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Cognitive enrichment to increase fish welfare in aquaculture: a review

Aude Kleiber[1,3,8]*, Mathilde Stomp[2]*, Mélanie Rouby[8], Vitor Hugo Bessa Ferreira[3], Marie-Laure Bégout[4], David Benhaïm[5], Laurent Labbé[6], Aurélien Tocqueville[2], Marine Levadoux[7], Ludovic Calandreau[3]‡, Vanessa Guesdon[1]‡, Violaine Colson[8]‡

[1] JUNIA, Comportement Animal et Systèmes d'Elevage, F-59000 Lille, France

[2] ITAVI, Filière piscicole, 76000 Rouen, France

[3] INRAE, CNRS, IFCE, Université de Tours, Centre Val de Loire UMR Physiologie de la Reproduction et des Comportements, 37380 Nouzilly, France

[4] MARBEC, Université de Montpellier, CNRS, Ifremer, IRD, F-34250 Palavas-Les-Flots, France

[5] Department of Aquaculture and Fish Biology, Hólar University, Sauðárkrókur, Iceland

[6] INRAE, PEIMA, 29450 Sizun, France

[7] CIPA, 75010 Paris, France

[8] INRAE, LPGP, Campus de Beaulieu, 35042 Rennes, France

* These authors share the first authorship
Corresponding author: Aude Kleiber, aude.kleiber@outlook.fr

‡ These authors share the last authorship

Abstract

While most animals have received increasing attention for their welfare, consideration for fish welfare has started more recently, particularly since the recognition that fish have emotions and complex cognitive abilities. Housing conditions in fish farms do not always meet fish ethological requirements as these conditions lack sufficient sensory and cognitive stimulations. An approach to address this issue involves enriching the rearing environment by including social, food, physical, or cognitive stimuli. Cognitive enrichment (CE) is a recent but promising concept to improve fish welfare by manipulating the predictability and controllability of their environment. It relies not only on the ability of fish to predict positive and negative events but also on their ability to perform and succeed in operant conditioning. In our present review, we identified four categories of CE: (i) feeding predictability, (ii) predictability of a negative event, (iii) operant conditioning through self-feeders, and (iv) learning experiences. Existing CEs were reviewed for their effects on behaviour, brain, zootechnical performances, and welfare in terms of physiological stress or physical integrity in the aquarium and farmed teleost fish. The review highlights unbalanced categories and the lack of adequate multidisciplinary analyses to assess the effects of these categories on fish welfare. Providing free access to self-feeders seems to be a good strategy, given its positive effects on zootechnical and physiological parameters. Other categories showed contradictory and species-dependent results; hence, further studies are required to confirm the benefits of CE on fish welfare. Finally, further investigations should also validate current CE systems and assess other strategies that may trigger positive emotions in fish.

Keywords: Feeding predictability, fish farming system, fish welfare, negative event predictability, occupational enrichment, self-feeder

1. Introduction

Animal welfare of captive animals is currently a key issue in our society, and its definition is constantly changing not only to adapt and include new scientific knowledge but also to meet new societal and legislative demands. The definition of animal welfare generally varies depending on whether one considers the function-, feeling- or nature-based approaches (for discussion on this, see Saraiva et al., 2018). A commonly used definition for the welfare of an animal is 'its state as regards its attempts to cope with its environment' (Broom, 1986). This definition clearly emphasises the importance of considering an animal's perspective and expectations, or in other words, its cognition. As cognition is 'the way animals perceive, process, acquire, store and act upon information coming from their environment' (Shettleworth, 1998), we can say that cognition is an integral part of animal welfare.

Since the early 2000s, the concept of positive welfare has emerged, and it can be defined as the 'mental and physical states that exceed what is strictly necessary for short-term survival' (Fife-Cook & Franks, 2019). To be guaranteed, welfare implies the absence of negative or constraining experiences (fear, illnesses, and stress) and the possibility of experiencing positive emotions (joy and pleasure) (Boissy et al., 2007), which can be achieved by meeting the animal's behavioural and physiological needs and expectations (ANSES, 2018). Nevertheless, captive conditions often involve impoverished environments that prevent the animal from fully meeting its ethological and physiological needs, with very few sensory and cognitive stimuli (Zebunke et al., 2013). Captive animals also often lack control over their environment, *i.e.,* successive failures in attempts to cope with a challenging situation which may result in behavioural and/or health disorders such as chronic stress, stereotypies (Dawkins, 1988), depression-like states (Fureix et al., 2015; Fureix & Meagher, 2015), degradation of brain functions (Lovallo, 2015), increased aggressiveness (Popescu & Diugan, 2013) and decreased growth rate or immunity (Ursin & Eriksen, 2004). Aquaculture husbandry practices also involve unpredictable events such as cleaning, transfers, sorting, oocyte collection, sudden lighting, weighing and vaccinations, which make farming conditions unpredictable and uncontrollable and thus potentially stressful for fish (Colson et al., 2019; D'orbcastel et al., 2009; Karakatsouli et al., 2007; North et al., 2006; Tschirren et al., 2021). In barren tanks, captive fish do not have any opportunity to escape from threats; in contrast, in natural habitats, wild fish can hide or flee during an unpredictable event, which may enable them to cope more easily and/or rapidly with such events. It is, therefore, important to find strategies for mitigating the stressful effects due to the unpredictability of the environment used for maintaining fish in captivity.

While several animal production processes have received considerable attention from major regulatory authorities and the general public regarding animal welfare, this is an emerging issue for fish production. Today, in Europe, even though the WOAH (World Organisation for Animal Health), formerly known as the OIE (Office International des Epizooties), has established standards (*i.e.* general principles and recommendations) for aquatic animal welfare, including farmed fish (OIE, 2021), there are still no directive targeting specifically fish welfare (Giménez-Candela et al., 2020). Research on welfare improvement strategies for fish have started only recently in the last two decades (Grimsrud et al., 2013). Such research studies are currently increasingly necessary, particularly because it has now been recognised that fish can experience pain and perceive different emotions such as fear, frustration, and anticipation (Kittilsen, 2013; Salena et al., 2021; Sneddon & Brown, 2020). Fish also possess complex cognitive abilities comparable to those of non-human primates even if they lack a neocortex (Bshary et al., 2002; Salena et al., 2021; Sneddon & Brown, 2020). Learning concepts – which require decision-making, associative learning and problem-solving abilities – are examples of a large spectrum of cognitive abilities possessed by fish. When conditioned to discrimination paradigms, fish learn to differentiate between shapes or objects (Schluessel et al., 2012), even if partially masked (Sovrano & Bisazza, 2008; Wyzisk & Neumeyer, 2007); sizes (Siebeck et al., 2009); and colours (Bloch et al., 2019; Maia et al., 2017; Oliveira et al., 2015) and to solve numerical rules (Agrillo et al., 2010; Agrillo & Bisazza, 2014; DeLong et al., 2017). For example, teleost fish can discriminate between shoal size or between small and large quantities of 2D and 3D objects (Agrillo et al., 2017); similarly, archerfish (*Toxotes chatareus*) can identify 44 different human faces (Newport et al., 2016). Some fish species are even capable of self-recognition (*Labroides dimidiatus*: Kohda et al., 2019; *Pelvicachromis taeniatus*: Thünken et al., 2009). Goldfish can orient in their environment by using a particular turn response (egocentric strategy) or environmental cues (allocentric strategy) (Rodriguez et al., 1994). Tool use was also demonstrated in some fish species, such as the Atlantic cod (*Gadus morhua*), which can use an external tag to operate the trigger of a self-feeder (Millot et al., 2014), or the six-bar wrasse (*Thalassoma hardwicke*), which uses rocks with rough surfaces as support to break food pellets into small pieces that are easier to swallow (Paśko, 2010). Fish have thus developed different memory systems that can hold working memory – a short-term memory that allows reasoning, learning, and comprehension – and episodic-like memory – which enables them to recall the context of a past event, including *what* happened and *when* and *where* to mobilise – and use it in the present scenario (*Danio rerio*: Gerlai, 2017; Hamilton et al., 2016; *Labroides dimidiatus*: Salwiczek & Bshary, 2011). All these studies demonstrate that high cognitive abilities are not restricted to large-brain vertebrates (Vail et al., 2013). Thus, improving welfare in aquaculture and aquariology is a real challenge given the high diversity in cognitive skills, lifestyles and behaviours among fish species (Saraiva et al., 2022).

To further improve captive fish welfare, in this review, we present the current state of the art on cognitive enrichment (CE) strategies that have been tested on captive fish (aquarium and farmed) and how these strategies affect their welfare. After a rapid overview of the different types of environmental enrichments, we focus on CEs and describe in greater detail the cognitive abilities that enable fish to derive benefits from each type of CE. We then describe the different methodologies used to design CEs, followed by reporting the effects of CEs on fish welfare and zootechnical performances. The final part of this review presents the current limitations and recommendations to design appropriate CEs.

