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## In praise of fishes

Précis of *What a fish knows* (Balcombe 2016)

**Jonathan Balcombe**

Humane Society Institute for Science and Policy  
The Humane Society of the United States

**Abstract:** Our relationship to fishes in the modern era is deeply problematic. We kill and consume more of them than any other group of vertebrates. At the same time, advances in our knowledge of fishes and their capabilities are gaining speed. Fish species diversity exceeds that of all other vertebrates combined, with a wide range of sensory adaptations, some of them (e.g., geomagnetism, water pressure and movement detection, and communication via electricity) alien to our own sensory experience. The evidence for pain in fishes (despite persistent detractors) is strongly supported by anatomical, physiological and behavioral studies. It is likely that fishes also seek pleasure, as evidenced by their willingness to approach divers to receive caresses that may mimic those given out by cleaner-fishes who seek to curry favor with valued clients. Observations of play behavior in fishes present another possible source of pleasure, or at least relief from boredom. Some fishes are also subject to emotional stress and will take action to relieve it. Fishes routinely recognize other individuals. Their social lives involve cooperation, virtue, democracy, deception, and cumulative monitoring. Courtship and sexual behavior are highly variable across species, and parental care is known for about a quarter of all fish species. Based on the cumulative research now available, we may conclude that fishes are deserving of levels of protections comparable to those deemed suitable for any other vertebrate. Currently, however, our treatment of fishes falls far short of such a standard.

**Keywords:** fishes, cognition, emotion, social behavior, exploitation



[Jonathan Balcombe](#), Director of Animal Sentience at the Humane Society Institute for Science and Policy, writes and speaks about animal thinking, feeling, and protection. His forthcoming book *What A Fish Knows* explores the inner lives of the world's most exploited vertebrates. Other books include *Second Nature* and *Pleasurable Kingdom*. He has appeared on the National Geographic Channel, *The Nature of Things* (CBC), and in several

documentary films, and his work has appeared in *The New York Times*, *The Washington Post*, *The Wall Street Journal*, *Nature*, and others. <http://www.jonathanbalcombe.com>

## Introduction

**T**here is no shortage of superlatives for fishes. They were the planet's first vertebrates. They probably invented most of the senses as we know them, including color vision. They almost certainly invented consciousness, and, according to a recent fossil discovery, penetrative sex. They can claim the longest known age at reaching sexual maturity (45 years), and the longest gestation (3 years). In diversity, fishes outnumber all other vertebrates combined. The age of mammals is long past; we are living in an age of fishes — or, to be more precise, an age of teleosts (bony fishes) (Helfman et al. 2009).

Fishes also can claim an unenviable superlative: the species most exploited by us. Depending on who's doing the counting, we destroy between 150 billion and 2 trillion fishes each year — to eat them, feed them to farmed fishes, feed them to livestock or pets, or toss them back, usually dead or dying, as unwanted bycatch (Cooke & Cowx 2004; Mood 2010).

If fishes were mindless and insensate, our toll on them would be environmental travesty enough. But with advances in underwater technologies, and the rise in scientific interest in animal sapience and sentience, modern research is revealing that fishes are not only sentient but anything but primitive (in the sense of being simple by dint of having ancient ancestry). Nor are their lives dull. Instead, as my book *What A Fish Knows* (hereafter, *WAFK*) aims to show, fishes have sophisticated perceptual, cognitive, emotional, and social capacities, which in some cases rival those of the most vaunted of vertebrates: the primates.

## Perceptions

With qualities like that, it is dismaying that some still question fishes' capacity to feel pain (see Key 2016, and the many accompanying commentaries in this journal). The sense of pain in fishes is supported by extensive and robust evidence. One particularly elegant demonstration was a study in which zebrafishes<sup>1</sup> could choose to swim in a barren, brightly lit chamber or a less brightly lit chamber enriched by a stimulus shoal, gravel and plants. The fishes showed a clear preference for the enriched chamber, a preference that persisted after they were injected with either painful acid or innocuous saline. However, if an analgesic (lidocaine) was dissolved in the water of the barren chamber, acid-treated fishes began to prefer the barren chamber. The saline-treated fishes' unchanged preference for the enriched chamber shows that the lidocaine had neither an addictive nor a sedative effect (Sneddon, 2012). This study shows that fishes' reaction to noxious stimuli is nuanced and that they will take action to relieve pain.

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<sup>1</sup> I use the plural "fishes," and, for example, "zebrafishes" to reflect the fact that each is an individual with a unique physical and psychological profile.

