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REVIEWS IN Aquaculture

REVIEW

Environmental enrichment in fish aquaculture: A review of fundamental and practical aspects

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Abstract

Environmental enrichment (EE) can improve the welfare of captive fish. Its objective is to provide new sensorial and motor stimulation in order to help meet their behavioural, physiological, morphological and psychological needs, whilst reducing stress and frequency of abnormal behaviours. In fish farms, rearing environments are usually designed from a human perspective and based on economic requirements, mainly for practical reasons for the farmer, with little consideration for animal welfare. Throughout aquaculture production cycles, many farming operations can be stressful for fish, and EE may not only help them cope with these stressful events but also improve their overall welfare. In recent years, increasing interest on the effects of EE in captive fish has focussed mainly on structural enrichment. However, there are many other enrichment strategies that merit attention (e.g. sensorial, occupational, social and dietary enrichment) and which may be of interest for fish farming. Here, we review in depth the existing literature on EE and its effects on the welfare of a wide range of farmed fish species, discussing the feasibility and potential applications of different EE strategies to promote fish welfare at a commercial scale. We also present a practical framework to address the design, validation and implementation of EE by the aquaculture industry, taking in consideration the technical challenges of providing enrichment for farmed fish.

KEYWORDS
aquaculture, environmental enrichment, fish welfare, management, positive stimulus, stress response

1 | INTRODUCTION

The aquaculture industry has been growing globally over the past few years due to the increasing demand of protein consumption by human population worldwide, and fish are the most farmed animals in this animal production system. Under farm conditions, the environments where fish are kept have been frequently arranged based just on economic and ergonomic requirements, thereby neglecting considerations related to fish welfare. Moreover, it is evident that, whilst fish farming is of fundamental importance for the animal production system on a worldwide scale, these animals are commonly exposed to poor and unfavourable conditions under farm systems that can severely impair their welfare state and the quality of the final product for the farmers. Several farm procedures, including fish handling processes, pre-slaughter and slaughter, may also evoke a strong stress response in fish,[1] with an important negative effect both on fish welfare and on the quality of fish flesh.[2,3] This is worsened by the low level of domestication of many widely-farmed fish species,[4] as such species can be more severely affected in captivity.[5] On the other hand, there is an increasing awareness amongst the public (and thus amongst the potential consumers), about the importance of taking the welfare conditions of fish into account.[6] A recent survey within the European Union showed that consumers are becoming more demanding in relation to the conditions in which fish are farmed.[7] This, coupled with the idea that better welfare conditions also help to improve the product quality and potentially the profitability, opens the door to the use of environmental enrichment (EE) techniques to improve the quality of life for fish in farms by giving them the opportunity to experience positive aspects in their environment.[8] In this sense, EE in aquaculture can be understood as providing new environmental stimuli (motor or sensor stimulation) to help captive fish to meet with their physiological, behavioural and psychological needs. This EE definition encompasses the three main aspects defining animal welfare in terms of proper biological functioning: functional, natural and feeling-based.[9] In fact, the Council of Europe Directive 98/58/EC of 20 July 1998, concerning the protection of animals kept for farming purposes (which includes fish), states that the biological characteristics and different species-specific needs of the fishes should be taken into account in husbandry practices, especially “with respect to the requirements for water conditions, social behaviour and environmental structures”.[10] In order to avoid detrimental effects on fish welfare, it is important to consider how biological characteristics interact with farming systems using both scientific and practical knowledge, and how EE can be successfully applied in fish culture conditions.

The benefits of using EE on land-farm animal welfare and productivity have been widely demonstrated,[11] but the EE needs of aquatic farmed animals have been largely overlooked.[6] The neglect of aquatic EE is mostly due to the debate on whether fish are sentient and capable of suffering (which now is clear),[12-15] as well as to the difficulty of observing aquatic animal behaviour in farming settings. In addition to this, there is the specificity of EE needs in the wide range of farmed aquatic species, which comprise very diverse taxonomic groups,[16] contrary to land-farmed animals. At this point, it is relevant to consider that giving positive stimuli to fish, which can elicit some positive feelings, is as important as the need to prevent or minimise fish suffering under captive conditions. Accordingly, the reformulated proposal of the ‘five domains’—nutrition, environment, health, behaviour and affective experiences—which should be considered to properly evaluate the welfare state of an animal,[17] also addresses the positive aspects of welfare instead of focussing just on the negative ones. For example, when considering the behaviour domain, not only the restrictions of behavioural expressions should be taken into account, but also if the animal has the possibility to express rewarding behaviours (e.g. environment-focussed exploration, food acquisition activities, animal-to-animal interactive activities), all of which can generate various forms of comfort, pleasure, interest, confidence and a sense of control.[18] The same should be regarded for all the other welfare domains. This is also in agreement with the concept of quality of life, which addresses the overall balance between negative and positive experiences at a particular period of the animal's life.[19] Thus, a ‘life worth living’ (as proposed by UK Farm Animal Welfare Council) is reached when positive events predominate in this balance over the whole life of the animal. A good way to improve such positive experiences for fish, as for other animals, is to properly implement techniques of EE.

Because of the variety of EE that can be provided, as well as the wide range of species that can benefit from it, EE science is constantly improving. Even though there is extensive information about the effects of EE on fish welfare concerning physiology and behaviour of laboratory (e.g. zebrafish, three-spined stickleback) and ornamental fish (e.g. guppies, goldfish),[20-22] this review focuses only on fish species of aquaculture interest. Unlike other sectors with captive fish (laboratory and ornamental fish), aquaculture produces fish for human consumption, and therefore, aspects related not only to ethical issues (e.g. welfare) but also reputation and production efficiency (e.g. growth performance, feasibility, certifications) are essential. In this sense, there are some very comprehensive reviews on physical enrichment or specific colour preferences in cultured fish,[23-25] but there is no work to date that encompasses all five recognised categories of EE (physical, sensorial, occupational, social and dietary enrichments). Therefore, the main goal of the recent review is expanding the over-the-horizon views on different strategies and alternatives for enriching the fish environment in world-wide aquaculture, compiling the existing knowledge on the effects on fish welfare, assessing possible benefits for the industry or applications at industrial scale and providing guidelines for fish-farmers, researchers and other stakeholders.

To fulfil the aim for this review, relevant peer-reviewed literature were sought for using Google Scholar and Web of Science databases. We retrieved articles based on their relevance to the search strings including fish species of aquaculture interest and the five enrichment strategies, as well as the different methodologies that could be used within each enrichment strategy. Additional articles and technical reports provided by experts in the field were also included. In addition, articles were checked for relevance and grouped into general categories (EE strategies) for discussion, comprising research foci on fundamentals and discussing feasibility and further steps of EE in aquaculture.

2 | ENVIRONMENTAL ENRICHMENT STRATEGIES

2.1 | Physical enrichment

Physical enrichment consists of adding physical complexity with structures, objects or any structural modification to increase heterogeneity of the rearing environment.[23] Some species use substrate or shelters in their natural environment, and, therefore, may also make frequent use of physical enrichment when in captivity. Such enrichment strategy can be created with a wide variety of features in many shapes and sizes, and they can be classified into two main types: (1) structures, which can provide shelter or simply add heterogeneity and complexity to the rearing environment; and (2) substrates, which are more appropriate for bottom-dwelling or bottom-user species, during their whole life or at specific life-stages (e.g. incubation). Structural enrichment is probably the best-known EE strategy and, therefore, the most used from laboratories to farms nowadays.

Physical enrichment for captive fishes has been addressed in depth by several recent reviews,[22-24] which highlight the growing interest in this type of enrichment as well as the extent of its effects on fish welfare. We nonetheless include an overview here for the sake of completeness, with some additional studies and a focus on relevance to aquaculture for food production.

2.1.1 | Structures

There is a wide range of studies on different fish species regarding physical EE that provided shelter in captivity. For instance, some work on catfishes (i.e. *Clarias gariepinus*, *Heterobranchus longifilis*, *Silurus glanis*, *S. asotus*) demonstrated that simple structures in the rearing environment, such as plastic strips, shreddings, or tubes, can provide hiding places, inhibit cannibalism and aggressive behaviours and increase growth and survival (e.g.[26-30]). A study on mangrove red snapper (*Lutjanus argentimaculatus*) showed that juveniles grow faster when provided with hard, complex structures, such as rock piles and mangrove roots.[31] Similarly, studies on different salmonids showed that EE structures, such as plastic tubes and shredding, not only can improve growth and survival, but also swimming agility and physiological stress response (e.g. reduced plasma cortisol levels) when presented with stressors (e.g. air exposure, handling, crowding), as well as decreased fin damage and related fin infections (e.g.[23,32-34]). Indeed, studies on the Atlantic salmon (*Salmo salar*) demonstrated that adding complexity in the rearing environment not only promotes cognitive abilities and improves brain plasticity,[35,36] but also decreases parasite occurrence and improves infection resistance and survival.[37,38] Rearing Atlantic cod (*Gadus morhua*) in physically enriched environments that provide hiding places improves their learning capabilities and increases resting behaviour, thus affecting swimming activity and shoaling behaviour in the tank.[39-42] In this sense, the level or intensity of physical structures (i.e. number of structures) reduces aggression and increases social stability of territorial species, such as black rockfish (*Sebastes schlegelii*) and fat greenling (*Hexagrammos otakii*).[43] Similarly, the number of plastic plants provided as structural enrichment has direct effects on territoriality of cichlids, such as Nile tilapia (*Oreochromis niloticus*), redbreast tilapia (*Tilapia rendalli*) and convict cichlid (*Amatitlania nigrofasciata*), and reduces aggression.[44-46]

Recent studies have combined different types and levels of physical structures and plastic plants on larval and juvenile black rockfish.[47-51] These studies indicated that enrichment levels have significant positive effects on growth performance, behaviour (especially aggression), brain plasticity and neurogenesis, physiological condition and stress-related physiological responses. The authors suggested that providing a medium-amount (approximately 50% basal-area coverage) of structural enrichment might be optimal for enhancing welfare and behavioural flexibility in the aquaculture industry. However, changes in behavioural responses to structural enrichment depend on ontogenetic life-stages of reared fish.[52] Furthermore, Saraiva and Pompeu[53] demonstrated that structural EE (submerged logs and artificial aquatic plants) can induce morphological differentiation in two Neotropical species (*Prochilodus lineatus*, *Brycon orbignyanus*) through phenotypic plasticity, potentially generating phenotypes more adapted to exploiting a complex environment. In addition, the use of nets in hatchery and nursery tanks is known to be widely used in gilthead seabream (*Sparus aurata*) and European seabass (*Dicentrarchus labrax*) farms (Arechavala-Lopez P. *pers. obs.*), with the aim of disrupting their circular swimming pattern when shoaling, thereby reducing vertebral malformations, although this has not yet been empirically tested. It is also known that some aquaculture companies use submerged rings that release curtains of air bubbles inside the net-pen (Sea Pen Aeration systems; KAESER ®, https://www.kaeser.com/int-en/solutions/aquaculture/), which increase the oxygen saturation of the water, thus lowering the feed conversion ratio, as well as preventing algae and plankton (including planktonic stages of sea lice *Lepeophtheirus salmonis*) from entering the sea cage, and improving the overall health of the fish (Kadri, S. *pers, com.*).

In this context, even if structural enrichment does not provide shelter, it can simply add environmental complexity and heterogeneity that can also improve the welfare conditions of captive fish. For example, adding vertically-suspended structures can modify the water flow and velocity profiles in fish tanks,[54,55] and it has been demonstrated that substantial benefits can be accrued during rearing of four salmonid species. Jones et al.[56] demonstrated that feed conversion rate can be improved in Atlantic salmon by inserting an array of suspended plastic conduits in the rearing tank, but did not report significant differences in individual fish length, total weight gain, individual weight or condition factor. White et al.[57] conducted a similar study on brown trout (*Salmo trutta*) and rainbow trout (*Oncorhynchus mykiss*) and reported that total tank weight gain and feed conversion ratio can be significantly improved for both species reared with suspended conduit as enrichment. Other studies on rainbow trout tested different designs and densities of vertically-suspended structures (e.g. aluminium rods, aluminium angles, strings of coloured balls) in circular rearing tanks and reported benefits in total tank weight gain, feed conversion ratio and individual performance in the structurally complex tanks, with minimal effects on regular tank cleaning.[58-64] Rosburg et al.[65] showed that rearing chinook salmon (*Oncorhynchus tshawytscha*) in tanks with vertically-suspended arrays of polyvinyl chloride pipes or six golf balls fixed vertically on threaded rods can improve fish length, weight-gain and fin condition. Similarly, Voorhees et al.[66] reported that vertically-suspended structures (aluminium angles) in tanks, combined with an exercise routine, may be beneficial during the rearing of juvenile landlocked fall Chinook salmon. On the other hand, an experiment on brown trout, chinook salmon and Atlantic salmon reared in circular tanks with vertically-suspended aluminium rods as enrichment structures did not show any effect on growth for any species, probably due to the short experimental period or underfed fish.[57] Moreover, colours of vertically-suspended structures seemed to have no relevant effects on growth performance of hatchery-reared chinook salmon and rainbow trout.[67,68] This highlights the need to provide ethologically relevant EE features to the species of interest, under the risk of null or even negative effects. Vertically suspended plant-fibre ropes can also be successfully used as an EE strategy for farmed fish, as it has been demonstrated for gilthead seabream.[69-71] Arechavala-Lopez et al.[69] demonstrated that such simple structures can reduce aggressiveness in juvenile seabream and modify the distribution of fish, leading to better fin condition and less interactions with the net pen (e.g. less bites and fins rubbing), but no effects were reported on fish condition, growth and mortality. Arechavala-Lopez et al.[70] showed that vertical ropes can enhance seabream cognition, exploratory behaviour and brain physiological functions. Suspended ropes were also applied in experimental sea-cages of on-growing seabream, which increased their spatial use in the net-pen, so such ropes were recommended as a passive and non-invasive tool for improving welfare of intensively cultured seabream.[71]

2.1.2 | Substrates

Providing floor substrate (sand, pebbles, gravel, stones, etc.) can be seen as another type of physical EE to improve or guarantee the welfare of fish,[23,24] mostly for those species that regularly interact with the bottom or live closely associated to it during its whole life (e.g. benthic fish). For example, flatfish are benthic organisms inhabiting sandy or muddy bottoms, but are commonly cultured in smooth-substrate tanks where they often develop skin lesions on the blind (abocular) side, decreasing their welfare, but also causing economic losses to the farmers.[72-75] Therefore, adding substrate to the tanks could address some of the biological needs of these species and/or provide some welfare benefits. Dou et al.[76] reported an increase in resting behaviour, a reduction of metabolic rate and a decrease in cannibalism in olive flounder (*Paralichthys olivaceus*) after adding gravel to the bottom of the rearing tank wherein fish can bury themselves or hide. Studies on the Atlantic halibut (*Hippoglossus hippoglossus*) showed that substrate-covered bottoms (e.g. sand, gravel) can reduce skin lesions, infections and hyperpigmentation.[73,77] Ambicolouration or blind-side hypermelanosis on olive flounder and starry flounder (*Platichthys stellatus*) can be also reduced, or even eliminated, by providing gravel as substrate enrichment in rearing tanks.[74,78-80] Furthermore, sandy substrates in tanks also play an important role as a prophylactic measure and even for the treatment of skin diseases, for example in Dover sole (*Solea solea*),[72,81] whereas improving plain cement bottoms by blending with silica fume (10%) improves growth, fin erosion, skin lesions and abnormal pigmentation patterns in Senegalese sole (*Solea senegalensis*).[82] Reiser et al.[83] found that natural and artificial substrate enrichment can modulate epigenetic patterns in rainbow trout, affecting global DNA methylation in the brain at the egg and alevin stage, the period during development where the animals are in close physical contact with the substrate. Additionally, cobble substrates provided in concrete raceways can improve fin condition and decrease related infections of rainbow trout and cutthroat trout (*Oncorhynchus clarkii*).[84-86] Similarly, artificial seaweed (AquaMats®), specifically designed to provide structural enrichment in pond bottoms, improve the growth and fin condition of rainbow trout, whilst allowing the growth of aquatic plants and invertebrates as an additional nutritional source to cultured species.[87]

The gilthead seabream is a demersal species that usually forages on the bottom substrate. Some studies on juveniles revealed that adding a uniform layer of single colour glass gravel as enrichment in rearing tanks can induce positive effects on fish condition and growth performance (i.e. final mass, specific growth rate, mass gain, food conversion ratio), and also reduces aggressiveness, increases fish-bottom interactions, improves the stress response (reduce brain serotonergic activity) and promotes better fillet quality.[88-91] Therefore, although different bottom colours and densities can lead to different effects (see Sections 2.2 and 2.4 respectively), these authors pointed out that improvement of the fish rearing environment with substrate may have multiple beneficial aspects for both fish welfare and producers. Murtaza et al.[92] reported a significant benefit of enriched early rearing environment (including multi-coloured gravel substrate, cobbles and plants) on the physiologic stress response to net capture and confinement of grass carp (*Ctenopharyngodon idella*). Authors recommended the use of this kind of EE to produce fish with better ability to cope with stressful events.[92] Similarly, Tatemoto et al.[93] demonstrated through novel-object tests that substrate in more complex environments (i.e. mostly gravel substrate with some glass balls and small coloured PVC pipes) improves the affective states and welfare of Nile tilapia.

Substrate enrichment can also be applied to incubation processes. Salmonid alevins (yolk-sac fry) hatch from eggs buried in gravel and spend the first stage of their life within this substrate. Adding hatching mats to the bottom of the tanks provides a wide range of positive effects, as it has been demonstrated on different salmonid species (e.g.[23,94]). These hatching mats improve growth and survival of alevins, reduce yolk-sac constrictions and improve yolk conversion efficiency, reduce alevins swimming activity and malformations and permit resting on the bottom in normal body-position. Hatching mats also promote positive physiological changes, increase brain growth and decrease high activity and oxygen consumption due to stress.[23] Indeed, several commercial salmon hatching mats are already available.[16]

Similar positive effects on hatchlings have been shown for Atlantic sturgeon (*Acipenser oxyrinchus*) and white sturgeon (*A. transmontanus*) when adding sand and gravel to the bottom of the tanks as incubation substrate.[95-97] Substrate plays a crucial role in many cichlid species that exhibit substrate-oriented activities during the breeding season, such as males digging pits or nests in soft bottoms, displaying courtship behaviours to attract females and establishing territories.[98] Male Nile tilapia prefer small-grained gravel or sand substrate to stones to dig spawning nests.[99,100] In the case of Mozambique tilapia (*Oreochromis mossambicus*), sandy bottoms can reduce aggressiveness during courtship and nest-building and, therefore, reduce stress and increase welfare of breeding males.[101,102] Altogether, these studies reveal that the lack of substrate is particularly deleterious in a reproductive context for these species and, thus, it is likely to decrease the welfare state of breeding fish and hatchling offspring.

