

Premises for digital twins reporting on Atlantic salmon wellbeing

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ABSTRACT

Many species of fish, birds and mammals commonly live in human captivity; Atlantic salmon *Salmo salar* is one of them. The international legal status of the welfare of captive animals is slowly developing and still requires rigorous specification. For example, even though fish have complex cognition and elements of sentience, The United Nations' animal welfare principles still take a functional health-centred perspective overlooking the cognitive-affective component. Wellbeing problems remain a major source of slow growth and high mortality in intensive aquaculture of Atlantic salmon. The value system for decision making in vertebrates is based on expectations of emotional wellbeing for the options available and is linked with the individual's assessment of its future. We propose a new approach for monitoring and improving the welfare of salmon (or any other captive or wild vertebrate) based on modelling the salmon's wellbeing system by digital twins, which are simulation models that implement major bodily mechanisms of the organism. Indeed, predictions on boredom, stress and wellbeing can all be captured by a computational evolutionary model of the factors underlying behaviour. We explain how such an agent-based model of salmon digital twins can be constructed by modelling a salmon's subjective wellbeing experience along with prediction of its near future and allostasis (the bodily preparation for the expected near future). We attempt to identify the building blocks required in digital twin models to deliver early warnings about escalating issues that could eventually lead to negative effects on salmon health in aquaculture. These models would provide critical insights for optimizing production processes and could significantly reduce the reliance on animal experiments. Overall, reports of a population of digital twins could support the implementation of 3Rs - replacement, reduction, refinement - by offering actionable information to fish farmers as well as consumers, voters, politicians and regulators on relevant issues as well as guide experimental work on animal wellbeing across species.

1. Introduction

Today, most Atlantic salmon live in captivity (FAO, 2023), as do also many of the world's birds and non-human mammals (Bar-On, Phillips, and Milo, 2018; Greenspoon et al., 2023). Fish welfare is a major concern in intensive aquaculture in many countries (Wickens, 2020; Browning, 2023; Ciliberti, Alfano, and Petralia, 2023), and humans have responsibility for the welfare of captive animals (Farm Animal Welfare

Council, 2009; Bovenkerk and Meijboom, 2020; van de Vis et al., 2020; Cooper et al., 2023), but this is not fully reflected in international laws and agreements.

The aim of this paper is to outline the theoretical basis for monitoring and predicting the wellbeing of Atlantic salmon by constructing a population of digital twins—simulation models that implement major proximate mechanisms—where their wellbeing (defined in Box 1) is the output. This is an ambitious goal. It will require far deeper resolution of

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cognitive and emotional mechanisms than in most other agent-based models, but this is necessary to be able to model how a salmon would experience, for instance, a procedure, how the procedure can be made less stressful for the salmon and how one can estimate the degree of wellbeing of salmon in a facility or in an operation. A description of the many bodily mechanisms that should be incorporated in a salmon digital twin are discussed in Budaev et al. (2024).

The *method* of building such a salmon digital twin involves mechanistic models of decision making and wellbeing with a genetic algorithm that evolves a whole agent-based population of twins, which can capture individual variation among fish in an aquaculture facility. The *purpose* is discussed thoroughly in Budaev et al. (2024); here we will briefly describe the four challenges the digital twins can assist to address. (1)

Improve aquaculture productivity, i.e. growth and feed conversion and reduce mortality. (2) Promote and implement the 3Rs (replacement, reduction, refinement) in research on animals (Russell and Burch, 1959; Grimm et al., 2023) and in research for aquaculture (Hawkins et al., 2011; Eguiraun et al., 2018; Sloman et al., 2019). (3) The challenge from the public (and thereafter from politicians and regulators) for transparency about fish welfare, where reports from digital twins may act as honest brokers (Pielke Jr, 2007) for all these groups. (4) A digital twin is an instrument for the advancement of science: when assembling it from its parts, it will become clear where are the important gaps in scientific knowledge, enabling an iterative process between trials and modelling.

To study wellbeing, we must begin with decision making, as behaviour and wellbeing are closely linked. Decision making needs a

Box 1

Concepts in wellbeing for a digital twin model.

Note that the underlying concepts may differ across different research areas and contexts. The definitions in this box are provided to explain their usage in his paper.

Agency: the ability of an autonomous entity to set its own goal-directed behaviour.

Allostasis: the budgeting of resources required for effective preparative regulation of the body before a need arises.

Allostatic load: a continuum from hypo- (boredom) to hyper stimulation (chronic stress).

Allostatic overload: an allostatic load that exceeds the individual's ability to cope.

Animal welfare: the human third-person perspective on animal wellbeing out of care for the animal.

Animal wellbeing: an individual's own prediction of its near-future emotional state.

Awareness: ability to integrate subjective internal models with one's current goals and emotions to guide behaviour.

Basic needs: necessary factors to ensure the health and safety of an individual.

Boredom: the aversive experience to not be able to engage in satisfying activity and to not be able to keep attention engaged.

Degeneracy: the ability of structurally different components to perform the same function so that absence or malfunction of one component can be compensated elsewhere.

Digital twin: a modelled representation of an object or a system designed to reflect it accurately.

Emotion: a functional state of the brain that plays a broad role in decision making, responses to reward and punishment, involves inter-connected neural circuits, and includes affective component (feeling) described by valence and arousal.

Episodic-like memory: the ability to remember what/where/when information from an experience.

Experience: a subjective process by which an organism perceives its external and internal environment with awareness.

Global organismic state: the organism's centralized emotional state as defined by the currently dominant survival circuit.

Modularity: the independence of components in a serial architecture.

Motivation: the neural activity that transforms bodily needs to behavioural goals.

Neurobiological state: the current emotional arousal in a survival circuit, e.g. the level of fear in the brain.

Neuronal response function: the conversion from metric units to a subjective numerical value in a subjective internal model of real or imagined sensory data.

Prediction error: the difference between the *a priori* predicted state of the body or the environment and the *a posteriori* interpretation of the same by the sensory system.

Robustness: an organism's ability to remain in a favourable state for future reproduction.

Sentience: the capacity to experience subjective emotions.

Stress: a non-specific physiological, behavioural or cognitive state as well as the response of the organism to cope with real or anticipated challenges to its normal functioning.

Subjective internal model: an internal representation or model of an aspect of itself or the environment currently held in the working memory of the organism.

Subjective: internal processes and states of the organism that exist from its first-person point of view; their existence is inseparable from and cannot be defined independently of the experiencing organism.

Survival circuit: a highly integrated neural pathway that responds to a specific class of subjective internal models and controls a specific set of neurobiological, physiological and behavioural responses.

Unlimited associative learning: a general ability to learn from novel sensory data combinations.

value system to rank options (McNamara and Houston, 1986, 2009; Cabanac, 1992; Mendl and Paul, 2020; Jablonka and Ginsburg, 2022), and in vertebrates this value is the animal's prediction of its emotional wellbeing that will result from each option (Cabanac, 1979; Schultz, 2024; Giske et al., 2025). This value system enables boredom, stress and wellbeing, which can therefore be captured in a digital twin.

The rest of the paper consists of two main parts: a review of the biological machinery that informs an individual salmon about its wellbeing followed by a proposal for how these can be assembled in a wellbeing-explicit digital twin model. But first we discuss the slow developments in the thinking about animal welfare in United Nations documents, and then point out that the mortality and wellbeing of salmon in aquaculture is linked to the production technology. We end with some perspectives on the usage of a wellbeing-explicit digital twin.

