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Behavioural fever, fish welfare and what farmers and fishers know

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Highlights:

- Fish of several species move to warmer water when they detect a pathogen, thereby increasing their body temperature (or showing behavioural fever); this can stimulate a strong immune response, allowing the fish effectively to cure themselves of the responsible pathogen.
- The occurrence of behavioural fever in fish raises the possibility of allowing cultured fish to 'self-medicate' by giving them access to temperature gradients (behavioural prophylaxis).
- Experienced fish farmers have discovered that their fish make use of thermal gradients, which provides one example of the fact that those whose livelihoods depend on controlling or predicting fish behaviour often have a wealth of knowledge about fish ethology.
- A diffuse but extensive literature shows that this is the case, not just for fish farmers but also for fishers, who use their knowledge of fish ethology to enhance the efficiency of their fishing operations.

Abstract: In this article we first describe briefly how, like other ectotherms, wild fish promote effective functioning (for example, digestion and reproductive maturation) by moving through the temperature gradients that they experience in their natural habitats (showing behavioural thermoregulation). We then look in more detail at one particular example of behavioural thermoregulation in fish, specifically the phenomenon of behavioural fever; this refers to an acute, reversible increase in preferred water temperature in response to pathogen recognition. Behavioural fever promotes survival by stimulating an effective immune response to the responsible pathogen. An on-going project is described that explores the possibility of using this capacity for behavioural fever to promote disease resistance in fish in Nile tilapia farms. This project involved intensive discussion with experienced tilapia farmers, during which it emerged that a number of these farmers already knew how their fish make use of thermal gradients. Using this observation as a pivot, we then switch to consideration of the extensive non-scientific, traditional knowledge of fish ethology possessed by experienced fish farmers and fishers and discuss possible implications for fish culture.

1. Introduction

This article addresses two separate but linked issues concerning the behaviour of fishes; both were covered in presentations at the International Society for Applied Ethology 2019 conference in Bergen, Norway (FH Wood-Gush lecture: *Synergy between fundamental and applied behavioural science: lessons from a lifetime of fish watching*. FH, SR and colleague: Symposium on fish behaviour and welfare: *Using thermal choices as indicators for fish welfare*). By chance, the points we discuss relate to and develop some made by Temple Grandin in her opinion piece arising from the previous ISAE meeting, in which she calls for more training in ethology for students of animal sciences and veterinary medicine (Grandin, 2019; *Crossing the divide between academic research and practical application of ethology and animal behavior information on commercial livestock and poultry farms*).

The first of our two topics, both expanded in later sections, concerns the fact that, given access to a temperature gradient, fish in the wild and in captivity use behavioural choices to control their body temperature in such a way as to promote effective functioning. The second issue for consideration here is the fact that those whose livelihoods depend on controlling or predicting the behaviour of fishes often have a great wealth of knowledge about their behaviour; one might call such people the ultimate applied fish ethologists. The link between these two topics lies in the fact that some farmers already know from their own experience that fish make adaptive thermal choices and use this knowledge to improve the health of their stock.

2. Thermal choices, behavioural fever and the health of cultured fish

2.1 Thermal stratification in the aquatic environment

In nature, fish experience gradients in water temperature on a variety of spatial scales, for example in relation to depth and horizontal position. To give just one of thousands of possible examples, temperatures recorded on the same specific days in a large freshwater body in Malaysia varied at four offshore locations. On one representative day (in June 2014), temperatures varied from ca 31^{o}C at the surface to ca 25^{o}C at a depth of 20m, while at a particular depth (for example, 10m) it varied between ca 27°C and 31°C at different stations (Ling et al., 2018). Cultured fish also experience temperature gradients, from local areas of higher temperature around aquarium equipment, to horizontal and depth-related temperature variation within ponds and depth-based variation in cages. Again, by way of illustration, Atlantic salmon (*Salmo salar*) in sea cages (160m circumference X ca 17m depth) in Tasmania in February 2016 experienced temperatures ranging from ca 22°C at the surface to ca 14°C at 12m (Stehfest et al., 2017).