2. Environmental enrichment: an effective strategy to improve animal welfare

Among the different strategies investigated to enhance the welfare of captive animals, **environmental enrichment (EE)** is one of the most promising alternatives for achieving multiple positive outcomes in different species (Fox et al., 2006; Mason et al., 2007; Newberry, 1995; Reynolds et al., 2010). The EE concept was widely developed around three decades ago and has been mainly studied in the field of applied ethology (Broom, 1986; Mason, 1991; Newberry, 1995; Ödberg, 1987). EE is defined as a husbandry principle that describes how the environments of captive animals can be changed to promote positive behaviours and reduce maladaptive and aberrant traits such as aggression and stereotypies. Traits could be physiological, behavioural, morphological, and psychological and considered maladaptive in terms of fitness components (health, survival, reproduction, etc.) (Näslund & Johnsson, 2016). EE allows the animals to enhance their opportunities to interact with their environment and make choices to gain some control over it (Galhardo & Oliveira, 2009). Beyond the reduction in the risk of developing abnormal and agonistic behaviours, EE particularly seeks to meet the physiological, behavioural and psychological needs of captive animals (for reviews, see: Arechavala-Lopez et al., 2021; Näslund & Johnsson, 2016). Thus, EE works to increase the repertoire of animals' behavioural responses so that they can cope with challenges in a more flexible and adapted manner (Young, 2003). EE thus contributes to animals' welfare, and this has been confirmed in many animal species, including fish (reviews: Arechavala-Lopez et al., 2021; Näslund & Johnsson, 2016).

EE can assume several forms, such as food, social, physical and cognitive enrichments. The definitions of these forms, the different methods used for these enrichments and their outcomes are listed in a recent review on fish (Arechavala-Lopez et al., 2021). Briefly, **food enrichment**, which is also known as dietary enrichment, consists of modifying the provided food by acting on its physical aspect (size, form and state [pellets or live food, liquid or solid]) and its delivery (frequency, food location(s) and type of dispenser) and on food-related olfactory cues (appetence) (Young, 2003). In Atlantic salmon (*Salmo salar*), for example, the provision of live prey (brine shrimp) together with physical enrichment enhances its foraging performance and may thus improve the post-release survival rates of hatchery-reared fish (Brown et al., 2003). **Social enrichment** is the possibility to have temporary or permanent contacts with conspecifics (pair and group), other species or sensorial stimuli linked to social cues (odours, pheromones, sounds, vocalisations and mirror) (Young, 2003). However, food and social enrichments are not easily applicable in farming and aquariology because zootechnical parameters (*e.g.,* food delivery and fish density) are usually constant and based on husbandry practices. Furthermore, social enrichment may often be related to reduced group size in fish farming, which could increase the 'quality' of the social environment; however, fish may also start to fight more as a response to dominance-based social hierarchies (*i.e.,* in salmonids) – which is a more natural behaviour, but with negative effects on the welfare of some individuals (Roy et al., 2021). **Physical enrichment**, also known as structural enrichment, involves the modification of the animal's living environment by adding physical elements (structures/accessories, substrates and physical exercise) and/or sensorial stimuli (visual, auditory and others), either permanently or temporarily. Physical enrichment is the most studied EE in aquatic animals. The different methods used for physical enrichment and their outcomes are listed in three recent reviews (Arechavala-Lopez et al., 2021; Näslund & Johnsson, 2016; Zhang et al., 2022). The authors concluded that many, but not all, studies report positive effects of physical enrichment on the behaviour, growth performance, survival and physiology of fish. For instance, rainbow trout (*Oncorhynchus mykiss*) held in enriched conditions, including gravel, plants and covered areas, showed a better recovery and lesser adverse effects (immobile behaviour, opercular beat rate and high cortisol level) following exposure to a stressor (acetic acid injection) than trout reared in barren tanks (Pounder et al., 2016). A recent study showed that trout in an enriched environment had better growth and were less aggressive than those kept in barren tanks (Brunet et al., 2022). They were also less fearful when isolated in a novel tank and bolder when facing a novel object (Brunet et al., 2022). However, habituation, defined by Lieberman (2000) as 'an automatic process in the brain decreasing the strength of a reflex upon multiple exposures to a stimulus' and extinction phenomena can be easily observed with this type of enrichment and decreases the initial positive effect of such additions to the environment (Tarou & Bashaw, 2007). Moreover, physical enrichment is not easy to adapt to farming systems as it can create constraints with regard to time and cleaning for fish farmers (Kientz & Barnes, 2016; Näslund & Johnsson, 2016a). Therefore, although physical enrichments may present many advantages regarding fish welfare, reintroduction plans or zootechnical performances, farmers should use them with caution and choose appropriate structures that are easy to clean, non-damageable and non-fear-provoking (*i.e.,* generating neophobia) (Kientz & Barnes, 2016; Näslund & Johnsson, 2016a); fish farmers should also vary the location and/or the type of objects introduced into the tanks to avoid any habituation phenomenon.

3. CE: is this another promising strategy?

CE, which is also known as occupational or psychological enrichment, introduces the possibility for animals to meet moderate challenges by using their cognitive/learning abilities and to actively interact with their environment (Manteuffel et al., 2009; Meehan & Mench, 2007; Oesterwind et al., 2016). These challenges range from simple manipulations (*e.g.,* devices to obtain food) to more complex problems (*e.g.,* puzzle solving) that are tailored to the biology of the species. CE mainly aims to reduce psychological monotony within the environment by introducing animal-controllable variations and decreasing the environment unpredictability that can act as a source of stress or anxiety (Galhardo et al., 2011; Galhardo & Oliveira, 2009; Greiveldinger et al., 2009; Näslund & Johnsson, 2016). For instance, goats successively confronted with several visual discrimination tasks in their home pen showed a decreased heart rate while resting in response to their increased learning performance on consecutive tasks (Langbein et al., 2004). Acquiring information can thus be self-rewarding (Wood-Gush & Vestergaard, 1989), which can likely induce positive emotions on its own (Franks, 2017; Zebunke et al., 2013). Therefore, the welfare of captive animals may depend on the extent of cognitive stimulations they receive. Furthermore, the ability of animals to secure positive mental states and guard against negative ones depends on what they know and learn about their environment and thus depends on their cognitive capacity. Therefore, cognition and welfare are closely interrelated (Franks, 2017).

Many of the CE strategies established in farms are based on classical or operant conditioning, which makes the occurrence of events predictable and/or controllable. Classical (Pavlovian) conditioning, or classical associative learning, involves associating a usually neutral stimulus with either a positive or negative event. Operant conditioning is a learning process in which animals learn to associate their voluntary behaviour to its consequences (either positive or negative). These concepts will be explained in more detail in Section 4.

With regard to predictability notions, *i.e.,* having information about the regularity of salient daily events (Bassett & Buchanan-Smith, 2007), in the environment as an approach to CE, one can consider two kinds of predictability: (i) temporal predictability when one event can occur at fixed (temporally predictable) or variable (unpredictability) time intervals and (ii) signalled predictability when a stimulus is always preceded by a signal (mostly auditory or visual). Preference for predictability was determined through choice tests in humans and animals (Badia et al., 1973; Mineka & Hendersen, 1985). Some studies even showed that predictability reduces the stress effects of aversive experiences warned by a neutral stimulus (Bassett & Buchanan-Smith, 2007; Lovallo, 2015; Sapolsky, 2004). Therefore, predictability seems to have various advantages. First, it offers the animal the opportunity to obtain knowledge regarding its surroundings and then be better prepared and adapt more easily to environmental changes (Daan, 1981; Meehan & Mench, 2007; Millot, Nilsson, et al., 2014; Williams et al., 2014). Second, predictability may satisfy the animal's drive to be regularly engaged in cognitive challenges. Regularly training animals to anticipate positive reinforcements (*e.g.,* food reward) allows active 'anticipatory behaviours' (*e.g.,* mainly hyperactivity) (lambs: Anderson et al., 2015; pigs: Dudink et al., 2006; salmons: Vindas et al., 2014) to appear and can be rewarding in itself as anticipatory behaviours are linked to the activation of the reward neural circuits (*i.e.,* dopaminergic system) involved in positive emotions (Spruijt et al., 2001; van der Harst et al., 2003). However, even if captive animals tend to choose predictable events over the unpredictable ones (Badia et al., 1973; Mineka & Hendersen, 1985), several studies have shown that unpredictability in appetitive events may reduce boredom encountered with easily predictable environmental conditions and sometimes even enhances animal welfare by promoting a continual interest. This behavioural aspect was observed in captive black rhinoceros (*Diceros bicornis michaeli*) when provided with a simple but temporally unpredictable puzzle for food, which did not decrease their interest toward the feeder over time (Krebs & Watters, 2017). Therefore, the notion of predictability is an essential strategy to improve animal welfare in farms, including fish; however, this implies acquisition of detailed knowledge of species-specific preferences and problem-solving and cognitive abilities to implement appropriate CEs (Nawroth et al., 2019).