1.1. The legal status of fish welfare

Since the publication of the Environmental Manifest from the UN Conference on the Human Environment (United Nations, 1972), United Nations documents have in general only marginally considered animal welfare. In the sustainable development agenda from 2015, animals are not considered sentient beings (Nista et al., 2020). However, in 2019 the UN launched The Convention on Animal Health and Protection (UNCAHP) as a global initiative to protect animals, with the ambition that the General Assembly will adopt it at latest in 2029. Its draft principles (Pipia, 2020) begin with the responsibility, care and assistance of animals in human custody, and thereafter include the five freedoms from hunger, thirst, malnutrition, fear and distress and the right to express normal patterns of behaviour (Farm Animal Welfare Council, 2009) and finally the 3Rs (Russell and Burch, 1959; Grimm et al., 2023). The draft principles also state that animals have intrinsic value and are sentient beings with capacity for positive and negative feelings. Evidence suggests that sentience is a step too far for many kinds of animals (Ginsburg and Jablonka 2019), but should apply to fish (Low et al., 2012; Andrews et al., 2024; Giske et al., 2025). Korte, Olivier, and Koolhaas (2007) point out that the five freedoms are more based on ethics than on science, that they are not helpful in animal welfare, and that complete freedom is undesirable.

Meanwhile, the UN Food and Agriculture Organization (FAO) still recommends “function-based approach to fish welfare” (Segner et al., 2019) where welfare is reached when animals are in good health and show normal biological functioning and expected growth. Whereas this is good intended, we will later explain why this functional approach should be replaced by a sentence-based concept. However, the FAO also emphasizes that the rapid increase in knowledge of biological, social, and environmental capacities and needs of fish presents an opportunity to develop and update the approach to welfare regulations and monitoring of fish in aquaculture (Segner et al., 2019).

1.2. Mortality and welfare are linked to production strategies in aquaculture

In 2023, and in Norway alone, 105 million Atlantic salmon *Salmo salar* and rainbow trout *Oncorhynchus mykiss* died prematurely in intensive aquaculture; 13 million more than the year before (Sommerset et al., 2023, 2024). In the sea-phase of aquaculture in Norway in 2023, the mortality was 16.7 % of all salmon (total for 2023), which is the highest number observed (Sommerset et al., 2024). Several human-affected welfare factors contribute severely to this high mortality and includes both land-based and sea-based facilities. Typical factors are diseases, parasites, challenging water quality, fixed environmental conditions, fast growth strategies and repeated handling, all linked to high production intensity. Repeated episodes of stress adversely affect individual fish. This contributes to bad reputation among the public. Although we do not cover disease explicitly, several studies suggest that when an animal channels resources to tackle stress this increases the

likelihood of disease and generally poor health (Tort, 2011; Campbell, Dixon, and Whitehouse, 2021). Stress is a major contributor to this mortality (Vindas, Johansen et al., 2016; Overton et al., 2019). Factors inducing stress in the farm are i) production related treatments disturbing the fish (sometimes this can be excessive with panic during crowding, pumping, etc), and ii) the mismatch between production conditions and the individual salmon's biological requirement. The Salmon Welfare Index Model 1 (Stien et al., 2013) and 2 (Pettersen et al., 2014) identify the basic needs (Bracke, Spruijt, and Metz, 1999) for salmon in aquaculture (Fig. 1).

Wild salmon populations also live in increasingly anthropogenically-altered environments. Many restoration programs raise juveniles for release (Jonsson and Jonsson, 2006; Araki et al., 2008; Lennox et al., 2021) but there is often a substantial mismatch between the challenges a young salmon meets in a monotonous hatchery and those that are vital for learning survival skills, both in the wild and in aquaculture (Ebbesson and Braithwaite, 2012; Dunlap, 2016; Solås, Skoglund, and Salvanes, 2019). Boredom causes inadequate brain development (Zupanc, 2006) and is a poor preparation for later life. This is likely an important factor in human-controlled salmon mortality.

2. The machinery for experiencing wellbeing in salmon (and other vertebrates)

As wellbeing and behaviour are intertwined in vertebrates (Cabanac, 1979; Giske et al., 2025), we must discuss decision making before wellbeing, and here take advantage of recent advances in neuroscience and cognitive sciences (LeDoux, 2012; Barron and Klein, 2016; Feinberg and Mallatt, 2016; Barrett, 2017; Godfrey-Smith, 2017; Gygas, 2017; Ginsburg and Jablonka 2019; Seth, 2021; Chittka, 2022; Zacks, Ginsburg, and Jablonka, 2022; Del Giudice, 2023; Reid, 2023). We will briefly explain the main findings and we refer to Budaev et al. (2024) and Giske et al. (2025) for more thorough descriptions of how these findings are relevant for animal behaviour and wellbeing.

2.1. Major evolutionary transitions to wellbeing

Three major transitions in evolution made it possible for organisms

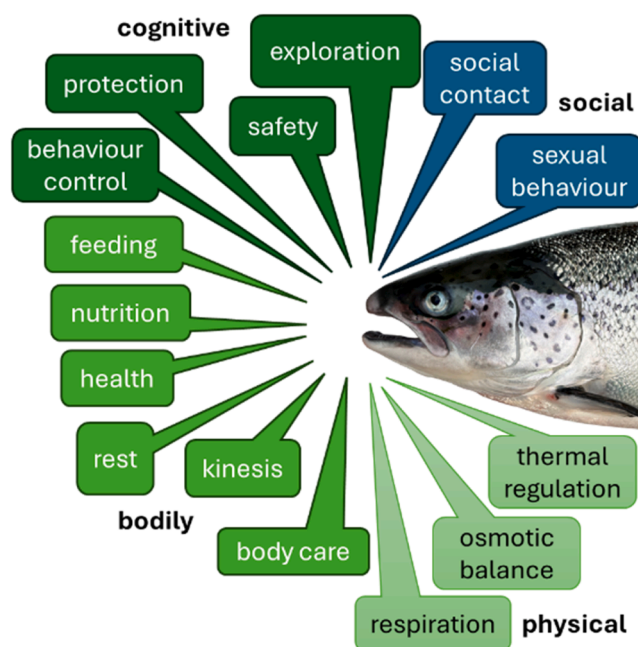


Fig. 1. Basic needs of Atlantic salmon are, according to the Salmon Welfare Index Model, a long list of physical, bodily, cognitive and social dimensions. See (Stien et al. 2013; Pettersen et al. 2014) for detailed descriptions of each.

to experience grades of wellbeing (Giske et al., 2025). The most recent transition seems to have happened during or shortly after the Cambrian explosion with evolution of episodic-like memory (remembering information about the where, what, when and with whom of an event, Clayton and Dickinson, 1998). As “what” in the episodic-like memory may contain an emotional experience (e.g., Damasio, 1999’s book entitled “The feeling of what happens”), these animals could use their experiences to predict grades of emotional wellbeing (Zacks, Ginsburg, and Jablonka, 2022) across behavioural alternatives (Giske et al., 2025). Dopamine neurons are central in the learning of these rewards (Karin and Alon, 2022; Schultz, 2024). This transition seems to have happened in early vertebrates (Gans and Northcutt, 1983; Zacks, Ginsburg, and Jablonka, 2022; Zacks and Jablonka, 2023), but parallel processes may have taken place in other lineages as well (Godfrey-Smith 2020; Elwood, 2021; Rößler et al., 2022; Farnsworth and Elwood, 2023). The combination of memories of with whom and the corresponding emotion also gradually enabled the capacity for sociality and even cooperation, which is also observed in teleosts (Croft et al., 2006; Heathcote et al., 2017; Busia and Griggio, 2020).