2.2 Adaptive thermal choices in fish

It is well known that, depending on ontogenetic stage, wild fish of many species move through the temperature gradients to which they are exposed in such a way as to promote effective functioning (see review by Huntingford et al., 2012). Again, to illustrate briefly, dogfish (*Scyliorhinus canicula)* lower their daily energy costs by adopting a 'hunt warm-rest cool' strategy, catching prey in warm, shallow water at night and digesting their meal in cool, deep water during the day (Sims et al., 2006). Upstream-migrating chum salmon track water temperatures that reduce the metabolic costs of swimming (Tanaka et al., 2000), while migrating sockeye salmon track temperatures that are optimal for sexual maturation (Newell and Quinn, 2005). Free-ranging common carp held in a pond (area: 70 X 20m) raise their body temperature above ambient by as much as 4°C by periodically basking in sunspots; the longer the time spent basking in this way, the faster the fish grow (Nordahl et al., 2019).

2.3 Behavioural fever in fish

Given the opportunity, cultured fish also move between areas of different temperatures to the benefit of their health, illustrated strikingly by their thermal responses to infection. In this context, while endotherms respond to infection with physiological fever (facilitating recovery), ectotherms may respond behaviourally, moving temporarily to places with a higher water temperature (Rakus et al., 2017a). Such an acute change in thermal preference following pathogen recognition is referred to as behavioural fever. Physiological fever in endotherms and behavioural fever in ectotherms depend on similar underlying pathways (Rakus et al., 2017a; Boltano et al. 2018), details of which are beyond the scope of this short article. Behavioural fever has been well documented in lizards (for example Vaughn et al., 1974), but until relatively recently has not been much studied in fishes (though see Reynolds et al., 1976; Covert and Reynolds, 1977 and Grans et al., 2012).

It is perhaps worth noting that behavioural fever, in which an increase in preferred temperature occurs in response to pathogen recognition, is distinct from stress-induced hypothermia (or emotional fever emotional fever as it is sometimes called. e.g. Cabanac and Gosselin, 1993), in which preferred temperature increases in response to a stressor, though both are examples of behavioural thermoregulation. Whether fish show stress-induced hyperthermia is an important but controversial topic (Rey et al. 2015; Key et al., 2017; Rey et al., 2017; Jones et al. 2019) that certainly requires resolution. However, our focus here is on pathogen-induced (behavioural) fever in fish, a few examples of which are given below.

Cultured zebrafish (*Danio rerio*) are normally housed at a fixed temperature within a narrow range of 26-28°C, identified as optimum for this species. When housed in tanks that provide a choice of temperatures, they make frequent visits to compartments above and below this recommended temperature. Zebrafish in tanks with a temperature gradient (ca18°C to 37°C) given a simulated viral infection spend more time at higher temperatures over a period of ca 24h (Figure 1a), thereby raising their body temperature; untreated fish and sham treated fish (handled and given an injection of phosphate buffered saline) show no such dramatic change (Boltana et al., 2013). An increase in preferred temperature in response to infection has been found in common carp (*Cyprinus carpio*) infected with Cyprinid herpes virus 3, the behavioural change appearing at a relatively advanced stage in the infection (ca 6 days post infection. Figure 1b. Rakus et al., 2017b). One interesting feature here is that the possibility of behavioural fever in infected fish was first identified by researchers by observing such fish congregating around their aquarium heaters. (Rakus et al. 2017b). Nile tilapia (*Oreochromis niloticus*) also show an increased temperature preference following infection with *Streprococcus iniae* (Cerqueira et al., 2016).

2.4 Behavioural fever and recovery from infection

When zebrafish infected with the highly virulent Spring viraemia virus are allowed access to a temperature gradient, as opposed to being held at a fixed temperature of 22 °C or 28°C, they are able to protect themselves against the disease, showing zero mortality, no external signs of infection (Figure 2a) and with no viral particles remaining in their body after a week. This enhanced protection in fish given the opportunity to express behavioural fever is associated with a major upregulation of anti-viral genes that is absent in control fish (Boltana et al., 2013). Similarly, in common carp infected with Cyprinid herpesvirus 3, no mortalities were reported in fish held in a thermal choice tank (with access to tanks at 24 °C, 28 °C and 32°C) and so able to move to warmer temperatures and express fever. Good survival was also found in carp given no thermal choice but held at 32°C (Figure 2b). The appearance of behavioural fever was associated with upregulation of inflammatory cytokines (Rakus et al., 2017). Similar results have been found in Atlantic salmon (Boltana et al., 2018).

