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Challenges and benefits of applying fish behaviour to improve production and welfare in industrial aquaculture

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Abstract

An understanding of behaviour is used in zoos, laboratories, and agriculture to reduce stressful aspects of the captive environment for animals. While fish are one of the most cultivated of all vertebrate groups, incorporating their behaviour into production management has proved elusive. Here, we evaluate the current evidence base relating to use of (1) innate behaviours of fish, and (2) their ability to learn new behaviours via human-mediated training or through social

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learning, in fish farms. Studies that tested habituation and conditioning (training) as a tool to improve welfare demonstrate positive effects for improving fish welfare and coping capacity. However, methods solely reliant on innate behavioural responses to stimuli will always be imperfect, due to variation in individual responses which are often context dependent. To date, there has been no successful demonstration of social learning as a tool for aquaculture. While many experimental scale studies report promising results, few have translated to commercial scale, highlighting a mismatch between theoretical and practical use and cautions against extrapolation of results from small-scale studies to commercial situations. While some promising evidence exists that fish behaviour can be integrated into farm management, logistical and scale-related hurdles must be overcome before this can occur. We conclude that fish behaviour is an additional and currently under-researched resource that could be integrated into farm practices to improve production and welfare in industrial aquaculture.

Introduction: aquaculture and farmed fish behaviour

Life as a farmed fish is seemingly a simple and monotonous existence. With an absence of predators, continuous food supply and structurally simple housing, the experience of farmed fish differs fundamentally from their wild counterparts. However, the aquaculture environment is often a stressful and cognitively challenging place for fish. Throughout the production cycle, from hatchery to harvest, farmed fish experience a series of stressors that do not arise in wild environments. Cultured fish are exposed to high stocking densities, temporarily unfavourable environmental conditions that may be unavoidable, and have a lack of control over food type, habitat and conspecific choice (Fernö *et al.* 2006). Many routine farm procedures necessary to complete a standard production cycle cause major and sudden environmental change which can induce a strong stress response in fish (Folkedal *et al.* 2010; Vieira Madureira *et al.* 2019). Generally, coping with new environments is enhanced by a high degree of variation in experience. A monotonous culture environment coupled with unpredictable disturbances creates a lack of opportunity for fish to learn, meaning fish may not be able to anticipate subsequent stressors. Increased stress levels lead to poor animal welfare, which is not only adverse for the fish themselves, but can reduce productivity for farmers (Bagni *et al.* 2007). To achieve sustainable, ethical, and optimal fish production in the future, the industry must endeavour to develop and improve current practices.

Today, aquaculture production has overtaken that of beef (Larsen & Roney 2013). While aquaculture is by no means a young practice, dating back to at least 500 BC in Asia (Liao

2000), industrialisation of fish farming only began to take off globally in the 1960s (Teletchea & Fontaine 2014), compared to industrial land-based animal farming that took place in the early 1900s (Ikerd 1996). With land-based animal production dominated by four species (cows, pigs, sheep and chickens), humans have had more time to observe, understand, and work with the behaviour of these domesticated species. This has allowed producers to tailor the farm environment to terrestrial domesticated animals and vice versa, through selective breeding, to achieve a level of sophistication in land-based animal farming. In contrast, over 300 different species of fish are farmed around the globe for human consumption, with less than half of these produced in large quantities (Huntingford *et al.* 2011). Several of the fish species produced in the highest abundance are not yet considered fully domesticated (Teletchea & Fontaine 2014).

In land-based farming, most of our knowledge concerning farm animal behaviour and animal husbandry is built on the relationship between farmer and animal (Føre *et al.* 2017). This is more difficult to achieve in aquaculture when there are thousands to millions of small-bodied individuals living underwater at any farm site. Additionally, there are relatively few examples of how to translate behaviour to production advantage for fish, so the impetus has not been strong enough to investigate the full behavioural repertoire of each species. Moreover, human perception of fish has also likely played a role in this lack of knowledge.

The perception that fish are unintelligent and behaviourally obstinate is gradually changing (Laland *et al.* 2003), with the amount of studies exploring learning and cognition increasing. A review of fish intelligence by Brown (2015) highlighted complex cognitive abilities and behaviours in fish including tool use, development of traditions, spatial orientation, discrimination between stimuli, Machiavellian intelligence, ability to cooperate with and recognise others, long-term memory, and more recently wrasse passed the mirror self-recognition test (Kohda *et al.* 2019). These attributes make fish viable candidates to apply their behaviour in a practical sense.

Research focusing on the application of fish behaviour in aquaculture for human consumption can be broadly split into two categories; 1) using existent inherent behaviours; and 2) encouraging new behaviours through learning regimes, that are either human mediated (conditioning or habituation) or via social learning. The suggested applications of both categories of behaviour are aimed at facilitating animal husbandry, optimising production and enhancing fish welfare. Here, we summarise the current evidence for applying behaviour in

aquaculture, discuss the limitations associated with behavioural principles being put into practice, and suggest ways to incorporate behaviour into farm management.