With their rich diversity and prolonged tenure on the blue planet, fishes have evolved some remarkable sensory adaptations. Their eyes — controlled by the same trio of muscle pairs that allow our eyes to swivel on all axes — allow them to see as well underwater as we do in air. Some fishes can swivel each eye independently, like a chameleon. Others, including swordfishes, sharpen their hunting vision by shunting warm blood from their powerful trunk muscles to their eyes, heating them by up to 30 degrees (Fritsches et al. 2005). Ambon damselfishes identify each other covertly by unique facial “fingerprints” visible only in the UV light spectrum, which are not detectable to their predators (Siebeck et al. 2010).

Contrary to the common belief that fishes are silent, they communicate with a veritable symphony of sounds by vibrating their swim bladders, grating or grinding their teeth, rubbing bones together, stridulating their gill covers and even, in the case of herrings, expelling bubbles from their anuses (Helfman et al. 2009; Wilson et al. 2003). Some fishes can hear in the ultrasound range, allowing them to detect the presence of predatory dolphins (Mann et al. 1997, 1998); detection of infrasound by others is thought to aid migration by tuning in to ocean currents, tides, and waves colliding with objects (Sand & Karlsen 2000).

Fishes also have some notable olfactory adaptations, including the supreme chemical sensitivity that allows a salmon to return to her natal stream to breed, and a fear chemical called schreckstoff (German: “scary stuff”) that can be used to warn other fishes of the presence of a predator (von Frisch 1942). Taste and touch also find rich expression in fishes. The entire body surface of some catfishes is cloaked with taste-buds (Finger et al. 1991). Touch is pleasurable, as demonstrated by groupers and moray eels who will approach trusted divers to be petted and stroked, without food rewards. Cleaner-fishes curry favor with valued client fishes by pausing to deliver gentle caresses with their fins. Touch is also therapeutic, as demonstrated when stressed surgeonfishes repeatedly sidled up to a mechanical wand (painted to resemble a cleaner-fish) to receive strokes that measurably lowered their stress hormones. They ignored a stationary wand (Soares et al. 2011).

Then there are senses largely alien to us: polarized cells that afford the detection of geomagnetic fields; a lateral line of cells that detect minute pressure changes and allow night-time navigation; and the electroreception system of sharks that enables detection of prey hiding beneath the sand. The African elephantnose fishes and the South American knifefishes have elevated electricity to a mode of communication; their electric organ discharges (EODs) facilitate individual identification and communication. Dominant individuals may chase trespassers off their territories when they detect the trespasser’s EOD, which probably explains why others will deferentially go “silent” when swimming through a neighbor’s territory (Scheffel & Kramer 2006).

## **Feelings**

Aligned with their excellent perceptions, fishes possess both physiological substrates and behavioral repertoires befitting emotional animals. The medial pallium of a fish’s brain appears to perform the role of the mammalian amygdala, which helps drive emotional

reactions, memory, and decision making (Broglia et al. 2005). In response to a predatory attack, a fish responds as we might expect if they are feeling afraid: they breathe faster and release alarm pheromones, and they show classical behaviors shown by land animals: fleeing, freezing, trying to look bigger, and/or changing color. For some time afterward they also stop feeding and avoid the area where the attack occurred. Fishes produce hormones that can have nuanced effects on behavior and mirror those of related compounds in mammals. For instance, injections of isotocin (the fish version of mammalian oxytocin) caused high-ranking daffodil cichlids to become more aggressive in defending their territories, while the effect on mid-ranking cichlids was to boost submissive behavior (Reddon et al. 2012).

As an expression of positive emotion, play has for decades been suspected of occurring in fishes (Burghardt 2005), but it is only recently that formal definitions of play behavior are being satisfied by fishes. Burghardt et al. (2014) describe what appears to be object play, by three male cichlids (*Tropheus duboisi*), in this case repetitive, idiosyncratic interactions with a submersible, partially buoyant thermometer. Generally, the behaviors most resembled the way these fishes make quick jabs at rivals, but were more repetitive — rather like a boxer practicing on a bag — and were engaged in only when the fishes were alone, unstressed, and perhaps understimulated. These interactions also did not align with predatory, feeding, or sexual behavior. There are many anecdotal accounts of fishes engaging in social play as well as solitary play — as when an aquarium-bound fish repeatedly rides the current from a water pump, or the ascending bubbles from a water stone (Burghardt 2005).