2.1.3 | Combinations

Physical EE can provide shelter, substrate and complexity in a rearing environment at the same time, and can also allow the cohabitation of different species. This is the case of enrichment structures for cleaner-fish in salmon aquaculture. Lumpfish (*Cyclopterus lumpus*) and several wrasse species (e.g. *Labrus bergylta*, *Ctenolabrus rupestris*, *Centrolabrus exoletus*, *Symphodus melops*, *Labrus mixtus*, *Tautogolabrus adspersus*) are the most common cleaner-fish currently used as a biological control for sea lice on farmed salmon (sea-cages) in Europe and Canada.[103] The use of cleaner-fish seems to be an alternative method of louse control, but for it to be efficient and ethical, the health and welfare of the cleaner-fish is also of major importance.[104]

Juvenile lumpfish are typically found amongst kelp during their first year of life, both attached and free floating; therefore, those stocked in commercial salmon cages will need some type of shelter or substrate to attach to when resting, and to shelter to during periods of inactivity or adverse environmental conditions.[103] Imsland et al.[105] demonstrated that juvenile lumpfish are able to adhere and rest on smooth flat vertical or floating plastic surfaces, which may mimic their natural requirements for surface adhesion. Structures made of pipes or artificial kelp are also provided to wrasse stocked in commercial salmon cages, providing shelter and resting hides for their overnight inactivity.[103,106] Consequently, and given the quick expansion of the use of cleaner-fish in commercial salmon cages, several companies manufacture a varied range of vertical substrates or 'kelp curtains', resembling artificial kelp made of PVC.[103] In this line, Leclercq et al.[106] developed sinking hides of plastic fake-kelp for ballan wrasse (*L. bergylta*) stocked in commercial salmon cages. These structures had hanging feeders or 'feed blocks' (water-stable agar-based diet on PVC pipes or trays), forming altogether a complex vertically suspended shelter and supplementary feeding for cleaner fish. These feed blocks were also specially designed for lumpfish—which quickly accepted and grazed on them—and successfully reduced the prevalence of cataracts compared to supplementary pelleted-commercial feed.[107,108] Kelp-curtains, shelters and feed-blocks can be used for any cleaner-fishes in farming conditions. However, it is important to highlight that, given the behavioural and biological differences amongst species,[109,110] they must be specifically designed for each cleaner-fish species. Moreover, the farming strategies and rearing conditions should also be taken into account to avoid undesirable effects.[111] A further point worth considering when providing kelp-curtains, shelters, and feed-blocks for cleaner-fish that coexist with Atlantic salmon in commercial cages, is that the complexity of the rearing environment is increased for both species and, of course, such provided structures must not cause any detrimental effect to either co-habitant's welfare.

Another example of physical EE combining both structures and substrates is periphyton-based aquaculture.[23] Periphyton is a matrix of bacteria, algae and microorganisms embedded in a mucopolysaccharide matrix that colonises structures placed in earthen ponds, and that can be consumed by fish, increasing the productivity and efficiency of aquaculture systems.[112] Application of periphyton structures can be mostly found in Asian and African ponds rearing cichlids or cyprinids. Periphyton structures can be made of organic materials, such as bamboo, rice straw or sugarcane fibrous matter or made with PVC pipes or plastic slides, but the former provide higher benefits in of growth, immunity and survival.[112] To summarise, physical EE is probably the main type of EE to be considered in fish farming, but the fundamental questions surrounding their deployment (what type, how much, when and how) should be answered in advanced.[24] It is therefore important to consider the nuances and details of its implementation, which should first and foremost consider the ethology of the species in question,[5] and consequently the functional relevance on the physical structures to be implemented.

2.2 | Sensorial enrichment

In the wild, animals are exposed to an ever-changing array of sensory stimuli that triggers the diverse senses of fish, whereas captive environments are generally much more deficient in terms of the sensory cues.[113] However, to successfully provide sensory stimuli and implement sensorial EE in captive environments, it is essential to have a good knowledge of the biological needs and the sensory worlds of the targeted species.[5] This is especially relevant for fish, given that there are substantial differences in their sensory systems compared to terrestrial animals, due to differing ecological and evolutionary pressures.[15] In order to promote better welfare of captive fish, different sensory stimulation must be explored as potential methods of EE for these animals, including visual, auditory, chemical (olfactory, taste), hydromechanical and electrical stimuli.

2.2.1 | Visual stimuli: lighting, covers and colours

Light is a key environmental factor that synchronises all life-stages of fish, from embryonic development to sexual maturation.[114] Some researchers have extensively explored the effects of light characteristics (periodicity, intensity, spectrum) in a wide variety of species, life-stages and rearing environments, suggesting different strategies of sensorial enrichment through visual stimuli. The diversity of fish visual systems, which might change during their life-history, or even within life stages, together with the enormous variety in eye anatomy and brain structures that process visual information,[115,116] make visual enrichment very challenging. In addition, light behaves differently underwater than at the surface, and can not only be influenced by many physical and biological factors, but also fluctuates within daytime, season or natural weather conditions.[5] At indoor fish-farm facilities, however, farmers can simulate natural light conditions to promote natural chronobiology, although artificial lights may differ greatly from natural solar light.[117] Classic light bulbs (incandescent filaments) produce a reddish inefficient light underwater, whilst fluorescent tubes produce sharp peaks at specific wavelengths far from natural daylight, but modern light-emitting diode (LED) technology provides versatile and better cost-effective lighting systems which can be used for different purposes in aquatic research and captive environments.[118] Overall, efficiency of production and quality of aquacultural products can be improved if the activities of fish husbandry are timed to coincide with the biological rhythms of fish.[119]

Light characteristics (intensity and spectrum) and circadian clock (periodicity) represent key regulators of many aspects of fish biology. They can be artificially controlled and are frequently manipulated as part of strategies designed to maximise productivity in fish farms, but can also be used to guarantee good welfare conditions. In fact, the species-specific behavioural and physiological responses to acute stressors depend heavily on the time of the day when the stress occurs; this has been extensively reported in many species of farming interest.[117] The effects of environmental cycles, biological rhythms and artificial lighting conditions during early development have been extensively studied and reviewed for many species of commercial interest.[117,120,121] In general, the overall performance, development and welfare of fish larvae are significantly affected by light characteristics, obtaining better results under the closest conditions to their natural environment.[117] Juvenile and adult fish also present daily cycles of locomotor and food anticipatory activities, which are directly affected by lighting conditions.[122] Therefore, understanding the circadian timing system of fish is essential for optimization of rearing protocols and the improvement of their well-being in farming environments.

Similarly, light spectrum might have physiological and behavioural effects on fish in captivity. In the underwater photo-environment, the spectral composition of both solar and artificial radiation changes greatly and is absorbed differently by the water column.[123] Therefore, shortwave radiation (violet and blue) diffuses more, whilst longwave radiation (red and orange) diffuses less.[123] For early developmental stages, juveniles and breeders, it is generally recommended providing short wavelength lights (blue and/or green colours) which, in combination with proper light periodicity and intensity, induces positive effects on growth and performance, enhances locomotor and feeding activity, reduces stress and mortalities, promotes spawning behaviour and affects organoleptic properties.[117,120,124] Moreover, the antibacterial and anti-protozoal activities of blue LED light-emitting diode light (405–465 nm) have been demonstrated for some farmed species, without apparently causing side effects (in contrast to UV light).[125,126] Therefore, it is recommended avoiding long wavelength light (red colour), as well as constant light or constant darkness, which negatively affects fish welfare in terms of embryo, larvae and juvenile development, spawning, malformations, eye damages and mortality.[117]

Some studies on the Atlantic salmon have also reported direct effects on behaviour induced by light intensity and positioning in cages.[127-129] Herbert et al.[127] applied a central lighting device that provided an apparently moving light pattern to induce sustained exercise in salmon, which enhanced growth rates and feed conversion, and reduced plasma cortisol. On the other hand, Bui et al.[128] reported that fish groups exposed to high and medium intensity of blue LED light showed a marked change in vertical distribution, displaying erratic swimming and increasing surface activity, both symptoms of stress. Wright et al.[129] showed how Atlantic salmon instantaneously follow vertical light movements in sea cages. The authors suggested that positioning of lights may help move salmon away from fluctuating unsuitable depths (e.g. lice-rich depths) into temporary favourable depths (e.g. surface brackish waters to treat against stenohaline parasites), and throughout cages to avoid crowding in narrow depth ranges. However, responses to different light conditions may vary depending on the species, especially due to specific physiological needs or behaviours (e.g. phototaxis), and also on the adaptation to different environments within the same species (e.g. living at different latitudes).

Likewise, covers can be used to modify lighting conditions in a more indirect way, reducing the amount of light and providing shades. Several studies on salmonids demonstrated that the use of covers can prevent sun-burn and UVR-induced effects, whilst also preventing jump-out and predation, improving fish performance and reducing stress (e.g.[130-138]). Most of these studies pointed towards partially covered conditions as the most beneficial for fish performance and welfare. A recent study on Nile tilapia, however, showed that providing partially covered environments in rearing tanks can induce stressful conditions, compared to fully covered or uncovered tanks.[139] Rearing tanks can be manufactured in a wide variety of colours, offering high flexibility to aquaculture production, considering that most cultured fish can distinguish colour and thus be affected by the colour of their rearing environment. Tank colour and depth, together with light source and water clarity, impact the degree at which light is absorbed, reflected, scattered and attenuated in the rearing environment. McLean[25] reviewed the effects that tank colour (floor and walls) may have on various physiological and behavioural processes in larval and post-larval fishes. The author compiled a vast number of studies on a wide range of species demonstrating that different background colours can influence fish performance and survival, health, level of stress and even level of aggressiveness; effects that can be negative or positive depending on species and life-stage.[25] Diverse patterns of wall and bottom tanks can be also applied as sensory enrichment, stimulating the visual system. For example, studies on Pacific bluefin tuna (*Thunnus orientalis*) reported that coloured wall patterns (lattice and polka dot coloured patterns) increased the survival of juveniles during growing and transportation, decreasing collisions, bone injuries and physiological stress.[140,141] Similarly, striped coloured walls and lattice coloured bottoms were successfully applied on rearing tanks of juvenile Atlantic bluefin tuna (*Thunnus thynnus*) to modify swimming activity, reducing collisions and, consequently, injuries and mortalities.[142] Additionally, fish pigmentation is also strongly influenced by background colour, which can lead to significant consequences at consumer levels, mostly for species sold skin-on whole/gutted.[25]

Some research has indicated the potential use of mirrors and other reflective devices as a method for visual stimulation or enrichment for captive animals, particularly for individuals subject to social isolation.[113] However, in the case of aquaculture, fish are not reared in isolation and the use of mirrors is not recommended, since they may induce negative effects. For example, mirror images simulate intrusions in territorial fish (e.g. cichlids), triggering aggressive responses with their mirror image in unresolved disputes,[143,144] which can lead to dysfunctional or even fearful states.[145] A recent study, using a complex operant conditioning device, demonstrated that rainbow trout are able to discriminate 2-D photographs of conspecifics from different visual stimuli, suggesting the positive effects of developing visual-based enrichments for fish cognition.[146] Therefore, there is ample scientific evidence that the use of visual stimuli as sensory enrichment can induce positive effects on fish welfare, despite the existence of important differences amongst light and colour sources, and species. However, the potential adverse effects of light systems, protocols and background colours need to be assessed before implementing their use in aquaculture settings, ensuring that animal welfare is not compromised.

2.2.2 | Auditory stimuli: noise and music

Human activities in aquatic environments generate a wide range of waterborne noises and, consequently, fish are subjected to extreme levels of acute (transient) and chronic (continuous) noise, both in natural and cultured conditions, which may negatively affect their stress level and welfare.[113] Auditory capabilities and processing mechanisms of fish are highly sensitive and complex and differ amongst species.[147] In natural waters, human activities are the source of a wide range of sounds, generating acoustic stresses that are particularly important in coastal zones, where most of the sea-based aquaculture facilities are located. For example, underwater anthropogenic-derived noise (i.e. urban and shipping noise, drilling and piling) negatively affects the behaviour (swimming activity, group cohesion, distribution) and physiology (primary and secondary stress responses) of gilthead seabream and European seabass.[148-157] Negative behavioural effects of anthropogenic-derived noise (i.e. infrasound, surface disturbances, urban and shipping noises) were also reported on Atlantic salmon[158] and Nile tilapia.[159] In addition, an even greater amount of noise is generated in land-based aquaculture systems, especially in enclosed recirculation systems.[113,160]

High-frequency noise (1–2 kHz) is mostly generated by electrical motors, oscillating and collapsing air bubbles, aeration and water pump action, whereas low-frequency noise (25–1000 Hz), which is within the hearing range of most teleosts, is generated by water flows, ground vibrations, tank wall vibrations and electrical pumps.[113] Therefore, it is essential to take the appropriated measures (e.g. isolation and proper materials, spatial planning, etc.) to reduce background noise-related impacts, ensuring good welfare conditions of farmed fish. This approach might be considered a strategy closely related to a kind of sensory enrichment, since it masks or reduces negative auditory stimuli. This reduction of background noise might also allow better communication through naturally-generated sounds of the captive species, which are produced in various behavioural contexts (agonistic interactions, courtship, spawning, distress).[161] On the other hand, adding background sounds specific to a species' natural habitat is already considered an EE strategy through sensory stimulation in captive animals,[113] and even though some studies suggested the potential use of sea soundscape,[149,150] further studies are needed in this matter.

In addition, recognition of the direct effects associated with music for human well-being has prompted recent research into the value of auditory stimulation as a means of enriching the environment of captive animals, ultimately with the view of meeting one or more of the suggested goals of EE.[113] In this sense, some studies have assessed the potential effects of adding background music (i.e. rhythmic or systematic sound not typically found in the wild) on cultured fish. For example, it has been demonstrated that musical stimuli positively influence growth performance, feeding efficiency and stress reduction on common carp (*Cyprinus carpio*),[162-165] gilthead seabream[166,167] and rainbow trout,[168] mostly reared in recirculating water systems. Similarly, Catli et al.[169] reported that slow tempo music-induced positive effects on growth performance and feed intake of turbot (*Scophthalmus maeotica*), whereas fast tempo music-induced negative effects and stress in this species. Therefore, musical stimuli can be regarded as a stress relieving or inducing factor, but adequate selection of tempo, frequency and harmony may enhance welfare[170] and can be applied as a sensorial enrichment strategy in intensive aquaculture facilities. Overall, further studies are still needed, systematically exploring both behavioural and physiological effects of different auditory stimuli on a wider range of species at different developmental stages and environments.[171]

2.2.3 | Chemical stimuli: olfaction, taste and chemosensing

Chemical senses play an essential ecological role (fish-environment interactions) and are extremely relevant in communication contexts in all fish taxa (cyclostomes, elasmobranchs and teleosts).[5] Chemical sensing in fish is highly particular compared to terrestrial animals and exists in three modalities, the importance of which depends on species and life-stage; olfaction, taste and solitary chemosensory cells.[172] Chemical sensing is fundamental for intra-specific communication in fish, allowing not only males and females to find suitable partners,[173] but also the assessment and announcement of status in agonistic contexts, which are solved much quicker and less violently thanks to 'chemical diplomacy'.[144,174] On the other hand, chemical sensing also enables fish orientation and inter-specific interactions, such as predation, territorial aggressions, foraging and escaping from predators in dark or murky waters.[175,176] Biological waterborne chemical signals are ubiquitous in aquaculture systems, being released in agonistic encounters, during handling, feeding or breeding, and are prevalent at high stocking densities. A build-up of chemical cues might also occur, inducing higher stress conditions or undesirable behavioural and physiological responses.[177,178] For example, increased ventilation rate, decreased foraging and swimming activity, increased dashing and dorsal fin erection[176] or even morphological changes[179] are within the effects of exposing fish to chemical cues. These effects should not be taken lightly as many of the most farmed fish species have been characterised in terms of chemical sensing, such as salmonids,[180,181] tilapias,[182-184] carps,[185] European seabass,[186] gilthead seabream[187] or Senegalese sole.[188]

In this context, manipulation of odours or other chemical stimulations, whether in the form of olfactory stimuli that are specific or non-specific to an animal's natural habitat, or pheromonal in nature, have been proposed as potential EE for both land animals and captive fish. For example, releasing specific pheromones during dominance contests that modulates behaviour by reducing aggression would be a promising tool to promote welfare.[189] However, the applicability of this sensory enrichment on aquatic animals may be complex and the welfare advantages of introducing this kind of chemical stimuli on captive environments may not be straightforward. In fact, in some cases, the reduction of natural chemical signals in the water is actually a driver of poor welfare, as fish may rely on the chemical cues in the environment to stabilise the social system[98,190] and, therefore, avoiding the exchange of holding water may be considered a sensory enrichment strategy itself. It is also noteworthy that the use of chemicals during water treatments or bio-sanitary protocols may release other undesirable chemical stimuli into the rearing environment and, conversely, filtration systems may remove important chemical cues rendering the captive environment scant on meaningful chemical information for captive fish.[177]

Olfaction may function at a longer distance for all the roles described above, whereas gustation (i.e. the sense of taste) is usually limited to very close range detection of food, being located in the head and mouth of fish,[175] and used mostly during oral food evaluation.[172] In fish farming, food chemical signals may function in two ways as enrichments: chemical attraction and feeding stimulation. In the first case, enrichment may rely on the use of attractants for faster detection, possibly reducing energy expenditure for the fish whilst mainly reducing waste (with the consequential positive effects on water quality and feed cost). In the second case, feeding stimulants have an effect on satiation and modulate food ingestion, with relevant effects on growth.[191] These stimulants are different for carnivorous and herbivorous fish[192] and there is at least theoretical potential to use chemicals to stimulate and enrich the environments of farmed fish whilst reducing the ecological and social impacts of forage fisheries.[193] However, other ecological problems may arise in certain farming systems (cages, ponds) where feeding stimulants could be detrimental for local fauna. Interestingly, tryptophan is known to be both an attractant[194] and a stimulant[195] in fish feeds, whilst simultaneously showing positive effects in welfare by reducing stress and aggression in many farmed species,[196] and can be used in combination with other EE strategies.[197] However, these effects vary in magnitude and even direction,[196] so the strategy and type of chemical stimulation should be pondered in a case-by-case basis.

2.2.4 | Tactile stimuli and other sensory systems

Fish are widely covered by tactile receptors and may also possess various tactile organs, mostly cutaneous outgrowths (e.g. barbels, free rays of fins, rostrum, breeding tubercles, or dermal teeth). Tactile organs are highly significant in orientation, reproduction, defence, social interactions, exploration and food searching behaviour.[198,199] The fins have been found to function as proprioceptors, by providing feedback on fin ray position and movement, and as tactile sensors, by encoding pressures applied to the fin surface.[200,201] Intra-oral tactile reception also has an important role in estimating the texture and attractiveness of food objects.[198] It is also known that cleaner-fish provide tactile stimulation with the pelvic and pectoral fins to their clients in coral reefs.[202] This tactile stimulation is beneficial for clients, by lowering their stress and removing parasites, and dead and infected tissues, and for cleaners, by helping to keep clients available for longer and reducing conflicts.[203] In aquaculture, however, whether the tactile stimulation of cleaner-fish (e.g. lumpfish and some wrasse species) reduces the stress and social conflicts on the clients (i.e. salmonids) or not, remains to be proven. Recent studies on Nile tilapia suggest that, although tactile stimulation does not lower blood cortisol levels in the short-term, it can reduce aggressiveness[204,205] and may also reduce the overall stress associated with social interactions in long-term. Moreover, a recent study reported that koi carp (*Cyprinus rubrofuscus*) showed interest in physical contact (tactile interaction) with humans, suggesting that interacting with human skin, a novel substance and texture, might serve as a source of tactile and/or sensory enrichment.[206] However, further studies are still needed to test several effects of tactile stimulation on fish welfare.[205]

There are other sensory systems, such as hydromechanical and electro-sensing, which are involved in diverse biological and ecological functions.[5] Fish are able to detect and perceive the hydrodynamic and physical environment they inhabit and process this sensory information through their mechanosensory lateral-line system. The lateral-line system consists of up to several thousand neuromasts distributed across the entire body of the animal. Using the lateral-line system, fishes perceive water movements (i.e. hydrodynamic stimuli) of both biotic and abiotic origin, such as those generated by conspecifics, predators and prey, and therefore acting as a communication tool.[207] In addition, electro-sensing is present in certain teleost species, being able to detect electric fields from a multitude of sources, including the earth's magnetic field and the bodies of all aquatic organisms including the electro-sensing fish itself.[208,209] The extremely high sensitivity of fish to these fields enables orientation, navigation, communication and even detection and localization of other fish, both prey and conspecifics.[208,209] Nevertheless, the stimulation of these last sensory systems in captivity is not yet assessed, and may be indirectly addressed through other enrichment strategies, such as social, occupational, or even physical enrichment, as well as by good welfare practices and management at fish farms.