The development of subjective experience in addition to basic associative learning and instinctive responses (Ginsburg and Jablonka, 2010, 2019; Feinberg and Mallatt, 2013; Godfrey-Smith, 2017) seems to have happened slightly earlier in arthropods and chordates (Ginsburg and Jablonka, 2010; Feinberg and Mallatt, 2013) and much later in some molluscs (Godfrey-Smith, 2017). With subjective experience, the animal got a self – a “person within” – that could balance needs and emotions in a globally available memory (Baars, 1988; Dehaene, Kerszberg, and Changeux, 1998; Damasio 2003; Godfrey-Smith 2024). Agency, that is the ability to live and behave for the organism’s own goals, ultimately reproduction (Ruiz-Mirazo, Pereto, and Moreno, 2004; Thompson, 2007), appeared at the dawn of life on Earth (Kauffman, 2007). Gradually, a range of robustness mechanisms evolved in agentic populations because they had helped the phenotype remain within a window of favourable states for achieving those goals (Fernandez-Leon 2011a, 2011b; Wingfield, 2013).

2.2. Decision making

With agency and subjective experience, behaviour and decision making became parts of a vital robustness complex including sensing, emotion and attention (Ginsburg and Jablonka 2019). We follow LeDoux (2000) who named a highly integrated neuronal pathway from sensing via attention to behaviour a “survival circuit”, which is an evolved neural mechanism for efficient direction of the animal’s motivation to serve the current need. In a survival circuit, the animal’s subjective internal models of itself and its surroundings feed into neurobiological states (Giske et al., 2013), such as the levels of fear, hunger or curiosity (Fig. 2). (Despite the name, the evolutionary drive for the adaptation into these circuits was reproduction, not survival.)

Often the activated survival circuits compete for control of the body (Godfrey-Smith, 2017). At other times, none of them are activated. We begin with the situation in which one or more survival circuits are activated. Then, animals have the ability of attaining a centralised emotional state (Anderson and Adolphs, 2014; Barron and Klein, 2016) called the global organismic state (LeDoux, 2012), which controls the whole body for a limited amount of time. An individual in a global organismic state can focus its attention on its most urgent challenge (Mendl, 1999) and increase its sensory resolution of phenomena most relevant (Trimmer et al., 2008; Feldman and Friston, 2010).

Episodic-like memory (Zacks, Ginsburg, and Jablonka, 2022) and dopamine-based learning of rewards (Karin and Alon, 2022; Schultz, 2024) explain why vertebrates have predictive brains (Bubic, Von Cramon, and Schubotz, 2010; Soylu, 2016). Using prediction, a vertebrate estimates how each possible behavioural option would feel, if chosen (Crump et al., 2020; Giske et al., 2025). This is the crucial link between behaviour and wellbeing in all vertebrates: To decide its behaviour, a vertebrate assesses and compares its expected wellbeing benefits (Cabanac, 1992; Schultz, 2024; Giske et al., 2025). The motivation for behaviour in a vertebrate is to maximize wellbeing, and its behavioural choice is the option it regards will most likely maximize wellbeing, immediately or later (Aellen, Dufour, and Bshary, 2021). This is the proximate behavioural rule salmon have evolved to follow and is also what digital twins will have to use. Rather than the ultimate question “what is the optimal decision now?”, which may be very hard to

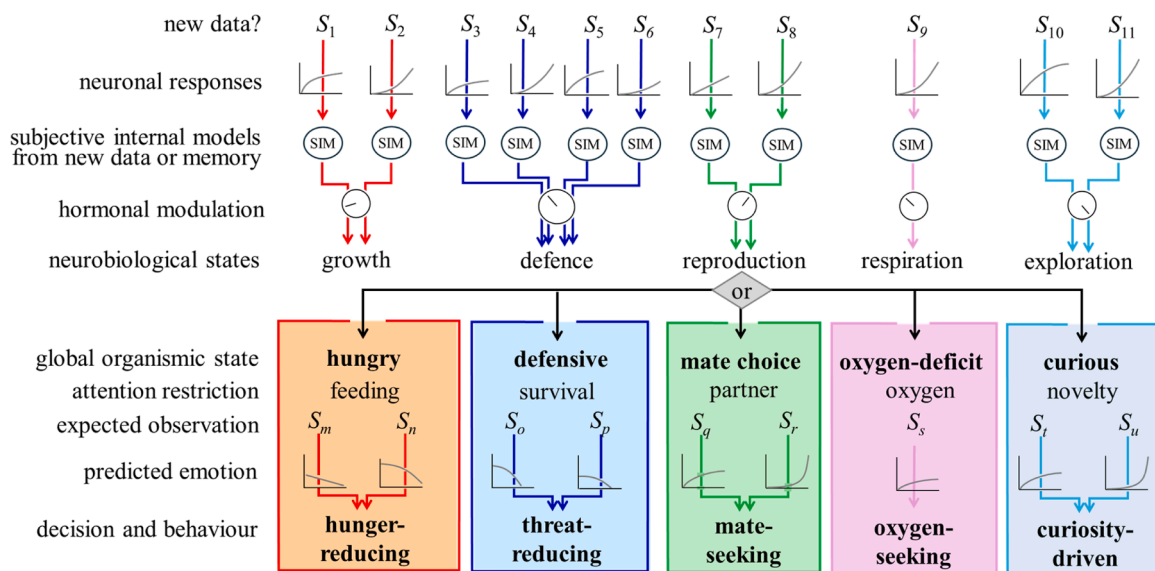


Fig. 2. A survival circuit is a highly integrated neuronal pathway from memory or new sensing via attention to behaviour. The small graphs illustrate the conversions from sensing ($S_1 \dots S_u$; the value of e.g. light intensity and food availability produced by the model) to an individual’s internal representation of that value in its subjective internal model (Andersen et al. 2016; Giske et al. 2025). The hormonal modulation helps the organism change its priorities through life with the same survival circuits. Salmon have many survival circuits (five illustrated here) which as illustrated can take one or more data as input. When activated, survival circuits compete for control of the body by the affect strength of their neurobiological states. The survival circuits are evolutionarily co-adapted proximate mechanisms for motivated behaviour that can through survival result in reproduction. See text for more explanation.

calculate in many situations both for fish and researchers, fish answer the proximate question “how is my wellbeing best improved?” (Cabanac, 1979, 1992; Klopff, 1983; Giske et al., 2025). This is easier to answer for the fish than the optimality question but harder for researchers. Prediction errors will occur, and more often and severely in an environment or situation the fish is not adapted to or has not learned about. However, satisfaction is a moving target (Spruijt, van den Bos, and Pijlman, 2001), and the competition between adapted emotions (Fig. 2) will balance out the animal’s wellbeing priorities.

After decision making and behaviour, a salmon uses sensing to compare its predictions to its observations; prediction error (Bubic, Von Cramon, and Schubotz, 2010; Adams, Shipp, and Friston, 2013) then becomes the basis for learning and for updating its subjective internal models.