2.5 Potential applications in fish culture

The beneficial effects of holding fish at high temperature for protection against disease has already been noted and used in fish culture. For example, aquaculture researchers in Israel studying the lethal Koi herpes virus of common carp have shown that fish exposed to the virus for a few days within the virus's permissive temperature range (18 °C to 25°C) and then moved them to a higher, non-permissive temperature of 30°C developed resistance to subsequent infection, associated with high plasma levels of virus-specific antibodies. At a farm level, such 'naturally resistant' carp have significantly reduced mortalities (from 80-90% to ca 40%. See Ronen et al., 2003). Asian seabass (*Lates calcarifer*) farmers in Vietnam have discovered that, when they notice signs of a specific viral disease, holding fish at hotter temperature reduces disease prevalence and mortality levels (Dr. Sean Monaghan, fish immunologist at the Institute of Aquaculture, University of Stirling, UK. Pers. comm.).

The potential significance of behavioural fever in this context lies in the fact that access to a temperature gradient would potentially allow fish to dose themselves to increased temperature if required, rather than their needing to be moved by farm workers. This forms the basis of a recent project by SR and colleagues on farmed Nile tilapia in Egypt, funded by the British Council and the Newton Institutional Links programme (*Behavioural prophylaxis informing improved culture system design and management for enhanced fish health and sustainable intensification of the Egyptian tilapia industry).* Tilapia farming, which is typically carried out by traditional, semi-intensive methods in large earthen ponds, is of considerable social and economic importance. The project started with intensive discussion between researchers and experienced farmers about, among other things, temperature gradients within their ponds and ways in which these might be manipulated by changing the pond design. The most promising and feasible methods have been implemented and the behaviour of the tilapia in response to such gradients is being monitored, as is resistance to a range of diseases (including *Streptococcus*, *Aeromonas* and *Vibrio* spp). The data from this study have still to be analysed, but some of the farmers involved are of the clear opinion that final production is better in the modified ponds (Ahmed Hamza, veterinary partner in the project; pers. comm.).

3. Non-scientific and traditional ethological knowledge: what farmers and fishers know

3.1 Ethological knowledge and good stockmanship

All of the tilapia farmers who took part in the project described above know and understand the temperature profiles of their rearing ponds. Some farmers already place greenhouses in the ponds for wintering, to benefit fish health, and some report that their fish congregate in warmer locations. Such knowledge by farmers of how fish respond to temperature gradients provides a specific example of the second point we wish to make in this article, namely that (under the right circumstances) those whose livelihoods depend on being able to control or capture fish (in effect those who need to be able to predict what fish will do) often have extensive knowledge about aspects of their ethology. This relates to a point made by Grandin (2019) about the importance of good stockmanship for the welfare of farmed terrestrial animals; she suggests, for example, that experienced stock people are often highly skilled behavioural observers, for example being alert to early behavioural signs of fear.

In another context, FH and MMQ have recently carried out a review of behavioural knowledge held by fishers (both for food and for sport), using literature published in academic journals (for example from the fields of sociology, geography and anthropology) and books written by anglers for anglers. In what follows we combine these various sources with information from aquaculture to illustrate the breadth and depth of such non-scientific, sometimes traditional, ethological knowledge and how it is used. By way of a disclaimer, our aim in this brief commentary is to highlight and appreciate the detailed ethological knowledge held by many farmers and fishers and not to discuss fish sentience and its implications for the rights and wrongs of fish farming and fishing. These are very important topics, but complex and beyond the scope of this commentary.

3.2 Pervasive general knowledge of fish behaviour among farmers and fishers

It is recognised by those familiar with practices on well-run fish farms, where good husbandry is allowed to inform decision making, that experienced farmers make use of a number of behavioural cues when monitoring the well-being of their fish; these include early signs of loss of appetite and changes in swimming patterns that relate to stress or sickness. Such cues were picked up by farm staff in a study carried out by FH and colleagues on stocking density and welfare in Atlantic salmon held in sea cages, who became concerned about the status of fish in some of the higher-density cages and took appropriate action. Retrospective analysis using a complex scientific multivariate welfare indicator (based on indices of fin and body condition and several blood biochemistry variables) showed that the fish in cage identified as problematic by farm staff did indeed have significantly lower-than-average welfare scores (Turnbull et al., 2005). It is also noteworthy that FH and colleagues first started studying the behaviour of farmed fish in response to an approach from the (then) Scottish Salmon Farmers Association (now the Scottish Salmon Producers Organisation). The Association was responding to concerns expressed by members, based on their own observations, that aggressive interactions seemed to be causing unequal distribution of food within sea cages. Systematic ethological studies showed that they were correct (Kadri et al. 1996), resonating with Grandin's identification of aggressively maintained dominance hierarchies in terrestrial livestock as an important training topic (Grandin, 2019).