2.3 | Occupational enrichment

In nature, fish are continuously exposed to physical and psychological challenges and, therefore, occupational EE aims to introduce diverse challenges into the rearing environment that are important to prevent monotony and, consequently, boredom. Occupational enrichment can encompass psychological devices that provide animals with challenges or control over their environment, as well as enrichment encouraging physical exercise.[210]

2.3.1 | Hydrodynamism: flow, currents, and exercise

The exercise levels and swimming capacity of fish cultured in ponds, recirculating systems, raceways and cages are generally lower than those in the wild, but depend heavily on species, life-stage of development, and rearing systems. The study of fluid dynamics (water flows, currents, waves, etc.) within aquaculture facilities, and how it influences swimming behaviour, has proven to be of great importance for designing captive environments, both on-land and offshore cage systems.[211,212] Some studies on Atlantic salmon open-sea cages, where the fish can be exposed to diverse environmental challenges, demonstrated that waves and currents have a direct effect on the group shoaling behaviour and distribution inside the net-pen.[213,214] Similarly, turbulence and water flow in land-based systems have been shown to have both positive and negative effects on fish swimming, feeding and energetics, usually with negative impacts at very low and at high levels, with least effects and, sometimes, positive ones at intermediate levels.[215]

Forcing the fish to swim in a certain water-flow can promote swimming exercise and could represent a natural, non-invasive, and economical approach to improve growth, resilience, robustness and welfare.[216] Optimal exercise may have beneficial effects of major importance for aquaculture and, therefore, is a potential occupational enrichment strategy to be considered by the industry. Exercise-induced growth is optimal at specific speeds, most likely near optimal swimming speeds (U_{opt}) where the cost of transport is the lowest and the energetic efficiency the highest.[216] At swimming speeds lower than U_{opt}, energy is lost due to higher spontaneous activities (e.g. flight responses), whilst at higher speeds, swimming becomes unsustainable, stressful, and can finally cause fatigue.[217] It must be noted that critical swimming speed varies with group shoaling behaviour,[218] and also that fish densities and other structures can alter the water flow.[219,220]

In salmonid fish, the stimulatory effects of sustained moderate swimming on growth performance have been widely demonstrated. When juvenile salmonids are reared in flowing water (0.75–1.5 body length per second; BL s^{-1}), they tend to grow faster, making more efficient use of the food and showing uniformity of growth rates and a reduced size range at harvest.[221] Some studies on Artic charr (*Salvelinus alpinus*) also showed that exercised fish presented not only better growth performance, but also different body composition (lower fat and higher protein) than control fish.[222,223] An increase in swimming speed caused a marked increase in schooling behaviour and lower levels of aggressive interactions, but the moderately exercised fish presented the highest growth performance. Additionally, Herbert et al.[127] induced sustained exercise in Atlantic salmon using a lighting device centrally placed in semi-commercial tanks that provided an apparently moving light pattern. Exercised salmon (exposed to 1.5 BL s^{-1}) presented enhanced rates of growth and feed conversion, and reduced levels of plasma cortisol, improving productivity and welfare. Water current velocities can be also regulated in closed containment systems (e.g. closing cages) placed in the sea. Nilsen et al.[224] demonstrated that moderate water velocity (0.36–0.63 BL s^{-1}) can be favourable for growth rates and performance of post-smolt Atlantic salmon during the entire on-growing period in commercial closed contained systems.

Contradictory effects of water flow are also reported. More recent studies on chinook salmon and rainbow trout reported lack of positive effects on growth performance and post-transportation stress response between fish reared at different water flows.[225,226] The authors indicated that a moderate velocity (1.5 BL s^{-1}), which is necessary for circular tanks to be self-cleaning, is not detrimental to fish growth or condition, whereas a faster water velocity (3.0 BL s^{-1}) may negatively affect fish growth and food utilization in the long-term.[225] They also highlighted the importance of pairing exercise with adequate food intake to avoid undesired effects.[226] Similarly, no clear effects on growth performance were reported on exercised rainbow trout under intermittent or constant water-flow regimens, combined with vertically-suspended structural enrichment, which directly influences the water flow.[58,61,64,66] However, a combination of structural enrichment and water-flow is important for fish habitat preference and, therefore, the potential effects of multiple factors simultaneously deserve further attention.[227] Villaroel et al.[228] found no evidence of positive effects of water-induced exercise on growth performance of rainbow trout. However, exercised fish presented a better adaptation to acute stress. Reiser et al.[229] reared juvenile brown and rainbow trout in commercial earthen ponds exposing fish to a sustained swimming condition, by using paddle-wheel aerators to create circular flow patterns with a range of current speeds in the system at minimal or no additional costs. Brown trout reared with that current had higher protein and lower fat, but no effects were observed on growth, whereas water current positively affected the growth of rainbow trout that presented lower fat and lower energy.[229]

Much less information is available on the potential stimulatory effects of swimming exercise in non-salmonid species. Ibarz et al.[230] showed that swimming exercise stimulates growth in gilthead seabream. Palstra et al.[231] demonstrated that, in the same species, water flow-induced swimming exercise near U_{opt} (at 1 BL s^{-1}) provided optimal conditions for growth and uniformity, but also physiological stress, robustness and energy mobilisation. However, the percentage of lordotic fish increased with exercise and the authors suggested that exposing fish to random waters currents (instead of constant flows) could bring welfare benefits.[231] Shi et al.[232] demonstrated that sustained swimming training have direct effects on filet texture of European seabass. Moreover, different flow velocities had significant effects on the growth, digestive enzyme activities, antioxidant capabilities, and immune capabilities of juvenile largemouth bass (*Micropterus salmoides*) in recirculating systems (RAS).[233] A study on Nile tilapia showed that water flow can help the fish to cope better with stressful events, such as being introduced into novel environments.[234] In addition, optimal exercise may also have beneficial effects on reproduction control.[216] Swimming exercise may thus represent a way to significantly control puberty in farmed fish,[235] at least amongst female migrant anguillids (e.g. *Anguilla anguilla*) besides salmonids. Induced-swimming exercise can trigger lipid mobilisation, delay of sexual maturation, prevent precocious maturation, and extend the growth period.[216] Therefore, together with induced growth, enhanced flesh quality, increased survival, robustness and fitness and increase welfare by lowered stress, the potential benefits of this type of occupational enrichment deserves further attention by the industry.

2.3.2 | Predictability and variability

Fish are exposed to highly variable environmental stimuli and challenges in the wild. Some are unpredictable, such as predation risks, food availability and human threats. Other external stimuli can be somehow predictable, presenting temporal patterns and constant fluctuations, such as solar and lunar cycles, tides, and daily temperature variations. The right amount of environmental predictability reduces the uncertainty that animals are exposed to, improves their cognitive skills, such as learning and spatial memory, and favours engrained behaviours.[236] However, human-induced environmental predictability can create evolutionary traps that are detrimental to an animal's fitness; for example, predictable feeding induces high competition and thereby increases dangerous or lethal injuries.[237] Thus, when having fish in captivity, the right balance between predictability and uncertainty is necessary, adjusting the variability within predictable events to ensure that animals do not get accustomed to the same exact routines, and thus do not reach allostatic overload when they are exposed to unpredictable events.[238]

Fish learn to predict events when they always take place at the same time of the day.[239-241] Several studies have shown that fish can be trained to predict events via classical conditioning.[242-246] Thus, fish can be trained to predict negative events and then habituate to stressors, inducing a low physiological stress response, as shown in Atlantic salmon parr.[247] On the other hand, predictability of a positive event, such as feeding, can be detrimental for the welfare of fish in some species, such as Atlantic salmon parr, to which it induces higher levels of aggression.[240] Moreover, spatially and temporally predictable feeding regimes in brown trout induced aggression and territoriality, which increased growth in individuals with high resting metabolic rate.[248] However, implementing unpredictable feeding regimes as an alternative strategy can also be detrimental to welfare. For example, in Atlantic salmon parr, this generated a dissociation of roles within their network, with heavier and longer fish initiating attacks towards smaller individuals, which had higher dorsal fin damage as a consequence.[240] In gilthead seabream, an unpredictable feeding regime was also detrimental for welfare, since it increased cortisol and glucose, and overall locomotor activity which, together, suggests that unpredictability induces stress.[239]

All these studies bring forward the importance of considering the stimulus valence (i.e. whether a stimulus is positive or negative) when studying stimulus salience (i.e. whether it is predictable or unpredictable). In fact, several studies have shown that the different combinations of valence and salience of a stimulus have different effects in the behaviour of fish,[242] as well as in their physiological and neuromolecular states.[243,244] For example, in gilthead seabream, appetitive stimuli (feeding) promoted social interactions, aversive stimuli (physical constraint) triggered escape attempts, and predictability increased the frequency of these behaviours in contrast to unpredictability. The same authors found that aversive stimuli increased cortisol levels compared to appetitive stimuli, and unpredictability elicited higher cortisol levels compared to predictable regimes. More importantly, each experimental treatment (appetitive-predictable, appetitive-unpredictable, aversive-predictable, and aversive-unpredictable) generated different patterns of gene expression in three brain regions related to reward and aversion processing.[243] This study shows that both the valence and the salience of the stimulus affect the behaviour, physiology and neural activation of fish in different ways, inducing emotion-like states. Cerqueira et al.[244] showed in European seabass that an unpredictable negative stimulus (confinement) increased shoal cohesion and freezing and escape behaviours, reduced exploratory behaviour and increased cortisol levels and neural activation of the dorsomedial telencephalon (putative teleost homologue of the mammalian amygdala) compared to a predictable negative stimulus, meaning that an unpredictable stressor triggers a stress response in this species. Similarly, Galhardo et al.[242] showed that Mozambique tilapia trained to predict a negative event (confinement) showed lower stress-related signs than a group exposed to an unpredictable visual sign and had lower cortisol levels during isolation. Alternatively, when exposed to a positive event (feeding) the fish trained to predict it showed higher anticipatory behaviour and activity compared to the fish exposed to the unpredictable sign, and the latter had lower cortisol levels compared to their baseline levels.[242] The authors discussed that anticipatory behaviour might be linked to negative emotions, generating expectations, frustrations and loss of control. In fact, in a study on Atlantic salmon, omission for 30 minutes of an expected reward induced higher levels of aggression and a stronger hierarchical conformation of the group, although this change in behaviour did not result in changes of cortisol levels.[245] Furthermore, the omission of an expected reward can affect not only the behaviour, but also the biochemistry and structural organisation of the brain.[246] Overall, these studies show that both predictable and unpredictable conditions in the environments have the potential to create welfare issues, and thus a balance between the two (i.e. adding certain variability to a predictable environment) may be a solution, although further research is needed to confirm this hypothesis.

In this line, a good way of preparing adult fish to the unpredictability of their environments, both in farms and natural habitats, is adding environmental variability to their rearing setup during their growing stages. For example, hatchery-reared Atlantic cod raised in barren environments receive more attacks, flee more often and have a lower shelter-use than conspecifics reared in variable enriched environments.[39] Similarly, early exposure to variable spatial cues and food regimes generated Atlantic cod more attracted to live prey and faster consumption, with lower latency to explore novel areas, and with faster recovery from a stressful event compared to those reared in barren environments.[249] An unpredictable food regime also alters the development of European sea bass, which grew slower and were bolder than conspecifics raised in a predictable feeding schedule.[241] In Atlantic salmon parr, adding shelter and variability in the water level and direction and velocity of the currents at production-scale densities increased the feeding rates on natural prey,[250] and in smolts, these rearing conditions increased migration speed and survival rate in the wild.[35] Therefore, fish raised in environments with some degree of variability seem to learn and develop flexible behaviour that better prepares them to confront environmental unpredictability compared with fish raised in barren environments. However, spatial variability of the enrichment might not be beneficial for all species. For example, a study on steelhead trout (*O. mykiss*) showed that those exposed to 4 weeks of stable EE had lower latency to explore a novel environment compared to steelhead trouts exposed to either unstable EE or to barren environments.[251] The data dispersion of the steelhead trouts raised in unstable-enriched and barren environments were higher compared to the ones raised in stable EE, which might indicate that the former environmental situations might promote a wider behavioural repertoire, which could include unnatural or maladaptive behaviours.[251] Although the differences between the steelhead trout studies and the previously mentioned research may be due to differences in methodology, it is nonetheless important to test the effects of EE variability in the species of interest before implementing a programme to ensure that the added variability will promote a suitable behavioural repertoire and positive welfare.

2.3.3 | Play and joy

Play is defined as the voluntary and repetitive manipulation of a non-food object, excluding instances of intention/purpose.[252] In this sense, some fish species display behaviours likely to involve positively valenced experiences, or even likely to have the ability to play.[252] Various studies identified three different play behaviour subtypes in fishes: locomotor (e.g. bubble jets/air stone), object manipulation (novel/stimulatory) and social (including human interaction).[206,252-254] Regarding species of aquaculture interest, it is known that salmonids and other fishes can jump into the air from the water, which is highly relevant in net-pen culture since this behaviour can be related to buoyancy regulation, parasitic infections or stress. However, Fagen[255] suggested that some salmonid jumping behaviour may be also a form of play. Encouraging play behaviour, therefore, might be considered as occupational EE, though whether it involves positive emotions in fish is still under debate, and further research is still needed in this field.[256,257]

2.4 | Social enrichment

Social enrichment comprises not only the presence of other individuals and their social interactions, but also the availability of space to interact or avoid other fish, either conspecifics or different species. In this sense, it is important to know whether the reared species is solitary, or likely to shoal in small or big groups at different life-stages, as well as if they usually co-habit with other fish species in the wild. For example, many fish species form shoals in the wild and thus, in captivity, these species may suffer in isolation or in inappropriate spaces to properly shoal. On the other hand, most farmed species that do not shoal in the wild, or associate with other species, are territorial and can engage in aggressive behaviours with conspecifics, which in both cases may be a big problem in the high stocking densities of captive environments.

Stocking density is one of the major aspects to consider in improving fish welfare in monospecific intensive aquaculture, which is the most widespread practice. Diverse studies have demonstrated that different stocking densities can have direct effects on the stress response, growth rate, health and condition of intensively farmed fish. For example, in most farmed fish species, lower densities can improve growth rates and fin condition, reduce injures, promote a better stress response and increase size-homogeneity, and may also lead to positive effects on fish distribution and spatial use.[258,259] Nevertheless, discrepancies found within the literature[259] have highlighted that the effects of stocking density are complex and appear to consist of numerous interacting and case-specific factors[1] and, therefore, require careful consideration.[260] For example, Adams et al.[261] reported that both low and high densities can compromise welfare in Atlantic salmon, and the overall welfare was best at an intermediate density. Appropriate density depends heavily on the behavioural and physiological requirements of each farmed species, as well as on life-stage, rearing system, food availability, social interactions and other environmental parameters (i.e. variations and alterations of water quality).[6,258,259,262,263] Some species, such as catfish species, can tolerate high stocking densities in different farming systems.[264-266] Farming catfish at high densities can lead to higher net fish yields and financial benefits, but exceeding specific stocking densities can also lead to impaired welfare (e.g. skin lessons, infections, mortalities) and problems to ensure long-term sustainability.[28,266-270] Even low stocking densities can have negative effects on welfare of some species and life-stages, mostly affecting social interactions, as social interactions in small groups of fish usually lead to the formation of dominance hierarchies.[271,272] Individuals within the same population are often differentially responsive to risk and use different tactics to compete for limited resources.[272] In general, dominant fish can show more territoriality, holding better positions in the environment and better access to available food, being aggressive towards subordinate fish, which suffer behavioural inhibition, including reduced activity, feeding or mating.[101,102,271] One of the main consequences of high concern for fish farmers is that these social hierarchies can lead to a high inter-individual growth variability, and even increase mortality within the rearing system, suggested as an adaptative strategy to optimise survival of the population in a restricted space.[273]

Social interactions are also influenced by the physiological and behavioural differences in stress responses of each individual within a population or rearing unit, namely stress copying styles or personalities, which can have relevant consequences for aquaculture.[274] In addition, several studies have demonstrated the ability of diverse farmed fish to recognise familiar conspecifics and consequent positive effects on social interactions.[29,146,275] Familiarity stabilises the hierarchical structure of a group, and governs behavioural modifications (e.g. agonistic behaviours) that promote feeding and growth, leading to higher fitness and survival.[29,275] Therefore, besides being affected by densities in relation to space, food distribution and food quantity, social interactions are also affected by familiarity and personality, and all these factors might be modulated through social enrichment, but also through feeding strategies (see dietary enrichment, section 2.5). Moreover, it is also important to consider that in farm conditions, it is possible to find more than one species in the same rearing unit, with some associated effects for welfare. For example, cleaner-fish such as lumpish and diverse wrasse species are reared in net-pens together with adult salmon to reduce their parasitic load by feeding on the salmon lice copepod,[103] although recent evidence highlights the questions on welfare and sustainability benefits of such practices, especially for the lumpfish and wrasse themselves.[276] Noble et al.[277] reported that growth performance and welfare of white-spotted charr (*Salvelinus leucomaenis*), which are poor self-feeders, may be improved by growing them in tandem with experienced and proficient self-feeding rainbow trout. Recently, Thomas et al.[278] showed positive effects on growth parameters and behavioural changes of juvenile zander (*Sander lucioperca*) cultured in recirculating systems (RAS) with other species, such as sterlet (*Acipenser ruthenus*) or tench (*Tinca tinca*). Another example of co-existing different species, and therefore another kind of social enrichment strategy, is the polyculture in Asian and African ponds, where mainly several species of carps (e.g. *Hypophthalmichthys molitrix*, *Aristichthys nobilis*, *Cyprinus spp.*) are reared together given their compatible spatial-trophic habits.[279] In addition, diverse fish species can also be reared together in extensive and semi-intensive earthen ponds in estuarine areas of Southern Europe, such as European eel (*Anguila anguila*), grey mullet (*Liza spp.*) or flatfishes (*Solea spp.*), which already co-exist in natural conditions.[280,281]

Finally, Fife-Cook and Franks[206] recently suggested the possibility of directed fish-human interaction. According to these authors, this kind of inter-specific interaction may be motivated by curiosity, presenting an opportunity to explore and exercise agency, which could serve as a source of cognitive stimulation for some species of captive fish. However, before considering fish–human interaction as social enrichment, further work is still needed to explore this possibility.

2.5 | Dietary enrichment

The last, but not the least, strategy to enrich the environment and thus the lives of captive fish is related to their diet. Dietary enrichment refers to the food type or feeding strategy (distribution, quantity, periodicity, etc.) which mostly affects foraging behaviour or food intake, but it does not include the composition of the diet (which would be considered "internal or nutritional" enrichment). Feeding strategies play an important role here as dietary enrichment, given that feeding regimens, schedules and procedures can highly affect, positively or negatively, fish welfare status.[1,282] An appropriate feeding strategy adjusted to the biological needs of each species and life-stage can help control foraging behaviour and reduce undesired behavioural responses and social interactions. However, foraging behaviour is one of the widest and most complex areas of investigation, and it is difficult to develop a universal feeding strategy.[283] Many species-specific factors are involved in the feeding strategies and tactics of fish, such as feeding rhythms, food ratio and feeding time.