Play behavior is generally regarded as pleasurable. Pleasure in fishes has scarcely been given any attention by researchers, but as a powerful motivator of adaptive behaviors we may expect to find it in sentient animals (Balcombe 2009). Cleanerfishes will pause from their cleaning activities to deliver gentle caresses to clients with their pectoral fins — a behavior that may serve to make the cleaner more desirable for future visits (Bshary & Würth 2001). Presumably, it is the pleasure of such treatment that makes it effective. Indeed, I posit that the chief motivator for frequent visits to cleaner stations is the proximal experience of pleasure and not the ultimate fitness benefits from having parasites removed. That certain fishes including groupers and large wrasses will approach trusted divers to receive strokes (with no parasite removal service) bolsters the interpretation that it is pleasurable (Figure 1).



Figure 1: Grouper fish receiving caresses from a trusted diver. Courtesy, Cathy Unruh.

## **Minds**

While the study of fish play is still in its infancy, research on fish cognition is not. In the early 20<sup>th</sup> Century, Jacob Reighard, a biologist at the University of Michigan, fed dead sardines to snapper fishes. The snappers readily ate the sardines whether or not they had been dyed red; but when Reighard made the red ones unpalatable (he sewed stinging anemones into the sardine's mouths), the snappers quickly learned to avoid the red food, and retained the aversion two weeks later (Reighard 1908). This is also a form of cognition we term *avoidance learning*.

Fish memory achieves greater heights. In experiments from the late 1940s to the 1970s, Lester Aronson of the American Museum of Natural History conducted spatial memory experiments with frillfin gobies. He documented these intertidal fishes' remarkable ability to learn, in one trial, the topography of rockpools while swimming over them at high tide. This can be a critical survival skill to avoid having to make a leap of faith when a goby finds herself stranded in a shrinking pool. Experienced gobies successfully leaped to neighboring pools with 97 percent accuracy, whereas naïve fishes with no high-tide experience were only 15 percent successful (Aronson 1971). They still remembered the tide-pool layout 40 days later.

All the fishes mentioned so far are teleosts, or bony fishes, which make up over 96 percent of all fishes. How does the other group, the chondrichthyans, or cartilaginous fishes (such as sharks and rays), compare with their distant bony relatives? A study of problem-solving by five vermiculate river stingrays (*Potamotrygon castexi*) offers some insight. Presented with hard-to-reach food hidden inside an 8-inch piece of plastic PVC pipe, the rays soon discovered how to draw the morsel out by one of two methods: creating a suction with their disc-like bodies, or undulating their fins to create a current (Kuba et al. 2010). When the research team put a black cap with a mesh barrier on one end of the pipe, and an open white cap on the other end, all five rays were successfully removing food morsels after eight trials. Most went from either using the suction or the fin undulation method to using a combination of the two. One male also blew jets of water from his mouth into the pipe to force the food out. Moving away from a strongly attractive cue — the smell of food at one end of the tube — and trying the other side is not a trivial thing, for it requires working against a natural impulse to follow chemical cues. While this is a small-sample study of just one species, it nevertheless reveals the mental capacities of a chondrichthyan, including cognition, flexibility, innovation, and determination. Another ray, the giant manta, has the largest brain of any fish, and a new captive study suggests that they are capable of recognizing themselves in a mirror (Csilla & D'Agostino 2016).

Perhaps the holy grail of animal cognition is tool-use. Lacking hands or feet, fishes are physically limited in their options for manipulating objects. Nonetheless, tuskfishes and wrasses have been seen using rocks as anvils against which to smash mollusks they have uncovered by blowing water at the sand (Bernardi 2012). Water-blowing itself, as we also

saw from the rays retrieving food from PVC pipes, could be considered a form of tool-use, for it involves the manipulation of an external agent (water) to attain a goal (Paško 2010).

Water takes on another purpose for archerfishes, noted for being able to pick off perching or flying insects by shooting jets of water up to ten feet through the air. Their ballistic skills are not innate; they must be learned, and archerfishes learn them both from trial and error and from watching experienced archerfishes. Novice fishes cannot hit an object moving just a half inch per second, but after watching a thousand attempts (successful and unsuccessful) by another fish to hit a moving target, novices can hit rapidly moving targets. Archerfishes use two different techniques to aim and fire at flying prey. With the “predictive leading” strategy, the fish shoots like a football quarterback, aiming the water jet ahead of the speeding target. The “turn and shoot” strategy is generally reserved for lower-flying prey: the fish unloads directly at the target while rotating its body horizontally to match the target’s lateral movement. As a further measure of the flexibility of these fishes, most of the time they feed in the conventional fashion, on submerged food, and when stalking airborne quarry, they may forego shooting in favor of leaping from the water to nab prey directly.