If previous needs are satisfied and no new needs have appeared, then no survival circuit is activated and the salmon does not attain a global organismic state. It may then with low attention to each, consider several weak needs at the same time in its wellbeing assessment, for instance, to consider its weak appetite, its low level of fear, and some curiosity (Budaev et al., 2024; Giske et al., 2025). (See Fig. 3: two parallel routes towards the right at the bottom.)

Through evolutionarily very old forms of learning, sensitization and habituation (Cheng, 2021), most animals can modulate the impact of sensory stimuli on their behaviour (Ginsburg and Jablonka 2019). For instance, salmon parr can gradually habituate to sudden changes from darkness to light (Folkedal et al., 2010). Reinforcement learning is central in the learning of subjective rewards, where dopamine neurons provide excitations when the obtained reward is larger than predicted, and inhibitions when lower (Schultz, 2024). For example, Atlantic salmon can by Pavlovian conditioning habituate to light flashes that initially provoke fear (Bratland et al., 2010), which in sea bream is found sustained if not paired with reward (Folkedal et al., 2017).

With these cognitive capacities, a vertebrate can forge connections between an unfamiliar sensory input and its significance and adapt its response accordingly. This involves the creation of new synaptic connections within the brain, linking the sensory data to a subjective internal model and to a specific neurobiological state, and ultimately guides behavioural responses. Furthermore, through episodic-like

memory, this process extends to the anticipation of favourable or unfavourable outcomes.

2.3. Boredom and stress

Before discussing wellbeing as a concept, we need some background to two important wellbeing challenges, boredom and stress, which are two ends of a continuum. Boredom can be defined as the experience of not being able to engage in satisfying activity and to not be able to keep attention engaged (Eastwood et al., 2012). Prolonged boredom is bad for both humans (Britton and Shipley, 2010) and animals (Burn, 2017; Meagher, 2019). For fish, we consider the negative aspects of boredom at two different time scales. On the short scale, boredom and stereotypical conditions are not good welfare (Korte, Olivier, and Koolhaas, 2007; Rose, Nash, and Riley, 2017; See definition in Box 1). On the longer scale, lack of stimulation, often studied through environmental enrichment experiments (Arechavala-Lopez et al., 2022) is shown to alter brain organisation (Dumitru and Opdal, 2024) and can prevent the fish from learning important survival skills (Strand et al., 2010; Ebbesson and Braithwaite, 2012; Dunlap, 2016; Ward et al., 2024) and stress management (Martin, Sadlo, and Stew, 2006; Salvanes et al., 2013; Alnes et al., 2021). This lack of learning opportunity during prolonged boredom prevents the fish brain from developing normally (Braithwaite and Salvanes, 2005; Salvanes et al., 2013; Mes et al., 2019; Näslund, Rosengren, and Johnsson, 2019; Ward et al., 2024), a process which in fish, as opposed to mammals, continues throughout life (Zupanc, 2006).

For salmon, several studies have shown that experiencing mild stress in early life improves the ability to cope with stress later in life (Moberg, and Braithwaite 2007; Burns, Saravanan, and Rodd, 2009; Gonda, Herczeg, and Merila, 2009; Jonsson and Jonsson, 2014; Rosengren et al., 2017; Lai et al., 2024). Madaro et al. (2020) call this improvement in robustness via allostasis (see below). Here, repeated mildly stressful experiences improve the individual's ability to cope with the next (Korte, Olivier, and Koolhaas, 2007), ensure healthy adaptation (e.g., McEwen, 1998), and/or efficiently downregulate stress so that it can attend to other goals (Del Giudice, Ellis, and Shirtcliff, 2011). Early development in a stable RAS environment reduces robustness of the Atlantic salmon following transfer to natural environmental

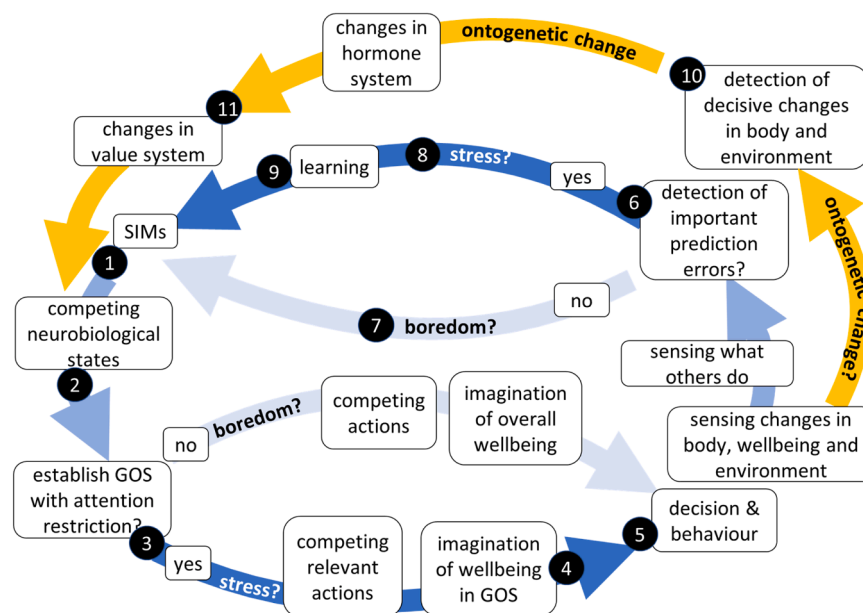


Fig. 3. Wellbeing reports from a salmon digital twin model. The decision-making process is illustrated by a fast cognitive (blue tones) and a slow ontogenetic (orange) loop. The cognitive loop has two branching points: sensing may or may not detect important prediction errors and competition between survival circuits due to the animal's subjective internal models (SIMs) may or may not lead to a global organismic state (GOS) with focussed attention. See text for explanation of the figure and to the numbers and the reporting from the digital twin. Modified from [Giske et al. \(2025\)](#).

unpredictability in sea cages (Lai et al., 2024). Stress management in salmon thus appear to be linked to developmental plasticity, associative learning and habituation and probably to the high capacity for brain change in fish (Zupanc, 2006).

Allostasis (Sterling, 2012; Barrett 2020) is the predominant framework for understanding stress. In this model, organisms anticipate their imminent needs and prepare for a coming challenge by modulating hormones, physiology, attention and behaviour. However, the costs of allostatic regulation can escalate under specific circumstances (Korte, Olivier, and Koolhaas, 2007): if there is a significant error in predicting the upcoming challenge, if the challenge surpasses the organism's capacity or reserves or if the challenge persists over an extended period.

Costs of persistent allostatic activation may accumulate to have adverse effects on the health and wellbeing of the organism. With even higher costs, allostatic overload can be pathological and genome-damaging (McEwen et al., 2015). These mechanisms likely contribute substantially to mortality in intensive salmon aquaculture. Finally, if allostatic load is extreme or long lasting and largely exceeds the capacity of the organism, the most robust response is to switch to the emergency life history stage where energy is redirected to self-maintenance at the expense of growth, reproduction and all non-essential processes (Wingfield et al., 1998).

These stress mechanisms in Atlantic salmon are demonstrated in an intriguing series of studies showing (i) anticipatory feeding behaviour (Bratland et al., 2010; Folkedal, Torgersen et al., 2012; Vindas et al., 2012), (ii) change in the anticipation after the experience of a dangerous disturbance (Folkedal, Stien et al., 2012; Folkedal, Torgersen et al., 2012), (iii) frustration when feeding anticipations are not met (Vindas et al., 2012, 2014) and (iv) salmon in the emergency life history stage (Vindas, Johansen et al., 2016) where (v) treatment with an antidepressant reduced maladaptive behavioural inhibition in Atlantic salmon and rainbow trout (Vindas et al., 2019; Shapouri et al., 2024). A successful digital twin must detect and report on such developments to prevent escalations.

