Detour tests reveal task- and stimulus-specific neural lateralization in mosquitofish (*Gambusia holbrooki*). *Behavioural Brain Research*, 89, 237–242.

Boissy, A., Manteuffel, G., Bak Jensen, M., Oppermann Moe, R., Spruijt, B., Keeling, L. J., Winckler, C., Forkman, B., Dimitrov, I., Langbein, J., Bakken, M., Veissier, I., & Aubert, A., 2007. Assessment of positive emotions in animals to improve their welfare. *Physiology & Behavior, 92,* 375–397.

Bovenkerk, B., Meijboom F. L. B., 2012. The Moral Status of Fish. The importance and limitations of a fundamental discussion for practical ethical questions in fish farming. *Journal of Agricultural and Environmental Ethics*, 25, 843–860.

Braithwaite, V., 2010. Do Fish Feel Pain? Oxford University Press, Oxford, UK.

Braithwaite, V.A., Huntingford, F., van den Bos, R., 2013. Variation in emotion and cognition among fishes. *Journal of Agricultural and Environmental Ethics*, 26, 7–23, DOI 10.1007/s10806-011-9355-x

Broglio C, Gómez A, Durán E, Ocańa FM, Jiménez-Moya F, Rodríguez, R, Salas C., 2005. Hallmarks of a common forebrain vertebrate plan: specialized pallial areas for spatial, temporal and emotional memory in actinopterygian fish. *Brain Res Bull*, 66:277–281.

Broglio C, Rodríguez, R, Salas C., 2003. Spatial cognition and its neural basis in teleost fish. *Fish and Fisheries*, 4, 247-255.

Broom, D.M., 1991. Animal Welfare. Concepts and Measurement, *Journal of Animal Science*, 69, pp. 4167–4175.

Id., 2013. The welfare of invertebrate animals such as insects, spiders, snails and worms. In Animal Suffering: From Science to Law, International Symposium, ed. Kemp, T. A. van der and Lachance, M., 135-152. Paris: Éditions Yvon Blais.Broom, D., 2014. Welfare and Animal Sentience. CABI Publishing, Wallingford, UK.

Brown, C., 2015. Fish intelligence, sentience and ethics. *Animal Cognition*, 18(1), 1–17.

Brydges, N.M., Boulcott, P., Ellis, T., Braithwaite, V.A., 2009. Quantifying stress responses induced by different handling methods in three species of fish. *Applied Animal Behaviour Science*, 116, 295–301.

Bsary, R., Brown, C., 2014. Fish cognition. *Current Biology*, 24(19), R948.

Bshari, R., Gingins, S., Vail, A. L., 2014. Social cognition in fishes. *Trends in Cognitive Sciences*, 18(9), 465-471.

Bshary, R., Horner, A., Ait-el-Djoudi K., Frickle, H., 2006. Interspecific communicative and coordinated hunting between groupers and giant moray eels in the Red Sea . *Plos Biology*, 4(12), 2393-2398, e431, DOI: 10.1371/journal.pbio.0040431.

Bullock, T. H., Orkand, R. and Grinnell, A. 1977. Introduction to nervous systems. San Francisco, CA: W. H. Freeman.

Burghardt, G., 2013. The origins of play. IEC2013 abstract book, p. 18.

Carruthers, P., 2007. Invertebrate minds: a challenge for ethical theory. *The Journal of Ethics*, 11, 275–297.

Chandroo, K. P., Duncan, I. J. H., Moccia, R. D., 2004. Can fish suffer? Perspectives on sentience, pain, fear and stress. *Applied Animal Behaviour Science*, 86, 225–250.

Cheeseman, J. F., Millar, C. D., Gregger, U., Lehmann, K., Pawley, M. D. M., Gallistel, C. R., Warman, G. R., Menzel, R., 2014. Way-finding in displaced clock-shifted bees proves bees use a cognitive map. *PNAS*, 111, 24, pp. 8949–8954.