4. Upon which cognitive abilities of fish does CE rely?

Before considering the different CE strategies mentioned in the literature, it is essential to assess which cognitive skills fish need to use CE properly and which limits one might encounter when requiring fish to perform a specific task. CE is mainly based on animals' ability to appraise events and to retain information, thereby giving them the capacity to anticipate and control their environment by using either classical or operant conditioning paradigm. In the following section, we will thus focus on the appraisal skills of the fish and on these two specific cognitive skills widely investigated in fish cognition which paves the way for the possible CE considered in this review.

Appraisal of events and long-term memory

Faustino et al. (2015) defined appraisal as 'a multi-component and interactive process between the individual and the environment, in which the individual must evaluate the significance of a stimulus to generate an adaptive response'. According to Scherer's theory (2001), novelty, predictability, controllability, pleasantness, coping and discrepancy from expectations are appraisal components that allow fish to evaluate the significance of an event or a stimulus, according to their affective state and their environmental conditions (Faustino et al., 2015). Fish can appraise the affective valence (positive/negative) of an event, privileging the positive event (food) and avoiding the negative one (chasing with a dip net) (Millot, Cerqueira, et al., 2014). For example, sea bream (*Sparus aurata*) retains memories of events with positive (food) and negative (chasing) valence as shown by a conditioned place preference test; thus, allowing them to increase the time spent in the cued appetitive side and avoid the aversive one (Millot, Cerqueira, et al., 2014). In another study, zebrafish learned to avoid an electric shock (unconditioned stimulus) by swimming from a bright compartment (conditioned stimulus) to a darker compartment (Xu et al., 2007). According to Scherer's theory (2001), the repeated suddenness of stimuli in an unpredictable environment where the fish has no control may then trigger a negative appraisal of the situation, which is associated with negative emotions (Greiveldinger et al., 2007). Conversely, a pleasant predictable event will trigger positive emotions (Boissy et al., 2007).

More than appraising the valence of an event, fish can also retain a highly aversive event from one month up to one year and are further able to avoid it (cleaner wrasse: Triki & Bshary, 2020; *Cyprinus carpio*: Beukema, 1969; *Pagrus major*: Takahashi & Masuda, 2021). Fish can also remember an appetitive event from one to eight months (*Tridentiger trigonocephalus*: Sakai et al., 2013; *Pagrus major*: Fujiya et al., 1980; *Gadus morhua*: Björnsson et al., 1999; salmonids: Tlusty et al., 2008; *Cyprinus carpio*: Sloan et al., 2013). It is thus important to consider that fish have the capacity of long-term memory retention, which justifies the use of CEs based on associative learning.

Classical conditioning to anticipate positive or aversive stimuli

Classical conditioning, or classical associative learning, consists of associating a usually neutral stimulus (conditioned stimulus [CS]) with either a positive or a negative unconditioned stimulus (US). The two stimuli either overlap in time (delay-conditioning) or are separated in time (trace-conditioning); this implies short-term memory.

Positive unconditioned stimuli

In fish experiments, positive stimuli used as US in classical conditioning are mainly food distributions. In associating a food reward with a neutral stimulus (for example, light as the CS), previous studies have demonstrated that Atlantic salmon, Atlantic cod, Atlantic halibut (*Hippoglossus hippoglossus*) or rainbow trout can exhibit a conditioned response evidenced by an increased activity when the signal was emitted alone after few trials. In the study of Thomassen & Fjæra (1991), salmons were successfully conditioned to a light stimulus as the CS after 72 to 144 trials, while Bratland et al. (2010) and Vindas et al. (2012) showed that salmons required around 19–56 trials to be successfully conditioned. Thomassen & Fjæra (1991) used trace-conditioning with 72 trials per day, while Bratland et al. (2010) and Vindas et al. (2012) used delay-conditioning with 2 to 7 trials per day. Thus, salmons took more time to learn under trace-conditioning than under delay-conditioning. This could be explained by the fact that trace-conditioning involves more complex brain functions than delay-conditioning where the CS and US overlap in time (Nilsson et al., 2008a) and/or by the shorter intertrial interval (Holland, 2000). In contrast, rainbow trout took less than 10 trials to exhibit a food anticipatory activity with a trace-conditioning procedure (Nordgreen et al., 2010). Nilsson et al. (2008a) reported that Atlantic cod can associate stimuli from 20 to 120 s apart from one another (trace) within only 8 trials and that fish in the 20-s trace groups remember the association for at least 3 months. In another study, the same authors showed that Atlantic halibut associated stimuli separated from 20 to 120 s apart within 6 to 70 trials (Nilsson et al., 2010). These results show a large variation between the different fish species on the basis of their abilities to associate two events separated in time and also the impressive ability of some of these species to retain a positive association in only a few trials and over a long period of time. However, one should note that the differences in the time required to reach conditioned responses may be due to the conditioning strategy (number of trials, salience of the US: more preferred food) or due to zootechnical parameters (density and photoperiod) rather than because of species-specifics differences alone.

Negative unconditioned stimuli

Similar to positive conditioning, fish can be successfully conditioned to a negative stimulus (Portavella et al., 2004; Portavella & Vargas, 2005). Aversive conditioning is known to be successful with different forms of US, such as an electric shock (Xu et al., 2007), chasing (Madaro et al., 2016), confinement (Cerqueira et al., 2020; Galhardo et al., 2011), dewatering (Cerqueira et al., 2017), and chemical alarm cues (Reddon & Hurd, 2009). As an example, Portavella et al. (2004) successfully trained goldfish (*Carassius auratus*) individually under delay-conditioning and trace-conditioning to associate a light stimulus (CS) with an electric shock (US) after 80 to 150 and 120 to 180 trials, respectively. After only 3 trials of trace-conditioning with the presentation of an object as the CS followed 1 min later by net chasing as the US, zebrafish exhibited anticipatory behavioural and neuroendocrine (cortisol and stress-related gene expression) responses when the object was presented (Samaras & Pavlidis, 2020).

Operant conditioning

Operant conditioning – also known as instrumental conditioning – is a learning process in which animals learn associations between their voluntary behaviour and its consequences (Skinner, 1937). For positive reinforcement, an animal will voluntarily cooperate in the task by repeating a particular behaviour, while for positive or negative punishment, the animal will tend to reduce or avoid it. Operant conditioning may involve a large set of cognitive abilities, such as spatial orientation, object recognition, temporal association of environmental cues, and tool use. Many fish species have already demonstrated these abilities (Jurado-Parras et al., 2013; Kleiber et al., 2021; Millot, Nilsson et al., 2014).

The self-feeder is an operant conditioning device commonly used by fish farmers. It allows fish to play an active role in their feeding schedule as they activate a trigger accessible from their rearing tank to receive their meals. By using self-feeders, fish can self-regulate and adapt their feeding behaviour in stressful situations (Endo et al., 2002; Ferter & Meyer-Rochow, 2010; Gélineau et al., 1998). Many fish species learn how to operate self-feeders in few trials in group (*Perca fluviatilis*: Ferter & Meyer-Rochow, 2010; *Seriola quinqueradiata*: Kohbara et al., 2000; *Gadus morhua*: Nilsson & Torgersen, 2010; *Oncorhynchus mykiss*: Noble et al., 2012; *Verasper moseri*:

Sunuma et al., 2007; *Dicentrarchus labrax*: Benhaïm et al., 2017; *Arapaima gigas*: de Mattos et al., 2016; *Carassius auratus:* Sánchez-Vázquez et al., 1999; *Pagrus pagrus*: Doxa et al., 2011; *Solea senegalensis*: Navarro et al., 2009); *Seriola dumerili*: Chen et al., 2007) or individually (*Oncorhynchus mykiss*: Kleiber et al., 2021; *Tinca tinca*: Herrero et al., 2005). However, fish species may differ in the extent to which they learn and operate the self-feeder; a group of white-spotted charr (*Salvelinus leucomaenis*) took 71 days to start activating the trigger, while a group of rainbow trout took 25 days to reach a stable level of self-feeding (Alanärä, 1996; Noble et al., 2012). The use of social learning by mixing naïve fish with the experimented ones is an interesting approach to achieve a faster performance in self-feeding (Flood et al., 2010; Kentouri et al., 1986; Noble et al., 2012). In a recent study, isolated rainbow trout learned to voluntary cooperate in a discrimination test by activating self-feeders positioned in the front of visual stimuli displayed on a screen (Kleiber et al., 2021). Fish can also differentiate signals indicating either a positive (food) or an aversive (confinement) stimulus by using the same operant paradigm and inhibit their operant behaviour toward the trigger if the signal predicts an aversive stimulus (Yue et al., 2008). Sea bass (*Dicentrarchus labrax*) can discriminate a self-feeder from a similar device in shape that allows them to gain access to physical exercise: an induced water current (Valverde et al., 2005); thus, demonstrating their need to perform more physical exercise, which is an under-explored enrichment strategy in fish farms (McKenzie et al., 2021). Fish are thus capable of performing different operant conditioning tasks, which allows them to control their environment for food access and even for more physical exercise.