Methods

We conducted a search of the literature for publications up to April 2020 on using fish behaviour in aquaculture by searching for the following terms using *Web of Science*: ((aquaculture OR fish farm) AND fish behav* AND (social* OR social learning OR guided learning OR conditioning OR behavioural transfer OR informed leader OR naïve OR experienced OR conditioned OR habituation OR acclimation OR positive reward OR response OR stimulus OR attraction OR aversive OR avoidance OR manipulation OR exploiting OR innate)). This initial search resulted in ~1100 results. Search results were manually vetted by title and abstract alone where the subject matter was obviously unrelated, or else after reading the full text. Other articles missed by our original search were uncovered using exploratory searches using *Google Scholar* and *Scopus* and by examining the reference lists of all appropriate articles found by our original search, up to April 2020. Our search focused on species of finfish that are produced in a commercial capacity and on studies that used or tested fish behaviour in an explicit attempt to benefit some aspect of aquaculture production (parasite management, transport, welfare improvement, size grading, adaptation to feed).

Table 1

To be included in Table 1, studies had to provide quantitative data adequate to calculate an effect size. Many studies lacked a true control and so were not included in **Table 1**. Effect sizes were calculated for responses that directly measured the success of the application of behaviour. For example, if the main purpose of the study was to reduce lice loads, then the effect size for the response that measured this (e.g. mean no. of lice) was calculated, and not for instance, fish growth. Natural log response ratios were calculated for each variable: $RR = \ln(T/C)$, where T is the treatment mean and C is the control mean. Taking the natural log of the response ratio standardizes the error distribution by reducing the effect of positive responses (Hedges *et al.* 1999). Studies used a range of methods and a variety of different responses were measured. In studies where authors attempted to find the optimal conditions for a response to stimuli, we calculated the effect size for those optimal conditions. This was done to prevent studies that provided data on numerous treatments from having a disproportionate influence on our findings and to reduce the number of correlated effect sizes (non-independence), while outlining the conditions that are needed to induce the best response compared to control

conditions. When a negative number indicated a success (i.e. a lower average abundance of lice on treatment fish compared to a control), the sign was inverted.

Results

Our search discovered 39 relevant studies that investigated some aspect of fish behaviour applied for the purpose of improving commercial aquaculture production processes or fish welfare between 1993 and 2020. 12 of these studies had a true control and were included in **Table 1**, as effect sizes for these studies could be calculated.

1. Innate behaviours of fish

1.1 Use of innate behaviours for fisheries or conservation purposes

Evolving attraction or avoidance responses to abiotic environmental conditions and stimuli allow fish to react appropriately to their environment. Humans have exploited behavioural responses in wild fish for decades to locate and capture fisheries species (Bardach 1980). For example, fishers routinely use the fact that tuna aggregate in large numbers in the waters surrounding natural floating objects, such as logs, in the mid ocean as part of strategies to locate and fish them (Dempster & Taquet 2004). This has resulted in tens of thousands of artificial floating objects (fish aggregation devices; FADS) deployed worldwide each year (Dagorn *et al.* 2013). Fish behavioural patterns are also used to boost conservation outcomes. Orientation towards flow and the inclination to dive when stressed is exploited to promote self-grading and reduce mortality in fish bypass systems for juvenile salmonids (Gessel *et al.* 1985). Other innate behaviours, such as inherent avoidance responses to various stimuli (e.g. electrical, acoustic, chemical stimuli) are used at water inlets of power plants to reduce wild fish mortality with varying levels of success (Ross *et al.* 1993; Maes *et al.* 2004; Sonny *et al.* 2006; Noatch & Suski 2012). Behaviour is also a component of pest management strategies in wild ecosystems. Specialised traps that harness the jumping and pushing behaviour of European carp (*Cyprinus carpio*) effectively remove this species from wetlands where it is invasive (Stuart *et al.* 2006; Thwaites *et al.* 2010; Conallin *et al.* 2016).

1.2 Harnessing innate behaviours in aquaculture

The potential benefits and constraints of using fish behaviour in farm settings differ markedly from the wild. In aquaculture, behavioural patterns are expressed in confinement and differ to those behaviours expressed by wild conspecifics. Much of the research surrounding the use of fish behaviour in farm settings involves manipulating fish behaviour through innate

behavioural responses to relevant stimuli. Below we outline examples from the literature that explore the use of fish behaviour to expedite farm operations.

Inducing voluntary movement of fish to different locations within a farm site has been investigated in several studies. Allowing fish to move themselves reduces stress for fish and decreases labour. A behavioural response to an aversive stimuli through the carbon dioxide avoidance response in rainbow trout (*Oncorhynchus mykiss*) has been used to move fish from an on-growing tank to a harvest tank with success (Clingerman *et al.* 2007; Summerfelt *et al.* 2009). Positive phototaxis (Lekang & Fjæra 1995) and orientation toward flow in Atlantic salmon (*Salmo salar*) (Lekang *et al.* 1996) have been explored as mechanisms to encourage self-transport between land-based tanks in a similar manner. Positive phototaxis is also a known mechanism to rapidly alter the swimming depths of Atlantic salmon in sea cages as they follow lights moved vertically in the water column over the scale of minutes (Wright *et al.* 2015).

Inducing voluntary grading reduces stress and injury to fish during hand or mechanical grading (Conte 2004). This was demonstrated in farmed turbot (*Scophthalmus maximus*) by using innate attraction to light, colour and food stimulus to attract turbot through a stationary grading apparatus (Bögner *et al.* 2017) and in larval pikeperch (*Sander lucioperca*) to reduce cannibalistic behaviour (Tielmann *et al.* 2016). Preventing self-inflicted injury and harmful behaviour is important in certain species of farmed fish. Natural colour preferences deter farmed striped trumpeter (*Latris lineata*) larvae from ‘walling’ behaviour (swimming into tank walls) that causes jaw deformities. Cobcroft and Battaglene (2009) found 25-44% more fish walled in coloured rearing tanks (blue, green, red), with only 3.4% of fish walling in tanks with a marbled pattern.