2.4. Wellbeing

Absence of disease, injury, hunger and thirst are seen as basic animal welfare components, such as in The Five Freedoms (Farm Animal Welfare Council, 2009), the Five Domains (Mellor et al., 2020) the Four Principles of EU's Welfare Quality Assessment (Botreau, Veissier, and Pery, 2009) and in UN's UNCAHP initiative (Pipia, 2020). However, this absence is not common in nature, and the absences do not address boredom (Korte, Olivier, and Koolhaas, 2007). There has also been a focus on a species' natural behaviour (e.g., Bracke and Hopster, 2006). However, it is natural for salmon to die young. Further, natural behaviour does not necessarily imply good wellbeing (Barnard, 2007; Dawkins, 2023).

Animal wellbeing takes the perspective of the individual and should be seen in the context of body control by robustness and allostasis (Korte, Olivier, and Koolhaas, 2007), as emphasised by the studies cited above showing grades of stress in salmon. Korte, Olivier, and Koolhaas (2007, p. 426) concluded that "good animal welfare is characterized by a broad predictive physiological and behavioural capacity to anticipate environmental challenges" and "only conditions that produce high allostatic load or inadequately low allostatic load may threaten good health and good animal welfare". (We presume Korte, Olivier, and Koolhaas 2007 meant wellbeing when writing welfare in this quote.) From this, we can define an operational wellbeing concept as

a fish will have positive wellbeing if it predicts that it can reach a window of rewarding (as opposed to punishing) emotional states and this prediction is not significantly challenged by the actual environment.

This operational definition of wellbeing can be built into salmon's

digital twin. Then, the third-person perspective of good animal welfare means that the human observer considers that a salmon's predicted wellbeing outcomes of its behavioural options contains one or more emotionally positive alternatives (Giske et al., 2025). But whether those alternatives existed in the ancestral environment is not important.

3. A digital twin for salmon welfare

A salmon digital twin must be built to address all four purposes mentioned in the Introduction: aquaculture productivity and mortality, the 3Rs, fish welfare concerns and advancement of science. There are very few simulation models related to farm animal welfare. Collins and Part (2013) link this to lack of available quantitative data. However, even big data are easier to interpret via a theory (Coveney, Dougherty, and Highfield, 2016). In this paper, we lay out the theory for how animal welfare can be addressed by modelling the wellbeing of digital twins. Some of the challenges in nature and aquacultural management of salmon can be investigated and improved by computational modelling tools that explore and report on the assumed inner life of the fish (Budaev et al., 2024). Whereas most empirical welfare indices score the researcher's view from outside (Fig. 1), we seek a first person-report from inside the fish (Budaev et al., 2019, 2020, 2024; Giske et al., 2025). Because this report is not available directly, we need a digital twin to report on behalf of the fish.

A digital twin is a simulation model that aims to accurately represent an object of the physical world (Rasheed et al., 2020; VanderHorn and Mahadevan, 2021; Tao et al., 2022). It is much faster, easier, cheaper and safer to study a digital copy than the object itself, but for it to be useful we need evidence that a salmon digital twin produces responses with sufficient fidelity to natural salmon such that it addresses welfare problems in aquaculture. A digital twin for aquaculture must be integrated with near-real-time data from the facility, particularly data that may impact the wellbeing for the fish (see top row of Fig. 2). We discuss the potential outputs from the digital twin model below. If developed transparently, aided by empirical research and tested towards empirical production data from several and different aquaculture facilities, a digital twin can be an honest broker (Pielke Jr, 2007) on fish welfare for fish farmers, consumers, voters, politicians, regulators and researchers. Many other aspects than wellbeing must also be in place before a digital twin can represent a natural fish, such as physiology, ontogeny, the hormone and immune systems, sensing and behaviour. We regard the knowledge to build a digital salmon from a natural salmon's genome not to be available in the near future. This paper does therefore not end with a digital twin simulation model but with a description of a potential model of the digital twin's cognition and wellbeing. This being said, however, simpler digital twin like models have already been developed for salmonid appetite, feeding and growth (Budaev, Cusimano, and Rønnestad, 2024).

At this time, we cannot construct a twin that truly represents the inner life of a particular salmon, because we would not have the data. However, we can model a population of digital twins to represent major traits in a group of salmon (Budaev et al., 2024), so that this population of digital twins can report on the experiences of the natural fish that the digital twins represent. This approach may allow us to explore how to solve the stress and brain development issues without additional massive deaths (Hawkins et al., 2011; Eguiraun et al., 2018; Sloman et al., 2019).

Our focus is not to find the *optimal* behaviour a salmon could have taken in a stressful or boring situation (Taborsky et al., 2021, 2022), but its wellbeing status and the *actual* behaviour it is likely to undertake in a fish farm or during a procedure. To be used for monitoring the development of stress and wellbeing, the model must be agent-based (Grimm and Railsback, 2013). Only with a robust naturally reacting and behaving modelled salmon, can one investigate its likely response to stressful situations.

3.1. Construction of wellbeing in a salmon digital twin

The AHA model (Adapted Heuristics and Architecture; Budaev, Giske, and Eliassen, 2018) can provide a starting point for salmon digital twin models (Budaev et al., 2024). It uses evolutionary simulations by a genetic algorithm (Sumida et al., 1990; Huse and Giske, 1998; Mitchell, 1998; Ruxton and Beauchamp, 2008) to optimise a population of fish with sensing, emotion, cognition and behaviour (Giske et al., 2013; Andersen et al., 2016; Eliassen et al., 2016; Budaev, Giske, and Eliassen, 2018) in an aquatic habitat with environmental variation and stochasticity and with predators and prey. AHA has been used to simulate how individuals select what is important and what is irrelevant (either for feeding or predator avoidance), sample and select information, produce agentic behaviour and update their internal models (Giske et al., 2013, 2014; Budaev et al., 2019, 2020). Some extensions related to natural Atlantic salmon ontogeny, such as sexual maturation, anorexia during winter, smoltification and ocean migration are discussed in Budaev et al. (2024). Here we focus on making the salmon wellbeing mechanisms explicit in the digital twin.

One can ask whether a simpler representation than Fig. 2 would be better for the digital twin as it could take away much model uncertainty. However, we think these robustness mechanisms must be represented if a digital twin is to be sophisticated enough to replace an animal in an experiment (Russell and Burch, 1959; Hawkins et al., 2011; Eguiraun et al., 2018; Sloman et al., 2019; Grimm et al., 2023). Secondly, salmon (and the twin) have a complex decision architecture because modularity and degeneracy have improved decision making and adaptive evolution: The modular architecture (top-down) of each survival circuit (Fig. 2) allows for replacement of a component by an alternative formulation (by natural selection) without affecting the other components in the series (Chen and Crilly, 2014), which has given faster adaptive evolution in an agent-based model (Giske et al., 2014; Eliassen et al., 2016) and in nature (Wagner, 1996; Clune, Mouret, and Lipson, 2013). The survival circuits also contain parallel alternatives, for example that a fish can become afraid due to several environmental factors or by detecting fear in conspecifics. This parallelism is an example of degeneracy that is a vital robustness mechanism (Chen and Crilly, 2014).