Prediction by temporality

Although some environmental changes are unpredictable (tank cleaning, weighing and transfer), other cyclic fluctuations (currents, day length, moon phases and seasons) are predictable and thus appraisable by fish's biological clock (review: Sánchez-Vázquez et al., 2019). Because the biological clock is inherent to each organism, animals can predict and use temporal regularities of their environment by synchronising their behavioural and physiological processes for the different events they experience (Balsam et al., 2009; Lazado et al., 2017; López-Olmeda et al., 2012; López-Olmeda, 2017; Mistlberger et al., 1996). Circadian rhythmicity helps fish to estimate time intervals and relies strongly on environmental cues (food availability and temperature) and on their synchronisation with photoperiod. Interestingly, the circadian rhythm may show intra- and inter-species variations (reviews: Frøland Steindal & Whitmore, 2019; Madrid et al., 2001; Zhdanova & Reebs, 2005); furthermore, even in the absence of any environmental cues, the biological clock autonomously oscillates with a circadian period (Zhdanova & Reebs, 2005). Fish can thus temporally predict and differentiate feed and non-feed periods (Benhaïm et al., 2017; López-Olmeda et al., 2012).

Feed prediction

When feed delivery is restricted to the same time every day, either under a light-dark cycle or under continuous light, fish synchronise their daily activities to this specific time period (López-Olmeda, Sánchez-Vázquez, 2010; Madrid et al., 2001; Zhdanova & Reebs, 2005). Thus, they can make temporal anticipation of feed delivery schedules, which often leads to increased locomotor activity before the forthcoming meal; this behaviour can be observed in group (Cañon Jones et al., 2012; Chapman et al., 2010; Reebs & Lague, 2000; Sánchez et al., 2009; Ferrari et al., 2016) or individually (Ali & Wootton, 2001; Holley et al., 2014). This phenomenon is called 'food anticipatory activity' (FAA) (Mistlberger, 1994). FAA allows fish to prepare themselves both internally and externally for the forthcoming food by optimising their digestive and metabolic processes through the secretion of digestive enzymes (Bassett & Buchanan-Smith, 2007; Lazado et al., 2017; Montoya et al., 2010; Sánchez et al., 2009a; Vera et al., 2007). For instance, Reebs & Lague (2000) demonstrated that fish conditioned to fixed daily feeding schedules exhibited FAA from up to 4.5 h before mealtime and that 78% of them were still anticipating when food was omitted.

In goldfish, the number of bites on the trigger of a self-feeder increases during a restricted access of one hour per day (Gee et al., 1994). The same behaviour was also observed in Artic charr (*Salvelinus alpinus*) (Brännäs, Berglund, & Eriksson, 2005) and sea bass (Azzaydi et al., 1998). For a restricted time of self-feeding, fish learn to inhibit their operant behaviour (triggering activity) when they are unrewarded (Benhaïm, Ferrari, et al., 2017; Nilsson & Torgersen, 2010); thus, concentrating their feeding activity only to the time-restricted periods of access (Azzaydi et al., 1998, 2007; Maragoudaki et al., 2001; Shi et al., 2017).

Throughout this section, we described the cognitive abilities of fish that enable them to predict or control events. Fish are capable of appraising events as positive or negative, and they are endowed with a long-term memory; thus, providing them the ability to respond to positive and aversive conditioning (classical and operant). They also possess a biological clock that allows them to predict the time of their meal. These findings indicate the promising cognitive abilities of farmed fish to use appropriately a CE that already exists or could be developed for future fish farming systems. In the next section, we describe the effects of existing CEs on fish welfare.

5. Methodology of literature search used to assess welfare effects of CE

EE is a recent topic, and this is also true for CE, which is currently the least investigated type of enrichment for both terrestrial and aquatic captive animals. In a meta-analysis of research studies conducted on EE, CE alone accounted for 3.5% of the 744 reviewed articles in total – all species and EE types combined – for the period from 1985 to 2004, and none of these research studies included fish (de Azevedo et al., 2007). However, the authors did not include other CE terminologies, such as 'occupational enrichment' and 'psychological enrichment' in their review, which may have led to an underestimation of the total number of articles available in the literature. Langbein et al. (2006), Puppe et al. (2007), and Manteuffel et al. (2009) are among the first authors to use the terms 'cognitive enrichment' in the context of farm animals. Searching appropriate studies for the present review was therefore challenging because of the lack of mention of the terms 'cognitive enrichment' or any of its synonyms. Moreover, the boundary between the different types of EE is not entirely clear. Therefore, as suggested by Clark (2017), for the present review, we used a large panel of keywords to make the search as comprehensive as possible (see supplementary materials for the search history). The literature search was conducted for relevant articles listed in the Web of Science between 1995 and 2022. For studies prior to 1995, an additional search was conducted using Google Scholar and included the same keywords that accounted for CE combined with words representing more broad categories: 'fish', 'farmed fish', 'ornamental fish' and 'wild fish'. By using this method, and after agreeing on the definition of CE (see Section 3), we classified studies on CEs and their respective effects on zootechnical performances, behaviour and welfare in four distinct categories according to the required cognitive ability of the fish. **Category 1** assesses the impact of giving fish the possibility to predict mealtime. In **category 2,** fish are given the opportunity to anticipate the occurrence of a negative event (*e.g.* confinement due to tank cleaning) through conditioning. Such CE procedures are based on the concept of increasing the predictability of relevant events for fish. **Category 3** includes studies that investigate the effect of giving fish more control over their living conditions. These studies mainly involve providing the possibility for fish to use self-feeders, through operant conditioning, to improve their control over feeding. **Category 4** contains articles that are not easily classifiable. Their common topic is to use learning experiences as a reward in themselves, which is thus considered as CE.

All the articles obtained using this methodological search were classified according to the four previously mentioned categories of CE. For each article, we indicated the fish species; the ontogenic stage; CE duration; the group size; and types of effects obtained, namely behavioural, cognitive, zootechnical and/or physiological effects. We discuss these in detail in the next section.

6. Different effects of CE: results of literature search and discussion

The reviewed studies that investigated the effects of CEs on captive teleost fish are fully described in Table 1. A total of 81% of the selected studies (*N = 42*) focused on the effects of CE on farmed fish species: namely salmonid species (38.1%) – *Oncorhynchus mykiss, Salmo salar, Salvelinus alpinus* and *Oncorhynchus tshawytscha* – followed by sparid species (26.2%) – *Sparus aurata, Pagrus pagrus, Pagrus major* and *Pagellus bogaraveo* – and others species (16.7%) – *Gadus morhua, Oreochromis mossambicus, Oreochromis niloticus, Arapaima gigas* and *Colossoma macropomum*. The remaining 19% studies discussed laboratory or aquarium fish: *Danio rerio, Gasterosteus aculeatus, Poecilia reticulata*, *Carassius auratus* and *Epinephelus fuscoguttatus*. In the reviewed literature, the authors mainly investigated CE for their effects on zootechnical performances, behaviour and welfare in terms of physiological stress or physical integrity (targeted sector in Table 1).

Categories 1 (predictability of mealtime) and **3** (self-feeders) were the most represented with 14 and 22 articles, respectively (Table 1). **Category 2** (predictability of a negative event) was the least represented one, with only 4 articles. **Category 4** (learning experiences) included 6 articles. Table 1 highlights the unbalanced representation of these four categories, probably because of the novelty of using CE for fish, with temporality and operant conditioning being the most investigated topics. However, these studies mostly focused on zootechnical performances and physiological effects. In general, effects on cognitive abilities and/or brain and behaviour were poorly investigated.

Category 1: Giving fish the possibility to anticipate mealtime

A fixed feeding schedule is a routine husbandry practice, and some studies used this procedure as a CE because it increases the predictability of mealtime. Manipulating feeding schedules is known to alter the diversity of behavioural phenotypes within individuals, with predictable feeding schedules causing differences in the capacity of fish to take risks (Holley et al., 2014) (Table 1). An environment where mealtime is unpredictable – randomly distributed in time – leads to bolder individuals (Chapman et al., 2010; Ferrari et al., 2016; Salvanes & Braithwaite, 2005). The authors suggest that individuals living in an unpredictable environment are more likely to perceive benefits from engaging in a risky behaviour when they need to find opportunities to feed. However, despite this adaptive advantage, unpredictability in feeding under farming conditions seems to cause a constant state of alertness, with higher activity between meals (Saiz et al., 2021; Sánchez et al., 2009; Xu et al., 2022), which could be energetically costly in the long term and could result in lower immunocompetence (Cañon Jones et al., 2012), high stress (Saiz et al., 2021; Sánchez et al., 2009; Xu et al., 2022) and reduced growth (Ferrari et al., 2016; Xu et al., 2022). As mentioned previously, predictable feeding time produces FAA, a possible marker of positive emotions (Martins et al., 2012; Sánchez et al., 2009). However, FAA is often coupled with an increase in agonistic interactions in salmonid species

(Fife-Cook & Franks, 2019; Franks et al., 2017; Heydarnejad & Purser, 2009; Kittilsen, 2013). In line with this, FAA induced more frequent agonistic behaviours in two salmonid species reared in an environment where feeding time was predictable as compared to treatments where feeding time was unpredictable (Cañon Jones et al., 2012; Kleiber et al., 2022) (Table 1). However, aggressive behaviour alone is not necessarily indicative of altered welfare, but it does when coupled with fin injuries and damages (Martins et al., 2012), which were not observed for salmons (Cañon Jones et al., 2012). The possibility to predict feeding time does not seem to significantly affect zootechnical performances although, in some cases, it was associated with higher weight and lower fin damages (Braithwaite & Salvanes, 2005; Cañon Jones et al., 2012.; Ferrari et al., 2016; Sánchez et al., 2009; Xu et al., 2022). Overall, an environment where feeding time is predictable appears to be a promising CE strategy given the positive effects reported on fish welfare. However, the studies reviewed here, although concerning different fish species and different captive conditions, did not fully examine all aspects of behaviours, physiology, and in general, fish welfare.