Parasite prevention is another area where utilising farmed fish behaviour has been explored. Infestations of ectoparasitic salmon lice (*Lepeophtheirus salmonis*) on farmed salmon are a major threat to sustainability of the industry (Taranger *et al.* 2014). Salmon lice negatively affect farmed salmon health and welfare (Wagner *et al.* 2008) and have detrimental ecological impacts for wild salmonid populations (Thorstad *et al.* 2012). Salmon behaviour has been explored as an alternative strategy to prevent and control lice infestations. Salmon are inherently attracted to light and feed (Oppedal *et al.* 2007; Oppedal *et al.* 2011; Stien *et al.* 2014). Deep lights and deep feeding stations deployed in sea-cages modify the swimming depth of salmon, and reduce physical interactions between farmed salmon and infective lice, that are

most abundant at the surface (Bui *et al.* 2013; Frenzl *et al.* 2014; Bui *et al.* 2020). Salmon have an open swim bladder and require surface access to refill their swim bladder and regulate buoyancy (Macaulay *et al.* 2020b). This innate surfacing behaviour has also been explored as a mechanism for lice control. By encouraging salmon to increase the frequency of jumping via forced submergence and different stimuli, salmon could effectively treat themselves, via jumping through an oil-based delousing chemotherapeutant placed at the surface of the sea-cage (Dempster *et al.* 2011; Dempster *et al.* 2019). These studies demonstrate proof-of-concept, showing the possibilities of how fish behaviour could be used, yet whether they have been adopted by industry remains unclear. Deep lights and deep feeding stations to improve lice control are used in some commercial salmon sea-cages, but the use and efficacy of this behavioural application is poorly documented (Barrett *et al.* *in press*).

1.3 Challenges to applying innate behaviours at fish farms

The idea of using fish behaviour is not new, yet few ideas have been widely implemented in commercial aquaculture. In the studies reviewed, there was substantial variation in the effect of exploiting the innate responses of fish (**Table 1**), indicating that success in implementing a behavioural method was highly context dependent. Scaling-up from small-scale experimental testing to large-scale applications of fish behaviour in commercial sized operations is challenging. Some infrastructure required to elicit desired responses (e.g. lights, grids, coloured surfaces) could be relatively cost-effective to implement and are scalable. However, commercial stocking densities will likely affect the expression of innate responses and behavioural patterns, and farm environments provide difficult settings to ensure that all individuals perform a desired behaviour or respond to the stimulus in the same way. Methods to control fish using their innate behavioural responses to different stimuli (e.g. attraction to light, avoidance of CO₂) and natural behavioural patterns can either be effective or provide no real effect at all (**Table 1**). For example, Lekang and Fjæra (1995) induced voluntary transport through positive phototaxis, with 74% of fish the highest percentage of voluntary movement when there was no light in the occupied tank and the transfer pipe was lit with 15 lux light intensity for 30 min. As fish behaviour is complex, it is improbable that any method to passively control fish that relies solely on attraction or avoidance responses would work seamlessly. Further, it is impossible to anticipate the interactive effect of all stimuli present in a commercial environment on how fish respond. Along with variation in responses, different aquaculture environments present unique challenges for implementing responses to stimuli.

1.3.1 Stimuli in different farm environments

Hatcheries, land-based tanks, semi-natural ponds and on-growing sea cages all vary in the level of control the farmer has over the environmental conditions that influence fish behaviour. Using behavioural responses of fish might be a more viable option in production settings where the farmer has a higher level of control over environmental conditions, such as in indoor tanks or hatcheries. For example, Herbert *et al.* (2011) investigated using light rings to induce an optomotor response in Atlantic salmon smolts as a tool to induce sustained swimming at optimal speeds to improve productivity. While these light-rings did optimise swimming speeds in a tank environment, this technology was never used commercially, due to the logistical constraints of deploying light rings in sea-cages. Environmental conditions and exposure to disease, parasites and pollutants are largely out of human control in extensive outdoor production systems. In these systems, attraction to a stimulus might be overridden by preference seeking. For example, sea-caged salmon seek out optimal temperature over optimal light conditions (Oppedal *et al.* 2011). This makes manipulating behaviour with environmental stimulus difficult in such production environments. Also, variable management procedures may be needed at different times of day and season including more active management on some occasions (forcing fish to swim deep) compared to passive (attract fish to swim deep) at others.

1.3.2 Variation in responses

Not all individuals will be motivated by the relevant stimulus. For instance, sea-cage salmon do not engage in feeding every time feed enters a cage (Juell & Westerberg 1993). If a fish is not motivated by a certain stimulus, an attraction technique based on that stimulus will not function. Additionally, with the increasing trend for mariculture to use larger cages (Oldham *et al.* 2018) and to be located in ever more exposed locations, environmental manipulation to induce behavioural responses may prove more difficult in the future (Klinger *et al.* 2017).