In general, a self-feeding system improves fish welfare, allowing fish to choose their optimal feeding time and food ratio.[283] However, automatic feeders can be used to deliver small quantities of feed at short intervals, whereas hand feeding allows better observation of fish reaction to the feed and reduces feed wastage, although increasing the labour demand. Farmers can also use feed spreaders that facilitate a more uniform and automatic distribution of feed throughout the rearing unit.[284,285] It is noteworthy that a combination of feeding strategies appears most appropriate, but the observation of fish feeding response is essential and allows a quick adjustment of feeding strategies and diets, as well as a reduction of feed waste. Therefore, fish hunger and food availability are the main factors affecting fish welfare and effective production.[282,286] A proper food availability consists on adequate distribution of food in time and space, food ration size, and food particle characteristics.[282] In addition, farmers can benefit from current innovative, rapid, and non-invasive technology, such as intelligent feeding control methods (i.e. mathematical models, acoustic methods, optical sensors, and computer vision), which have improved drastically in recent years[287,288] and are moving aquaculture towards a precision farming activity.[289,290] Nevertheless, the implementation of technological developments is not feasible in all aquaculture facilities, as the initial financial investment may be high.

On the other hand, the selection of the appropriate type of feed as an enrichment strategy is also important. Feeds can be formulated diets (pelleted/extruded) or live prey, such as those used in hatcheries or in extensive and polyculture aquaculture. Indeed, periphyton-based aquaculture in earthern ponds, which is considered physical EE (see section 2.1.3), can be considered also dietary EE, given that the structures provide well-oxygenated surfaces for periphyton to grow on, and the periphyton serves as food for many cichlids and cyprinids in aquaculture.[112] Regarding formulated diets, they can be of different sizes and shapes, flavours, enhancers, texture, palatability and colour.[291] Feeds can be also formulated to sink or float depending on where the fish usually feed within the water column. Taste preference or evaluation of sensory quality of grasped food items is a well-developed sense in fish, consisting mainly of the gustatory system.[292] Such preferences in fishes are widely known for the many carnivorous species of farming interest, but also for some herbivorous species, and such knowledge is highly relevant for the feeding behaviour and preferences of each farmed species, also considering its life-stage and rearing systems, in order to improve the welfare status of captive fish (see section 2.2.3). Feed manufacturers already consider all these characteristics, and fish farmers can follow the manufacturer's suggestions, choosing and selecting those feeds that are best suited to their fish.

3 | ENVIRONMENTAL ENRICHMENT AT FARMS: GUIDELINES AND CONSIDERATIONS

This review presents compelling evidence that EE influences the biological functions of fish in captivity. Appropriate enrichment increases the biological relevance of the living environment and promotes good welfare, both through overall health improvements and increased resilience to stressors. This is, to our knowledge, the most complete collection of studies regarding the full spectrum of EE and its effects in farmed fish to date. Nevertheless, these effects often vary in direction and magnitude, and each species and life-stage needs special consideration with respect to its natural history and preferences. In order to apply appropriate EE strategies, a possible first approach could be to evaluate specific preferences[293] for different environmental resources or characteristics. This allows us to better identify which resources or characteristics fish really want, which is in line with the idea that to improve animal welfare, we should pay more attention to the wants and needs of the animals.[294,295] In addition, determining their motivation to access specific resources is a complementary strategy that tells us *how much* the animal wants such preferable resources,[296] thus highlighting which of them are more important than others. Preference and motivation tests differ in their approach (e.g.[102,242,293,297,298]), but they both present an integrative view of what resources fish want and how much they want it. It is also important to consider that some EE features may be actively avoided and may represent a behavioural barrier preventing fish to access specific areas of the environment,[299] and thus should also be taken into account for welfare purposes. The implementation of EE based on preferences and avoidances of fish is challenging, because fish are known to have considerable individual variability of preference responses.[298,300] However, determining group preferences or, at least, which characteristics are preferred or avoided by the majority can help to better plan and implement EE strategies for farmed fish. This determination of fish needs and wants may be best achieved by an ethological approach: by addressing the causes and functions of behaviour (known as Tinbergen's 4 questions[301]), fish farmers can identify EE opportunities with the best probability of resulting in relevant improvements for their animals.[302] For example, benthic species should benefit from substrate enrichment, which should nevertheless be appropriate for the life-stage in size and type. Conversely, there may be little advantage in providing physical enrichment for pelagic species or life-stages; instead, these fish would benefit more from occupational enrichment under the form of currents, or sensory enrichment such as wall/substrate colour patterns. This nature-based approach towards EE departs from the assumption that domestication in fish is very recent,[4,5,302,303] and therefore, farmed fish species have essentially the same fundamental needs as their wild counterparts. The biology of fish in the wild is also highly informative on their welfare state because farmers can, for example, compare the behaviour observed in their systems with the known behaviours in the natural environment and use those comparisons as indicators of welfare.[304] This is a central message of this review: the implementation of EE should be based on scientific knowledge of the animal, adapt the methods to the species and life stage and use the biology in the wild as a guideline, yet having in consideration the technical limitations (and possibilities) of each rearing systems.

The effective implementation of EE strategies at a commercial scale is still incipient. This may have two main sets of reasons:

1. *Apparent cacophony of results*: Several studies showed contradictory, undesired or unexpected results, which in most cases may reflect the use of inadequate design (or materials) for each species, life-stage and rearing condition. The effects of structural enrichment (probably the most direct form of EE) have been shown to be inconsistent amongst species, and therefore enrichment techniques may need to be adapted according to species-specific considerations. It should be noted that the specific items used as enrichment features vary between and within studies[23,24] and may be responsible for the differences found. Reporting fine-scale characteristics of items used as enrichment in studies may help to reveal these last factors.[24] Natural environments cannot be exactly recreated in farming systems, so the objective when designing enrichment is to modify elements of the artificial environments in order to provide welfare benefits without compromising the biosecurity of the farms. Hygiene and biosecurity currently seem to be the main concerns regarding physical EE; some structures or objects may accumulate food particles and faeces, making cleaning and disinfection difficult and compromising fish health and overall welfare. It can also happen that the structures leak out potentially hazardous chemicals to the environment (e.g. PVC phthalates), or that their design is inadequate and causes physical or psychological disturbances or damage to the fish (e.g. small holes, cracks, protrusions, noise), increasing the risk of infection, stress or mortality. All these factors should be considered when planning EE, and contingency plans as well as corrective actions (e.g. increasing or modifying cleaning

routines, monitoring fish behaviour upon deployment of EE, quickness to respond to negative effects) must be considered. Another aspect to consider is that the introduction of new objects in the environment can cause negative mental states ("neophobia") in some fish, or an increase of territoriality and aggressive/defensive attacks.[45,305] In addition, the type and intensity of EE should take into consideration the ethology of the species, so that the method is adapted to the fish and not the other way around,[5,306] as well as the allostatic effect of the enrichment measures: whilst too little (or inefficient) stimulation will not produce positive effects, too much (or wrong) stimulation will produce distress.[5,307] For example, in the case of forced-swimming exercise, currents may differ in different areas of the tank, subjecting some fish to too much or too little exercise; and social enrichment can cause stress by densities being too high[262,308] or too low.[309,310] Potential synergistic effects of two or more types of enrichment or stimulus that can amplify, reduce or even eliminate one another should also be considered when implementing EE strategies for farmed fish. In this sense, it should be noted that many types of EE may have already been tested in many more species than is known but, due to publication bias, the existing knowledge may be limited to the few that produced clearly visible or short-term effects.

2. *Industry hesitation*: Existing fish farming methods are mostly designed on practical, functional, economic and ergonomic requirements. Consequently, operational protocols in fish farms have been built on efficiency standards for such systems. However, most systems and methods have been designed when the science behind fish welfare, and specifically EE, was still in its early days. The implementation of EE requires a transformation of existing methods and protocols, so there may be an understandable resistance to change by the industry stakeholders, especially in a case where the results of such transformation do not seem to be consistent (see previous point). Any transformation or implementation at industrial scale entails a considerable financial investment, including time and personnel, and final results must be reputational and economically profitable. Furthermore, the challenges to implement EE differ regarding the type of system; whilst in extensive and semi-intensive farming, the deployment of EE may be feasible without much disruption to operational protocols, in intensive or ultra-intensive systems any small change may require large transformations in the procedures and may impact a huge number of animals (both negatively or positively). Finally, enrichment protocols may be protected by corporate secrecy, or there may simply be lack of stimulation to disseminate and share knowledge publicly. The industry would greatly benefit from consistent, reliable studies at a commercial scale, since much of the information remains in pilot or laboratory scale. This is especially relevant when market environments are changing; in the case of certification schemes, major labels are moving towards welfare standards and new requirements. The Friend Of the Sea ® label, for example, now requires at least some form of EE for most of their certified farmed fish species.[311] It would therefore be in the best interest of the sector to respond to these market requirements. Comparing with the poultry and pig farming industry, these sectors stand out for how long there has been a push towards more welfare-friendly practices,[312] and how recent are the advances in welfare requirements, specifically in EE.[313,314] This represents an opportunity of the fish farming sector to catch up with its terrestrial counterpart, learn from its path and gain traction. Regardless of the main driver for this change (ethical, reputational, economic) what should be noted is that fish welfare awareness is already at an advanced stage, especially in the EU, from campaigns and retailer bans to certification and legislation (e.g.[7,10,311,315,316]). It is therefore time for research and industry to join forces so that EE in fish effectively works for the benefit of all parts.

Overall, EE strategies show the same pattern; there is no single silver bullet to design a fit-for-all EE strategy in any category. Interventions should be carefully planned, always considering that each combination of species, life stage, size, and type of group, density, type of rearing methods, type of operation, and so on, renders a unique arrangement that must be taken into account when designing and implementing EE[260,317] in a commercial setting. The implementation of EE is, therefore, a process that requires caution and validation at each step. Consequently, we propose a decision-making framework to assist the process of implementation of EE in aquaculture in order to obtain positive benefits for the fish and the company (Figure 1). The selection, design and development of each EE strategy must be nourished with relevant information on both the target fish and farming facilities from the outset. Each strategy must then be validated by following a series of steps aimed at obtaining the desired results, starting from experimental approaches and scaling up. Based on these results, a cost-benefit analysis must be performed, considering the potential rewards expected from the EE implementation but also the total costs associated with taking that action or strategy in place. Farming companies have production demands whilst simultaneously need to meet the regulators and market expectations, which can lead to conflicts between protection and production.[318] Ideally, an appropriate EE strategy must provide benefits for the fish and the company, such as improving the health and welfare of the captive fish, increasing the growth performance and resistance to diseases, which increases the product quality, reduces associated economic costs, improves rearing standards and overall improves the ethics and public perception of the company. If desired results are obtained from these analyses, implementation will then proceed. However, a close long-term monitoring of the implemented strategy should be carried out in order to evaluate its effects and to be able to apply corrective measures if necessary. Indeed, the application of operational welfare indicators (OWIs) throughout this process, such as specific behaviours or physiological parameters,[319] is highly recommended for a much more accurate and successful assessment of the selected EE strategy on fish welfare. In addition, the use of precision fish farming tools[289,290] could provide a technological support for farmers to monitor OWIs and safely implement measures that have the potential to greatly

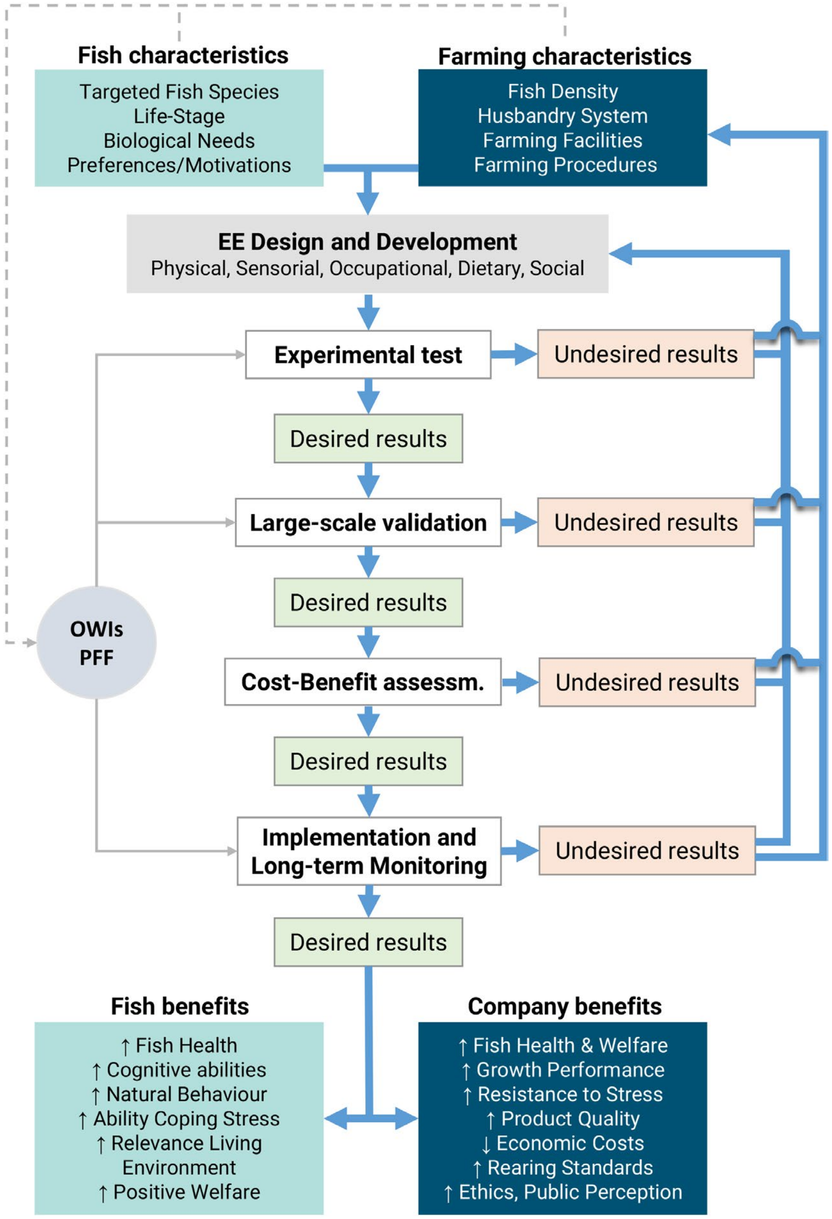

FIGURE 1 Decision-making scheme about the procedures from designing and developing environmental enrichment (EE) strategies to validation, final implementation and monitoring at commercial scale, to obtain both fish and company benefits in fish aquaculture. Abbreviations: OWIs, operational welfare indicators; PFF, precision fish farming

improve the lives of countless farmed individuals. In case of undesired results in any of the steps described above, modifications in the design and development of the strategy should be made, applying the experience gained so far. In addition, the possibility of making modifications to some of the characteristics of the aquaculture facilities so that these, together with the EE strategy, are adapted to the fish, should be also reconsidered.

4 | CONCLUDING REMARKS

This paper reviews the range of possibilities and strategies for EE to be applied to different species of commercial interest and farming systems, in order to guarantee or improve the welfare of captive fish. It is clear that EE can improve the well-being of fish in captivity, providing stimulation to help meet their behavioural, physiological and psychological needs, increasing resilience and consequently reducing factors that impair not only welfare but also production. However, the effects of different EE often vary in direction and magnitude, and highly depend on each species and life-stage needs, preferences and natural history, combined with the characteristics of the fish farming system. Based on scientific knowledge, we discuss the feasibility and potential applications of different EE strategies, considering challenges and benefits for the aquaculture sector. We also provide a decision-making framework to address the design, validation and application of EE at industrial scale. Nevertheless, the evidence base on this topic is still growing, and as such there are knowledge gaps regarding how environmental conditions should be modified to achieve all of the desired fish welfare and commercial benefits. Therefore, there is a need for further research and knowledge on the context-specific effects of different enrichment strategies for as many species and farming systems as possible, but above all, to demonstrate on-farm the applicability and feasibility of these strategies at commercial scale.

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REFERENCES

1. Ashley PJ. Fish welfare: Current issues in aquaculture. *Appl Anim Behav Sci*. 2007;104(3):199-235. https://doi.org/10.1016/j.applanim.2006.09.001
2. Poli BM. Farmed fish welfare-suffering assessment and impact on product quality. *Ital J Anim Sci*. 2009;8(sup1):139-160. https://doi.org/10.4081/ijas.2009.s1.139
3. Poli BM, Parisi G, Scappini F, Zampacavallo G. Fish welfare and quality as affected by pre-slaughter and slaughter management. *Aquac Int*. 2005;13(1):29-49. https://doi.org/10.1007/s10499-004-9035-1
4. Teletchea F, Fontaine P. Levels of domestication in fish: implications for the sustainable future of aquaculture. *Fish Fish*. 2012;15(2):181-195. https://doi.org/10.1111/faf.12006
5. Saraiva JL, Castanheira MF, Arechavala-López P, Volstorf J, Heinzpeter SB. Domestication and welfare in farmed fish. In Teletchea F ed. *Animal domestication*. IntechOpen; 2018:29. https://doi.org/10.5772/intechopen.77251
6. Huntingford FA, Adams C, Braithwaite VA, et al. Current issues in fish welfare. *J Fish Biol*. 2006;68(2):332-372. https://doi.org/10.1111/j.0022-1112.2006.001046.x
7. Eurogroup for Animals, Compassion in World Farming. *Fish Welfare Survey*; 2018. Accessed October 21, 2019. https://www.comresglobal.com/polls/eurogroup-for-animals-ciwf-fish-welfare-survey/
8. Brydges NM, Braithwaite VA. Does environmental enrichment affect the behaviour of fish commonly used in laboratory work? *Appl Anim Behav Sci*. 2009;118(3–4):137-143. https://doi.org/10.1016/j.applanim.2009.02.017
9. Huntingford FA, Kadri S. Defining, assessing and promoting the welfare of farmed fish. *Rev Sci Tech OIE*. 2014;33(1):233-244. https://doi.org/10.20506/rst.33.1.2286
10. Giménez-Candela T, Saraiva JL, Bauer H. The legal protection of farmed fish in Europe : analysing the range of EU legislation and the impact of international animal welfare standards for the fishes in European aquaculture. *Derecho Anim Forum Anim Law Stud*. 2020;11(1):0065-0118. https://doi.org/10.5565/rev/da.460
11. Bolt SL, George AJ. The use of environmental enrichment on farms benefits animal welfare and productivity. *Livestock*. 2019;24(4):183-188. https://doi.org/10.12968/live.2019.24.4.183
12. Brown C. Fish intelligence, sentience and ethics. *Anim Cogn*. 2015;18(1):1-17. https://doi.org/10.1007/s10071-014-0761-0
13. Brown C. Fish pain: An inconvenient truth. *Anim Sentience*. 2016;1(3). https://animalstudiesrepository.org/animsent/vol1/iss3/32
14. Sneddon L, Lopez-Luna J, Wolfenden D, et al. Fish sentience denial: Muddying the waters. *Anim Sentience*. 2018;3(21). https://animalstudiesrepository.org/animsent/vol3/iss21/1
15. Sneddon LU. Comparative physiology of nociception and pain. *Physiology*. 2018;33(1):63-73. https://doi.org/10.1152/physiol.00022.2017
16. Gerber B, Stamer A, Stadtlander T. *Environmental Enrichment and Its Effects on Welfare in Fish*. nic Aquacultre; 2015:74.
17. Mellor D, Beausoleil N. Extending the "Five Domains" model for animal welfare assessment to incorporate positive welfare states. *Anim Welf*. 2015;24(3):241-253. https://doi.org/10.7120/09627286.24.3.241
18. Mellor DJ. Updating animal welfare thinking: Moving beyond the "Five Freedoms" towards "A Life Worth Living". *Animals*. 2016;6(3):21. https://doi.org/10.3390/ani6030021
19. Green TC, Mellor DJ. Extending ideas about animal welfare assessment to include 'quality of life' and related concepts. *N Z Vet J*. 2011;59(6):263-271. https://doi.org/10.1080/00480169.2011.610283
20. Williams TD, Readman GD, Owen SF. Key issues concerning environmental enrichment for laboratory-held fish species. *Lab Anim*. 2009;43(2):107-120. https://doi.org/10.1258/la.2007.007023
21. Stevens CH, Croft DP, Paull GC, Tyler CR. Stress and welfare in ornamental fishes: what can be learned from aquaculture?: stress and welfare in ornamental fishes. *J Fish Biol*. 2017;91(2):409-428. https://doi.org/10.1111/jfb.13377
22. Stevens CH, Reed BT, Hawkins P. Enrichment for laboratory zebrafish—A review of the evidence and the challenges. *Animals*. 2021;11(3):698. https://doi.org/10.3390/ani11030698
23. Näslund J, Johnsson JI. Environmental enrichment for fish in captive environments: effects of physical structures and substrates. *Fish Fish*. 2016;17(1):1-30. https://doi.org/10.1111/faf.12088
24. Jones NAR, Webster M, Vea Salvanes AG. Physical enrichment research for captive fish: time to focus on the DETAILS. *J Fish Biol*. 99(3), 704-725. https://doi.org/10.1111/jfb.14773
25. McLean E. Fish tank color: An overview. *Aquaculture*. 2021;530:735750. https://doi.org/10.1016/j.aquaculture.2020.735750
26. Hecht T, Appelbaum S. Observations on intraspecific aggression and coeval sibling cannibalism by larval and juvenile *Claias gariepinus* (Clariidae: Pisces) under controlled conditions. *J Zool*. 1988;214(1):21-44. https://doi.org/10.1111/j.1469-7998.1988.tb04984.x
27. Hossain MAR, Beveridge MCM, Haylor GS. The effects of density, light and shelter on the growth and survival of African catfish (*Clarias gariepinus* Burchell, 1822) fingerlings. *Aquaculture*. 1998;160(3–4):251-258. https://doi.org/10.1016/S0044-8486(97)00250-0
28. Coulibaly A, Ouattara IN, Koné T, et al. First results of floating cage culture of the African catfish Heterobranchus longifilis Valenciennes, 1840: Effect of stocking density on survival and growth rates. *Aquaculture*. 2007;263(1–4):61-67. https://doi.org/10.1016/j.aquaculture.2006.11.022
29. Slavík O, Maciak M, Horký P. Shelter use of familiar and unfamiliar groups of juvenile European catfish Silurus glanis. *Appl Anim Behav Sci*. 2012;142(1–2):116-123. https://doi.org/10.1016/j.applanim.2012.09.005
30. Arsin NE, Estim A, Mustafa S. Behaviour and response of Japanese Catfish (*Silurus asotus*) in captivity provided with an artificial microhabitat mosaic. *Aquat Res*. 2018;1(3):136-139. https://doi.org/10.3153/AR18015