The detailed knowledge that good, experienced farmers have of fish behaviour is illustrated indirectly by their role in a recent study in which Qualitative Behavioural Assessment (QBA) was applied to farmed salmon (Dunn, 2017). QBA is a method developed by social scientists that is increasingly used in animal welfare science to reach an informed consensus about affective (emotional) states in animals of a given species held in particular circumstances (Wemelsfelder and Millard, 2009). The basis of QBA is that human observers can form reliable judgements about such states from fine details of an animal's behaviour and body language. The first step is for experienced observers to formalise the behaviour of the species concerned into an agreed set of qualitative descriptors (e.g. relaxed, anxious), with associated behavioural symptoms. In Dunn's (2017) application of QBA to salmon, discussion with and among experienced fish farmers generated 20 such descriptors (Table 1). A panel of observers then used these descriptors to characterise the status of salmon from a sample of video clips. The choices of different panellists were then compared statistically and, where there was good agreement among panellists, scores based on the QBA descriptors were compared with the results of a classical quantitative ethological analysis of the videoclips (i.e. using ethograms). In some cases (for example, the distinction between the *tense* and *calm* descriptors) there was good agreement between to the two approaches. Such results suggest that QBA could be used to provide sensitive, objective, low-tech indicators of the affective state of these fish from a knowledge of their behaviour (Dunn, 2017). The fact that experienced salmon farmers were able to use their behavioural observations to generate clear descriptors that successfully encapsulated the affective state of their stock speaks for the breadth and depth of their knowledge of fish ethology.

Extensive general ethological knowledge also exists among indigenous fishers, epitomised by the fact that they often identify and name fish species with reference to by their behaviour. For example, artisanal coastal fishers from north-eastern Brazil identify more than 16 species of fish, based on various aspects of behaviour. These include movement and migration, activity rhythms, feeding, predator avoidance, social interactions (aggression and communication) and reproductive behaviour (Table 2). Their classification agrees well with those of scientific fish taxonomists (Costa-Neto, 2000).

3.3 Knowledge about learning in fish

Grandin (2019) identified animal learning as one of the topics that veterinary and agricultural science students need to be taught about to manage terrestrial livestock effectively. Certainly, many procedures carried out on fish farms depend on the ability of fishes to learn from experience; for example when young fish are being weaned from live prey onto unfamiliar pelleted food they need to learn that these are nutritious (Raubenheimer et al., 2012). Here we concentrate on of what fishers know about fish learning, giving just a few examples from a large, if diffuse, literature. Not surprisingly, fishers have extensive knowledge of the abilities of fish to change their behaviour in response to the adverse experience of encounters with fishing gear. Anglers are well aware that fish often learn quickly to avoid both the places where they have experienced capture attempts and the bait and lures used for this purpose. For example, in an early classic text about angling Isaak Walton (1653) writes of carp fishing: “After several days’ fishing, your game will be very wary and you shall hardly get a bite. Then your only way is to desist from your sport two or three days … (meanwhile providing worms without hooks) … Then you may enjoy your former recreation.”. Responses of a group of coarse fishers in the UK to questions about the behaviour of their prey include comments such as: “The fish know where the fishermen are, so they go where the fishermen aren’t” and “…what I found was that the fish (carp) weren’t feeding during the day because they were being pressured by all the anglers, so they'd wait until dark and they'd feed all night."(Bear and Eden, 2011).

The fact that Atlantic salmon learn the smells of their natal stream and use these to direct their return migration is a classic example of (olfactory) imprinting (Hvidsen et al., 1994). Interestingly, Isaak Walton knew about this remarkable (learned) homing ability, writing as follows (using Walton's spelling and grammar): "…it is said (of the Atlantic salmon) that after he is got to the sea, he becomes from a Samlet not so big as a gudgeon, to be a Salmon…Much of this has been observed by tying a riband or some known tape or thread to the tail of some young Salmons which have been taken in weirs as they have swimmed towards the salt water, and then by taking a part of them again, with the known mark, at the same place, at their return from sea…; and like the experiments that have been tried upon young swallows who have…been observed returning to the same chimney, there to make their nests…" (Walton,1653).