Natural behaviours of different species and the way they approach or respond to a stimulus is directly affected by differences in natural history and life stage. For example, anticipatory behaviour in post-smolt Atlantic salmon to a conditioned stimulus involves crowding the food delivery area (Bratland *et al.* 2010; Folkedal *et al.* 2012a), while salmon parr situate themselves further away from the conditioned stimulus (Folkedal *et al.* 2012b). This reflects the change in foraging activity with life stage, as parr are stationary predators that wait for food and post-smolts are cruising predators (Folkedal *et al.* 2012b). While there are definite challenges to

exploiting behavioural responses in fish, some methods could be incorporated into a framework of fish management as an additional tool in modern aquaculture.

1.4 Incorporating innate behaviours into current practices

Though using innate responses to relevant stimuli is an imperfect tool, these methods could be used in conjunction with current practices. For example, the ‘deep lights and deep feeding’ technique is currently being trialled in Norway as a method to reduce lice loads on farmed salmon (Frenzl *et al.* 2014). By attracting salmon with light positioned deep in the water column and feeding salmon underwater, this deters salmon from swimming in the lice-infested surface waters (Bui *et al.* 2020). When the lights or feed fail to attract salmon, other more traditional lice control measures could be applied. Similarly, with voluntary transport or grading, if the best rate of voluntary movement is 80% using attractive stimuli, then automated or hand-grading could then be used to complete the practice (Fig. 1).

Another example of lice-preventative technology that requires an understanding of salmon behaviour is the ‘snorkel’ cage. Snorkel cages have a deep net roof, forcing salmon to swim deep and reduce contact with lice, but also have a tube impermeable to lice leading the surface (Stien *et al.* 2016; Oppedal *et al.* 2017; Wright *et al.* 2017; Geitung *et al.* 2019). This tube or snorkel was designed to permit salmon to swim to the surface, without encountering lice, and express their natural surfacing behaviour, so they can gulp air and regulate their buoyancy. Snorkel cages are now being trialled commercially (AKVA, 2020) and demonstrate how knowledge of farmed fish behaviour can be catered to and secure fish welfare in new farming environments.

An emerging technology, known as ‘iFarm’, is an individualised fish farm concept that exploits the innate surfacing behaviour of salmon to control lice (Cermaq, 2020). Individual salmon that are surfacing to refill their swim bladder are guided through a narrow funnel and photographed. Then, in future, each individual fish can be scored for weight, welfare, lice levels and potentially be sorted, depending on their condition. However, if fish are unwilling to enter the narrow pipe, then this concept will not be commercially applicable. Pilot trials that have been developing the cage construction based on salmon behaviour, to ensure the fish voluntarily enter and exit the sorting mechanism, have had promising results (pers comm. Jonatan Nilsson, IMR). These more complex rearing environments rely on the capacity fish have for being behaviourally adaptable and coping with environmental change. Improving behavioural plasticity by using the ability of fish to learn is another way to exploit fish

behaviour, however, this requires more time and effort for producers than simply using innate behaviours.

2. Harnessing fish cognition in aquaculture: training fish to improve their welfare

While behavioural adaptation, by means of acclimation and conditioning, improves welfare in zoos and terrestrial animal agriculture, it has not gained traction in aquaculture (Bui *et al.* 2019). Classical or Pavlovian conditioning happens when a biologically relevant stimulus (unconditioned stimulus) overlaps with a formerly neutral stimulus (conditioned stimulus), forming an association between the two stimuli that can be rewarding (reward or positive conditioning), or aversive (fear conditioning) (Fernö *et al.* 2006). Habituation is thought to be a natural process, where fish become accustomed to a stimulus through repeated exposure which decreases its stress response to that stimulus over time (Lieberman 1990). Unplanned fear conditioning is commonplace in fish farms. Sudden movements or loud noises from machinery or farm workers can cause reflexive stress responses in fish (Conte 2004), which can decrease feed intake. Although these disturbances are rarely harmful to the fish, they are instinctively stressful. This is especially true for farmed fish as they do not have the freedom to move away from the stressor as they would in the wild (Bratland *et al.* 2010). Experimental scale studies have suggested that by using conditioning or habituation the innate stress response caused by disturbances at fish farms can be reduced (Madaró *et al.* 2015). Sudden light is a typical stressful event for salmon parr in tanks, and a normal management practice is to change from the 24 h lighting phase from start feeding to a 12 h light: dark cycle, initiating the smoltification process. Part of this stressful event is habituated away within a week of daily exposures (Folkedal *et al.* 2010).

Farmed fish can be habituated to aversive events through positive conditioning. Schreck *et al.* (1995) observed an increased resistance to pathogens, reduced mortality during transport and decreased physiological response to other stressors in juvenile Chinook salmon (*Oncorhynchus tshawytscha*) that underwent a positive conditioning regime to associate dewatering for transport with feeding. Both Atlantic salmon and gilthead sea bream (*Sparus aurata*) went from being frightened by an initially aversive stimulus (flashing lights) to exhibiting anticipatory behaviour toward the same stimulus after undergoing positive conditioning and habituation (Bratland *et al.* 2010; Folkedal *et al.* 2018). Reward conditioning has been used to successfully reduce the stress response of Atlantic cod (*Gadus morhua*) to the moving of a dip net in the water (Nilsson *et al.* 2012).