The cognitive feats of certain fishes refute the common prejudice that animals must possess big brains to be able to perform complex mental tasks. Depending on the test, a small fish may outperform a great ape. For example, cleaner wrasses perform better than chimpanzees, orangutans, and capuchin monkeys in a test that requires learning, memory, and time-tracking (Salwiczek et al. 2012). Cleaner-fishes are so-named for their “profession” of providing a spa treatment to client fishes in exchange for a light meal of parasites, algae, and other undesirables removed from the client’s body. It is estimated that a cleaner wrasse can recognize 100 or more different client species, and probably individual clients.

The benefits to cleaner wrasses of being able to recognize client fishes and to remembering when they last serviced them may explain their superior performance compared to captive primates. In a test in which red plates bearing food were soon removed and blue food plates were not, only cleaner-fishes ( $n = 6$ ) learned to eat first from the red plate within fifty trials; of four chimpanzees, four orangutans, and eight capuchin monkeys, only two of the chimps solved the problem within 100 trials (60 and 70 trials) (Salwiczek et al. 2012). Several juvenile cleaner wrasses were also tested. They performed markedly worse than the adult fishes, indicating that this is a mental skill that must be learned. These results render all the more dubious a *corticocentric* viewpoint still defended by some — that only animals whose brain has a neocortex are conscious and can feel pain (Rose et al. 2012; Key 2016 and accompanying commentaries).

The cleaner-client mutualism has given rise to other social dynamics whose sophistication exceeds what we might have expected of a fish. Systems built on trust are vulnerable to exploitation by freeloaders. A cleaner-fish is not above occasionally nipping a mote of nutritious mucus from a client’s body. Imposters, like the sawtooth blenny, imitate cleaner wrasses and when the client is least expecting it, nip a chunk of fin before fleeing to safety. Clients know there are risks, and they are not passive victims; they jolt noticeably if a

cleaner nips too hard, which sends a signal to the cleaner that s/he has transgressed and that the client knows it. Waiting clients are vigilant of cleaners' performance; they keep accounts, forming "image scores" for known cleaners, and preferentially visit those who cause fewer jolts. In one of several known piscine examples of audience effects, cleaners perform better cleaning services when they are being watched by clients (Fernald 2011).

### **Individual Recognition**

Needless to say, all this requires individual recognition, which is widespread and possibly universal among fishes. Being able to recognize other individuals is useful, such as in the social hierarchies of guppies, who can infer that if fish A is higher ranking than fish B, and fish B higher than fish C, then fish A must be higher ranking than fish C (Grosenick et al. 2007). Individual recognition has also been used by fishes in making mate choice and foraging decisions. For example, European minnows prefer to associate with shoalmates who are poorer competitors for food (Metcalf & Thomson 1995).

A further function of recognition is social bonding. There are countless anecdotes of fishes appearing to bond emotionally with others, or with human guardians. These take the form of fishes providing physical support to an ailing comrade, fishes who swim repeatedly into a caregiver's hand to be stroked, and sharks, groupers and other species that recognize friendly divers and approach and linger for caresses. Sharks may enter a hyper-relaxed state of "tonic immobility" when stroked repeatedly by trusted divers (Figure 2).



Figure 2: A Caribbean reef shark relaxing while being stroked by familiar divers. Courtesy, Cristina Zenato.

Being able to recognize others may also be useful for defending one's area of surf and turf. When resident threespot damselfishes were presented with two rival male threespots (contained in glass bottles), one a familiar neighbor and the other a stranger, the resident fishes vigorously attacked the strangers, ramming the bottle and trying to bite them through the confounding barrier. In contrast, they virtually ignored the familiar neighbor, apparently recognizing that he was not a threat (Thresher 1979).



Some of the most interesting and revealing aspects of fish social lives are those that cross species lines. Cooperative hunting has been described for both intraspecies (e.g., lionfishes), and interspecies pairings (Lönnstedt et al. 2014). Interspecies hunting occurs between groupers and moray eels. Groupers appear to be the more proactive participants. A hungry grouper, upon spying a moray eel, will swim over and signal the desire to collaborate with a distinctive head-shake or body-shimmy gesture. If the moray eel is amenable, the pair of fishes swims off over the reef, like friends on a stroll. If a targeted prey fish hides among the coral, the slender moray goes after it. The grouper hovers nearby ready to snatch the fish if it manages to flee into open water. A grouper will also angle its body to point to a fish that has hidden in the reef, which notifies the eel that there is something there worth pursuing. This behavior meets the criteria for a referential signaling, a form of communication previously only known in species noted for high intelligence — great apes, dolphins, and ravens (Vail et al. 2013).