Colson, V., Mure, A., Valotaire, C., Le Calvez, J. M., Goardon, L., Labbé, L., Leguen, I., Prunet, P., 2019. A novel emotional and cognitive approach to welfare phenotyping

in rainbow trout exposed to poor water quality. *Applied Animal Behaviour Science*, 210, 103–112.

Dawkins, M.S., 1980, Animal Suffering: the Science of Animal Welfare, London, UK: Chapman and Hall.

Id., 1990, From an animal's point of view: motivation, fitness, and animal welfare, "Behavioural Brain Science", 13, pp.1-9 and 54-61.

Id., 2015. Chapter Two - Animal Welfare and the Paradox of Animal Consciousness. Advances in the Study of Behavior, 47, 5-38.

Id., 2017, Animal welfare with and without consciousness, "Journal of Zoology", 301, 1, pp. 1-10.

De Grazia, D., 2008. Moral status as a matter of degree. *The Southern Journal of Philosophy* XLVI, 181-198.

DeLong, C. M., Barbato, S., O'Leary, T., Wilcox, K. T., 2017. Small and large number discrimination in goldfish (*Carassius auratus*) with extensive training. *Behavioural Processes*, 141, 172–183.

Demin, K. A., Lakstygal, A. M., Kalueff, A. V., 2018. Time to (finally) acknowledge that fish have emotionality and pain. *Animal Sentience*, 2018.146

Denti A, Dimant B and Maldonado, H. 1988. Passive avoidance learning in the crab *Chasmagnathus granulatus*. *Physiology and Behavior*, 43: 317-320. http://dx.doi.org/10.1016/0031-9384(88)90194

De Santi, A., Sovrano V.A.; Bisazza A.; Vallortigara G., 2001. Mosquitofish display differential left- and right-eye use during mirror image scrutiny and predator inspection responses. *Animal Behaviour*. 61(2): pp. 305-310.

Diggles, B. K., 2018. Review of some scientific issues related to crustacean welfare. *ICES Journal of Marine Science*, doi:10.1093/icesjms/fsy058

Duncan, I. J. H., 1993. Welfare is to do with what animals feel, *Journal of Agricultural and Environmental Ethics*, 6, pp. 8–14.

Id., 2016. Is sentience only a nonessential component of animal welfare? *Animal Sentience*, 52, pp. 1-6.

Duncan I.J.H., Stamp Dawkins M., 1983. The problem of assessing "wellbeing" and "suffering" in farm animals, in D. Smidt (ed.), Indicators relevant to farm animal welfare, Martinus Nijhoff, The Hague, pp. 13-24.

Dunlop, R., Laming, P., 2005. Mechanoreceptive and nociceptive responses in the central nervous system of goldfish (*Carassius auratus*) and trout (*Oncorhyncus mykiss*). *Journal of Pain*, 6: pp. 561-568

Dunlop, R., Millsopp, S., Laming, P., 2006. Avoidance learning in goldfish (*Carassius auratus*) and trout (*Oncorhyncus mykiss*) and implication for pain perception, *Applied Animal Behaviour Science*, 97: pp. 255-271.

Edelman, D. B., 2016. Leaving the door open for fish pain: Evolutionary convergence and the utility of 'just-so stories'. *Animal Sentience*, 2016.062

Edelman, D. B, Seth, A. K., 2009. Animal consciousness: a synthetic approach. *Trends in Neurosciences*, 32(9), 476-484.

EFSA, 2009. Scientific Opinion of the Panel on Animal Health and Welfare on a request from European Commission on General approach to fish welfare and to the concept of sentience in fish. The EFSA Journal, 954, 1-26.

Elwood, LW, 2012. Evidence for pain in decapod crustaceans. Animal Welfare, 21(S2): 23-27.

Elwood, R. W., Appel, M., 2009. Pain experience in hermit crabs? *Animal Behaviour*, 77, 1243–1246.