Habituation or acclimatisation has also been explored as a mechanism to improve parasite eating behaviour by cleaner fish, in salmon aquaculture. Lumpfish (*Cyclopterus lumpus* L.) are a type of cleaner fish used commercially for grazing ectoparasitic lice off farmed Atlantic salmon in sea-cages (Powell *et al.* 2018). Before sea-transfer, lumpfish are fed on standard pelleted feed, with no prior experience of foraging on lice on salmon. In a recent study by Imsland *et al.* (2019), lumpfish were habituated to frozen salmon lice as feed in tanks. After transfer to experimental scale sea cages with salmon, the salmon that were placed with the lice-habituated lumpfish had 23% less lice than salmon placed with lumpfish that were reared with standard feed pellets. Ballan wrasse (*Labrus bergylta*), another species used as cleaner fish in salmon sea-cages, that were acclimatised to lice-infested salmon in sea cages ate more lice on salmon than wrasse that had no prior encounters with lice-infested salmon (Gentry *et al.* 2018).

2.2 Challenges to training fish in aquaculture

2.2.1 Farm environment

The predictable nature of exposure to aversive stimuli in experimental scale studies may have enhanced the rate of habituation and conditioning to a stimulus. In a realistic farm situation, exposure to disturbances would likely be spatially and temporally unpredictable, which may affect the success of and speed at which habituation or conditioning would occur (Nilsson *et al.* 2012). Furthermore, implementing procedures to condition or habituate the large amounts of individual fish held in commercial stocking densities is another area of uncertainty. The number of individuals used in the conditioning studies reviewed was typically low, and more studies on how large groups of fish can be taught a new behaviour are required. However, there are studies on habituation or acclimation that were conducted at higher densities and have demonstrated that these kinds of regimes to encourage behavioural plasticity at a larger scale are possible (Gentry *et al.* 2018; Macaulay *et al.* 2020a).

2.2.2 Incomplete habituation

Another unknown is whether habituation is ever total, or if the stress response in fish is reduced but not totally extinguished (Christoffersen 1997). Bratland *et al.* (2010) found that during days 4-6 of an experiment on conditioning salmon to flashing lights, salmon swam away from conditioned stimulus (light flashes), but then returned to the feeding area prior to the delivery of food. This shows the dichotomy of habituation and conditioning, as during this period fright and anticipation occurred simultaneously. The consequence of concurrent stress and eagerness

responses for fish welfare is unknown. Methods to encourage behavioural adaptation may be logistically challenging, as training regimes will likely disrupt or alter the production cycle.

2.2.3. Timing of training

Several studies highlight the importance of early experiences on forming individual behavioural patterns (Jones & Waddington 1992; Timmermans *et al.* 1994; Braithwaite & Salvanes 2005; Salvanes *et al.* 2007). Neurogenesis, the process involved in neuronal proliferation and acquiring new information and associated with flexibility and memory forming is more active in younger individuals of many species (Tello-Ramos *et al.* 2019). Age at which the fish undergo conditioning or habituation is therefore likely important. Conditioning a behaviour early in the production environment may enhance the retention of the target behaviour. Little research has been done on whether older fish are capable of learning and retaining a learned behaviour. Regardless, it seems logical to teach fish when they are younger because then they can take these life-skills with them throughout the production cycle.

How a behaviour that was learned in a hatchery or juvenile growing tank would translate to an on-growing environment is another area of uncertainty. Macaulay *et al.* (2020a) found that salmon, with previous experience of surface-based air domes in freshwater tanks, refilled their swim bladders at a submerged dome at sea more frequently than salmon that were reared in plain tanks. Similarly, the lumpfish that Imsland *et al.* (2019) acclimated to frozen lice as feed in tanks were more effective lice grazers after sea transfer. Both studies demonstrate that a behaviour learned early in life was transferred to a substantially different culture environment.

2.2.4. Implementing environmental enrichment

Some studies demonstrate that enrichment in the early rearing environment causes fish to be more behaviourally flexible and quicker to learn tasks compared to fish reared in plain environments (Braithwaite & Salvanes 2005; Strand *et al.* 2010; Salvanes *et al.* 2013). However, implementing structural enrichment in hatcheries comes with drawbacks. Incorporating structures into rearing environments makes these environments much more difficult to clean compared to a plain environment. Installing structures for enrichment can lead to a build-up of faecal matter or food waste, and they may also harbor pathogens (Tuckey & Smith 2001). Unsuitable enrichment can result in injury, stress, disturbances and increased aggression, therefore degrading fish welfare (review of effects of enrichment on captive fish Näslund and Johnsson (2016)).

2.3 Incorporating training into current practices

Incorporating learning into aquaculture practices may require increased effort compared to utilising innate behaviours already evolved by the fish. Our review of studies revealed that habituation or conditioning typically had only small to moderate effects (**Table 1**). However, habituation and conditioning to encourage learning could be used in various ways in aquaculture to develop new desirable behaviours in fish that improve welfare. These include familiarisation with new farm technologies (Macaulay *et al.* 2020a), and improving parasite control by acclimating cleaner-fish to lice as food (Gentry *et al.* 2018; Imsland *et al.* 2019;). Certain positive conditioning regimes could be relatively easy to establish to improve welfare by conditioning fish to aversive elements of the farm environment. For example, Bratland *et al.* (2010) suggested a positive reward to condition farmed fish to human presence with motion sensors that trigger automatic feeders when they detect human activity. A similar approach could be used for lowering water levels or presence of machinery.