There is good scientific evidence that young, naïve fish of many species learn traditional migration routes from older, experienced conspecifics. For example, Norwegian herring (*Clupea harengus*) move between traditional feeding and spawning grounds along population-specific routes. This involves using sequences of landmarks learned by younger cohorts from older schooling companions and transmitted between generations by social learning (e.g. Fernö et al., 1998; Corten, 2001; Huse et al., 2010). According to tradition among Norwegian fishers, the massive schools of herring migrating to spawning grounds were led by a larger fish species called the "herring king" (the giant oarfish, *Regalecus glesne*). This is partly accurate, because as described above, the herring do indeed follow larger fish to the spawning grounds, but is also partially mistaken, because these leaders are older herring and not oarfish. The fishers had identified the phenomenon of socially-learned migration routes in fish (later reported by scientists), even though they were wrong about the 'tutor' species (Ferno et al., 2011).

3.4 How traditional ethological knowledge is used

Such knowledge of the behavioural capacities of fish may be learned by individual experience, the reinforcement being more effective capture, but the knowledge is also often passed on from experienced to inexperienced fishers, along with broader traditional ecological knowledge (Ruddle, 1993; Silvano and Valbo-Jørgensen, 2008). Thus, indigenous fishers of the Godavari River, India, use their extensive knowledge of the behaviour of the 12 most intensely fished species to target particular prey (Shivaji et al., 2014). In the case of feeding behaviour, for example, experienced fishers describe how two species of fish that they hunt (*Notopterus kapirat* and *Channa marulius*) construct rafts of air bubbles at the water surface; they lie below these and ambush the dragonflies that are attracted to the shining surface of the bubbles. Local fishers use the floating air bubbles and the presence of dragonflies to locate and capture these species (Shivaji et al., 2014). In the case of anti-predator behaviour, fishers in the Godavari River call the omnivorous *Rhinomugil cephalus* ‘rocket fish’ because it escapes attack by jumping above the water surface for few feet. These fish feed in shoals in shallow water and fishers set one net across the water flow to catch the main shoal and another 3-4 feet beyond it, to catch the jumpers (Shavaji et al., 2014).

Like the rocket fish, many fish that are targeted by fishers belong to shoaling or schooling species and there is extensive traditional knowledge of this form of social behaviour (some already exemplified in Table 2). Fishers in the Marovo Lagoon, Solomon Islands, have at least 16 different terms for fish schools, characterised partly by behaviour of the schooling fish (Johannes and Hviding, 2000). For example, they distinguish between schools of quiet, resting fish, perhaps under cover (*Sakoto*), large groups of actively swimming, non-feeding fish (*Baini)* and tightly packed schools that stop periodically to feed on the bottom (*Uduma*. Johannes and Hviding, 2000). Knowing that fish often respond to predators by forming tighter schools, Marovo spear fishers tap their spears on the bottom of shallow sea areas where rabbitfish (Siganidae) are found, causing the fish to form tight clumps and making them easier to catch (Johannes and MacFarlane, 1991).

To put some numbers on this, experienced beach seine fishers from Sri Lanka are able to predict in advance the size and species composition of the schools of fish captured at each seine deployment.

Over 74 seining events, a positive and highly significant relationship was found between fishers' expectation (quantified from interviews prior to each throw) and the realised catch ($R = 0.814$, $p<0.001$). Predictions were based on a number of cues, some of which involved fish behaviour; informative cues include glimpses of fins, characteristic vortices on the water surface caused by species-specific swimming patterns, species-specific smells detectable in the water, the presence of floating objects (known to be attractive to particular fish species) and also by the presence of particular categories of predator (Deepananda et al., 2015).