FAWC (Farm Animal Welfare Council), 1979, *First Press Notice*, 5/12, London, MAFF.

Id., 2009. Farm Animal Welfare in Great Britain: Past, Present and Future, London, UK: FAWC. Accessed at: http://www.ongehoord.info/wp-content/uploads/2017/12/11-1.pdf, on 15/06/2019.

Feinberg, T. E., Mallat, J., 2016. The nature of primary consciousness. A new synthesis. *Consciousness and Cognition*, 43, 113–127.

Fenton, A., 2012. On the need to redress an inadequacy in animal welfare science: toward an internally coherent framework. *Biology of Philosophy*, 27:73–93; DOI 10.1007/s10539-011-9291-1.

Fraser D., 2008. Understanding Animal Welfare. Science in its cultural context, UFAW, Blackwell.

Id., 2009. Assessing animal welfare: different philosophies, different scientific approaches, *Zoo Biology*, 28, 6, pp. 507-518.

Galhardo, L., Vital, J., Oliveira R.F., 2011a. The role of predictability in the stress response of a cichlid fish. *Physiology & Behavior*, 102, 367–372

Galhardo L, Almeida O, Oliveira R.F., 2011b. Measuring motivation in a cichlid fish: an adaptation of the push-door paradigm. *Applied Animal Behavioural Science*, 130:60–70.

Gibson, W. T., Gonzalez, C. R., Fernandez, C., Ramasamy, L., Tabachnik, T., Du, R. R., Felsen, P. D., Maire, M. R., Perona, P., Anderson, 2015. Behavioral responses to a repetitive visual threat stimulus express a persistent state of defensive arousal in drosophila. *Current Biology*. 25, 1401–1415, http://dx.doi.org/10.1016/j.cub.2015.03.058

Giurfa, M, Zhang, S, Jenett, A, Menzel, R, Srinivasan, M. V. 2001. The concepts of 'sameness' and 'difference' in an insect. *Nature*, 410, pp. 930–933, doi:10.1038/35073582

Giurfa, M., 2013. Cognition with few neurons: higher-order learning in insects. *Trends in Neurosciences*, 36, 285-294.

Giurfa, M. 2015. Learning and cognition in insects. *WIREs Cogn Sci*, 2015, 6:383–395. doi: 10.1002/wcs.1348

Graham, C., von Keyserlingk M. A. G., Franks, B., 2018a. Zebrafish welfare: Natural history, social motivation and behaviour. *Applied Animal Behaviour Science*. 200, 13–22.

Graham, C., von Keyserlingk M. A. G., Franks, B., 2018b. Free-choice exploration increases affiliative behaviour in zebrafish. *Applied Animal Behaviour Science*. 203, 103–110.

Griffin D.R., 1976. The question of animal awareness, Rockfeller University Press.

Grosenick, Logan; Clement, Tricia S.; Fernald, Russell D. (2007). Fish can infer social rank by observation alone. *Nature*, 445(7126), 429-432, DOI: 10.1038/nature05511.

Håstein T., Scarfe A.D., Lund V.L, 2005, Science-based assessment of welfare: aquatic animals. *Rev. sci. tech. Off. int. Epiz.*, 24(2), 529-547.

Horvath, K., Angeletti, D., Nascetti, G., Carere, C., 2013. Invertebrate welfare: an overlooked issue. *Annali dell'Istituto Superiore di Sanità*, 49(1), 9-17

IASP (International Association for the Study of Pain), 1979. Pain terms: a list with definitions and notes on usage. *Pain*, 6, 249-252.