Another example could be to acclimate fish to an oncoming stressor such as transport or vaccination. Repeatedly exposing fish to dip nets and lowered water levels in tanks could reduce their initial stress response. Evidence suggests that exposing farmed fish to mild stress can improve their capacity to cope with challenges in the future (Vindas *et al.* 2016; Vindas *et al.* 2018). Madaro *et al.* (2015) subjected Atlantic salmon parr to an ‘unpredictable chronic stressor (UCS) paradigm’ where fish were exposed to random stressors such as tank emptying, noise, brief hypoxia, temperature changes, chasing, lowering the water level and netting, three times a day for 3 weeks. UCS fish had a lower cortisol response when exposed to a novel stressor after the trial period compared to a control group. However, at the end of the trial, control fish had grown by 41% on average, compared to 8.5% growth for the chronically stressed fish, coinciding with stressed fish having a decreased appetite. This indicates that ‘stress training’ is beneficial for the future welfare of fish but could be costly while the fish are undergoing training. Younger fish may become more resilient to stress, as early life experiences can form lasting behavioural patterns (Chapman *et al.* 2010). Therefore, it may be useful to implement ‘training’ programs in the hatchery with the aim of preparing farmed fish for the frequent disturbances that occur over a production cycle. Though fish can learn new behaviours through human-mediated regimes, they can also learn from each other.

3. Using social learning in aquaculture: can farmed fish teach each other?

Social learning occurs in a wide range of taxa and fish are no exception (see review of social learning in fish by Brown and Laland (2003)). Applying this aspect of fish behaviour, effectively ‘life-skills training’, could improve the post-release survival of hatchery reared fish for restocking programs (Suboski & Templeton 1989; Brown & Laland 2001). Social learning principles rely on developing transmission-chains, where inexperienced animals learn a behaviour from a trained demonstrator, then become the demonstrators to the next group of naïve individuals, and so on until a behavioural tradition is established (Laland & Williams 1997, 1998). This could permit the swift conditioning of all fish within a production unit, with only pre-training of a few individuals necessary (Brown & Laland 2001). Several studies have shown that anti-predator behaviour (Brown & Laland 2002b; Vilhunen *et al.* 2005) and foraging skills (Brown & Laland 2002a; Reader *et al.* 2003) can be taught from experienced fish to naïve fish via social learning in captivity. For example, the rate and amount of consumption of novel prey items was greater in wild trout that were in visual and olfactory contact with conspecifics compared to wild trout held in isolation (Sundström & Johnsson 2001). Using social learning as a tool in aquaculture for human consumption is a concept that has received very little attention. The handful of studies that have explored this idea have mainly focused on using interspecific ‘teacher’ fish to promote positive feeding habits in ‘student’ fish.

Proficient self-feeder actuators such as rainbow trout have been taught to be demonstrator fish to encourage other fish that are not efficient self-actuators such as amago (*Oncorhynchus masou masou*) (Flood *et al.* 2010) and white-spotted char (*Salvelinus leucomaenis*) (Noble *et al.* 2012). These studies had limited success. Some species (e.g. pikeperch *Sander lucioperca* and Eurasian perch *Perca fluviatilis*) reluctantly transition to a diet of pellets in the grow-out phase from fry to fingerlings as they are accustomed to receiving live prey. For these species, weaning is a key bottleneck in production (Policar *et al.* 2013). Brown trout (*Salmo trutta*) have been paired with Eurasian perch to facilitate perch fingerlings to accept pelleted feed (Härkönen *et al.* 2017), yet social transfer of feeding skills was unsuccessful. Similarly, demonstrator pikeperch and Eurasian perch paired with naïve pikeperch failed to facilitate the naïve pikeperch’s acceptance of pelleted feed (Horváth *et al.* 2013). However, Lepič *et al.* (2017) demonstrated that growth and rate of acceptance of pelleted feed in pikeperch fingerlings was greater in fingerlings that were paired with Vimba bream (*Vimba vimba*) tutors compared to fingerlings grown in monoculture. Most of these studies used one species as teacher fish and a different species as student fish. The actions of one species may be less

relevant to another species, which may explain the low rate of success in these studies. In addition, rearing fish in duo-culture to facilitate social learning comes with added biosecurity and logistical issues.

3.1 Challenges for using social learning in aquaculture

At present, the limited amount of studies that have explored using social learning in aquaculture have had little success (**Table 1**). Several factors may prevent the effectiveness of using social learning principles. Prior to applying social learning concepts, the fundamental mechanisms behind information transfer between demonstrator and observer individuals and the factors influencing this transmission must be understood. Capacity for social learning and to what extent socially acquired information is used should first be determined for the species being cultured (Brown & Laland 2001). Social cues can still stimulate learning in non-social species of fish (Webster & Laland 2017; Vila Pouca *et al.* 2020). The ‘costly information hypothesis’ proposes there is an evolutionary trade-off between dependable and expensive self-acquired information (through trial and error) and less dependable but cheap socially attained information (Chapman *et al.* 2008). Farmed fish may be less socially motivated due to the predictable and repetitive nature of aquaculture environments (Sundström & Johnsson 2001). Conversely, this type of environment may encourage exploratory behaviour (Sundström *et al.* 2004; Wechsler & Lea 2007). How the predictable nature of the aquaculture environment influences a fish’s decision to use socially acquired information requires further research. Furthermore, density effects on social transmission are likely important.