3.5 Traditional knowledge about how fish respond to temperature gradients

Coming back to our initial topic of the thermal choices made by fish, there is a huge scientific literature on the effects of spatial variation in water temperature on fish distributions, often on a fine scale. For example, numerous studies show that mackerel distributions and behaviour are influenced by fine scale differences in water temperature and that fishing effort maps onto these distributions. An acoustic survey of mackerel during spawning migrations along the coastal shelf off the Shetland Islands (UK) found the majority of schools at temperature between 8.00 and 8.75°C, none being observed in waters below 7.75°C (Walsh et al., 1995). This distribution seems to arise because fish increase their swimming speed when they enter colder water, but decrease their swimming speed on entering warmer water; together these responses keep them in a core of warm water near a costal shelf (Reid et al., 1997). Tracked fishing vessels also concentrate their activities within areas of relatively higher water temperature (Walsh et al., 1995).

Where fishers use sonar to detect fish schools, as is the case for these two studies (Walsh et al., 1995; Reid et al., 1997), this does not necessarily require them to know about the temperature preferences of the fish they capture. That fishers do have such knowledge is known but not well documented. It is reported, however, that Japanese nearshore fishers choose locations for fish aggregation devices on the basis on known habitat preferences of the fish species concerned, including preferred water temperature (Hamashima et al. 1969, cited in Parrish, 1999). Finally, to cite an anonymous referee, capelin in the Barents Sea prefer cold water, and fishers tend to turn back when they enter waters that are too warm (anonymous, pers. comm).

Taken as a whole, the examples described in this section, demonstrate that when the behaviour of fish is critical for their successful control or capture, even when such behaviour is complex, the knowledge of farmers and indigenous fishers can be both detailed and accurate.

4. Conclusions.

The existence of behavioural fever in fish and the beneficial effects for recovery from disease of being able to display this behaviour is of strong scientific interest. It is also of considerable applied importance, raising the interesting possibility that, given access to a temperature gradient, cultured fish could self-medicate, improving their health and reducing the need for medication.

The authors were greatly intrigued by these examples of the detailed ethological knowledge possessed by both farmers and fishers, which is what promoted us to describe them here. This point resonates with Temple Grandin's comments about the importance of good stockmanship and the need for students of veterinary medicine and animal science to learn about ethology (Grandin 2019). If such behavioural knowledge is sufficiently important to form the basis of what might be called traditional applied ethology among fishers and farmers, it is also important enough to be taught to those who are training to be responsible for the care of cultured fish, as indeed it sometimes is. In general. we fully endorse Grandin's thinking about the need for knowledge transfer between academia and practitioners and suggest that collecting, recognising and sharing the rich traditional ethological knowledge held by farmers and fishers could facilitate such transfer.

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Table 2. Behavioural ethnocategories of fish species identified by coastal fishers from Northern Brazil (adapted from Costa-Neto, 2000).

Figure legends

Figure 1. Examples of behavioural fever in fishes a) Zebrafish (Boltano et al., 2013) Mean (±SE) frequency of occupation of chambers with different water temperature by individual adult zebrafish following either a simulated viral infection (dsRNA) or sham infection (sham). Asterisks indicate significant differences between infected and sham infected fish. b) Common carp (Rakus et al., 2017b). Data from one representative replicate (of 3) in which fish infected with wild type (WT) carp herpovirus 3 on day 0 (broken vertical line). Y axis = mean no fish/compartment. Blue = 24°. Green = 28°C. Red = 32°C.