31. Chi VV, True JD. Effects of habitat structure and salinity on growth and survival of juvenile mangrove red snapper Lutjanus argentimaculatus (Forsskal, 1775). *Songklanakarin J Sci Technol*. Published online 2018. https://rdo.psu.ac.th/sjstweb/journal/40-6/2.pdf Accessed September 10, 2020.
32. Pounder KC, Mitchell JL, Thomson JS, Pottinger TG, Buckley J, Sneddon LU. Does environmental enrichment promote recovery from stress in rainbow trout? *Appl Anim Behav Sci*. 2016;176:136-142. https://doi.org/10.1016/j.applanim.2016.01.009
33. Ahlbeck Bergendahl I, Miller S, Depasquale C, Giralico L, Braithwaite VA. Becoming a better swimmer: structural complexity enhances agility in a captive-reared fish: structural complexity enhances agility. *J Fish Biol*. 2017;90(3):1112-1117. https://doi.org/10.1111/jfb.13232
34. Cogliati KM, Herron CL, Noakes DLG, Schreck CB. Reduced stress response in juvenile Chinook Salmon reared with structure. *Aquaculture*. 2019;504:96-101. https://doi.org/10.1016/j.aquaculture.2019.01.056
35. Hyvärinen P, Rodewald P. Enriched rearing improves survival of hatchery-reared Atlantic salmon smolts during migration in the River Tornionjoki. *Can J Fish Aquat Sci*. 2013;70(9):1386-1395. https://doi.org/10.1139/cjfas-2013-0147
36. Salvanes AGV, Moberg O, Ebbesson LOE, Nilsen TO, Jensen KH, Braithwaite VA. Environmental enrichment promotes neural plasticity and cognitive ability in fish. *Proc R Soc B Biol Sci*. 2013;280(1767):20131331. https://doi.org/10.1098/rspb.2013.1331
37. Karvonen A, Aalto-Araneda M, Virtala A-M, Kortet R, Koski P, Hyva P. Enriched rearing environment and wild genetic background can enhance survival and disease resistance of salmonid fishes during parasite epidemics. *J Appl Ecol*. 2016;53(1):213-221.
38. Räihä V, Sundberg L, Ashrafi R, Hyvärinen P, Karvonen A. Rearing background and exposure environment together explain higher survival of aquaculture fish during a bacterial outbreak. *J Appl Ecol*. 2019;56(7):1741-1750. https://doi.org/10.1111/1365-2664.13393
39. Salvanes AGV, Braithwaite VA. Exposure to variable spatial information in the early rearing environment generates asymmetries in social interactions in cod (*Gadus morhua*). *Behav Ecol Sociobiol*. 2005;59(2):250-257. https://doi.org/10.1007/s00265-005-0031-x
40. Salvanes AGV, Moberg O, Braithwaite VA. Effects of early experience on group behaviour in fish. *Anim Behav*. 2007;74(4):805-811. https://doi.org/10.1016/j.anbehav.2007.02.007
41. Moberg O, Braithwaite VA, Jensen KH, Salvanes AGV. Effects of habitat enrichment and food availability on the foraging behaviour of juvenile Atlantic Cod (*Gadus morhua* L). *Environ Biol Fishes*. 2011;91(4):449-457. https://doi.org/10.1007/s10641-011-9803-5
42. Zimmermann EW, Purchase CF, Fleming IA. Reducing the incidence of net cage biting and the expression of escape-related behaviors in Atlantic cod (*Gadus morhua*) with feeding and cage enrichment. *Appl Anim Behav Sci*. 2012;141(1–2):71-78. https://doi.org/10.1016/j.applanim.2012.07.009
43. Zhang Z, Fu Y, Zhang Z, Zhang X, Chen S. A Comparative Study on Two Territorial Fishes: The Influence of Physical Enrichment on Aggressive Behavior. *Animals*. 2021;11(7):1868. https://doi.org/10.3390/ani11071868
44. Barley AJ, Coleman RM. Habitat structure directly affects aggression in convict cichlids Archocentrus nigrofasciatus. *Curr Zool*. 2010;56(1):52-56. https://doi.org/10.1093/czoolo/56.1.52
45. Barreto RE, Carvalho GGA, Volpato GL. The aggressive behavior of Nile tilapia introduced into novel environments with variation in enrichment. *Zoology*. 2011;114(1):53-57. https://doi.org/10.1016/j.zool.2010.09.001
46. Torrezani CS, Pinho-Neto CF, Miyai CA, Sanches FHC, Barreto RE. Structural enrichment reduces aggression in *Tilapia rendalli*. *Mar Freshw Behav Physiol*. 2013;46(3):183-190. https://doi.org/10.1080/10236244.2013.805053
47. Zhang Z, Zhang X, Li Z, Zhang X. Effects of different levels of environmental enrichment on the sheltering behaviors, brain development and cortisol levels of black rockfish Sebastes schlegelii. *Appl Anim Behav Sci*. 2019;218:104825. https://doi.org/10.1016/j.applanim.2019.06.006
48. Zhang Z, Xu X, Wang Y, Zhang X. Effects of environmental enrichment on growth performance, aggressive behavior and stress-induced changes in cortisol release and neurogenesis of black rockfish Sebastes schlegelii. *Aquaculture*. 2020;528:735483. https://doi.org/10.1016/j.aquaculture.2020.735483
49. Zhang Z, Bai Q, Xu X, Guo H, Zhang X. Effects of environmental enrichment on the welfare of juvenile black rockfish Sebastes schlegelii: Growth, behavior and physiology. *Aquaculture*. 2020;518:734782. https://doi.org/10.1016/j.aquaculture.2019.734782
50. Zhang Z, Fu Y, Guo H, Zhang X. Effect of environmental enrichment on the stress response of juvenile black rockfish Sebastes schlegelii. *Aquaculture*. 2021;533:736088. https://doi.org/10.1016/j.aquaculture.2020.736088
51. Zhang Z, Fu Y, Shen F, Zhang Z, Guo H, Zhang X. Barren environment damages cognitive abilities in fish: Behavioral and transcriptome mechanisms. *Sci Total Environ*. 2021;794:148805. https://doi.org/10.1016/j.scitotenv.2021.148805
52. Alnes IB, Jensen KH, Skorping A, Salvanes AGV. Ontogenetic change in behavioral responses to structural enrichment from fry to parr in juvenile Atlantic Salmon (*Salmo salar* L.). *Front Vet Sci*. 2021;8:638888. https://doi.org/10.3389/fvets.2021.638888
53. Saraiva SDO, Pompeu PS The effect of structural enrichment in hatchery tanks on the morphology of two neotropical fish species. *Neotropical Ichthyol*. 2014;12(4):891-901. https://doi.org/10.1590/1982-0224-20130201
54. Muggli AM, Barnes JM, Barnes ME. Vertically-suspended environmental enrichment alters the velocity profiles of circular fish rearing tanks. *World J Eng Technol*. 2019;7:208-2016.
55. Caasi JMA, Barnes JM, Barnes ME. Impact of vertically-suspended environmental enrichment and two densities of fish on circular tank velocity profiles. *Engineering*. 2020;12(10):723-738. https://doi.org/10.4236/eng.2020.1210051
56. Jones MD, Krebs E, Huysman N, Voorhees JM, Barnes ME. Rearing performance of atlantic salmon grown in circular tanks with vertically-suspended environmental enrichment. *Open J Anim Sci*. 2019;09(02):249-257. https://doi.org/10.4236/ojas.2019.92021
57. White SC, Krebs E, Huysman N, Voorhees JM, Barnes ME. Use of suspended plastic conduit arrays during brown trout and rainbow trout rearing in circular tanks. *North Am J Aquac*. 2019;81(1):101-106. https://doi.org/10.1002/naaq.10076
58. Kientz JL, Barnes ME. Structural complexity improves the rearing performance of rainbow trout in circular tanks. *North Am J Aquac*. 2016;78(3):203-207. https://doi.org/10.1080/15222055.2016.1159629
59. Crank KM, Kientz JL, Barnes ME. An evaluation of vertically suspended environmental enrichment structures during rainbow trout rearing. *North Am J Aquac*. 2019;81(1):94-100. https://doi.org/10.1002/naaq.10064
60. Voorhees JM, Huysman N, Krebs E, Barnes ME. Influence of water velocity and vertically-suspended structures on rainbow trout rearing performance. *Open J Anim Sci*. 2019;10(1):152-161. https://doi.org/10.4236/ojas.2020.101008
61. Voorhees JM, Huysman N, Krebs E, Barnes ME. Use of exercise and structure during rainbow trout rearing. *Open J Appl Sci*. 2020;10(5):258-269. https://doi.org/10.4236/ojapps.2020.105020
62. Kientz JL, Crank KM, Barnes ME. Enrichment of circular tanks with vertically suspended strings of colored balls improves rainbow trout rearing performance. *North Am J Aquac*. 2018;80(2):162-167. https://doi.org/10.1002/naaq.10017

63. Huysman N, Krebs E, Voorhees JM, Barnes ME. Use of two vertically-suspended environmental enrichment arrays during rainbow trout rearing in circular tanks. *Int J Innov Stud Aquat Biol Fish*. 2019;5(1). https://doi.org/10.20431/2454-7670.0501005
64. Morris B, Voorhees JM, Huysman N, Krebs E, Barnes M. Effects of intermittent exercise during initial rainbow trout oncorhynchus mykiss rearing in tanks containing vertically-suspended environmental enrichment. *Aquac Fish Stud*. 2020;2(2):1-4. https://doi.org/10.31038/AFS.2020225
65. Rosburg AJ, Fletcher BL, Barnes ME, Treft CE, Bursell BR. Vertically-suspended environmental enrichment structures improve the growth of juvenile landlocked fall chinook salmon. *Int J Innov Stud Aquat Biol Fish*. 2019;5(1):17-24.
66. Voorhees JM, Huysman N, Krebs E, Barnes ME. Exercise and structure improve juvenile chinook salmon rearing performance. *Open J Mar Sci*. 2021;11(2):80-91. https://doi.org/10.4236/ojms.2021.112006
67. Jones MD, Voorhees JM, Huysman N, Krebs E, Barnes M. Use of different colours of vertically-suspended structure during the hatchery rearing of juvenile landlocked fall Chinook salmon (Oncorhynchus tshawytscha, Walbaum). *Int J Fish Aquac*. 2020;12(2):21-25. https://doi.org/10.5897/IJFA2019.0762
68. Meza E, Jones MD, Huysman N, Voorhees JM, Barnes ME. Color of vertically-suspended structure does not impact the growth of rainbow trout reared in circular tanks. *Open J Anim Sci*. 2020;10(04):706-713. https://doi.org/10.4236/ojas.2020.104045
69. Arechavala-Lopez P, Diaz-Gil C, Saraiva JL, et al. Effects of structural environmental enrichment on welfare of juvenile seabream (*Sparus aurata*). *Aquac Rep*. 2019;15:100224. https://doi.org/10.1016/j.aqrep.2019.100224
70. Arechavala-Lopez P, Caballero-Froilán JC, Jiménez-García M, et al. Enriched environments enhance cognition, exploratory behaviour and brain physiological functions of Sparus aurata. *Sci Rep*. 2020;10(1):11252. https://doi.org/10.1038/s41598-020-68306-6
71. Muñoz L, Aspillaga E, Palmer M, Saraiva JL, Arechavala-Lopez P. Acoustic telemetry: A tool to monitor fish swimming behavior in sea-cage aquaculture. *Front Mar Sci*. 2020;7:645. https://doi.org/10.3389/fmars.2020.00645
72. McVicar AH, White PG. The prevention and cure of an infectious disease in cultivated juvenile Dover sole, *Solea solea* (L.). *Aquaculture*. 1982;26(3–4):213-222. https://doi.org/10.1016/0044-8486(82)90157-0
73. Ottesen OH, Strand HK. Growth, development, and skin abnormalities of halibut (*Hippoglossus hippoglossus* L.) juveniles kept on different bottom substrates. *Aquaculture*. 1996;146(1):17-25. https://doi.org/10.1016/S0044-8486(96)01359-2
74. Kang D-Y, Kim H-C. Importance of bottom type and background color for growth and blind-side hypermelanosis of the olive flounder. *Paralichthys Olivaceus*. *Aquac Eng*. 2013;57:1-8. https://doi.org/10.1016/j.aquaeng.2013.05.001
75. Iwata N, Kikuchi K. Effects of sandy substrate and light on hypermelanosis of the blind side in cultured Japanese flounder Paralichthys olivaceus. *Environ Biol Fishes*. 1998;52(1–3):291-297. https://doi.org/10.1023/a:1007493913799
76. Dou S, Seikai T, Tsukamoto K. Cannibalism in Japanese flounder juveniles, Paralichthys olivaceus, reared under controlled conditions. *Aquaculture*. 2000;182(1):149-159. https://doi.org/10.1016/S0044-8486(99)00256-2
77. Ottesen OH, Noga EJ, Sandaa W. Effect of substrate on progression and healing of skin erosions and epidermal papillomas of Atlantic halibut, *Hippoglossus hippoglossus* (L.). *J Fish Dis*. 2007;30(1):43-53. https://doi.org/10.1111/j.1365-2761.2007.00780.x
78. Kang D-Y, Kim H-C. Relevance of environmental factors and physiological pigment hormones to blind-side hypermelanosis in the cultured flounder, *Paralichthys olivaceus*. *Aquaculture*. 2012;356–357:14-21. https://doi.org/10.1016/j.aquaculture.2012.05.041
79. Kang DY, Kim H-C, Myeong J-I, Min BH. Effect of infiltrating substrate on growth and double-sided pigmentation of flounder (*Paralichthys olivaceus*) fry. *Journal of the Korean Society for Fisheries Science*. 2014;47(4):406-412. https://doi.org/10.5657/KFAS.2014.0406
80. Kim W-J. Influence of background color and substratum on the blind-side hypermelanosis in starry flounder *Plathchthys stellatus*. *J Fish Mar Sci Educ*. 2016;28(3):841-847. https://doi.org/10.13000/JFMSE.2016.28.3.841
81. McVicar AH. Black patch necrosis of the skin of *Solea solea* (L.): the role of sand in prophylaxis and treatment. *J Fish Dis*. 1987;10(1):59-63. https://doi.org/10.1111/j.1365-2761.1987.tb00719.x
82. Almansa C, Oca J, Claramunt J, Reig L. Influence of tank bottom surface on growth and welfare of *Senegalese sole* (*Solea senegalensis*). *Aquac Eng*. 2017;78:205-215. https://doi.org/10.1016/j.aquaeng.2017.07.009
83. Reiser S, Pohlmann DM, Blancke T, Koops U, Trautner J. Environmental enrichment during early rearing provokes epigenetic changes in the brain of a salmonid fish. *Comp Biochem Physiol Part D Genomics Proteomics*. 2021;39:100838. https://doi.org/10.1016/j.cbd.2021.100838
84. Bosakowski T, Wagner EJ. Experimental use of cobble substrates in concrete raceways for improving fin condition of cutthroat (*Oncorhynchus clarki*) and rainbow trout (*O. mykiss*). *Aquaculture*. 1995;130(2):159-165. https://doi.org/10.1016/0044-8486(94)00223-B
85. Wagner EJ, Intelmann SS, Routledge MD. The effects of fry rearing density on hatchery performance, fin condition, and agonistic behavior of rainbow trout oncorhynchus mykiss fry. *J World Aquac Soc*. 1996;27(3):264-274. https://doi.org/10.1111/j.1749-7345.1996.tb00608.x
86. Arndt RE, Routledge MD, Wagner EJ, Mellenthin RF. Influence of raceway substrate and design on fin erosion and hatchery performance of rainbow trout. *North Am J Aquac*. 2001;63(4):312-320.
87. Arndt RE, Routledge MD, Wagner EJ, Mellenthin RF. The use of AquaMats® to enhance growth and improve fin condition among raceway cultured rainbow trout *Oncorhynchus mykiss* (Walbaum). *Aquac Res*. 2002;33(5):359-367. https://doi.org/10.1046/j.1365-2109.2002.00670.x
88. Batzina A, Karakatsouli N. The presence of substrate as a means of environmental enrichment in intensively reared gilthead seabream Sparus aurata: Growth and behavioral effects. *Aquaculture*. 2012;370–371:54-60. https://doi.org/10.1016/j.aquaculture.2012.10.005
89. Batzina A, Kalogiannis D, Dalla C, Papadopoulou-Daifoti Z, Chadio S, Karakatsouli N. Blue substrate modifies the time course of stress response in gilthead seabream Sparus aurata. *Aquaculture*. 2014;420–421:247-253. https://doi.org/10.1016/j.aquaculture.2013.11.016
90. Batzina A, Dalla C, Tsopelakos A, Papadopoulou-Daifoti Z, Karakatsouli N. Environmental enrichment induces changes in brain monoamine levels in gilthead seabream Sparus aurata. *Physiol Behav*. 2014;130:85-90. https://doi.org/10.1016/j.physbeh.2014.03.023
91. Batzina A, Dalla C, Papadopoulou-Daifoti Z, Karakatsouli N. Effects of environmental enrichment on growth, aggressive behaviour and brain monoamines of gilthead seabream Sparus aurata reared under different social conditions. *Comp Biochem Physiol A Mol Integr Physiol*. 2014;169:25-32. https://doi.org/10.1016/j.cbpa.2013.12.001
92. Murtaza MUH, Zuberi A, Ahmad M, Amir I, Kamran M, Ahmad M. Influence of early rearing environment on water-borne cortisol and expression of stress-related genes in grass carp