Commercial rearing densities of fish may impede social transmission of information (Berejikian *et al.* 2000). Guppies raised at low densities are more proficient at learning socially about foraging than those reared at higher densities (Chapman *et al.* 2008). Crowded conditions in production environments may reduce the ability of one individual to track another individual’s behaviour (Sundström & Johnsson 2001). Finding the right ratio of teacher: student is also essential for establishing a successful transmission chain and this will likely be species-specific. Too many knowledgeable demonstrators might impede learning (Vilhunen *et al.* 2005), while too few may not stimulate learning. Quality of the ‘demonstration’ is also important, as demonstrators that are too efficient may mean they carry out a behaviour too quickly for student fish to follow (Swaney *et al.* 2001). Social learning is clearly complex. Further research is necessary for social learning to be incorporated into aquaculture management.

4. Future research

To increase the likelihood of fish behaviour being applied in industrial aquaculture, further testing is required to validate methods at commercial scale. Behavioural observation of fish is difficult at commercial scale, yet monitoring behaviour is essential to understand why an animal is behaving the way it is. Building comprehensive knowledge of the behaviour and biology of the fish species being farmed is essential to successfully use behavioural responses. What stimulus elicits the desired response? How long before a stimulus does not induce the response or becomes ignored by the fish? Will fish become habituated to the stimulus, no longer respond, and therefore render a method of fish control obsolete? Under what conditions do fish no longer perceive or respond to a stimulus? These important questions must be explored before methods that use stimuli to manipulate fish (e.g. attraction to light to induce movement) could be feasible on large-scale fish farms and should be a priority in future research.

More large-scale studies with adequate replication are required to observe how behavioural principles operate in a commercial environment with industrially relevant stocking densities. An example that highlights the importance of validating methods in a commercial setting is Foss *et al.* (2020), where blue lights were placed inside fish traps to lure and recapture lumpfish in salmon sea-cages. Reusing lumpfish is essential if the cleaner-fish industry is to improve its sustainability, yet recapturing lumpfish in a commercial sea-cage is a laborious and challenging task. In a small-scale tank study, blue light traps effectively attracted and caught lumpfish. However, when a prototype was deployed in a sea-cage, the traps had very low capture rate (Foss *et al.* 2020). This example demonstrates how a clear mismatch between small-scale tank studies and commercial realities can arise. Similarly, substantiating welfare improvement tools that rely on fish cognition, such as acclimation and social learning, requires more research at commercially relevant scale. Additional factors that could affect the success of a conditioning or habituation regime include; individual animal personality, commercial stocking densities, ontogenetic shifts in learning capacity (Takahashi *et al.* 2010), gender (Lucon-Xiccato & Bisazza 2014) and strong preferences (Roy *et al.* 2019). Investigating these aspects should form the basis for future research in commercial settings into using fish cognition.

5. Conclusion

Currently, many of the animal husbandry practices required to complete a standard production cycle in aquaculture are stressful for fish and can be laborious and costly for producers. Future

production of finfish is set to continue to grow, with a trend toward intensification, technological advancement, and diversification in the types of species being produced. As the industry expands, improving fish welfare and optimising production will only become more important; new approaches to fish husbandry are required for this to be achieved. There is potential for practical application of fish behaviour to create low-stress methods for fish husbandry that improve farm operations and fish welfare. Encouraging behavioural plasticity and providing learning opportunities can increase the coping capacity of farmed fish to environmental disturbances. However, there are also obvious challenges involved in the use of behaviour over a production cycle. These challenges are species-specific, environmental, scale-related, and logistical in nature. Future research should focus on how learned and inherent behaviours are expressed over time in commercial environments and how they vary with stocking density. Although fish behaviour is complex, it is an additional resource that could be integrated into aquaculture management and pave the way for new approaches to fish husbandry.

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Figure Captions

Figure 1 – An example of how behaviour could be incorporated into production management in the routine farm practice of size grading.

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Table 1 - Characteristics of peer-reviewed studies identified through our literature search demonstrating how fish behaviour could be applied to industrial aquaculture. Data include: a short summary of how behaviour was used in the study, species studied, number of fish per unit replicate, stocking density, average fish size, volume of unit replicate (tank or cage), number of unit replicates (tank or cages), explanation of observed responses that measured the effect of behavioural application, associated controls, effect size (natural log: lnRR), the suggested benefit of the behavioural application and the environment that each study was conducted in. Effect size gives a measure of how well the behavioural treatment worked relative to controls (a higher lnRR value means a greater difference between treatment and control). Effect sizes were calculated for responses that directly measured the success of the application of behaviour. For example, if the main purpose of the study was to reduce lice loads, then the effect size for the response that measured this (e.g. mean no. of lice) was calculated. Multiple effect sizes were calculated for several studies that tested several responses that measured the success of the behavioural application (e.g. R1, R2, R3). See supplementary material 1 for further information on the multiple responses observed.