Johnson W. A., Carder J. W., 2012. *Drosophila* nociceptors mediate larval aversion to dry surface environments utilizing both the painless TRP channel and the DEG/ENaC subunit, PPK1. *PLoS One*, 7:e32878. 10.1371/journal.pone.0032878

Jones, R.C., 2016. Fish sentience and the precautionary principle. *Animal Sentience*, 2016.016

Karenina K. A., Giljov, A. N., Malashichev, Y. B., 2013. Eye as a key element of conspecific image eliciting lateralized response in fish. *Animal Cognition*, 16, 287–300

Key, B., 2015. Fish do not feel pain and its implications for understanding phenomenal consciousness. *Biology & Philosophy*, 30(2), 149–165.

Key, B., 2016. Why fish do not feel pain. *Animal Sentience*, 2016.003.

Kistler C, Hegglin D, Würbel H, König B., 2011. Preference for structured environment in zebrafish (*Danio rerio*) and checker barbs (*Puntius oligolepis*). *Applied Animal Behaviour Science*, 135, 318– 327.

Kittilsen, S., 2013. Functional aspects of emotions in fish. *Behavioural Processes* 100, 153– 159.

Knutsson, S., Munthe, C., 2018. A Virtue of Precaution Regarding the Moral Status of Animals with Uncertain Sentience. *Journal of Agricultural and Environmental Ethics*, 30(2), 213–224.

Lee, SA; Vallortigara, G; Ruga, V; Sovrano, VA., 2012. Independent effects of geometry and landmark in a spontaneous reorientation task: a study of two species of fish. *Animal Cognition*, 15(5), 861-870.

Lockwood, J. A., 1987. The moral standing of insects and the ethics of extinction. *The Florida Entomologist*, 70(1), 70-89.

Lozada, M., Romano, A., Maldonado, H., 1988. Effect of morphine and naloxone on a defensive response of the crab *Chasmagnathus granulatus*. *Pharmacology Biochemistry and Behavior*, 30(3), 635-640.

Lucon-Xiccato, T.,Bisazza, A., 2017. Individual differences in cognition among teleost fishes. *Behavioural Processes*, 141, 184–195.

Lüschen W, Willig A, Peter P and Jaros P.P., 1993. The role of biogenic amines in the control of blood glucose level in the decapod crustacean, *Carcinus maenas* L. Comparative Biochemistry and Physiology Part C: *Comparative Pharmacology*, 105: 291-296

Martins C. I. M., Galhardo L., Noble C., Damsgård B., Spedicato M.T., Zupa W., Beauchaud M., Kulczykowska E., Massabuau J-C., Carter T., Rey Planellas S., Kristiansen, T., 2012. Behavioural indicators of welfare in farmed fish. *Fish Physiol Biochem*, 38:17–41.

Mason. G. J., 2011. Invertebrate welfare: where is the real evidence for conscious affective states? *Trends in Ecology and Evolution*, 26(5), 212-213.

Meijboom, F. L. B., Bovenkerk, B., 2013. Fish Welfare: Challenge for Science and Ethics—Why Fish Makes the Difference. *Journal of Agricultural and Environmental Ethics*, 26, 1–6.

Menzel, R., De Marco, R. J., Greggers, U., 2006. Spatial memory, navigation and dance behaviour in *Apis mellifera*. *Journal of Comparative Physiology A*, 192, pp. 889–903.

Milinski, M., Kulling, D. and Kettler, R., 1990. Tit for Tat: sticklebacks (*Gasterosteus aculeatus*) "trusting" a cooperating partner. *Behavioral Ecology*, 1(1), 7-11.

Milsopp, S. Laming, P., 2008. Trade-offs between feeding and shock avoidance in goldfish (*Carassius auratus*). *Applied Animal Behaviour Science 113*, 247–254

Millot, S., Cerqueira, M., Castanheira, M. F., Øverli, Ø., Martins, C. I. M., Oliveira, R. F., 2014. Use of conditioned place preference/avoidance tests to assess affective states in fish. *Applied Animal Behaviour Science* 154, 104-111.