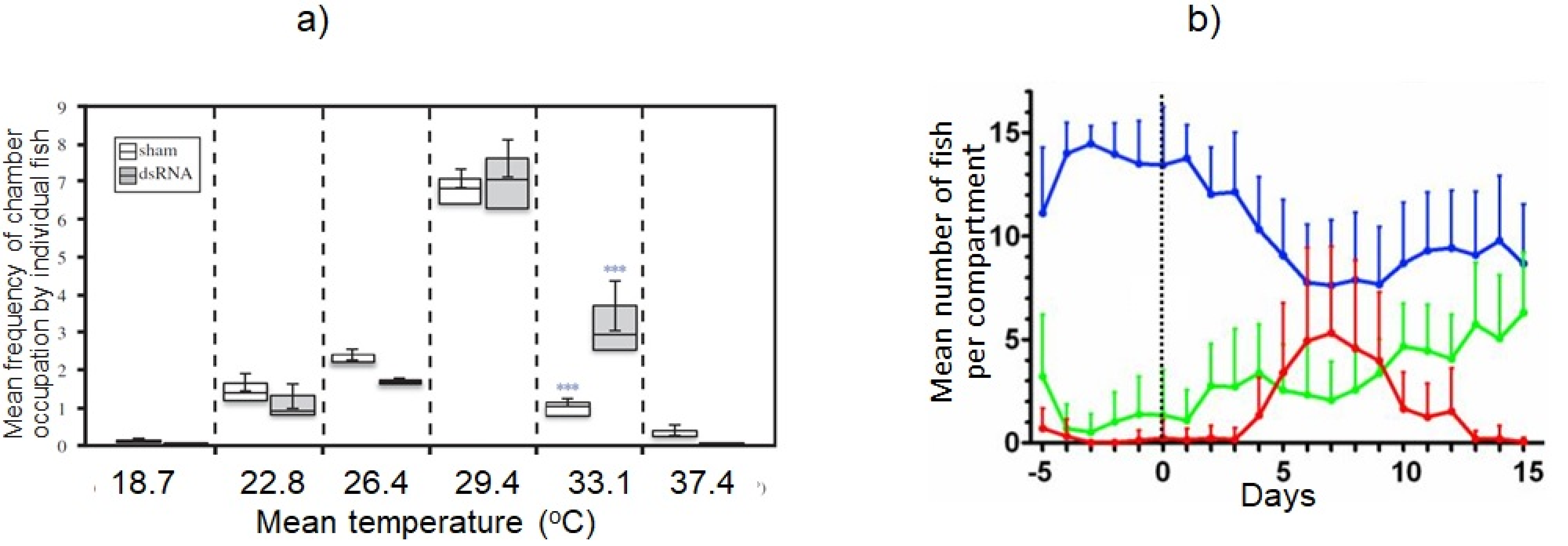
Figure 2. Beneficial effects of behavioural fever on recovery from infection. a) Number of zebrafish with clinical signs of disease on successive days post infection with Spring viraemia virus and held either at a fixed temperature of 22°C (black diamonds), or a fixed temperature of 28°C (black squares) or in a temperature gradient centred on 28°C (black triangles. Boltana et al., 2013) b) Survival rate in common carp in days following infection with wild type carp herpovirus 3 (day 0) under various temperature regimes. SCT: fish held in a fixed temperature tank at 24°C, 28°C, or 32°C. MCT: Fish held a multi chamber tank offering a choice of s chambers maintained at 24°C, 28°C, or 32°C. MCT blocked: fish restricted to one of the 3 temps within MCT (Rakus et al., 2017b).

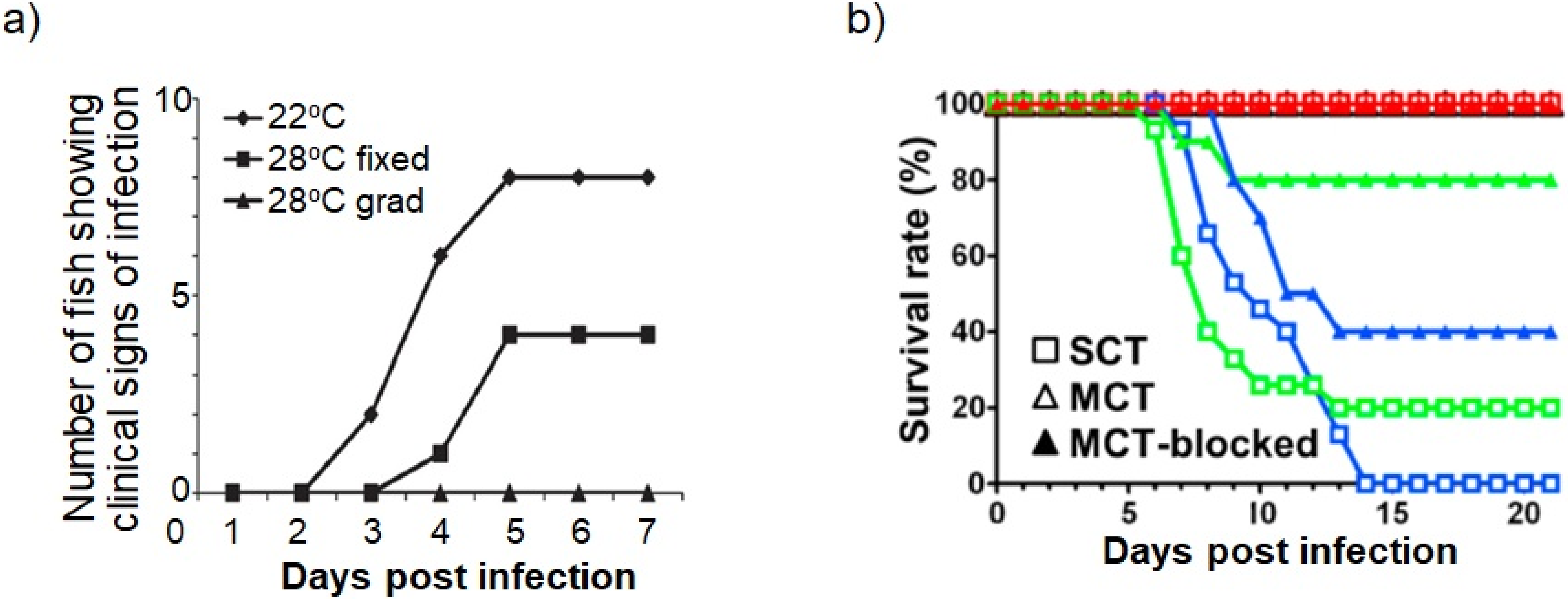
Table 1. List of descriptors and agreed synonyms developed by experienced fish farmers for use in a Qualitative Behavioural Assessment (QBA) study of famed Atlantic salmon (Dunn 2017).