Study	Summary	Species	No. fish per replicate	Density (kg/m ³)	Mean fish size (kg)	Volume (m ³)	No. replicates	Observed response	Control	Effect size (lnRR)	Suggested benefit	Environment
Clingerman <i>et al.</i> (2007)	Voluntary transfer between tanks induced by CO ₂ avoidance response	<i>Oncorhynchus mykiss</i>	507 – 2,993	40–60	0.2 - 1.3	11	3	Mean % of fish moved after 2 hours with different speeds of levelling off CO ₂	No CO ₂ for 2 hours	R1: 3.14 R2: 3.61 R3: 3.76 R4: 3.99	Reduce labour and stress in fish	Indoor tanks with connecting pipe system
Lekang and Fjæra (1995)	Voluntary transfer between tanks induced by attraction to light	<i>Salmo salar</i>	75	18	1.8	7.5	3	Mean % of fish moved after 30 min with different lux over canal and tank	15 lux over tank and 15 lux over transfer canal after 30 min	R1: 1.01 R2: 0.32 R3: 0.00 R4: -0.52 R5: -0.57	Reduce labour and stress in fish	Indoor tanks with connecting pipe system

										R6: -0.48		
Bögner <i>et al.</i> (2017)	Voluntary size grading induced by colour, light, food stimuli	<i>Scophthalmus maximus</i>	60	0.63 – 1.14	Gradable: 0.315 Non-gradable: 0.571	30	3	Daily mean grading success (%) with colour, light, feed and combintaions of all (day 6)	No stimulus (day 6)	R1: -0.17 R2: -0.08 R3: 0.38 R4: 0.37 R5: 0.66	Improve welfare, reduce fish stress, injury cannibalism	Indoor tanks
Frenzl <i>et al.</i> (2014)	Parasite control using attraction to deep lights and deep feeding	<i>Salmo salar</i>	45,078	15.6	4.4 at end of trial	12739	2	Mean juvenile sea louse abundance per fish	Surface lights, surface feeding	R1: 1.17 R2: 0.80	Reduce lice loads	Sea-cages
Bui <i>et al.</i> (2013)	Parasite control by encouraging salmon's jumping behaviour	<i>Salmo salar</i>	10	0.01	0.333	272	5	Mean % of fish that jumped after surface access reinstated	Surface access denied through submergence of the cage	R1: 0.49 R2: 0.52 R3: 0.34	Reduce lice loads	Sea-cages
Schreck <i>et al.</i> (1995)	Acclimation to transport – random stress conditioning and positive reward conditioing to dewatering stress	<i>Oncorhynchus tshawytscha</i>	79-89	5.5 – 6.2	0.028	0.4	2	Cortisol blood level (ng/mL) 2, 4, 12, 26, 122 hrs after transport	No conditioning	R1: 0.82 R2: 1.13 R3: 0.10 R4: 0.19 R5: 0.66 R6: 0.45 R7: 3.22 R8: 2.37	Increase survival during transport, reduce stress post transfer	Indoor tanks

										R9: 0.68 R10: 1.26		
Härkönen <i>et al.</i> (2017)	Habituating perch to tank culture conditions during cold-water seasons	<i>Perca fluviatilis</i>	100	-	110 mm	-	2	Survival (%)	No habituation to tank conditions	R1: 0.58	Increase survival	Hatchery
Imslund <i>et al.</i> (2019)	Acclimating lumpfish to frozen lice as juveniles before sea-cage transfer	<i>Cyclopterus lumpus</i> , <i>Salmo salar</i>	30 lumpfish 300 salmon	1.63	0.118 lumpfish 0.668 salmon	125	2	Av. no. of all stages of <i>L. salmonis</i> per fish counted on day; 19, 34, 49, 62 of the trial (30 salmon lice counted very two weeks)	Lumpfish fed on standard marine pellets as juveniles	R1: 0.60 R2: 0.81 R3: -0.53 R4: 0.97 R5: 0.63	Improve lice grazing in lumpfish to reduce lice loads	Hatchery
Macaulay <i>et al.</i> (2020a)	Acclimating salmon to air domes to pre-emptively modify swim bladder refilling behaviour	<i>Salmo salar</i>	1000	0.7	0.118	175	3	No. individual tags registered at the dome, no. of refills, mean relative echo strength	No habituation to domes	R1: 0.92 R2: 1.21 R3: 0.21	Habituate salmon to new cage technologies before cage deployment	Indoor tanks, sea-cages

Lepič <i>et al.</i> (2017)	Adapting early life stages of pikeperch to pelleted feed using social learning with teacher bream	Teacher: <i>Vimba vimba</i> Student: <i>Sander lucioperca</i>	Control: 3600 pikeperch Treatment: 3600 pikeperch + 720 bream	Control 1.69 Treatment 2.39	Pikeperch: 0.0004 Bream: 0.0008	0.8	3	Pikeperch specific growth rate (SGR) % per day	Direct application of pellet feed only (no social learning)	R1: 0.17 R2: -0.06	Increase rate of acceptance of pelleted feed	Hatchery
Noble <i>et al.</i> (2012)	Teach char how to use self-actuator feeder using social learning with proficient self-feeder teacher trout	Teacher: <i>Oncorhynchus mykiss</i> Student: <i>Salvelinus leucomaenis</i>	Control: 15 naïve char Treatment: 14 char + 1 trout	Control 2.6 Treatment 3.5	Control Naïve char: 0.035 Treatment char: 0.037 Trout: 0.169	0.2	4	Actuations per hour	Naïve charr only	R1: 0.47	Improve self-actuator use to reduce feed waste	Indoor tanks / Hatchery
Vindas <i>et al.</i> (2016)	Early life unpredictable chronic stress (UCS) regime to improve coping capacity to stressors later in life	<i>Salmo salar</i>	124 – 111 per tank	17.5 - 19.5	0.063	0.4	3	Specific Growth Rate (SGR) Sampling 2. after smoltification Sampling 3. after sea transfer	No stress	R1: 0.4 R2: 0.12	Improve coping capacity later in life in aquaculture environment	Indoor tanks / Hatchery

Figure 1

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