The neuronal response function in Fig. 2 also plays an important role in the architecture. It converts the numeric value of a bodily or environmental variable into the subjective value in the salmon brain. Each neuronal response is based on a two-parameter (two-gene) non-linear function (Andersen et al., 2016; Giske et al., 2025) that is zero in absence of data input and can take almost any shape that increases with signal strength, as illustrated in Fig. 2. Thus, each individual has many neuronal response functions, and the allele of each gene can vary between individuals. Each modelled twin receives its alleles from its two parents in diploid sexual reproduction in the genetic algorithm. The result of this complexity can be a population of digital twins that reflects the variation in natural salmon in a fish farm where e.g. large individual variations in spatial decision making is found (Johansson et al., 2009).

Each basic need in salmon (Fig. 1) can be expressed as a survival circuit (Fig. 2) or as element of one. Each wellbeing component then needs to connect an environmental factor or a physiological mechanism with a sensory capacity (Atema et al., 1988; Giske, Huse, and Fiksen, 1998; von der Emde, Mogdans, and Kapoor, 2012) and with physiological and behavioural outcomes (LeDoux, 2012). A good beginning is to investigate and simulate those that most likely may lead to poor wellbeing.

The construction of a digital twin can reveal important unknowns and thus guide empirical research on natural salmon. The genetic algorithm is likely to find an adaptive solution to most problems. But it is not necessarily the same solution as Atlantic salmon found during its evolution. To avoid unrealistic solutions for salmon, simulation experiments can be performed towards each basic need in Fig. 1, one by one, and force the model to produce the affect of the neurobiological state to be higher than a given value to become a global organismic state. After a

digital twin population has been evolved to a quasi-stable solution (as evolution does not stabilise), with all relevant survival circuits, senses, physiological and hormonal mechanisms, these training experiments can ensure that the wellbeing challenges in natural salmon are detected by the twin's survival circuits and that the twin responds adequately towards all of them. When this is done, a new population and gene pool can be established with adaptive salmon-like solutions to all wellbeing challenges. Thereafter, test this new digital twin population repeatedly against combinations of challenges (Fig. 1) to ensure it behaves adequately.

3.2. Predictions from modelling wellbeing

The componential approach to experience (*sensu* Ginsburg and Jablonka 2019) in a digital twin can use the wellbeing definitions of Korte, Olivier, and Koolhaas (2007) and our own in Section 2.4 to provide a multifaceted wellbeing report. For example, there are potential wellbeing challenges in most of the steps in the cognitive cycle in Fig. 3 that all could be detected and reported by the digital twin model. Further, our wellbeing definition in Section 2.4 includes minimization of the uncertainty of the sensory systems (Trimmer et al., 2008; Friston et al., 2010) and in the predictions (Peters, McEwen, and Friston, 2017) for avoiding stress. The aim for building a digital twin is importantly also to detect and report upcoming challenges long before the criteria in Korte, Olivier, and Koolhaas (2007) and our in Section 2.4 have been reached.

Fig. 3 pictures decision making as a predominantly cognitive process, however, intents over many different time scales affect it: i) the present sensing, the state of the body and the current ontogenetic hormonal profile (Budaev et al., 2024), ii) learning throughout life, including learning from others (Brown, 2023), iii) the genetic adaptation in the 20 past salmon generations in Norwegian aquaculture (Besnier et al., 2022) and in the last 10–15 million years as natural Atlantic salmon (Crête-Lafrenière, Weir, and Bernatchez, 2012) and iv) back to the three major transitions described above. Yet, whereas the causation is multi-layered, the goal of the decision making is simple: wellbeing (Giske et al., 2025). That all these processes impact a salmon's wellbeing priorities is why a single digital twin cannot represent the behavioural diversity in a group of fish, why a population of digital twins should be evolved as a historic process by a genetic algorithm, and why the individuals should develop historically through ontogeny (Giske et al., 2013, 2014; Budaev et al., 2024). This is very different from a rational choice optimisation approach, where the behaviour-determining state is usually one or a few current physiological traits and the goal is fitness.

3.2.1. Stress

The digital twin model can monitor stress development (#3–5 and #8 in Fig. 3), as the model of vertebrate decision making (Giske et al., 2025) involves what to expect about the future, how to prepare for it, what to do about it and how to react to prediction errors (Budaev et al., 2020).

The model can monitor neurobiological states (#2 in Fig. 3) over time and across the population. Simultaneous and lasting high activation of several survival circuits in an individual will lead to prolonged competition between neurobiological states and problems in focusing on a global organismic state. Thus, the fish may in frustration not solve any of its current challenges. Synchronisation of neurobiological states across the population of digital twins would signal that much or all the population is affected by the same external pressures.

The model can report on periods of extensive prediction errors (#6 in Fig. 3) in the digital twin population. Predictable but not monotonous environments (e.g. enriched environments) can induce good wellbeing. Omission of predicted reward can lead to disappointment, and from there to depression or aggression, which can be stressful for other fish, particularly smaller or subdominant individuals (Vindas et al., 2012). Frequent mismatch between the sensing and expectations from the

subjective internal models after previous prediction error and learning, increases the informational uncertainty in the sensory system and reduces the reliability of the prediction ability (Friston et al., 2010). Costs of allostatic regulation can become disproportionately high if i) there is an excessive prediction error (#6) in the estimation of the challenge, ii) the challenge exceeds the capacity or reserves of the fish, or iii) the challenge is chronic and will continue for a long time (Korte, Olivier, and Koolhaas, 2007).

The model can monitor learning (#9 in Fig. 3), both habituation and associative learning (Ginsburg and Jablonka 2019; Schultz, 2024). Fish brains can change both due to new experiences and to lack of experiences (Braithwaite and Salvanes, 2005; Salvanes et al., 2013; Mes et al., 2019; Näslund, Rosengren, and Johnsson, 2019), thus fish can learn to cope with stressors (Vindas, Madaro et al., 2016; Moghadam et al., 2017; Madaro, Kristiansen, and Pavlidis, 2020; Alnes et al., 2021). For coping with stressors, the challenge is not “whether”, but “how much” and “how fast” (Folkedal et al., 2010).

Data uncertainty constitutes a learning challenge (#1 in Fig. 3) that a separate survival circuit is needed to handle. New types of sensory data, such as what a new sound represents and what future wellbeing consequence it may have, need to go through associative learning (Ginsburg and Jablonka 2019) or habituation/sensitisation (Cheng, 2021) before a fish knows how to deal with it (Bratland et al., 2010). Meanwhile, interpretation uncertainty can feed the new subjective internal model into a defensive survival circuit (Friston et al., 2017). On the other hand, building new subjective internal models from new sensory data or data combinations (#1) can also be vital for normal brain development (Zupanc, 2006).

Mismatch between cues about the state of the body and the state of the environment, compared to what salmon evolved to expect, are common in intensive aquaculture and may lead to ontogenetic confusion (#10 in Fig. 3) and stress (Duncan, Mitchell, and Bromage, 1999; Alnes et al., 2021; Martinez et al., 2023; Budaev et al., 2024) and to a dysfunctional value system (#11) for the individual in its current situation (Budaev et al., 2024; Giske et al., 2025). The model can be analysed for which factors contribute to unwanted developmental decisions (Budaev et al., 2024) so that conditions and procedures can be changed to reduce the incidence of these mistakes.