(*Ctenopharyngodon idella*). *Mol Biol Rep*. 2020;47(7):5051-5060. https://doi.org/10.1007/s11033-020-05574-5

93. Tatemoto P, Valença-Silva G, Queiroz MR, Broom DM. Living with low environmental complexity increases fear indicators in Nile tilapia. *Anim Behav*. 2021;174:169-174. https://doi.org/10.1016/j.anbehav.2021.02.006
94. Reiser S, Pohlmann DM, Koops U, Gröger JP, Focken U. Using gravel for environmental enrichment in salmonid hatcheries: The effect of gravel size during egg incubation, endogenous and first feeding in rainbow trout. *J Appl Ichthyol*. 2019;35(2):465-472. https://doi.org/10.1111/jai.13884
95. Gessner J, Kamerichs CM, Kloas W, Wuertz S. Behavioural and physiological responses in early life phases of Atlantic sturgeon (Acipenser oxyrinchus Mitchill 1815) towards different substrates. *J Appl Ichthyol*. 2009;25:83-90. https://doi.org/10.1111/j.1439-0426.2009.01246.x
96. Boucher MA, McAdam SO, Shrimpton JM. The effect of temperature and substrate on the growth, development and survival of larval white sturgeon. *Aquaculture*. 2014;430:139-148. https://doi.org/10.1016/j.aquaculture.2014.03.011
97. Wiszniewski G, Duda A, Kolma R. Wplyw warunkow przetrzymywania larw jesiotra ostroosego na ich wzrost i przezywalnosc. *Komun Rybackie*. 2010;2:8-10.
98. Gonçalves-de-Freitas E, Bolognesi M, Gauy A, Brandão M, Giaquinto P, Fernandes-Castilho M. Social behavior and welfare in Nile tilapia. *Fishes*. 2019;4(2):23. https://doi.org/10.3390/fishes4020023
99. Mendonça FZ, Volpato GL, Costa-Ferreira RS, Gonçalves-de-Freitas E. Substratum choice for nesting in male Nile tilapia Oreochromis niloticus. *J Fish Biol*. 2010;77(6):1439-1445. https://doi.org/10.1111/j.1095-8649.2010.02754.x
100. Freitas RHA, Volpato GL. Motivation and time of day affect decision-making for substratum granulometry in the Nile tilapia Oreochromis niloticus. *J Appl Ichthyol*. 2013;29:239-241.
101. Galhardo L, Correia J, Oliveira R. The effect of substrate availability on behavioural and physiological indicators of welfare in the African cichlid (*Oreochromis mossambicus*). *Anim Welf*. 2008:16.
102. Galhardo L, Almeida O, Oliveira RF. Preference for the presence of substrate in male cichlid fish: Effects of social dominance and context. *Appl Anim Behav Sci*. 2009;120(3–4):224-230. https://doi.org/10.1016/j.applanim.2009.07.001
103. Haugland GT, Imsland AKD, Reynolds P, Treasurer J. 10-Application of biological control: Use of cleaner fish. *Aquaculture Health Management. Elsevier*. 2020:319-369. https://doi.org/10.1016/B978-0-12-813359-0.00010-5
104. Overton K, Barrett L, Oppedal F, Kristiansen T, Dempster T. Sea lice removal by cleaner fish in salmon aquaculture: a review of the evidence base. *Aquac Environ Interact*. 2020;12:31-44. https://doi.org/10.3354/aei00345
105. Imsland AK, Reynolds P, Eliassen G, et al. Assessment of suitable substrates for lumpfish in sea pens. *Aquac Int*. 2015;23(2):639-645. https://doi.org/10.1007/s10499-014-9840-0
106. Leclercq E, Graham P, Migaud H. Development of a water-stable agar-based diet for the supplementary feeding of cleaner fish ballan wrasse (Labrus bergylta) deployed within commercial Atlantic salmon (Salmon salar) net-pens. *Anim Feed Sci Technol*. 2015;208:98-106. https://doi.org/10.1016/j.anifeedsci.2015.06.026
107. Imsland AKD, Reynolds P, Jonassen TM, et al. Comparison of diet composition, feeding, growth and health of lumpfish (*Cyclopterus lumpus* L.) fed either feed blocks or pelleted commercial feed. *Aquac Res*. 2019;50(7):1952-1963. https://doi.org/10.1111/are.14083
108. Imsland AK, Reynolds P, Hangstad TA, et al. Feeding behaviour and growth of lumpfish (*Cyclopterus lumpus* L.) fed with feed blocks. *Aquac Res*. 2018;49(5):2006-2012. https://doi.org/10.1111/are.13657
109. Leclercq E, Zerafa B, Brooker AJ, Davie A, Migaud H. Application of passive-acoustic telemetry to explore the behaviour of ballan wrasse (*Labrus bergylta*) and lumpfish (*Cyclopterus lumpus*) in commercial Scottish salmon sea-pens. *Aquaculture*. 2018;495:1-12. https://doi.org/10.1016/j.aquaculture.2018.05.024
110. Geitung L, Wright DW, Oppedal F, Stien LH, Vågseth T, Madaro A. Cleaner fish growth, welfare and survival in Atlantic salmon sea cages during an autumn-winter production. *Aquaculture*. 2020;528:735623. https://doi.org/10.1016/j.aquaculture.2020.735623
111. Johannesen A, Joensen NE, Magnussen E. Shelters can negatively affect growth and welfare in lumpfish if feed is delivered continuously. *PeerJ*. 2018;6:e4837. https://doi.org/10.7717/peerj.4837
112. van Dam AA, Beveridge MCM, Azim ME, Verdegem MCJ. The potential of fish production based on periphyton. *Rev Fish Biol Fish*. 2002;12(1):1-31. https://doi.org/10.1023/A:1022639805031
113. Wells DL. Sensory stimulation as environmental enrichment for captive animals: A review. *Appl Anim Behav Sci*. 2009;118(1–2):1-11. https://doi.org/10.1016/j.applanim.2009.01.002
114. Naylor E. Chronobiology: implications for marine resource exploitation and management. *Sci Mar*. 2005;69(S1):157-167. https://doi.org/10.3989/scimar.2005.69s1157
115. Northcutt RG, Wullimann MF. The visual system in teleost fishes: morphological patterns and trends. In *Sensory Biology of Aquatic Animals*. Springer; 1988:515-552. https://doi.org/10.1007/978-1-4612-3714-3_21
116. Evans BI. A fish's eye view of habitat change. In von der Emde G, Mogdans J, Kapoor BG eds. *The Senses of Fish*. Springer; 2004:1-30. https://doi.org/10.1007/978-94-007-1060-3_1
117. Sánchez-Vázquez FJ, López-Olmeda JF, Vera LM, Migaud H, López-Patiño MA, Míguez JM. Environmental cycles, melatonin, and circadian control of stress response in fish. *Front Endocrinol*. 2019;10:279. https://doi.org/10.3389/fendo.2019.00279
118. Yeh N, Yeh P, Shih N, Byadgi O, Chih CT. Applications of light-emitting diodes in researches conducted in aquatic environment. *Renew Sustain Energy Rev*. 2014;32:611-618. https://doi.org/10.1016/j.rser.2014.01.047
119. Parker NC. Chronobiologic approach to aquaculture. *Trans Am Fish Soc*. 1984;113(4):545-552.
120. Villamizar N, Blanco-Vives B, Migaud H, Davie A, Carboni S, Sánchez-Vázquez FJ. Effects of light during early larval development of some aquacultured teleosts: A review. *Aquaculture*. 2011;315(1–2):86-94. https://doi.org/10.1016/j.aquaculture.2010.10.036
121. Villamizar N, Blanco-Vives B, Oliveira C, et al. Circadian rhythms of embryonic development and hatching in fish: A comparative study of Zebrafish (Diurnal), Senegalese Sole (Nocturnal), and Somalian Cavefish (Blind). *Chronobiol Int*. 2013;30(7):889-900. https://doi.org/10.3109/07420528.2013.784772
122. Ceinos RM, Chivite M, López-Patiño MA, et al. Differential circadian and light-driven rhythmicity of clock gene expression and behaviour in the turbot, Scophthalmus maximus. *PLoS One*. 2019;14(7):e0219153. https://doi.org/10.1371/journal.pone.0219153
123. Ruchin AB. Environmental colour impact on the life of lower aquatic vertebrates: development, growth, physiological and biochemical processes. *Rev Aquac*. 2020;12(1):310-327. https://doi.org/10.1111/raq.12319
124. Güller U, Önalan Ş, Arabacı M, Karataş B, Yaşar M, Küfrevioğlu Öİ. Effects of different LED light spectra on rainbow trout (Oncorhynchus mykiss): in vivo evaluation of the antioxidant status. *Fish Physiol Biochem*. 2020;46(6):2169-2180. https://doi.org/10.1007/s10695-020-00865-x
125. Roh HJ, Kang GS, Kim A, Kim NE, Nguyen TL, Kim D-H. Blue light-emitting diode photoinactivation inhibits edwardsiellosis in fancy carp (Cyprinus carpio). *Aquaculture*. 2018;483:1-7. https://doi.org/10.1016/j.aquaculture.2017.09.046

126. Roh HJ, Kim A, Kang GS, Kim BS, Kim D-H. Blue light-emitting diode light at 405 and 465 nm can inhibit a Miamiensis avidus infection in olive flounder. *Paralichthys Olivaceus*. *Aquaculture*. 2018;493:176-185. https://doi.org/10.1016/j.aquaculture.2018.04.045
127. Herbert NA, Kadri S, Huntingford FA. A moving light stimulus elicits a sustained swimming response in farmed Atlantic salmon, *Salmo salar* L. *Fish Physiol Biochem*. 2011;37(2):317-325. https://doi.org/10.1007/s10695-011-9499-7
128. Bui S, Oppedal F, Korsøen ØJ, Dempster T. Modifying Atlantic salmon behaviour with light or feed stimuli may improve parasite control techniques. *Aquac Environ Interact*. 2013;3:125-133. https://doi.org/10.3354/aei00055
129. Wright DW, Glaropoulos A, Solstorm D, Stien LH, Oppedal F. Atlantic salmon Salmo salar instantaneously follow vertical light movements in sea cages. *Aquac Environ Interact*. 2015;7(1):61-65. https://doi.org/10.3354/aei00136
130. Pickering AD, Griffiths R, Pottinger TG. A comparison of the effects of overhead cover on the growth, survival and haematology of juvenile Atlantic salmon, Salmo salar L., brown trout, Salmo trutta L., and rainbow trout, Salmo gairdneri Richardson. *Aquaculture*. 1987;66(2):109-124. https://doi.org/10.1016/0044-8486(87)90226-2
131. Kelly DJ, Bothwell ML. Avoidance of solar ultraviolet radiation by juvenile coho salmon (*Oncorhynchus kisutch*). 2002:10. Published online
132. Barnes M, Durben D. Effects of partial tank covers on the growth of juvenile feral rainbow trout during hatchery rearing. *North Am J Aquac*. 2003;65(4):344-348. https://doi.org/10.1577/C03-002
133. Barnes M, Miller J, Durben D. Partial overhead tank cover use during feral brown trout rearing. *North Am J Aquac*. 2005;67(4):319-323. https://doi.org/10.1577/A04-060.1
134. Holtby LB, Bothwell ML. Effects of solar ultraviolet radiation on the behaviour of juvenile coho salmon (*Oncorhynchus kisutch*): Avoidance, feeding, and agonistic interactions. *Can J Fish Aquat Sci*. 2008;65(4):701-711. https://doi.org/10.1139/f08-013
135. Nordgreen J, Bjørge MH, Janczak AM, et al. The time budget of Atlantic salmon (*Salmo salar*) held in enriched tanks. *Appl Anim Behav Sci*. 2013;144(3–4):147-152. https://doi.org/10.1016/j.applanim.2013.01.005
136. Walker LM, Parker TM, Barnes ME. Full and partial overhead tank cover improves rainbow trout rearing performance. *North Am J Aquac*. 2016;78(1):20-24. https://doi.org/10.1080/15222055.2015.1090504
137. Lawrence KP, Young AR, Diffey BL, Norval M. The impact of solar ultraviolet radiation on fish: Immunomodulation and photoprotective strategies. *Fish Fish*. 2020;21(1):104-119. https://doi.org/10.1111/faf.12420
138. Krebs E, Barnes ME, Crank KM, Krebs JR. Use of bottom structure and tank cover during rainbow trout rearing in circular tanks. *J Fish Livest Prod*. 2017;05(03). https://doi.org/10.4172/2332-2608.1000247
139. Saraiva JL, Nogueirinha M, Teodósio R, Aragão C, Engrola S, Arechavala-Lopez P. The effect of tank cover on welfare of farmed Nile tilapia. *Appl Anim Behav Sci*. 2021;241:105396. https://doi.org/10.1016/j.applanim.2021.105396
140. Ishibashi Y, Izumi T, Kurata M, Okada T. Effects of tank wall pattern on survival, bone injury rate, and stress response of juvenile Pacific bluefin tuna, Thunnus orientalis. *Aquac Eng*. 2013;56:13-17. https://doi.org/10.1016/j.aquaeng.2013.03.004
141. Okada T, Nakatani M, Sawada Y, Miyashita S, Kumai H, Ishibashi Y. Effect of tank wall colour and pattern on the survival rate of juvenile Pacific bluefin tuna Thunnus orientalis (Temminck and Schlegel) during ship transportation. *Aquac Res*. 2015;46(2):446-452. https://doi.org/10.1111/are.12196
142. de la Gándara F, Ortega A, Buentello A. Chapter 6 - Tuna Aquaculture in Europe. In Benetti DD, Partridge GJ, Buentello A eds. *Advances in Tuna Aquaculture*. Academic Press; 2016:115-157. https://doi.org/10.1016/B978-0-12-411459-3.00005-9
143. Oliveira RF, Carneiro LA, Canário AVM. No hormonal response in tied fights. *Nature*. 2005;437(7056):207-208. https://doi.org/10.1038/437207a
144. Saraiva JL, Keller-Costa T, Hubbard PC, Rato A, Canário AVM. Chemical diplomacy in male tilapia: urinary signal increases sex hormone and decreases aggression. *Sci Rep*. 2017;7(1):7636. https://doi.org/10.1038/s41598-017-07558-1
145. Desjardins JK, Fernald RD. What do fish make of mirror images? *Biol Lett*. 2010;6(6):744-747. https://doi.org/10.1098/rsbl.2010.0247
146. Kleiber A, Valotaire C, Patinote A, et al. Rainbow trout discriminate 2-D photographs of conspecifics from distracting stimuli using an innovative operant conditioning device. *Learning & Behavior*. 2021;49(3):292-306. https://doi.org/10.3758/s13420-020-00453-2
147. Popper AN, Fay RR. Sound detection and processing by fish: critical review and major research questions (Part 1 of 2). *Brain Behav Evol*. 1993;41(1):14-25. https://doi.org/10.1159/000113821
148. Buscaino G, Filiciotto F, Buffa G, et al. Impact of an acoustic stimulus on the motility and blood parameters of European sea bass (*Dicentrarchus labrax* L.) and gilthead sea bream (*Sparus aurata* L.). *Mar Environ Res*. 2010;69(3):136-142. https://doi.org/10.1016/j.marenvres.2009.09.004
149. Filiciotto F, Giacalone VM, Fazio F, et al. Effect of acoustic environment on gilthead sea bream (*Sparus aurata*): Sea and onshore aquaculture background noise. *Aquaculture*. 2013;414–415:36-45. https://doi.org/10.1016/j.aquaculture.2013.07.042
150. Filiciotto F, Cecchini S, Buscaino G, Maccarrone V, Piccione G, Fazio F. Impact of aquatic acoustic noise on oxidative status and some immune parameters in gilthead sea bream *Sparus aurata* (Linnaeus, 1758) juveniles. *Aquac Res*. 2017;48(4):1895-1903. https://doi.org/10.1111/are.13027
151. Debusschere E, De Coensel B, Bajek A, et al. In situ mortality experiments with juvenile sea bass (*Dicentrarchus labrax*) in relation to impulsive sound levels caused by pile driving of windmill foundations. *PLoS One*. 2014;9(10):e109280. https://doi.org/10.1371/journal.pone.0109280
152. Debusschere E, Hostens K, Adriaens D, et al. Acoustic stress responses in juvenile sea bass Dicentrarchus labrax induced by offshore pile driving. *Environ Pollut*. 2016;208:747-757. https://doi.org/10.1016/j.envpol.2015.10.055
153. Neo YY, Seitz J, Kastelein RA, Winter HV, ten Cate C, Slabbekoorn H. Temporal structure of sound affects behavioural recovery from noise impact in European seabass. *Biol Conserv*. 2014;178:65-73. https://doi.org/10.1016/j.biocon.2014.07.012
154. Neo YY, Hubert J, Bolle LJ, Winter HV, Slabbekoorn H. European seabass respond more strongly to noise exposure at night and habituate over repeated trials of sound exposure. *Environ Pollut*. 2018;239:367-374.
155. Celi M, Filiciotto F, Maricchiolo G, et al. Vessel noise pollution as a human threat to fish: assessment of the stress response in gilthead sea bream (Sparus aurata, Linnaeus 1758). *Fish Physiol Biochem*. 2016;42(2):631-641. https://doi.org/10.1007/s10695-015-0165-3
156. Spiga I, Aldred N, Caldwell GS. Anthropogenic noise compromises the anti-predator behaviour of the European seabass, Dicentrarchus labrax (L.). *Mar Pollut Bull*. 2017;122(1–2):297-305. https://doi.org/10.1016/j.marpolbul.2017.06.067
157. Mauro M, Pérez-Arjona I, Perez EJB, et al. The effect of low frequency noise on the behaviour of juvenile Sparus aurata. *J Acoust Soc Am*. 2020:14. Published online.
158. Bui S, Oppedal F, Korsøen ØJ, Sonny D, Dempster T. Group behavioural responses of Atlantic Salmon (*Salmo salar* L.) to light, infrasound and sound stimuli. *PLoS One*. 2013;8(5):e63696. https://doi.org/10.1371/journal.pone.0063696