### **Raising a Family**

If there is a part of life that rivals getting food, it is reproducing. True to their diversity, fishes exhibit a level of sexual plasticity and flexibility that exceeds all other vertebrates (Pandian 2011). The sexual playbook of fishes includes promiscuity, polygyny, polyandry, sequential and long-term monogamy, harem-keeping, territoriality, group-spawning, sneak copulations, satellite male strategies, and simultaneous and sequential hermaphroditism. Most fishes have external fertilization, with eggs and sperm being ejected from the body to unite in the water column; however, many species have internal fertilization, including the live-bearing fishes of the family Poeciliidae, and the sharks and rays.

About a quarter of all fishes engage in parental care that ranges from guarding eggs to looking after the young through their most vulnerable first few weeks of life (Mank et al. 2005). One of the most elaborate expressions of parental care in fishes is mouthbrooding, in which eggs or young are kept in the parent's mouth. Mouthbrooding occurs in at least nine fish families on four continents, including some 1,400 cichlids (Roots 2007). Parenting is disproportionately carried out by males, and some have been known to starve for weeks while harboring and even feeding their young in their mouths, which surely ranks among the noblest examples of restraint in the animal kingdom.

Reproductive restraint may also take the form of foregoing breeding to help someone else raise their young. Cooperative breeding of this sort is best known among birds, of which several hundred species are known to practice it (Brown 1987). A dozen or more fish species have helpers at the nest. Helpers perform a variety of tasks relating to the care and protection of eggs and young, such as cleaning and fanning eggs, newborns, and fry; removing sand and snails from the breeding area; and defending the parents' territory (Desjardins et al. 2007). Helping increases the helper's genetic fitness by benefiting kin who share the helper's genes. Helping also provides valuable skills training. Helping probably evolved via kin selection under conditions of limited resources that preclude nesting oneself. This so-called "resource constraints hypothesis" was supported by a four-month captive study of 32 pairs of wild-caught daffodil cichlids; when helpers were



provided with separate compartments with nesting shelters and supplies, they paired up and bred, but not if the compartment had no supplies (Bergmüller et al. 2005).

## **Why It All Matters**

My chief goal in writing *WAFK* is to raise the status of fishes by drawing attention to scientific discoveries about their lives that are largely unknown to the lay public (for whom I also share numerous stories and personal accounts). The accumulating scientific evidence regarding the perceptual, cognitive and emotional qualities of fishes leads forcefully to the conclusion that they are autonomous individuals with minds of their own. Because a precondition of being something of direct moral concern is that it be sentient, it follows, I think, that fishes deserve our moral consideration.

Currently, we fall far short of giving them the sort of consideration that their capacities demand. Notwithstanding coastal communities that have for centuries engaged in sustainable fishing practices, modern commercial fishing is driven by profit, not hunger. Technological advances have enabled modern fishermen to continue taking enormous numbers of fishes out of the oceans whose populations are nonetheless declining. Catching methods, which include purse seining, bottom trawling, and long-lining, are notoriously inhumane and indiscriminate. Whether kept or discarded, most commercially caught fishes die of asphyxiation in air, crushing in hoisted nets, or decompression when raised from the depths. The estimated daily bycatch (unwanted marine species including sea birds, sea turtles, and marine mammals) is 200 million pounds, most of it tossed away dead or dying (Davies et al. 2009).

One might see the rise of aquaculture — captive fish rearing and slaughter — as a welcome replacement for the ravages of commercial fishing. The truth is more complicated. Most of the “forage fish” captured on the seas (such as anchovies or herrings) are fed not to humans but to farmed fishes and to pigs and chickens on factory farms (McClure 2008). Over 85% of fish oil extracted from wild-caught fishes is fed to farmed fishes (FAO 2008). The overcrowded conditions on fish farms give rise to a host of problems, including parasitic sea lice that can plague the fishes, bacterial diseases, toxic chemicals used to treat them, and concentrated fish wastes. Sea pens are not designed to contain any of these undesirables, which then spread into the surrounding waters, affecting free-swimming fishes and their habitats (Lymbery 2002). Efforts to kill fishes less inhumanely are gradually being adopted, especially in parts of Europe. In Norway, for example, the use of carbon dioxide stunning was banned in 2010; but replacement methods — usually electricity or a blow to the head — are hardly exemplars of humane handling (FishCount 2014).

As concern for animal wellbeing grows, fishes are gradually being swept into the current. A million acts of kindness rescue individual fishes stranded or beached and return them to the water. Fish welfare organizations are sprouting on both sides of the Atlantic Ocean, and consumers are becoming more aware of food choices that are less harmful — or not

harmful at all — to fishes. With growing awareness of the importance of healthy aquatic ecosystems to planetary stability, we may hope that these nascent trends accelerate.

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