Mizukami E, Gunji YP, Migita M., 1999, Learning process by goldfish and its use of a local site as a map. *Biosystems* 54: 91–104

Morgan, C. L., 1903. An introduction to comparative psychology. London, U.K. W. Scott.

Morris, P., Knight, S. and Lesley, S. 2012. Belief in animal mind: does familiarity with animals influence beliefs about animal emotions? *Society & Animals* 20(3): 211-224.

Morton D.B., 2000. Self-consciousness and animal suffering, *Biologist*, 47 (2), 77-80.

Muszynski, N. M., Couvillon, P. A., 2015. Relational learning in honeybees (*Apis mellifera*): Oddity and nonoddity discrimination. *Behavioural Processes*, 115, 81–93.

Nordgreen, J., Horsberg, T. E, Ranheim B., Chen C. A. N., 2007. Somatosensory evoked potentials in the telencephalon of Atlantic salmon (*Salmo salar*) following galvanic stimulation of the tail. Journal of Comparative Physiology A 193: 1235-1242.

O'Connell, L.A., Fontenot, M.R., Hofmann, H.A., 2011. Characterization of the Dopaminergic System in the Brain of an African Cichlid Fish, *Astatotilapia burtoni. The Journal of Comparative Neurology,* 519, 75–92.

Panksepp J., 2005. Affective consciousness: Core emotional feelings in animals and humans, *Conscious Cognition*, 14, 1, 30-80.

Perrot-Minnot, M. J., Banchetry, L., and Cézilly, F., 2017. Anxiety-like behavior increases safety from fish predation in an amphipod crustacea. *R. Soc. Open Sci.*, 4:171558. doi: 10.1098/rsos.171558.

Perry, C. J., Baciadonna, L., 2017. Studying emotion in invertebrates: what has been done, what can be measured and what they can provide. *Journal of Experimental Biology*, 220, 3856-3868.

Perry, C. J., Baciadonna, L., Chittka, L. (2016). Unexpected rewards induce dopamine-dependent positive emotion-like state changes in bumblebees. *Science*, 353(6307), 1529–1531.

Perry CJ, Barron AB., 2013. Honey bees selectively avoid difficult choices. *Proceeding of the National Academy of Science, USA*, 110:19155–19159.

Plowright, C. M. S., 2017. Bumblebees at work in an emotion-like State. *Learning & Behavior*, 45(3), 207–208.

Porcher, I. F., 2018. Fish sentience, consciousness, and AI. *Animal Sentience*, 119.

Portavella, M., Vargas, J.P., Torres, B., Salas, C. (2002) The effects of telencephalic pallial lesions on spatial, temporal, and emotional learning in goldfish. *Brain Research Bulletin*, 57:397–399.

Portavella, M., Vargas, P., 2005. Emotional and spatial learning in goldfish is dependent on different telencephalic pallial systems. *European Journal of Neuroscience*, 21, 2800–2806.

Regan, T., 1983, *The Case for Animal Rights*, Berkeley, CA: University of California Press.

Rollin, B., 1989, The unheeded cry. Animal consciousness, animal pain and science, Oxford University Press.

Rose, J.D., 2002. The neurobehavioral nature of fishes and the question of awareness and pain. *Reviews in Fisheries Science*, 10(1): 1–38.

Rose, J.D., Arlinghaus, R., Cooke, S.J., Diggles, D.K., Sawynok, W., Stevens, E.D. & Wynne, C.D.L. (2014). Can fish really feel pain? *Fish and Fisheries, 15.1*, 97-133. doi: 10.1111/faf.12010

Rose, J. D., 2016. Pain in fish: Weighing the evidence. *Animal Sentience* 2016.032

Rose, J. D., Arlinghaus, R., Cooke, S. J., Diggles, B. K., Sawynok, W., Stevens, E. D., Wynne, C. D. L., 2014. Can fish really feel pain? *Fish and Fisheries*, 15, 97–133.