159. Kusku H. Acoustic sound–induced stress response of Nile tilapia (Oreochromis niloticus) to long-term underwater sound transmissions of urban and shipping noises. *Environ Sci Pollut Res*. 2020;27(29):36857-36864. https://doi.org/10.1007/s11356-020-09699-9
160. Davidson J, Bebak J, Mazik P. The effects of aquaculture production noise on the growth, condition factor, feed conversion, and survival of rainbow trout. *Oncorhynchus Mykiss. Aquaculture*. 2009;288(3):337-343. https://doi.org/10.1016/j.aquaculture.2008.11.037
161. Ladich F. Sound production and acoustic communication. In von der Emde G, Mogdans J, Kapoor BG eds. *The Senses of Fish*. Springer; 2004:210-230. https://doi.org/10.1007/978-94-007-1060-3_10
162. Vasantha L, Jeyakumar A, Pitchai MA. Influence of music on the growth of Koi Carp, Cyprinus carpio (Pisces: Cyprindae). *NAGA WorldFish Cent Q*. 2003;26(4):25-26.
163. Papoutsoglou SE, Karakatsouli N, Papoutsoglou ES, Vasilikos G. Common carp (*Cyprinus carpio*) response to two pieces of music ("Eine Kleine Nachtmusik" and "Romanza") combined with light intensity, using recirculating water system. *Fish Physiol Biochem*. 2010;36(3):539-554. https://doi.org/10.1007/s10695-009-9324-8
164. Papoutsoglou SE, Karakatsouli N, Louizos E, et al. Effect of Mozart's music (Romanze-Andante of "Eine Kleine Nacht Musik", sol major, K525) stimulus on common carp (*Cyprinus carpio* L.) physiology under different light conditions. *Aquac Eng*. 2007;36(1):61-72. https://doi.org/10.1016/j.aquaeng.2006.07.001
165. Kusku H, Ergun S, Yilmaz S, Guroy B, Yigit M. Impacts of urban noise and musical stimuli on growth performance and feed utilization of Koi fish (*Cyprinus carpio*) in recirculating water conditions. *Turk J Fish Aquat Sci*. 2018;19(6):513-523.
166. Papoutsoglou SE, Karakatsouli N, Batzina A, Papoutsoglou ES, Tsopelakos A. Effect of music stimulus on gilthead seabream Sparus aurata physiology under different light intensity in a re-circulating water system. *J Fish Biol*. 2008;73(4):980-1004. https://doi.org/10.1111/j.1095-8649.2008.02001.x
167. Papoutsoglou SE, Karakatsouli N, Psarrou A, et al. Gilthead seabream (*Sparus aurata*) response to three music stimuli (Mozart—"Eine Kleine Nachtmusik," Anonymous—"Romanza," Bach—"Violin Concerto No. 1") and white noise under recirculating water conditions. *Fish Physiol Biochem*. 2015;41(1):219-232. https://doi.org/10.1007/s10695-014-0018-5
168. Papoutsoglou SE, Karakatsouli N, Skouradakis C, et al. Effect of musical stimuli and white noise on rainbow trout (*Oncorhynchus mykiss*) growth and physiology in recirculating water conditions. *Aquac Eng*. 2013;55:16-22. https://doi.org/10.1016/j.aquaeng.2013.01.003
169. Catli T, Yildirim O, Turker A. The effect of different tempos of music during feeding, on growth performance, chemical body composition, and feed utilization of turbot (Psetta maeotica, Pallas 1814). *Isr J Aquac – Bamidgeh*. 2015;67:9.
170. Alworth LC, Buerkle SC. The effects of music on animal physiology, behavior and welfare. *Lab Anim*. 2013;42(2):54-61. https://doi.org/10.1038/laban.162
171. Popper AN, Hastings MC. The effects of human-generated sound on fish. *Integr Zool*. 2009;4(1):43-52. https://doi.org/10.1111/j.1749-4877.2008.00134.x
172. Valentinčič T. Taste and olfactory stimuli and behavior in fishes. In von der Emde G, Mogdans J, Kapoor BG eds. *The Senses of Fish*. Springer; 2004:90-108. https://doi.org/10.1007/978-94-007-1060-3_4
173. Sorensen PW, Wisenden BD. *Fish Pheromones and Related Cues*. John Wiley & Sons; 2015.
174. Keller-Costa T, Saraiva JL, Hubbard PC, Barata EN, Canário AVM. A multi-component pheromone in the urine of dominant male Tilapia (*Oreochromis mossambicus*) reduces aggression in rivals. *J Chem Ecol*. 2016;42(2):173-182. https://doi.org/10.1007/s10886-016-0668-0
175. Hansen A, Reutter K. Chemosensory systems in fish: Structural, functional and ecological aspects. In von der Emde G, Mogdans J, Kapoor BG eds. *The Senses of Fish*. Springer; 2004:55-89. https://doi.org/10.1007/978-94-007-1060-3_3
176. Arvigo AL, Miyai CA, Sanches FHC, Barreto RE, Costa TM. Combined effects of predator odor and alarm substance on behavioral and physiological responses of the pearl cichlid. *Physiol Behav*. 2019;206:259-263. https://doi.org/10.1016/j.physbeh.2019.02.032
177. van de Nieuwegiessen PG, Zhao H, Verreth JAJ, Schrama JW. Chemical alarm cues in juvenile African catfish, Clarias gariepinus Burchell: A potential stressor in aquaculture? *Aquaculture*. 2009;286(1–2):95-99. https://doi.org/10.1016/j.aquaculture.2008.09.015
178. Mota VC, Martins CIM, Eding EH, Canário AVM, Verreth JAJ. Steroids accumulate in the rearing water of commercial recirculating aquaculture systems. *Aquac Eng*. 2014;62:9-16. https://doi.org/10.1016/j.aquaeng.2014.07.004
179. Díaz-Gil C, Alós J, Arechavala-Lopez P, et al. Reversible morphological changes in a juvenile marine fish after exposure to predatory alarm cues. *R Soc Open Sci*. 2020;7(5):191945. https://doi.org/10.1098/rsos.191945
180. Toa DG, Afonso LOB, Iwama GK. Stress response of juvenile rainbow trout (*Oncorhynchus mykiss*) to chemical cues released from stressed conspecifics. *Fish Physiol Biochem*. 2004;30(2):103-108. https://doi.org/10.1007/s10695-005-0266-5
181. Madsen SS, Winther SST, Bollinger RJ, Steiner U, Larsen MH. Differential expression of olfactory genes in Atlantic salmon (*Salmo salar*) during the parr–smolt transformation. *Ecol Evol*. 2019;9(24):14085-14100. https://doi.org/10.1002/ece3.5845
182. Giaquinto PC, Volpato GL. Chemical communication, aggression, and conspecific recognition in the fish Nile Tilapia. *Physiol Behav*. 1997;62(6):1333-1338. https://doi.org/10.1016/S0031-9384(97)00347-8
183. Hubbard PC, Mota VC, Keller-Costa T, da Silva JP, Canário AVM. Chemical communication in tilapia: A comparison of Oreochromis mossambicus with O. niloticus. *Gen Comp Endocrinol*. 2014;207:13-20. https://doi.org/10.1016/j.ygcen.2014.06.022
184. Keller-Costa T, Canário AVM, Hubbard PC. Chemical communication in cichlids: A mini-review. *Gen Comp Endocrinol*. 2015;221:64-74. https://doi.org/10.1016/j.ygcen.2015.01.001
185. Pashchenko NI, Kasumyan AO. Development of the olfactory organ in the ontogeny of carps (Cyprinidae). *J Ichthyol*. 2017;57(1):136-151. https://doi.org/10.1134/S0032945217010088
186. Saraiva JL, Martins RS, Hubbard PC, Canário AVM. Lack of evidence for a role of olfaction on first maturation in farmed sea bass Dicentrarchus labrax. *Gen Comp Endocrinol*. 2015;221:114-119. https://doi.org/10.1016/j.ygcen.2015.02.017
187. Hubbard PC, Barata EN, Canário AVM. Olfactory sensitivity to catecholamines and their metabolites in the goldfish. *Chem Senses*. 2003;28(3):207-218. https://doi.org/10.1093/chemse/28.3.207
188. Fatsini E, Carazo I, Chauvigné F, et al. Olfactory sensitivity of the marine flatfish *Solea senegalensis* to conspecific body fluids. *J Exp Biol*. 2017;220(11):2057-2065. https://doi.org/10.1242/jeb.150318
189. da Silva MC, Canário AVM, Hubbard PC, Gonçalves DMF. Physiology, endocrinology and chemical communication in aggressive behaviour of fishes. *J Fish Biol*. 2021;98(5):1217-1233. https://doi.org/10.1111/jfb.14667
190. Gonçalves-de-Freitas E, Teresa FB, Gomes FS, Giaquinto PC. Effect of water renewal on dominance hierarchy of juvenile Nile tilapia. *Appl Anim Behav Sci*. 2008;112(1–2):187-195. https://doi.org/10.1016/j.applanim.2007.07.002
191. Morais S. The Physiology of taste in fish: potential implications for feeding stimulation and gut chemical sensing. *Rev Fish Sci Aquac*. 2017;25(2):133-149. https://doi.org/10.1080/23308249.2016.1249279

192. Adams MA, Johnsen PB. Chemical control of feeding in herbivorous and carnivorous fish. In Duvall D, Müller-Schwarze D, Silverstein RM eds. *Chemical Signals in Vertebrates 4: Ecology, Evolution, and Comparative Biology*. Springer; 1986:45-61. https://doi.org/10.1007/978-1-4613-2235-1_5
193. Alder J, Campbell B, Karpouzi V, Kaschner K, Pauly D. Forage fish: From ecosystems to markets. *Annu Rev Environ Resour*. 2008;33(1):153-166. https://doi.org/10.1146/annurev.environ.33.020807.143204
194. Velez Z, Hubbard PC, Hardege JD, Welham KJ, Barata EN, Canário AVM. Evidence that 1-methyl-l-tryptophan is a food-related odorant for the Senegalese sole (*Solea senegalensis*). *Aquaculture*. 2011;314(1–4):153-158. https://doi.org/10.1016/j.aquaculture.2011.01.025
195. Zou Q, Huang Y, Cao J, et al. Effects of four feeding stimulants in high plant-based diets on feed intake, growth performance, serum biochemical parameters, digestive enzyme activities and appetite-related genes expression of juvenile GIFT tilapia (*Oreochromis sp.*). *Aquac Nutr*. 2017;23(5):1076-1085. https://doi.org/10.1111/anu.12475
196. Herrera M, Mancera JM, Costas B. The use of dietary additives in fish stress mitigation: Comparative endocrine and physiological responses. *Front Endocrinol*. 2019;10:447. https://doi.org/10.3389/fendo.2019.00447
197. Neto JF, Giaquinto PC. Environmental enrichment techniques and tryptophan supplementation used to improve the quality of life and animal welfare of Nile tilapia. *Aquac Rep*. 2020;17:100354. https://doi.org/10.1016/j.aqrep.2020.100354
198. Kasumyan AO. Tactile reception and behavior of fish. *J Ichthyol*. 2011;51(11):1035-1103. https://doi.org/10.1134/S003294521111004X
199. Hardy AR, Hale ME. Sensing the structural characteristics of surfaces: texture encoding by a bottom-dwelling fish. *J Exp Biol*. 2020;223(21):jeb227280. https://doi.org/10.1242/jeb.227280
200. Williams Iv R, Neubarth N, Hale ME. The function of fin rays as proprioceptive sensors in fish. *Nat Commun*. 2013;4(1):1729. https://doi.org/10.1038/ncomms2751
201. Aiello BR, Hardy AR, Westneat MW, Hale ME. Fins as Mechanosensors for Movement and Touch-Related Behaviors. *Integr Comp Biol*. 2018;58(5):844-859. https://doi.org/10.1093/icb/icy065
202. Bshary R, Côté IM. New perspectives on marine cleaning mutualism. *CRC Press*. 2008:577-606. https://doi.org/10.1201/b10757-20
203. Soares MC, Oliveira RF, Ros AFH, Grutter AS, Bshary R. Tactile stimulation lowers stress in fish. *Nat Commun*. 2011;2(1):534. https://doi.org/10.1038/ncomms1547
204. Bolognesi MC, dos Santos Gauy AC, Gonçalves-de-Freitas E. Tactile stimulation reduces aggressiveness but does not lower stress in a territorial fish. *Sci Rep*. 2019;9(1):40. https://doi.org/10.1038/s41598-018-36876-1
205. Gauy ACdS, Bolognesi MC, Martins GD, Gonçalves-de-Freitas E. Preference and motivation tests for body tactile stimulation in fish. *Animals*. 2021;11(7):2042. https://doi.org/10.3390/ani11072042
206. Fife-Cook I, Franks B. Koi (*Cyprinus rubrofuscus*) seek out tactile interaction with humans: general patterns and individual differences. *Animals*. 2021;11(3):706. https://doi.org/10.3390/ani11030706
207. Mogdans J. Sensory ecology of the fish lateral-line system: Morphological and physiological adaptations for the perception of hydrodynamic stimuli. *J Fish Biol*. 2019:jfb.13966. Published online May 7, https://doi.org/10.1111/jfb.13966
208. Electroreception KCH. Strategies for separation of signals from noise. In *The Senses of Fish*. Springer; 2004:330-361. https://doi.org/10.1007/978-94-007-1060-3_15
209. Scheffel A, Kramer B. Intra-and interspecific electrocommunication among sympatric mormyrids in the Upper Zambezi River. 2006. Published online.
210. Bloomsmith MA, Brent LY, Schapiro SJ. Guidelines for developing and managing an environmental enrichment program for nonhuman primates. *Lab Anim Sci USA*. 1991;41(4):372-377.
211. Liao JC, Cotel A. Effects of turbulence on fish swimming in aquaculture. In Palstra AP, Planas JV eds. *Swimming Physiology of Fish: Towards Using Exercise to Farm a Fit Fish in Sustainable Aquaculture*. Springer; 2013:109-127. https://doi.org/10.1007/978-3-642-31049-2_5
212. Xu Z, Qin H. Fluid-structure interactions of cage based aquaculture: From structures to organisms. *Ocean Eng*. 2020;217:107961. https://doi.org/10.1016/j.oceaneng.2020.107961
213. Johansson D, Laursen F, Fernö A, et al. The interaction between water currents and salmon swimming behaviour in sea cages. *PLoS One*. 2014;9(5):e97635 https://doi.org/10.1371/journal.pone.0097635
214. Johannesen Á, Patursson Ø, Kristmundsson J, Dam SP, Klebert P. How caged salmon respond to waves depends on time of day and currents. *PeerJ*. 2020;8:e9313. https://doi.org/10.7717/peerj.9313
215. Webb PW, Cotel AJ. Assessing possible effects of fish-culture systems on fish swimming: the role of stability in turbulent flows. *Fish Physiol Biochem*. 2011;37(2):297-305. https://doi.org/10.1007/s10695-011-9497-9
216. Palstra AP, Planas JV. Fish under exercise. *Fish Physiol Biochem*. 2011;37(2):259-272. https://doi.org/10.1007/s10695-011-9505-0
217. Davison W. The effects of exercise training on teleost fish, a review of recent literature. *Comp Biochem Physiol A Physiol*. 1997;117(1):67-75. https://doi.org/10.1016/S0300-9629(96)00284-8
218. Remen M, Solstorm F, Bui S, et al. Critical swimming speed in groups of Atlantic salmon *Salmo salar*. *Aquac Environ Interact*. 2016;8:659-664. https://doi.org/10.3354/aei00207
219. Plew DR, Klebert P, Rosten TW, Aspaas S, Birkevold J. Changes to flow and turbulence caused by different concentrations of fish in a circular tank. *J Hydraul Res*. 2015;53(3):364-383. https://doi.org/10.1080/00221686.2015.1029016
220. Moine J, Barnes MEB, Kientz JL, Simpson G. Flow patterns in circular rearing tanks containing vertical structure. *J Fish Livest Prod*. 2016;04(04). https://doi.org/10.4172/2332-2608.1000204
221. Jobling M, Baardvik BM, Christiansen JS, Jørgensen EH. The effects of prolonged exercise training on growth performance and production parameters in fish. *Aquac Int*. 1993;1(2):95-111. https://doi.org/10.1007/BF00692614
222. Christiansen JS, Ringø E, Jobling M. Effects of sustained exercise on growth and body composition of first-feeding fry of Arctic charr, *Salvelinus alpinus* (L.). *Aquaculture*. 1989;79(1–4):329-335. https://doi.org/10.1016/0044-8486(89)90474-2
223. Christiansen JS, Jobling M. The behaviour and the relationship between food intake and growth of juvenile Arctic charr, *Salvelinus alpinus* L., subjected to sustained exercise. *Can J Zool*. 1990;68(10):2185-2191. https://doi.org/10.1139/z90-303
224. Nilsen A, Hagen Ø, Johnsen CA, et al. The importance of exercise: Increased water velocity improves growth of Atlantic salmon in closed cages. *Aquaculture*. 2019;501:537-546. https://doi.org/10.1016/j.aquaculture.2018.09.057
225. Parker TM, Barnes ME. Rearing velocity impacts on landlocked fall chinook salmon (%3ci%3eOncorhynchus tshawytscha%3c/i%3e) growth, condition, and survival. *Open J Anim Sci*. 2014;04(05):244-252. https://doi.org/10.4236/ojas.2014.45031
226. Parker TM, Barnes ME. Effects of different water velocities on the hatchery rearing performance and recovery from transportation of rainbow trout fed two different rations. *Trans Am Fish Soc*. 2015;144(5):882-890. https://doi.org/10.1080/00028487.2015.1047533