Category 2: Giving fish the possibility to anticipate negative events

Conditioning fish to anticipate negative events or practices (air exposure, net chasing and confinement) is a CE procedure that has been used to increase the predictability of their rearing environment. Indeed, the possibility to anticipate a negative event can provide fish a certain degree of control over this event, thereby allowing them to be prepared for its occurrence and thus reduce its negative value (Cerqueira et al., 2017, 2020; Galhardo et al., 2011; Madaro et al., 2016; Orsini et al., 2002). However, whether this type of CE induces positive or negative emotions in fish needs further investigations as previous studies have yielded contradictory results. For example, Atlantic salmon and Gilthead seabream conditioned to an aversive stimulus (dewatering and chasing, respectively) exhibited more fear-related behaviours (*i.e.* flight and loss of social cohesion) during the CS than fish receiving it unpredictably (Cerqueira et al., 2017; Madaro et al., 2016), while the opposite case was found for sea bream (Cerqueira et al., 2020) and tilapia (*Oreochromis mossambicus*) (Galhardo et al., 2011) (Table 1). In some cases, anticipating a negative event could thus be more stressful than an event occurring in an unpredictable manner, particularly when the fish have no option to avoid the stressor; thus, resulting in experiencing stress for an increased amount of time while expecting the event (Cerqueira et al., 2017; Madaro et al., 2016).

Category 3: Giving fish the possibility to control their feeding through self-feeders

Another procedure to enrich fish farming conditions is to provide a certain degree of control over feeding. To achieve this, several studies have assessed the effects of rearing fish with self-feeders, a device that allows fish to control the delivery of their own food through operant conditioning (Table

1). Free access to self-feeders seems to be the more efficient method to promote zootechnical performance and improve fish physiology as compared to a restricted access or automatic and hand-feeding delivery (Table 1). For instance, compared to individuals fed continuously with an automatic feeder, rainbow trout with free access to self-feeders were more homogeneous in weight and exhibited less mortality for the same final specific growth rate and feed efficiency (Shima et al., 2001). The use of self-feeders globally results in better size and weight homogeneity, reduces fin damages and lowers the conversion factor and protein efficiency ratio (Alanärä, 1992b, 1992a; Azzaydi et al., 1998; de Mattos et al., 2016; Figueiredo-Silva et al., 2010; Gélineau et al., 1998; Pedrosa et al., 2019; Shima, 2001; Suzuki et al., 2008). Behavioural correlates were not investigated for the selected studies in this category (Table 1). However, it is known that restricted access to the self-feeder causes more aggressive behaviours linked to an increased competition in certain fish species such as Atlantic salmon or Artic charr (Brännäs, Berglund, & Erikson, 2005) and that triggering activity depends on the coping style of fish to stress; thus, supporting the benefits of free access to self-feeders (Attia et al., 2012).

Considering the positive effects of using only one self-feeder on fish growth and size homogeneity, providing access to more than one self-feeder could be another strategic approach to increase the impact of CE. However, previous studies showed that rainbow trout (Boujard et al., 2002; Kohbara et al., 2001; Wagner et al., 1996) and yellowtail (*Seriola quinqueradiata*: Kohbara et al., 2001) provided with three self-feeders concentrated their activity to only one self-feeder at a time. Consequently, rainbow trout had a lower final body weight, reduced feed intake and higher growth heterogeneity as compared to trout with a single self-feeder access (Boujard et al., 2002; Kohbara et al., 2001; Wagner et al., 1996). This may reflect that only a few individuals learned to operate the feeders, as previously observed in seabass (*Dicentrarchus labrax*: Millot & Bégout, 2009), while all other individuals became dependent on the rhythm and behaviour of these few high-triggering fish. This highlights the limit of the self-feeders as a CE strategy in groups as the controllability of the environment may only benefit a small sample of fish.

Category 4: providing fish with cognitive challenges

Few other studies that could not be classified in previous categories also tested innovative CE procedures on fish behaviour or physiology. In one study based on conditioning, fish were repeatedly trained to associate an aversive event (dewatering) with a positive outcome, *i.e.,* food delivery. This procedure was efficient to reduce behavioural and physiological responses of fish when they subsequently faced a stressful event (Schreck et al., 1995) (Table 1). Other studies used repeated learning experiences (spatial learning and trace-conditioning) as possible CEs, which were associated with brain and cognitive modifications (Álvarez-Quintero et al., 2020; Fong et al., 2019; Luchiari & Chacon, 2013).

7. Recommendations for designing an appropriate CE

In the present review, we identified four categories of CEs used for captive fish. Most of the reviewed studies focused on increasing the possibility for fish to better predict events that occurred in their living environment through a conditioning procedure or fixed time schedules and to provide them the opportunity to gain control over it. Furthermore, most of these studies highlighted positive and promising outcomes of these CEs on fish welfare and therefore represent a relevant information basis for implementing a successful CE for fish welfare. However, a high variability was observed among the experiments, and several studies from categories 1, 2 and 3 indicated negative or no effects of the attempted CE strategies. These discrepancies could result from intra- and inter-species differences, differences in environmental conditions (seasons, indoor or outdoor environment, tank size and fish density) and experimental designs (time, duration or severity of exposure, reward relevance and photoperiod) (Biswas & Takii, 2017; Chapman et al., 2010; Madrid et al., 2001; Salvanes & Braithwaite, 2005).

In this section, we address some key elements to consider when designing and implementing CEs to ensure maximum efficiency.

To ensure the effectiveness of conditioning procedures, caution should be exercised regarding the choice of the conditioned stimulus. Several conditioned stimuli allowed to successfully condition fish to a positive stimulus, such as a light stimulus (Bratland et al., 2010; Nilsson et al., 2008a; Nordgreen et al., 2010; Thomassen & Fjæra, 1991), an air diffuser (Masuda & Ziemann, 2000), water level (Sakai et al., 2013), and a sound stimulus (Sloan et al., 2013; Zion et al., 2010, 2011). Additionally, conditioning to an aversive stimulus was successful with CS being light, sound (Zion et al., 2010) or an external cue (Cerqueira et al., 2020; Galhardo et al., 2011). However, some conditioned stimuli are more effective than others, depending on their salience. The use of light (visible throughout the tank) as the CS would be more appropriate to acquire learning in large tanks or raceways where fish have no direct visibility of the food source (Thomassen & Fjæra, 1991). Conversely, sound as the CS would not be appropriate in farms where ambient noise is omnipresent (Moore & Newman, 1956). Bubble diffusion used as a CS seems to reinforce FAA responses, which is potentially related to the attraction response it generates in fish (Guttridge & Brown, 2014; Kleiber et al., 2022). For instance, sharks (*Heterodontus portusjacksoni*) conditioned to receive feed after bubble diffusion as a CS showed higher anticipatory behaviours and higher retention memory than those receiving feed after a light signal for the same conditioning procedure (Guttridge & Brown, 2014). Moreover, depending on its incentive salience, CS on its own can increase FAA in response to a sign-tracking foraging-strategy behaviour directed to the CS, in contrast to a goal-tracking strategy (Serrano-Barroso et al., 2019). This has been observed for archer fish which responded to a CS light above the surface by spraying water at it when fruit flies (US) were delivered on the surface (Waxman and McCleave, 1978) or for Atlantic cod which approached the CS light before waiting under the US food area (Nilsson et al., 2008b). The sign-tracking strategy can therefore lead to efficient responses to cue signals for individuals exhibiting such foraging strategies. The choice of the CS thus appears to be essential to consider for effective conditioning, thereby privileging a salient stimulus. The number of presentations of the CS/US in classical conditioning is also a critical factor. Indeed, an excessive number of trials during the day could slow down the learning process due to reduced feeding motivation for positive conditioning and may lead to chronic stress when fish would have no time to cope with the stressor for aversive conditioning (Schreck, 2000; Thomassen & Fjæra, 1991). Lower food anticipatory activity has been observed in fish fed with more than three daily meals, because of a more difficult temporal discrimination (Oliveira & Sánchez-Vázquez, 2010; Purser & Chen, 2001). Appropriate positive or negative unconditioned stimuli also need to be chosen carefully. For reward conditioning, to avoid negative contrasts (*e.g.,* discrepancy between the obtained reward and the expected one), reward shifts should be avoided as much as possible (Greiveldinger et al., 2009). For aversive conditioning, the use of a very aversive stimulus may induce a state of chronic stress (Boissy et al., 2007). CE based on the conditioning strategy requires to be highly reliable for the fish, namely by using one unique and clear CS for the forthcoming event and avoiding all wrong signals that might interfere with the CS and lead to a state of frustration (Bassett & Buchanan-Smith, 2007). For trace-conditioning, the length of the time elapsed between the CS and US should be monitored (Doxa et al., 2011; Galhardo et al., 2011; Shima et al., 2003; Zimmerman et al., 2011): it should not be too long to avoid frustration and loss of control nor too short to give the fish enough time to anticipate the event and to recognise this particular moment, which could be considered self-rewarding for positive conditioning and likely to promote positive emotions in fish (Martins et al., 2012). In contrast, Vindas et al. (2012); Vindas, Johansen et al. (2014); and Vindas, Sørensen et al. (2014) showed that the omission of an expected reward causes frustration in Atlantic salmon which is expressed by harmful effects on growth, aggression, and neurobiology (brain monoamine activity and abundant expression of genes involved in neuroplasticity).