Roques, J. A. C., Abbink, W., Chereau, G., Fourneyron, A., Spanings, T., Burggraaf, D., van de Bos, R., van de Vis, H., Flik, G., 2012. Physiological and behavioral responses to an electrical stimulus in Mozambique tilapia (*Oreochromis mossambicus*). *Fish Physiol Biochem*, 38, 1019–1028, DOI 10.1007/s10695-011-9586-9

Roques, J.A.C., Abbink, W., Geurds, F., van de Vis, H., Flik, G., 2010. Tailfin clipping, a painful procedure: studies on Nile tilapia and common carp. *Physiology & Behaviour*, 101, 533–540.

Rose JD, Arlinghaus R, Cooke SJ, Diggles BK, Sawynok W, Stevens ED, Wynne CDL, 2014. Can fish really feel pain? *Fish*, 15:97–133.

Rosnow, R. L. (1978). The prophetic vision of Giambattista Vico: Implications for the state of social psychological theory. *Journal of Personality and Social Psychology*, 36(11), 1322-1331. http://dx.doi.org/10.1037/0022-3514.36.11.1322

Santiago Rucinque, D., Oliveira Souza, A. P., Maiolino Molento, C. F., 2017. Perception of Fish Sentience, Welfare and Humane Slaughter by Highly Educated Citizens of Bogotà, Colombia and Curitiba, Brazil. *PLoS One*, 12(1), 0168197.

Seber, H., 2016. Why babies do not feel pain, or: How structure-derived functional interpretations can go wrong. *Animal Sentience*, 2016.033.

Smith, S. A. (2014). Welfare of Laboratory Fishes. *Laboratory Animal Welfare*, pp. 301-311.

Smith, A., Gray, H. (2011). Goldfish in a tank: the effect of substrate on foraging behaviour in aquarium fish. *Animal Welfare*, 20: 311-319.

Sneddon, L. U., Braithwaite, V. A., Gentle, M. J., 2003a. Do fish have nociceptors? Evidence for the evolution of a vertebrate sensory system. *Proceedings of the Royal Society London B*, 270, pp. 1115–1121.

Sneddon, L. U., Braithwaite, V. A., Gentle, M. J., 2003b. Novel Object test: examining pain and fear in the rainbow trout. *Journal of Pain*, 4: 431-440.

Sneddon, L.U. 2002 Anatomical and electrophysiological analysis of the trigeminal nerve in the rainbow trout, Oncorhynchus mykiss. *Neurosci. Lett*, 319, 167–171.

Sneddon, L.U., 2012. Clinical anesthesia and analgesia in fish. *Journal of Exotic Pet Medicine*, 21, pp. 32–43.

Sneddon, L. U., Lopez-Luna1, J., Wolfenden, D. C. C., Leach, M. C., Valentim, A. M., Steenbergen, P. J., Bardine, N., Currie, A. D., Broom, D. M., Brown, C., 2018. Fish sentience denial: Muddying the waters. *Animal Sentience*, 2018.115.

Stancher, G Sovrano, VA Potrich, D Vallortigara, G., 2013. Discrimination of small quantities by fish (redtail splitfin, *Xenotoca eiseni*). *Animal Cognition*, 16(2), pp. 307-312.

Sullivan, M., Lawrence, C., Blache, D., 2016. Why did the fish cross the tank? Objectively measuring the value of enrichment for captive fish. *Applied Animal Behaviour Science*, 174, pp. 181–188.

Storm, J.F., Boly, M., Casali, A.G., Massimini, M., Olcese, U., Pennartz, C.M.A. & Wilke, M. (2017) Consciousness regained: Disentangling mechanisms, brain systems and behavioral responses. *Journal of Neuroscience*, 37(45): 10882-10893.

Strausfeld, N. J. (2002). Organization of the honey bee mushroom body: representation of the calyx within the vertical and gamma lobes. *Journal of Comparative Neurology*, 450, pp. 4-33.