3.2.2. Boredom

The model can report issues of boredom (#7 in Fig. 3) – which typically would reflect understimulation in captivity – when prediction errors (#6) become rare and when fish in a facility tend to remain in the same global organismic state for a very long time or do not enter a global organismic state much of the time (#2–3). These would be signals of low levels of learning and thus inadequate brain development and poor preparation for future challenges (Braithwaite and Salvanes, 2005; Zupanc, 2006; Salvanes et al., 2013; Mes et al., 2019; Näslund, Rosengren, and Johnsson, 2019; Dumitru and Opdal, 2024; Ward et al., 2024). Boring environments limit the potential for associative learning (Strand et al., 2010) (#9) and lead to false trust in connections between causes and effects (#1–5). Low variance in interconnections between observational data, and between data and rewarding behaviour, can lead to maladaptive stereotypic behaviour.

3.2.3. Wellbeing

The model can detect and report which basic needs (Fig. 1) that frequently lead to a global organismic state (#3 in Fig. 3), including their affective strengths, durations and severeness. Hence, the model may report on the most frequent, severe and dangerous wellbeing challenges in a facility or of operations such as delousing, transportation and vaccination. It is useful to detect persistent activation of a costly global organismic state as it will result in allostatic load (Korte et al., 2005) or even allostatic overload (McEwen et al., 2015).

The model can also detect when all available actions have bleak (or worse) prospects for the near future in the predictions of expected

emotional state (#4 in Fig. 3) (Korte, Olivier, and Koolhaas, 2007) in individuals and at the population level. Population-level increases in poor wellbeing can be an important “inside report” for managers and for machine learning models; approaches such as cost-sensitive learning (Elkan, 2001) or safe reinforcement learning (Garcia and Fernandez, 2015) could exploit these simulation data as worst-case scenario to improve the prediction accuracy and confidence of critical scenarios and better connect forecasts of poor wellbeing with external observation data (Måløy, 2020).

Low behavioural diversity (#5 in Fig. 3) in an individual during a period is a signal that its behavioural goals have not been met, thus that the animal may experience poor wellbeing. High behavioural diversity signals that the challenges that evoked a global organismic state were quickly solved, and the animal is generally in a good wellbeing status (Budaev et al., 2020). This can be assessed both at the individual and collective levels.

4. Summary and perspectives

Implementing these ideas requires constructing a population model of digital twins who can mimic the awareness of living beings, in our case salmon in aquaculture. Doing so leads to a collection of programmed machines that can speak on behalf of a group of animals. It will only be valuable to listen to them if they are credible representatives of natural fish. That is, the salmon digital twin must mimic wellbeing and behaviour, but also physiology, the hormone system, the immune system and the development from egg to adult in a complex environment. The process of assembling relevant pieces will illuminate in a different way what is not understood and thus needs to be studied from the insight gained in the normal reductionist program for understanding details better and better. This is what Richard Feynman meant with his famous blackboard text “What I cannot create, I do not understand” (Way, 2017). Hence, building the salmon digital twin will advance science, which was the fourth reason to develop a salmon digital twin (Budaev et al., 2024). The three other reasons are fish welfare, the 3Rs and aquaculture productivity and mortality.

4.1. Reports from the inside: fish welfare and the 3Rs

The digital twin approach will yield insights into fish wellbeing (Fig. 3) that are complementary to the many monitoring technologies and methods that mainly see the fish “from the outside” (Stien et al., 2013; Pettersen et al., 2014). Doing so will be the first step to the 3Rs (Russell and Burch, 1959; Grimm et al., 2023) in which digital twins are used to investigate and improve conditions for live fish in aquaculture (Hawkins et al., 2011; Eguiraun et al., 2018; Sloman et al., 2019). This requires i) evolution of the digital twin population to a quasi-stable adapted state, where naturally occurring stressful events are included (Fig. 1), and ii) subsequent simulation experiments with digital twins in presumably stressful situations, such as feeding, aggression, vaccination, de-lousing, transportation, human-made noise or light conditions or other environmental factors. The digital twin with wellbeing can be used to investigate how a facility or procedure can be modified to be less stressful for the digital salmon (and presumably for its natural twin).

The digital twin approach is computationally intensive (Budaev et al., 2020, 2024). The aquaculture industry is in early transition to continuous digital monitoring of the environment and the fish (Føre et al., 2018; Antonucci and Costa, 2020; Chatziantoniou et al., 2023; Royer and Pastres, 2023) in which machine learning and other artificial intelligence tools can aid the analyses (Mustapha et al., 2021). However, available monitoring data are neither sufficiently dense nor sufficiently diverse to easily capture fish wellbeing. Calibrating digital twins to data collected from digital monitoring and using them to run simulations would allow us to produce further reliable data, which could then be used by additional downstream AI models tuned with respect to specific objectives. As in other fields, highly accurate but non-transparent

end-to-end neural model could be trained to learn useful correlations in the data and provide early warnings of the critical state of the fish (Reichstein et al., 2024). Further, coarser but interpretable causal models (Schölkopf et al., 2021) may provide representations of the dynamics of interest at a level of abstraction high enough to devise effective control policies (Chalupka, Eberhardt, and Perona, 2017; Dyer et al., 2024). In particular, the learning of explainable mechanistic causal models able to explain the dynamics emergent from a digital twin would align with the foreseen need of enriching our current models with theoretical underpinnings, as argued by Coveney, Dougherty, and Highfield (2016) who entitled their paper “Big data need big theory too”. Thus, the digital twin and transparent and interpretable AI tools complement each other in research laboratories and fish farms.

Improved fish welfare is not only a goal for the seafood industry and regulators, but increasingly also for consumers and voters (Ankamah-Yeboah et al., 2019; Pulcini et al., 2020; Rickard et al., 2020; de Boer and Aiking, 2022). Seafood producers can come to realise that the twin (or AI-tools based on it) can be useful for testing hypotheses, validating policies and delivering reports to regulators and consumers. The engagement of voters and consumers encourages politicians to legislate more transparent industry regulations, supermarket chains to demand trustworthy food labels and producers to change production according to these demands (Gismervik et al., 2020; Gaffney and Lavery, 2022). A digital twin, thoroughly based on the species’ physiology, cognition and behaviour and implemented in transparent open source-code, can be a useful tool for an honest broker (Pielke Jr, 2007) for all these groups.

4.2. Lowering mortality in aquaculture

Certain aspects of a salmon digital twin can facilitate higher physiological efficiency and productivity (Budaev et al., 2024). But a focus on wellbeing can help reduce unwanted mortality. Fish in aquaculture are removed from its ancestral environment with boring facilities, unfamiliar sensory experiences, understimulation and alarming handling procedures. Even so, episodic-like memory, prediction and other robustness mechanisms (Kitano, 2004; Fernandez-Leon 2011a, 2011b) try to keep the animal in a state that has led its ancestors to reproduction. Adaptive mechanisms for dealing with a challenge is stress (Overton et al., 2019), depression and aggression (Vindas et al., 2014) even to the “loser fish” (Vindas, Johansen et al., 2016) in the emergency life-history stage where all non-essential life functions are switched off (Wingfield et al., 1998). Managers of aquacultural facilities and natural systems will benefit from acknowledging these mechanisms and facilitate the wanted survival, growth and development in salmon. Digital twin models can be valuable instruments for this as the models can report on phenomena that are hard to observe.