Before using a fixed time schedule to increase mealtime predictability, it is also important to consider the feeding rhythm of the fish species as it can change the temporal implementation for a CE. This is particularly important for nocturnal-feeding fish species such as the sole: the self-feeding activity restricted to daytime is known to increase mortality and aggressiveness in this fish species

(De la Roca et al., 2017). Other species, such as sea bass (Azzaydi et al., 2000; Begout, 1995; Boujard et al., 1996; Sánchez-Vázquez et al., 1998) and seabream (Sánchez-Muros et al., 2003) are quite flexible in their feeding rhythm. However, further investigations are required to determine whether the feeding rhythm of fish species synchronizes with food cues, light cues, both, or circadian clocks before implementing predictable feeding schedules or restricted access periods to the self-feeder as CE approaches. An inadequate photoperiod may also impair feeding rhythm and learning and increase agonistic behaviours (Almazán-Rueda et al., 2004; Kitagawa et al., 2015; Lee et al., 2020; Mizusawa et al., 2007; Pinheiro-da-Silva et al., 2018; Rubio et al., 2003). The type of feeding predictability used is also important to consider in designing an appropriate CE. Signalled predictability of feeding generates higher FAA in rainbow trout and reduces aggressive and abnormal behaviours (jumps and burst of accelerations) as compared to temporal predictable feedings (Kleiber et al., 2022).

The use of self-feeders as a CE showed that free access to self-feeders results in more positive effects on fish welfare than restricted access. Furthermore, free-access self-feeding enables fish to control their own feeding and to select both quantity and possibly nutritious value as well as timing according to their appetite (Attia et al., 2012). Caretakers can achieve accurate feed intake monitoring (by counting wastes) and assess the feeding rhythm of their fish in addition to saving labour and time to feed the fish (Attia et al., 2012; Azzaydi et al., 2007; de Mattos et al., 2016; Mukai et al., 2016; Pratiwy & Kohbara, 2018). However, it may imply more important food wastage and thus, an increased cleaning time (Furukawa et al., 2002; Gélineau et al., 1998; Shi et al., 2017; Stewart et al., 2012). To overcome this effect, several options have been suggested: limiting accidental trigger actuations (trigger positioned above the surface of the water or inhibition of the device after each activation), determining the correct number of pellets per activation (depending on tank size and fish species), or collecting feed wastage (Coves et al., 1998).

8. Conclusions

To conclude, in this review, we highlighted that few studies investigated the overall effects of CEs on fish behaviour and physiology and, more generally on fish welfare. This topic, therefore, deserves further consideration. To obtain a complete representation of CE effects, experimental designs need to assess a panel of traits such as behaviour, cognitive abilities, physiology, neurobiology, zootechnical performance, and their interrelations (Bassett & Buchanan-Smith, 2007; Broom & Fraser, 2015; Broom, 1986; Saraiva et al., 2018; Manteca, 1998; Noble et al., 2018). However, the current results available in the scientific literature support CE as a promising approach to improve fish welfare as it is based on animal cognition principles, and an increasing number of studies have highlighted the remarkable cognitive abilities possessed by fish (Noble et al., 2018; Salena et al., 2021; Salvanes et al., 2013). Moreover, CE could overcome some of the constraints encountered with other types of EE, such as habituation that has already been reported with physical enrichment. However, to be effective, CEs will probably need an appropriate level of cognitive stimulations with learnable and reliable patterns to avoid frustration and an appropriate level of predictability to avoid anxiety from an unpredictable environment or boredom from invariably predictable events; CEs will also need to be designed according to the species needs (ecology and ontogenic stage) (Clark, 2017; Franks, 2017; Galhardo & Oliveira, 2009; Meehan & Mench, 2007). Animal caretakers are already using CEs based on fixed feeding schedules or the use of sounds preceding feed delivery; however, there is still a need for standardisation to make these procedures effective and clearly perceived and appraised by fish species. Finally, further investigations should also address the validation of the current systems and explore other strategies that may trigger positive emotions in fish.

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Type of cognitive enrichment	Method used	Details of the method used	Targeted sector	Species	Ontogenic stage	Duration of the cognitive enrichment	Group size	Classes of effects				References
								Behaviour	Brain/ cognitive abilities	Zootechnical performances	Physiology	
Category 1 : Give fish the possibility to anticipate mealtime	Delay-conditioning	Predictabilty (signalled by light) vs unpredictability of feeding (4x/day)	Behaviour and welfare	*Sparus aurata*	Adult	15 days (12 acclimatation and 3 experiment)	4 fish/tank, 6 tanks/treatment (4)	**(+)** more social interactions during CS	**(-)** lower expression profile of immediate early genes in Dm		**(+)** lower plasma cortisol after CS	Cerqueira et al., 2017
	Trace-conditioning	Predictabilty (signalled by light) vs unpredictability of feeding (feed every 20 min) (CS 5s)	Zootechnical performances	*Salmo salar*	Smolts	40-65 days	148 fish/ tank, 4 tanks/treatment (2)			= growth rate, condition factor, food conversion factor (diurnal photoperiod, indoor) **(-)** lower growth rate and condition factor (continous light, outdoor)		Thomassen & Fjoera, 1991
		Predictabilty (signalled by bubble diffusion or by both time and bubble diffusion) vs unpredictability of feeding (5x/day) (CS 15s)	Behaviour and welfare	*Oncorhynchus mykiss*	Juvenile	14 days	156 fish/tank, 3 tanks/treatment (3)	**(+)** food anticipatory activity, lower agresssive behaviours, burst of accelerations, and jumps during feed omissions = emotional reactivity		= weight, body size, condition factor		Kleiber et al., 2022
		Predictability (signalled by card) vs unpredictability of feeding (4x/day)	Welfare	*Oreochromis mossambicus*	/	19 days (7 acclimatation, 4 training, 2 test)	24 fish and control: 19 fish, 1 fish/tank	= time in front the CS			**(-)** tendance for higher plasma cortisol after acute stress	Galhardo & Oliveira, 2011
	Temporal predictability of feeding	Temporally predictable (1x/day) vs unpredictable delivery schedules (4x/day)	Behaviour	*Dicentrarchus labrax*	Juvenile	60 days	52 fish/tank (6)	**(-)** less bolder individuals = exploratory behaviour		**(+)** higher specific growth rate	= hypoxia tolerance	Ferrari et al., 2016
		Temporally predictable vs unpredictable feed delivery schedules (1x/day)	Behaviour	*Sparus aurata*	Adult	60 days	8 fish/tank (6)	**(+)** more activity before mealtime, less daily locomotor activity		**(+)** higher weight at 30 days = weight after 60 days	**(+)** lower plasma cortisol and glucose = plasma lactacte	Sánchez et al., 2009
		Temporally predictable vs unpredictable feed delivery schedules (1x/day)	Behaviour and welfare	*Salmo salar*	Adult	15 days unpredictable or predictable + 13 days predictable	10 fish/tank (8)	**(-)** more agressive interactions (attacks, displacements, fin bites)		= weight, body size, condition factor **(+)** less numerous and severe fin dorsal erosion		Cañon Jones et al., 2012
		Temporally predictable vs unpredictable feed delivery schedules (5x/day)	Behaviour and welfare	*Oncorhynchus mykiss*	Juvenile	14 days	156 fish/tank, 3 tanks/treatment (2)	**(-)** more agressive interactions before feedings = emotional reactivity		= weight, body size, condition factor		Kleiber et al., 2022
		Temporally predictable vs unpredictable feed delivery schedules (1x/day) under two photoperiods (LL - 24L:0D and LD - 12L:12D), each under 3 feeding regimes: random feeding (R), mid-dark stage feeding (D), mid-light stage feeding (L)	Behaviour and zootechnical performances	*Oncorhynchus mykiss*	Juvenile	3 months	20 fish/tank, 7 tanks/treatment (6)	**(+)** LL-L and LD-L treatments: food anticipatory activity, less daily locomotor activity		**(+)** LL-L, LL-D, LD-L and LD-D treatments: higher growth and conversion factor	**(+)** synchronisation of the digestive enzyme activity to feeding schedule, rhytms in serum levels of glucose, triglyceride, total-cholesterol,serotonin levels and lower serum cortisol = serum insulin levels	Xu et al., 2022
		Temporally predictable (1x/day) vs unpredictable (4x/day) feed delivery schedules	Behaviour	*Poecilia reticulata*	Juvenile	Unpredictable schedule: 56 days/ Unpredictable or predictable early feeding regime: 49 days/ Predictable or unpredictable recent feeding regime: 7 days	4 fish/tank, 9 tanks/treatment (4)	**(-)** less bolder individuals, more time in a shoaling tendency, less exploratory behaviour (2 months) = after 1 week		= mortality, growth rate, body size, sex-ratio		Chapman et al., 2010
		Temporally predictable (1x/day) vs unpredictable (1/day) feed delivery schedule	Behaviour and welfare	*Carassius auratus*	Adult	30 days (3 weeks acclimatation)	9-10 fish/tank, 5 tanks/treatment (3)	**(+)** food anticipatory activity, less daily locomotor activity	**(+)** maintained rytmicity of clock-control genes		**(+)** lower plasma cortisol	Saiz et al., 2021
		Temporally predictable (constant) vs unpredictable (1-4x/day) feed delivery schedules, different feeding locations	Behaviour and rehabilitation	*Gadus morhua*	Juvenile	20 weeks	100 fish/treatment (4)	**(-)** Unpredictable/ Unpredictable feeding schedules and location/unpredictable location treatments: more bolder individuals **(-)** Unpredictable feeding schedules and location/unpredictable location treatments: faster to turn back to opercula beat-rate resting levels **(-)** Unpredictable feeding schedules and location treatment: faster to turn back to normal swimming activity **(-)** Unpredictable feeding schedules/ Unpredictable feeding schedules and location treatments: faster food recovery after acute stress		**(+)** constant feeding treatment: better growth rate		Braithwaite and Salvanes, 2005
		Temporally predictable (1-2x/day) vs unpredictable (1-3x/day) feed delivery schedules	Behaviour	*Danio rerio*	Adult	3 weeks	1 fish/tank, 6 tanks/treatment (4)	**(+)** twice more exploratory than before the treatment (predictable) **(-)** less exploratory than before the treatment (unpredictable)				Holley et al., 2014
		Temporally predictable vs unpredictable feed delivery schedules (1x/day)	Zootechnical performances	*Gasterosteus aculeatus*	Juvenile	21 days	1 fish/tank, 12 tanks/treatment (3)			= growth rate, gross growth efficiency, lipid and dry matter content, white muscle RNA:DNA ratio		Ali & Wootton, 2001