Sumpter, J.P., 1997. The endocrinology of stress. In: Iwama, G.K., Pickering, A.D., Sumpter, J.P., Schreck, C.B. (Eds.), Fish Stress and Health in Aquaculture, Society for

Experimental Biology, Seminar Series 62. Cambridge University Press, Cambridge, pp. 95–118.

Taylor, J. C., Dewberry, L. S., Totsch, S. K., Yessick, L. R., DeBerry, J. J., Watts, S. A., Sorge, R. E., 2017. A novel zebrafish-based model of nociception. Physiology & Behavior 174, 83–88.

The European Parliament and the Council Directive 2010/63/EU of 22 September 2010 on the protection of animals used for scientific purposes. [Online]. [Accessed 15 June 2019]. Available from: http://eur-lex.europa.eu/

Thomas, R., 2001. Lloyd Morgan's canon: A history of misrepresentation. *History & Theory of Psychology Eprint Archive*. https://faculty.franklin.uga.edu/rkthomas/sites/faculty.franklin.uga.edu.rkthomas/files/MCPrintOptimal.pdf, last retrived 15-06-2019

Topál J, Csányi V., 1999. Interactive learning in the paradise fish (*Macropodus opercularis*): an ethological interpretationof the second-order condition paradigm, *Animal Cognition*, 2:197–206.

Van de Veer, D., 1983, Interspecific justice and animal slaughter, in H.B. Miller, W.H. Williams (eds.), *Ethics and animals*, Clifton, NJ: Humana Press, pp. 147-164.

Vargas, J.P., Bingman, V.P., Portavella, M.l, López, J.C. (2006). Telencephalon and geometric space in goldfish. *European Journal of Neuroscience*, 24: 2870–2878.

Vila Pouca, C., Brown, C., 2017. Contemporary topics in fish cognition and behaviour. *Current Opinion in Behavioral Sciences*, 2017, 16:46–52.

Voltaire C., 1753. (trad. it. 1968), Dizionario filosofico, Milano, Mondadori.

Wadiwel, D., 2016. Fish and pain: The politics of doubt. *Animal Sentience* 2016.038

Walters, E. T. (2018). Nociceptive biology of molluscs and arthropods: evolutionary clues about functions and mechanisms potentially related to pain. *Frontiers in Physiology*, 9, 1049.

Wemesfelder, F., 2001, Assessing the 'whole animal': a free-choice profiling approach, *Animal Behaviour*, 62 (2), pp. 209-220.

Whates, C., 2010, "Lives worth living?", *Veterinary Record*, 166, pp. 468-469.

Whay, H. R., Main, D. C. J., Green, L. E., & Webster, A. J. F. (2003). Animal-based measures for the assessment of welfare state of dairy cattle, pigs and laying hens: Consensus of expert opinion. *Animal Welfare*, 12(2), 205-217.

White, L. J., Thomson, J. S., Pounder, K. C., Coleman, R. C., Sneddon, L. U., 2017. The impact of social context on behaviour and the recovery from welfare challenges in zebrafish, Danio rerio. *Animal Behaviour*, 132, 189-199.

Woodruff, M. L., 2017. Consciousness in teleosts: There is something it feels like to be a fish. *Animal Sentience*, 2017.010

Yue Cottee, S., 2012. Are fish the victims of 'speciesism'? A discussion about fear, pain and animal consciousness. *Fish Physiol Biochem*, 38, pp. 5–15.

Yue, S., Moccia, R. D., Duncan, I. J., H., 2004. Investigating fear in domestic rainbow trout (*Oncorhyncus mykiss*), using avoidance learning task. *Applied Animal Behaviour Science*, 87:343-354.

Yue, S., Duncan, I.J.H., Moccia, R.D., 2008. Investigating fear in rainbow trout (*Oncorhynchus mykiss*) using the conditioned-suppression paradigm. *Journal of Applied Animal Welfare Science*, 2008;11:14–27.