227. DePasquale C, Fettrow S, Sturgill J, Braithwaite VA. The impact of flow and physical enrichment on preferences in zebrafish. *Appl Anim Behav Sci*. 2019;215:77-81. https://doi.org/10.1016/j.applanim.2019.03.015
228. Villarroel M, Torrent F, Perez C, Chavarri E, de la Fuente J. Enriquecimiento ambiental y bienestar en peces. *Derecho Anim Forum Anim Law Stud*. 2019;10(4). https://doi.org/10.5565/rev/da.458
229. Reiser S, Sähn N, Pohlmann DM, Willenberg M, Focken U. Rearing juvenile brown *Salmo trutta* (L.), and rainbow trout *Oncorhynchus mykiss* (Walbaum), in earthen ponds with and without an induced current. *J Appl Aquac*. 2019:1-21. https://doi.org/10.1080/10454438.2019.1678545
230. Ibarz A, Felip O, Fernández-Borràs J, Martín-Pérez M, Blasco J, Torrella JR. Sustained swimming improves muscle growth and cellularity in gilthead sea bream. *J Comp Physiol B*. 2011;181(2):209-217. https://doi.org/10.1007/s00360-010-0516-4
231. Palstra AP, Roque A, Kruijt L, Jéhannet P, Pérez-Sánchez J, Dirks RP. Physiological effects of water flow induced swimming exercise in seabream sparus aurata. *Front Physiol*. 2020;11:610049. https://doi.org/10.3389/fphys.2020.610049
232. Shi C, Wang J, Yang Z, Gao X, Liu Y, Wang C. Sustained swimming training is associated with reversible filet texture changes of European Sea Bass (*Dicentrarchus labrax* L.). *Front Physiol*. 2019;10. https://doi.org/10.3389/fphys.2019.00725
233. Chen Z, Ye Z, Ji M, et al. Effects of flow velocity on growth and physiology of juvenile largemouth bass (*Micropterus salmoides*) in recirculating aquaculture systems. *Aquac Res*. 2021:are.15153. Published online. https://doi.org/10.1111/are.15153
234. Rozaesilva ML, Pereira RT, Arvigo AL, Zanuzzo FS, Barreto RE. Effects of water flow on ventilation rate and plasma cortisol in Nile tilapia introduced into novel environment. *Aquac Rep*. 2020;18:100531. https://doi.org/10.1016/j.aqrep.2020.100531
235. Taranger GL, Carrillo M, Schulz RW, et al. Control of puberty in farmed fish. *Gen Comp Endocrinol*. 2010;165(3):483-515. https://doi.org/10.1016/j.ygcen.2009.05.004
236. Riotte-Lambert L, Matthiopoulos J. Environmental predictability as a cause and consequence of animal movement. *Trends Ecol Evol*. 2020;35(2):163-174. https://doi.org/10.1016/j.tree.2019.09.009
237. Robertson BA, Rehage JS, Sih A. Ecological novelty and the emergence of evolutionary traps. *Trends Ecol Evol*. 2013;28(9):552-560. https://doi.org/10.1016/j.tree.2013.04.004
238. McEwen BS, Wingfield JC. The concept of allostasis in biology and biomedicine. *Horm Behav*. 2003;43(1):2-15.
239. Sánchez JA, López-Olmeda JF, Blanco-Vives B, Sánchez-Vázquez FJ. Effects of feeding schedule on locomotor activity rhythms and stress response in sea bream. *Physiol Behav*. 2009;98(1–2):125-129. https://doi.org/10.1016/j.physbeh.2009.04.020
240. Cañon Jones HA, Noble C, Damsgård B, Pearce GP. Investigating the influence of predictable and unpredictable feed delivery schedules upon the behaviour and welfare of Atlantic salmon parr (*Salmo salar*) using social network analysis and fin damage. *Appl Anim Behav Sci*. 2012;138(1–2):132-140. https://doi.org/10.1016/j.applanim.2012.01.019
241. Sébastien F, Leguay D, Vergnet A, Vidal M-O, Chatain B, Bégout M-L. Unpredictability in food supply during early life influences growth and boldness in European seabass, Dicentrarchus labrax. *Appl Anim Behav Sci*. 2016;180:147-156. https://doi.org/10.1016/j.applanim.2016.04.017
242. Galhardo L, Vital J, Oliveira RF. The role of predictability in the stress response of a cichlid fish. *Physiol Behav*. 2011;102(3–4):367-372. https://doi.org/10.1016/j.physbeh.2010.11.035
243. Cerqueira M, Millot S, Castanheira MF, et al. Cognitive appraisal of environmental stimuli induces emotion-like states in fish. *Sci Rep*. 2017;7(1):13181. https://doi.org/10.1038/s41598-017-13173-x
244. Cerqueira M, Millot S, Felix A, et al. Cognitive appraisal in fish: stressor predictability modulates the physiological and neurobehavioural stress response in sea bass. *Proc R Soc B Biol Sci*. 1923;2020(287):20192922. https://doi.org/10.1098/rspb.2019.2922
245. Vindas MA, Folkedal O, Kristiansen TS, et al. Omission of expected reward agitates Atlantic salmon (*Salmo salar*). *Anim Cogn*. 2012;15(5):903-911. https://doi.org/10.1007/s10071-012-0517-7
246. Vindas MA, Sørensen C, Johansen IB, et al. Coping with unpredictability: dopaminergic and neurotrophic responses to omission of expected reward in Atlantic Salmon (*Salmo salar* L.). *PLoS One*. 2014;9(1):e85543. https://doi.org/10.1371/journal.pone.0085543
247. Madaro A, Fernö A, Kristiansen TS, et al. Effect of predictability on the stress response to chasing in Atlantic salmon (Salmo salar L.) parr. *Physiol Behav*. 2016;153:1-6. https://doi.org/10.1016/j.physbeh.2015.10.002
248. Hoogenboom MO, Armstrong JD, Groothuis TGG, Metcalfe NB. The growth benefits of aggressive behavior vary with individual metabolism and resource predictability. *Behav Ecol*. 2013;24(1):253-261. https://doi.org/10.1093/beheco/ars161
249. Braithwaite VA, Salvanes AGV. Environmental variability in the early rearing environment generates behaviourally flexible cod: implications for rehabilitating wild populations. *Proc R Soc B Biol Sci*. 2005;272(1568):1107-1113. https://doi.org/10.1098/rspb.2005.3062
250. Rodewald P, Hyvärinen P, Hirvonen H. Wild origin and enriched environment promote foraging rate and learning to forage on natural prey of captive reared Atlantic salmon parr: Enriched rearing promotes foraging of juvenile salmon. *Ecol Freshw Fish*. 2011;20(4):569-579. https://doi.org/10.1111/j.1600-0633.2011.00505.x
251. Lee JSF, Berejikian BA. Effects of the rearing environment on average behaviour and behavioural variation in steelhead. *J Fish Biol*. 2008;72(7):1736-1749. https://doi.org/10.1111/j.1095-8649.2008.01848.x
252. Burghardt GM. Play in fishes, frogs and reptiles. *Curr Biol*. 2015;25(1):R9-R10. https://doi.org/10.1016/j.cub.2014.10.027
253. Burghardt GM, Dinets V, Murphy JB. Highly Repetitive Object Play in a Cichlid Fish (*Tropheus duboisi*). *Ethology*. 2015;121(1):38-44. https://doi.org/10.1111/eth.12312
254. Fife-Cook I, Franks B. Positive welfare for fishes: Rationale and areas for future study. *Fishes*. 2019;4(2):31. https://doi.org/10.3390/fishes4020031
255. Fagen R. Salmonid Jumping and Playing: Potential Cultural and Welfare Implications. *Animals*. 2017;7(12):42. https://doi.org/10.3390/ani7060042
256. Oliveira AFS, Rossi AO, Silva LFR, Lau MC, Barreto RE. Play behaviour in nonhuman animals and the animal welfare issue. *J Ethol*. 2010;28(1):1-5. https://doi.org/10.1007/s10164-009-0167-7
257. Franks B, Sebo J, Horowitz A. Fish are smart and feel pain: What about joy? *Anim Sentience*. 2018;3(21). https://doi.org/10.51291/2377-7478.1368
258. Turnbull JF, North BP, Ellis T, et al. Stocking density and the welfare of farmed salmonids. *Fish Welfare*. 2008:111-120.
259. Baldwin L. The effects of stocking density on fish welfare. *Plymouth Stud Sci*. 2010;4:372-383.
260. Toni M, Manciocco A, Angiulli E, Alleva E, Cioni C, Malavasi S. Review: Assessing fish welfare in research and aquaculture, with a focus on European directives. *Animal*. 2019;13(1):161-170. https://doi.org/10.1017/S1751731118000940
261. Adams CE, Turnbull JF, Bell A, Bron JE, Huntingford FA. Multiple determinants of welfare in farmed fish: stocking density, disturbance, and aggression in Atlantic salmon (*Salmo salar*). *Can J Fish Aquat Sci*. 2007;64(2):336-344. https://doi.org/10.1139/f07-018
262. Ellis T, North B, Scott AP, Bromage NR, Porter M, Gadd D. The relationships between stocking density and welfare in farmed rainbow

trout. *J Fish Biol*. 2002;61(3):493-531. https://doi.org/10.1111/j.1095-8649.2002.tb00893.x

263. Ma Z, Li H, Hu Y, Fan J, Liu Y. Growth performance, physiological, and feeding behavior effect of Dicentrarchus labrax under different culture scales. *Aquaculture*. 2021;534. https://doi.org/10.1016/j.aquaculture.2020.736291 736291.
264. Toko I, Fiogbe ED, Koukpode B, Kestemont P. Rearing of African catfish (*Clarias gariepinus*) and vundu catfish (*Heterobranchus longifilis*) in traditional fish ponds (whedos): Effect of stocking density on growth, production and body composition. *Aquaculture*. 2007;262(1):65-72. https://doi.org/10.1016/j.aquaculture.2006.08.054
265. van de Nieuwegiessen PG, Olwo J, Khong S, Verreth JAJ, Schrama JW. Effects of age and stocking density on the welfare of African catfish, Clarias gariepinus Burchell. *Aquaculture*. 2009;288(1–2):69-75. https://doi.org/10.1016/j.aquaculture.2008.11.009
266. van de Nieuwegiessen PG, Boerlage AS, Verreth JAJ, Schrama JW. Assessing the effects of a chronic stressor, stocking density, on welfare indicators of juvenile African catfish, Clarias gariepinus Burchell. *Appl Anim Behav Sci*. 2008;115(3–4):233-243. https://doi.org/10.1016/j.applanim.2008.05.008
267. Dai W, Wang X, Guo Y, Wang Q, Ma J. Growth performance, hematological and biochemical responses of African catfish (Clarias gariepinus) reared at different stocking densities. *Afr J Agric Res*. 2011;6(28):6177-6182. https://doi.org/10.5897/AJAR11.1278
268. Shoko AP, Limbu SM, Mgaya YD. Effect of stocking density on growth performance, survival, production, and financial benefits of African sharptooth catfish (*Clarias gariepinus*) monoculture in earthen ponds. *J Appl Aquac*. 2016;28(3):220-234. https://doi.org/10.1080/10454438.2016.1188338
269. Shoko AP, Limbu SM, Mrosso HDJ, Mkenda AF, Mgaya YD. Effect of stocking density on growth, production and economic benefits of mixed sex Nile tilapia (*Oreochromis niloticus*) and African sharptooth catfish (*Clarias gariepinus*) in polyculture and monoculture. *Aquac Res*. 2016;47(1):36-50. https://doi.org/10.1111/are.12463
270. Oké V, Goosen NJ. The effect of stocking density on profitability of African catfish (*Clarias gariepinus*) culture in extensive pond systems. *Aquaculture*. 2019;507:385-392. https://doi.org/10.1016/j.aquaculture.2019.04.043
271. Gilmour KM, DiBattista JD, Thomas JB. Physiological causes and consequences of social status in salmonid fish. *Integr Comp Biol*. 2005;45(2):263-273. https://doi.org/10.1093/icb/45.2.263
272. Huntingford F, Adams C. Behavioural syndromes in farmed fish: implications for production and welfare. *Behaviour*. 2005;142(9/10):1207-1221.
273. Volpato G, Fernandes MO. Social control of growth in fish. *Braz J Med Biol Res*. 1994;27:797-810.
274. Castanheira MF, Conceição Luís EC, Sandie M, et al. Coping styles in farmed fish: consequences for aquaculture. *Rev Aquac*. 2017;9(1):23-41. https://doi.org/10.1111/raq.12100
275. Höjesjö J, Johnsson JI, Petersson E, Järvi T. The importance of being familiar: individual recognition and social behavior in sea trout (*Salmo trutta*). *Behav Ecol*. 1998;9(5):445-451. https://doi.org/10.1093/beheco/9.5.445
276. Powell A, Treasurer JW, Pooley CL, et al. Use of lumpfish for sea-lice control in salmon farming: challenges and opportunities. *Rev Aquac*. 2018;10(3):683-702. https://doi.org/10.1111/raq.12194
277. Noble C. Using rainbow trout Oncorhynchus mykiss as self-feeding actuators for white-spotted charr Salvelinus leucomaenis: Implications for production and welfare. *Appl Anim Behav Sci*. 2012;138(1-2):125-131.
278. Thomas M, Lecocq T, Abregal C, et al. The effects of polyculture on behaviour and production of pikeperch in recirculation systems. *Aquac Rep*. 2020;17:100333. https://doi.org/10.1016/j.aqrep.2020.100333
279. Wahab MA, Ahmed ZF, Islam MA, Haq MS, Rahmatullah SM. Effects of introduction of common carp, *Cyprinus carpio* (L.), on the pond ecology and growth of fish in polyculture. *Aquac Res*. 1995;26(9):619-628. https://doi.org/10.1111/j.1365-2109.1995.tb00953.x
280. Yúfera M, Arias AM. Traditional polyculture in “Esteros” in the Bay of Cádiz (Spain). *Aquac Eur*. 2010;35(3):22-25.
281. Anras L, Boglione C, Cataudella S, et al. The current status of extensive and semi-intensive aquaculture practices in Southern Europe. *Aquac Eur*. 2010;35(2):12-16.
282. Juell J-E. The behaviour of Atlantic salmon in relation to efficient cage-rearing. *Rev Fish Biol Fish*. 1995;5(3):320-335. https://doi.org/10.1007/BF00043005
283. López-Olmeda JF, Noble C, Sánchez-Vázquez FJ. Does feeding time affect fish welfare? *Fish Physiol Biochem*. 2012;38(1):143-152. https://doi.org/10.1007/s10695-011-9523-y
284. Skøien KR, Alver MO, Alfredsen JA. Modelling and simulation of rotary feed spreaders with application to sea cage aquaculture – A study of common and alternative designs. *Aquac Eng*. 2018;82:1-11. https://doi.org/10.1016/j.aquaeng.2017.11.002
285. Lien AM, Schellewald C, Stahl A, Frank K, Skøien KR, Tjølsen JI. Determining spatial feed distribution in sea cage aquaculture using an aerial camera platform. *Aquac Eng*. 2019;87. https://doi.org/10.1016/j.aquaeng.2019.102018 102018.
286. Juell J-E, Fernö A, Furevik D, Huse I. Influence of hunger level and food availability on the spatial distribution of Atlantic salmon, Salmo salar L., in sea cages. *Aquac Res*. 1994;25(4):439-451. https://doi.org/10.1111/j.1365-2109.1994.tb00709.x
287. Saberioon M, Gholizadeh A, Cisar P, Pautsina A, Urban J. Application of machine vision systems in aquaculture with emphasis on fish: state-of-the-art and key issues. *Rev Aquac*. 2017;9(4):369-387.
288. Zhou C, Xu D, Lin K, Sun C, Yang X. Intelligent feeding control methods in aquaculture with an emphasis on fish: a review. *Rev Aquac*. 2018;10(4):975-993.
289. Føre M, Frank K, Norton T, et al. Precision fish farming: A new framework to improve production in aquaculture. *Biosyst Eng*. 2018;173:176-193. https://doi.org/10.1016/j.biosystemseng.2017.10.014
290. Antonucci F, Costa C. Precision aquaculture: a short review on engineering innovations. *Aquac Int*. 2020;28(1):41-57. https://doi.org/10.1007/s10499-019-00443-w
291. Kubitza F, Lovshin LL. Formulated diets, feeding strategies, and cannibalism control during intensive culture of juvenile carnivorous fishes. *Rev Fish Sci*. 1999;7(1):1-22. https://doi.org/10.1080/10641269991319171
292. Levina AD, Mikhailova ES, Kasumyan AO. Taste preferences and feeding behaviour in the facultative herbivorous fish, Nile tilapia Oreochromis niloticus. *J Fish Biol*. 2021:jfb.14675. Published online. https://doi.org/10.1111/jfb.14675
293. Maia CM, Volpato GL. A history-based method to estimate animal preference. *Sci Rep*. 2016;6(1):28328. https://doi.org/10.1038/srep28328
294. Dawkins MS. The science of animal suffering. *Ethology*. 2008;114(10):937-945.https://doi.org/10.1111/j.1439-0310.2008.01557.x
295. Dawkins MS. A user's guide to animal welfare science. *Trends Ecol Evol*. 2006;21(2):77-82. https://doi.org/10.1016/j.tree.2005.10.017
296. Duncan IJ. Science-based assessment of animal welfare: farm animals. *Rev Sci Tech-Off Int Epizoot*. 2005;24(2):483.
297. Maia CM, Ferguson B, Volpato GL, Braithwaite VA. Physical and psychological motivation tests of individual preferences in rainbow trout. *J Zool*. 2017;302(2):108-118. https://doi.org/10.1111/jzo.12438
298. Johnsson JI, Carlsson M, Sundström LF. Habitat preference increases territorial defence in brown trout (*Salmo trutta*). *Behav Ecol*

Sociobiol. 2000;48(5):373-377. https://doi.org/10.1007/s002650000244

299. Keep JK, Watson JR, Cramp RL, et al. Low light intensities increase avoidance behaviour of diurnal fish species: implications for use of road culverts by fish. *J Fish Biol*. 2021;98(3):634-642. https://doi.org/10.1111/jfb.14604
300. Maia CM, Volpato GL. Preference index supported by motivation tests in Nile tilapia. *PLoS One*. 2017;12(4):e0175821. https://doi.org/10.1371/journal.pone.0175821
301. Tinbergen N. On aims and methods of Ethology. *Z Für Tierpsychol*. 1963;20(4):410-433. https://doi.org/10.1111/j.1439-0310.1963.tb01161.x
302. Huntingford FA. Fish behaviour: determinants and implications for welfare. In Kristiansen TS, Fernö A, Pavlidis MA, van de Vis H eds. *The Welfare of Fish. Animal Welfare*. Springer; 2020:73-110. https://doi.org/10.1007/978-3-030-41675-1_4
303. Saraiva JL, Arechavala-Lopez P, Sneddon LU. The welfare of fish in aquaculture systems. In: Knight A, ed. *Routledge Handbook of Animal Welfare*. Taylor & Francis; 2022.
304. Martins CIM, Galhardo L, Noble C, et al. Behavioural indicators of welfare in farmed fish. *Fish Physiol Biochem*. 2012;38(1):17-41. https://doi.org/10.1007/s10695-011-9518-8
305. Castanheira MF, Herrera M, Costas B, Conceição LEC, Martins CIM. Linking cortisol responsiveness and aggressive behaviour in gilthead seabream Sparus aurata: Indication of divergent coping styles. *Appl Anim Behav Sci*. 2013;143(1):75-81. https://doi.org/10.1016/j.applanim.2012.11.008
306. Saraiva JL, Arechavala-Lopez P, Castanheira MF, Volstorf J, Heinzpeter SB. A Global Assessment of Welfare in Farmed Fishes: The FishEthoBase. *Fishes*. 2019;4(2):30. https://doi.org/10.3390/fishes4020030
307. Korte SM, Olivier B, Koolhaas JM. A new animal welfare concept based on allostasis. *Physiol Behav*. 2007;92(3):422-428. https://doi.org/10.1016/j.physbeh.2006.10.018
308. Champneys T, Castaldo G, Consuegra S, Garcia de Leaniz C. Density-dependent changes in neophobia and stress-coping styles in the world's oldest farmed fish. *R Soc Open Sci*. 2018;5(12):181473. https://doi.org/10.1098/rsos.181473
309. van de Nieuwegiessen PG, Ramli NM, Knegtel BPFJM, Verreth JAJ, Schrama JW. Coping strategies in farmed African catfish Clarias gariepinus. Does it affect their welfare? *J Fish Biol*. 2010;76(10):2486-2501. https://doi.org/10.1111/j.1095-8649.2010.02635.x
310. North BP, Turnbull JF, Ellis T, et al. The impact of stocking density on the welfare of rainbow trout (*Oncorhynchus mykiss*). *Aquaculture*. 2006;255(1–4):466-479. https://doi.org/10.1016/j.aquaculture.2006.01.004
311. Friend Of the Sea. Standard Improvement on Sustainable Certification of Products. Published 2021. https://friendofthesea.org/standard-improvement/
312. Brambell FWR. Report of the Technical Committee to Enquire into the Welfare of Animals Kept under Intensive Livestock Husbandry Systems; 1965.
313. Phibbs DV, Groves PJ, Muir WI, Phibbs DV, Groves PJ, Muir WI. Leg health of meat chickens: impact on welfare, consumer behaviour, and the role of environmental enrichment. *Anim Prod Sci*. 2021;61(12):1203. https://doi.org/10.1071/AN19511
314. van de Weerd H, Ison S. Providing effective environmental enrichment to pigs: how far have we come? *Animals*. 2019;9(5):254. https://doi.org/10.3390/ani9050254
315. Saraiva JL, Arechavala-Lopez P. Welfare of Fish—No Longer the Elephant in the Room. *Fishes*. 2019;4(3). https://doi.org/10.3390/fishes4030039
316. Saraiva JL, Arechavala-Lopez P, Cabrera-Álvarez MJ, Waley D. *Requested by the ANIT Committee: Particular Welfare Needs in Animal Transport: Aquatic Animals*. Policy Department for Structural and Cohesion Policies; 2021:56.
317. Sullivan M, Lawrence C, Blache D. Why did the fish cross the tank? Objectively measuring the value of enrichment for captive fish. *Appl Anim Behav Sci*. 2016;174:181-188. https://doi.org/10.1016/j.applanim.2015.10.011
318. Størkersen KV, Osmundsen TC, Stien LH, et al. Fish protection during fish production. Organizational conditions for fish welfare. *Mar Policy*. 2021;129:104530. https://doi.org/10.1016/j.marpol.2021.104530
319. Noble C, Gismervik K, Iversen MH, et al. *Welfare indicators for farmed Atlantic salmon: Tools for assessing fish welfare*; 2018. Accessed August 10, 2020. https://nofima.no/publikasjon/1636395/

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