Type of cognitive enrichment	Method used	Details of the method used	Targeted sector	Species	Ontogenic stage	Duration of the cognitive enrichment	Group size	Classes of effects				References
								Behaviour	Brain/ cognitive abilities	Zootechnical performances	Physiology	
Category 2 : Give fish the possibility to anticipate an aversive event	Delay-conditioning	Predictabilty (signalled by light) or unpredictability of negative (air exposure) events (4x/day)	Behaviour and welfare	*Sparus aurata*	Adult	15 days (12 acclimatation and 3 experiment)	4 fish/tank, 6 tanks/treatment (4)	**(-)** more escape attempts, less social interactions during CS	**(-)** lower expression profile of immediate early genes in Dm		**(+)** lower plasma cortisol after CS	Cerqueira et al., 2017
		Predictabilty (signalled by card) or unpredictability of a negative (confinement) events (4x/day)	Behaviour and Welfare	*Dicentrarchus labrax*	Adult	14 days (12 acclimatation and 2 experiment)	4 fish/tank, 6 tanks/treatment (3)	**(+)** less freezing, less escape attempts, less time spent in shoaling, more exploratory behaviour during CS	**(+)** higher expression profile of immediate early genes in Dm		**(+)** lower plasma cortisol after CS	Cerqueira et al., 2020
	Trace-conditioning	Predictability (signalled by card) or unpredictability of negative (confinement) events (4x/day)	Welfare	*Oreochromis mossambicus*	/	19 days (7 acclimatation, 4 training, 2 test)	29 fish, control: 19 fish, 1fish/tank	**(+)** more time in front the CS, less freezing			**(+)** lower plasma cortisol	Galhardo & Oliveira, 2011
		Predictabilty (signalled by light 30s before) or unpredictability of an aversive (chasing) events (15s, 5min) (CS: 30s) (2x/day)	Behaviour and Welfare	*Salmo salar*	Parr	7 days	400 fish/ tank, 3 tank/treatment (4)	**(-)** chaotic swimming pattern during CS = swimming pattern between 15s or 5min US			= plasma cortisol, oxygen consumtpion after US (15s or 5min)	Madaro et al., 2016

Type of cognitive enrichment	Method used	Details of the method used	Targeted sector	Species	Ontogenic stage	Duration of the cognitive enrichment	Group size	Classes of effects				References
								Behaviour	Brain/ cognitive abilities	Zootechnical performances	Physiology	
Category 3 : Give fish the possibility to control their feeding through self-feeders	Self-feeder vs other feed delivery methods	Unrestricted self-feeding vs hand-feeding at fix schedule (1x/day)	Zootechnical performances	*Oncorhynchus mykiss*	Juvenile	33 days	10 fish/tank, 3 tanks/treatment (2)			**(+)** lower dorsal fin damage, higher specific growth rate and weight = conversion factor		Suzuki et al., 2008
		Unrestricted self-feeding vs hand-feeding at fix schedule (4-6x/day)	Zootechnical performances	*Oncorhynchus mykiss*	Juvenile	133 days	3980 fish/raceway, 2 raceways/treatment (3)			= weight, body length, conversion factor, mortality, fin condition	= healthy, haematocrit rate	Wagner et al., 1996
		Unrestricted self-feeding vs Restricted ration self-feeding vs belt-feeders	Zootechnical performances	*Oncorhynchus mykiss*	Juvenile	125 days	100 fish/tank (3), 300 fish/tank (3), 500 fish/tank (3), 3 tanks/treatment (3)			= feed efficiency, condition factor **(-)** lower weight (for 300 and 500 fish/tank)		Boujard et al., 2002
		Unrestricted self-feeding vs hand-feeding at fix schedules (2x/day)	Zootechnical performances	*Oncorhynchus mykiss*	Juvenile	8 weeks	26 fish/tank, 3 tanks/treatment (2)			= feed waste, feed efficiency **(+)** more size homogeneity, feed intake **(-)** lower specific growth rate		Gélineau et al., 1998
		Unrestricted self-feeding vs unrestricted and restricted automatic-feeding (12h/day)	Zootechnical performances	*Oncorhynchus mykiss*	Juvenile	44 days	50 fish/tank, 5 tanks/treatment (3)			**(+)** lower coefficient of variation in mean body weight, mortality = mean body weight, condition factor, specific growth rate		Shima et al., 2001
		Unrestricted self-feeding vs fix feeding delivery schedules (every 10 min for 7h/day)	Zootechnical performances and Welfare	*Salmo salar*	Juvenile	35 days	61 847 fish/tank, 3 tanks/treatment (2)			**(+)** lower dorsal fin erosion, less time to feed fish = specific growth rate, conversion factor **(-)** more food wastage		Stewart et al., 2012 et Noble et al., 2008
		Unrestricted self-feeding vs restricted self-feeding or automatic-feeding at fix schedules (3x/day)	Zootechnical performances	*Dicentrarchus labrax*	Juvenile	78 days	15 fish/tank, 5 tanks/treatment (3)			**(+)** Higher weight and feed efficiency in unrestricted self-feeding, followed by restricted self-feeding = specific growth rate, coefficient of variation	= body composition	Azzaydi et al., 1998
		Unrestricted self-feeding vs automatic-feeding at fix schedules (3x/day)	Zootechnical performances	*Colossoma macropomum*	Juvenile	127 days	10 fish/tank, 5 tanks/treatment (2)			**(+)** better feed intake, conversion factor = growth, survival	**(+)** higher protein efficiency ratio, protein retention rate and lower water phosphorus = hemato-somatic index, lipo-somatic index, viscero-somatic index, body composition, total ammonia nitogen excretion	de Mattos et al., 2022
		Unrestricted self-feeding (with infrared light sensor) vs automatic-feeding at fix schedules (2x/day)	Zootechnical performances	*Epinephelus fuscoguttatus*	Juvenile	25 days	10 fish/tank, 3 tanks/treatment (2)			= standard length, weight, conversion factor		Mukai et al., 2016
		Unrestricted self-feeding vs hand-feeding at fix schedules (2 or 3x/day) in RAS	Zootechnical performances	*Arapaima gigas*	Juvenile	60 days	6 fish/tank, 3 tanks/treatment (3)			= specific growth rate, weight, body size, feed intake, conversion factor, survival	**(+)** higher protein efficiency ratio, lower TAN, P = plasma glucose, cholesterol, body composition, orthophosphoric monoesters phosphohydrolase pattern **(-)** lower aspartate aminotransferase	Pedrosa et al., 2019
		Unrestricted self-feeding vs hand-feeding at fix schedules (2x/day)	Zootechnical performances	*Pagellus bogaraveo*	Juvenile	90 days (30 days adaptation, 60 days experimental period)	5 fish/tank, 3 tanks/treatment (2)			= weight, body size, survival **(-)** lower feed intake **(+)** lower conversion factor	**(+)** higher protein efficiency ratio, lower nitrogen, lipid, and starch intakes = body composition, hepatosomatic index, viscerosomatic index, glycolytic enzymatic activity, plasma glucose, cholesterol, insulin, muscle and liver lipid content	Figueiredo-Silva et al., 2010
		Self-feeder compared to fix feeding delivery schedules (1x/day)	Welfare	*Oreochromis niloticus*	Juvenile	12 days	/				**(+)** paler skin colour, lower plasma cortisol, higher phagocytic activity of fish macrophages, higher antibody production and blood-circulating lymphocytes	Endo et al., 2002