QBA descriptor	Agreed synonyms
Content	Satisfied, at peace, restful
Stressed	Disturbed, upset, under pressure, mix of anxious and tense
Energetic	Active, lively, dynamic
Anxious	Worried, apprehensive
Mellow	Easy-going, tolerant, unphased
Skittish	Excitable, easily frightened
Irritated	Annoyed, frustrated
Tranquil	Still, quiet, serene
Fearful	Afraid, frightened
Aggressive	Hostile, assertive (violent)
Calm	Peaceful, undisturbed
Crowded	Claustrophobic, overwhelmed
Tense	On edge, strained
Startled	Spooked, surprised
Listless	Lethargic, lifeless
Flighty	Erratic, volatile, unpredictable
Relaxed	At ease, no urgency (not necessarily motionless)
Agitated	Disturbed, unsettled
Unsure	Cautious
Inquisitive	Interested, curious, engaged

Table 2. Behavioural ethnocategories of fish identified by coastal fishers from Northern Brazil (adapted from Costa-Neto, et al., 2000).

Behavioural ethnocategory	**Behaviour used in classification**	**Example**
MOVEMENT PATTERNS		
Jumping fish	Predator avoidance	Mullet
	Reproduction	Stingray
	Play	Mullet
Whirling fish	Predatory attack	Eye-horse jack
	Predator avoidance	Mullet
Travelling fish	Migration	Armoured catfish
ACTIVITY PATTERN		
Night walking fish	Nocturnal activity	Giant grouper
SOCIAL BEHAVIOUR AND COMMUNICATION		
Schooling fish	Social behaviour	Mojarra
Singing fish	Communication	Atlantic moonfish
Snoring fish	Communication	Barred grunt
REPRODUCTIVE BEHAVIOUR		
Mouth-brooder fish	Parental care	Catfish
Nest maker fish	Courtship and parental care	Piranha
Bed maker fish	Courtship and parental care	Trahira
Courageous / Fierce fish	Competition/protection of young	African cichlid
GENERAL BEHAVIOURAL ‘STYLE’		
Wild fish	Aggression	Atlantic tarpon
Violent fish	Predatory attack	Eye-horse jack
Stone answering fish	Investigation	Snook
Playing fish	Play	Puffer fish


a)
b)
Mean frequency of chamber occupation by individual fish
sham
dsRNA
***
***
0
1
2
3
4
5
6
7
8
9
18.7
22.8
26.4
29.4
33.1
37.4
Mean temperature (oC)
Mean number of fish per compartment
0
5
10
15
-5
0
5
10
15
Days


a)
Number of fish showing clinical signs of infection
10
5
0
0
1
2
3
4
5
6
7
Days post infection
22oC
28oC fixed
28oC grad
b)
Survival rate (%)
100
80
60
40
20
0
0
5
10
15
20
Days post infection
□ SCT
△ MCT
▲ MCT-blocked