Type of cognitive enrichment	Method used	Details of the method used	Targeted sector	Species	Ontogenic stage	Duration of the cognitive enrichment	Group size	Classes of effects				References
								Behaviour	Brain/ cognitive abilities	Zootechnical performances	Physiology	
Category 3 : Give fish the possibility to control their feeding through self-feeders	Free-access vs restricted access to self-feeder	Unrestricted vs restricted self-feeding (2x/day)	Behaviour	*Salvelinus alpinus*	Adult	20 weeks	17 fish/tank (5)	**(+)** strong food anticipatory activity **(-)** more aggressive behaviour				Brännäs et al., 2005
		Unrestricted self-feeding (SF) vs daytime- (SFD) or nighttime- (SFN) restricted self-feeding vs fix daytime- or nighttime- feeding delivery schedules (2x/day (2D or 2N), 4x/day (4D or 4N) or 6x/day (6D or 6N)	Zootechnical performances and Welfare	*Colossoma macropomum*	Juvenile	40 days	6 fish/tank, 3 tanks/treatment (9)			**(-)** lower final weight, weight gain, feed intake (all fixed daytime and nightime feeding schedules) = conversion factor (SF, SFD, SFN, 4D, 4N)	**(+)** lower triglyceride content (SF) = Cholesterol, high-density lipoproteins (SF, SFN, 2N, 4N, 6N) = glucose, albumin, low-density lipoprotein, aspartate transaminase, alanine transaminase	Guilherme et al., 2022
		Unrestricted self- feeding, restricted self-feeding, and restricted timer-controlled feeding	Zootechnical performances	*Oncorhynchus mykiss*	Adult	3 months	937 fish/tank, 2 tanks/treatment (3)			**(+)** better growth rate, conversion factor		Alanärä, 1992a
		Unrestricted vs restricted self-feeding (3x/day)	Zootechnical performances	*Salmo salar*	/	6 weeks	25 fish/tank, 3 tanks/treatment (2)			= specific growth rate, weight, condition factor, conversion factor size homogeneity **(+)** lower fin damages **(-)** more food wastage	= body composition, nutrient retention efficiency, plasma glucose level **(-)** lower digestive enzyme activity	Shi et al., 2017a & 2017b
		Unrestricted self-feeding vs restricted self-feeding for 7 different periods (1x/day)	Zootechnical performances	*Dicentrarchus labrax*	Juvenile	62 days	40 fish/tank, 3 tanks/treatment (8)			**(+)** Higher weight and specific growth rate = conversion factor, body composition, coefficient of variation, mortality		Boujard et al., 1996
		Unrestricted vs restricted self-feeding (2x/day)	Zootechnical performances	*Oncorhynchus mykiss*	Juvenile	8 weeks	26 fish/tank, 3 tanks/treatment (2)			= specific growth rate, feed efficiency, feed intake **(+)** more size homogeneity **(-)** more food wastage		Gélineau et al., 1998
		Unrestricted vs restricted self-feeding (only day-time)	Zootechnical performances	*Pagrus major*	Adult	8 weeks	105 fish/tank, 2 tanks/treatment (2)			= feed intake, growth rate **(-)** more food wastage, lower feed efficiency		Furukawa et al., 2002
		Unrestricted vs restricted self-feeding (3x/day)	Zootechnical performances	*Sparus aurata*	Adult	64 days	10 fish/tank, 2 tanks/treatment (2)			**(+)** higher specific growth rate, feed efficiency, feed intake, body composition = survival		Velázquez et al., 2006
		Unrestricted vs restricted self-feeding (1x/day at dawn or night)	Zootechnical performances	*Pagrus pagrus*	Juvenile	32 weeks (8 weeks for each season)	50 fish/tank or 100 fish/tank, 2 tanks/treatment (3)			**(+)** higher feed efficiency in automn = body composition, mortality, feed efficiency		Maragoudaki et al., 2001
		Unrestricted vs restricted self-feeding (1x 3,5 or 7h/day)	Zootechnical performances	*Oncorhynchus mykiss*	Adult	16 weeks	1875 fish/tank, 2 tanks/treatment (4)			**(+)** lower conversion factor = specific growth rate		Alanärä, 1992b

Type of cognitive enrichment	Method used	Details of the method used	Targeted sector	Species	Ontogenic stage	Duration of the cognitive enrichment	Group size	Classes of effects				References
								Behaviour	Brain/ cognitive abilities	Zootechnical performances	Physiology	
Category 4 : Give fish learning experiences	Positive conditioning to stress	Positive (food) conditioning to stress (dewatering) (2x/day)	Welfare	*Oncorhynchus tshawytscha*	Smolts	13 days	79-89 fish/tank, 2 tanks/treatment (3)			**(+)** 100% survival after transportation compared to 10% mortality for controls, higher survival after second stressor	**(+)** lower plasma cortisol, glucose and lactate during transportation, faster recovery, higher resistance to infection with pathogen (for similar antibody number)	Schreck et al., 1995
		Positive (food) trace-conditioning to stress (moving dip net) (6x/day)	Welfare	*Gadus morhua*	Adult	7 days	85 fish/tank, 4 tank/treatment (2)	**(+)** higher swimming activity after CS, lower swimming activity after CS in controls			= plasma cortisol, glucose, lactate during CS	Nilsson et al., 2012
	Learning challenges	Multiple training in early life and tested again 3 weeks after (learning to access food with 4 different apparatuses, 9 trials/ apparatus)	Behaviour	*Gasterosteus aculeatus*	Juvenile	68 days (17 days/task)	3-5 fish/tank, 30 tanks/treatment (2)	**(-)** more time to reach food for similar swimming activity, failed at being conditioned	**(-)** smaller optic tectum only for females, lower performance in a maze task later in life compared to before the cognitive challenge	**(-)** lower growth, weight, body size, survival		Álvarez-Quintero et al., 2020
		Learning challenges with reversal learning (3-6 trials/day, 96 trials in total) or with spatial learning (1 trial/day)	Cognition	*Poecilia reticulata*	Adult	14 days for spatial learning, 19-22 days for reversal learning	1 fish/tank, 20 tanks/treatment (4)		= brain morphology **(+)** brain and optic tectum size for spatial learning compared to reversal learning	= body size		Fong et al., 2019
	Working for physical exercise	Giving access to swimming exercise (1x/day), then trace-conditioning (CS: light, US: food) (1x/day)	Behaviour	*Danio rerio*	/	20 days of swimming exercise and 8 days of conditioning to food	4 fish/tank, 12 exercised fish and x control fish. Conditioning: 8 exercised fish and 8 control fish, 1 fish/tank		**(+)** higher learning performance in classical conditioning after providing fish with physical exercise			Luchiari & Chacon, 2013
		Operant conditioning to access physical exercise	Behaviour	*Dicentrarchus labrax*	Juvenile	25 days acclimatation to self-feeder or sensor for physical exercise, 28 days without the sensor, 28 days with the sensor	5-6 fish/tank, 2 tanks/treatment (2)	**(+)** Sea bass discriminate between a self-feeder and an exercise sensor and voluntary actuate them, better control of their feeding rhythm in adequation to their physical exercise				Valverde et al., 2005

Table 1: Different effects of implemented cognitive enrichments on aquarium and farmed teleost fish in the literature reviewed. The results are presented by reviewed article and are synthesized and classified according to the four defined categories of cognitive enrichment: 1) feeding predictability 2) predictability of a negative event 3) operant conditioning through self-feeders 4) learning experiences. A same reviewed article can appear in two different categories when the authors conduced several experiences. For each article, we gave the details on methods used, fish species tested, ontogenic stage, duration of the cognitive enrichment implemented, group size and types of effects obtained. The "targeted sector" concerns the general purpose of the authors for having studied cognitive enrichment. In the effects section, the symbol "(+)" means a positive effect and the symbol "(-)" means a negative effect of the type of cognitive enrichment used, while the symbol "=" refers to similar effects between the cognitively enriched and non-enriched conditions.