4.3. Legal status of fish welfare

Superficially, there are many similarities between FAO’s function-based approach to animal welfare (Segner et al., 2019) – that welfare is reached when animals are in good health and show normal biological functioning and expected growth – and the definition of Korte, Olivier, and Koolhaas (2007) that allostatic loads that are too low or too high threaten good welfare, although boredom is not covered by FAO. However, by emphasizing an individual’s own expectations to its future wellbeing, by allostasis or wellbeing prediction, the definitions of Korte, Olivier, and Koolhaas (2007) and our own in Section 2.4 regard fish as sentient beings. This is a standing challenge to the UN (Pipia, 2020) in line with The Cambridge Declaration on Consciousness (Low et al., 2012) which stated that “it is indisputable that all vertebrates, including fish and reptiles do possess the neurological substrates of consciousness”. The recent New York Declaration on Animal Consciousness (Andrews et al., 2024) arrived at the same position, yet with softer wordings.

4.4. Beyond aquaculture

Humankind should sense a great responsibility for animal welfare (Farm Animal Welfare Council, 2009; Bovenkerk and Meijboom, 2020; van de Vis et al., 2020; Cooper et al., 2023) of many species. So far, there are no published simulation models that combine physiology, behaviour and wellbeing for any farmed or wild animal (Collins and Part, 2013; Budaev et al., 2020; Neethirajan, 2021; Colditz, 2023). The principles we have laid out for studying and improving salmon wellbeing apply to all other meat production industries, and to almost all kinds of pet animals, as they are vertebrates with episodic-like memory (Zacks, Ginsburg, and Jablonka, 2022) who utilize prediction of their near-future wellbeing in their behavioural evaluations (Giske et al., 2025). This is also something to consider in urban planning and other area change, where natural populations are impacted by the spread of human presence (Schilthuizen, 2018).

CRedit authorship contribution statement

Giske Jarl: Writing – original draft, Visualization, Project administration, Funding acquisition, Conceptualization. **Dumitru Magda L.:** Writing – original draft. **Enberg Katja:** Writing – original draft. **Folkedal Ole:** Writing – original draft. **Handeland Sigurd Olav:** Writing – original draft. **Higginson Andrew D.:** Writing – original draft. **Opdal Anders F.:** Writing – original draft. **Rønnestad Ivar:** Writing – original draft, Funding acquisition. **Salvanes Anne Gro Veia:** Writing – original draft. **Vollset Knut Wiik:** Writing – original draft. **Zennaro Fabio M.:** Writing – original draft. **Mangel Marc:** Writing – original draft, Conceptualization. **Budaev Sergey:** Writing – original draft, Conceptualization.

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Data availability

No data was used for the research described in the article.

References

- Adams, R.A., Shipp, S., Friston, K.J., 2013. Predictions not commands: active inference in the motor system. *Brain Struct. Funct.* 218, 611–643. <https://doi.org/10.1007/s00429-012-0475-5>.
- Aellen, M., Dufour, V., Bshary, R., 2021. Cleaner fish and other wrasse match primates in their ability to delay gratification. *Anim. Behav.* 176, 125–143. <https://doi.org/10.1016/j.anbehav.2021.04.002>.
- Alnes, I.B., Jensen, K.H., Skorping, A., Salvanes, A.G.V., 2021. Ontogenetic change in behavioral responses to structural enrichment from fry to parr in juvenile Atlantic salmon (*Salmo salar* L.). *Front. Vet. Sci.* 8, 638888. <https://doi.org/10.3389/fvets.2021.638888>.
- Andersen, B.S., Jørgensen, C., Eliassen, S., Giske, J., 2016. The proximate architecture for decision-making in fish. *Fish Fish.* 17, 680–695. <https://doi.org/10.1111/faf.12139>.
- Anderson, D.J., Adolphs, R., 2014. A framework for studying emotions across species. *Cell* 157, 187–200. <https://doi.org/10.1016/j.cell.2014.03.003>.
- Andrews, K., Birch, J., Sebo, J., Sims, T., 2024. nydeclaration.com. Backgr. N. Y. Declar. Anim. Conscious.
- Ankamah-Yeboah, I., Jacobsen, J.B., Olsen, S.B., Nielsen, M., Nielsen, R., 2019. The impact of animal welfare and environmental information on the choice of organic fish: an empirical investigation of German trout consumers. *Mar. Resour. Econ.* 34, 247–266. <https://doi.org/10.1086/705235>.
- Antonucci, F., Costa, C., 2020. Precision aquaculture: a short review on engineering innovations. *Aquac. Int.* 28, 41–57. <https://doi.org/10.1007/s10499-019-00443-w>.
- Araki, H., Berejikian, B.A., Ford, M.J., Blouin, M.S., 2008. Fitness of hatchery-reared salmonids in the wild. *Evolut. Appl.* 1, 342–355. <https://doi.org/10.1111/j.1752-4571.2008.00026.x>.

- Arechavala-Lopez, P., Cabrera-alvarez, M.J., Maia, C.M., Saraiva, J.L., 2022. Environmental enrichment in fish aquaculture: a review of fundamental and practical aspects. *Rev. Aquac.* 14, 704–728. <https://doi.org/10.1111/raq.12620>.
- Atema, J., Fay, R.R., Popper, A.N., Tavolga, W.N., 1988. *Sensory biology of aquatic animals*. Springer, New York.
- Baars, B.J., 1988. *A cognitive theory of consciousness*. Cambridge University Press.
- Barnard, C., 2007. Ethical regulation and animal science: why animal behaviour is special. *Anim. Behav.* 74, 5–13. <https://doi.org/10.1016/j.anbehav.2007.04.002>.
- Bar-On, Y.M., Phillips, R., Milo, R., 2018. The biomass distribution on Earth. *Proc. Natl. Acad. Sci.* 115, 6506–6511. <https://doi.org/10.1073/pnas.1711842115>.
- Barrett, L.F., 2017. *How emotions are made: the secret life of the brain*. Pan Macmillan.
- Barrett, L.F., 2020. Seven and a half lessons about the brain. Houghton Mifflin.
- Barron, A.B., Klein, C., 2016. What insects can tell us about the origins of consciousness. *Proc. Natl. Acad. Sci. USA* 113, 4900–4908. <https://doi.org/10.1073/pnas.1520084113>.
- Besnier, F., Aylton, F., Skaala, Ø., Solberg, M.F., Fjeldheim, P.T., Anderson, K., Knutar, S., Glover, K.A., 2022. Introgression of domesticated salmon changes life history and phenology of a wild salmon population. *Evolut. Appl.* 15, 853–864. <https://doi.org/10.1111/eva.13375>.
- Botreau, R., Veissier, I., Perny, P., 2009. Overall assessment of animal welfare: strategy adopted in Welfare Quality (R). *Anim. Welf.* 18, 363–370. <https://doi.org/10.1017/S0962728600000762>.
- Bovenkerk, B., Meijboom, F., 2020. *Ethics and the welfare of fish*. In: Kristiansen, T.S., Fernø, A., Pavlidis, M.A., van de Vis, H. (Eds.), *The welfare of fish*. Springer.
- Bracke, M.B.M., Hopster, H., 2006. Assessing the importance of natural behaviour for animal welfare. *J. Agric. Environ. Ethics* 19, 77–89. <https://doi.org/10.1007/s10806-005-4493-7>.
- Bracke, M.B.M., Spruijt, B.M., Metz, J.H.M., 1999. Overall animal welfare reviewed. Part 3: Welfare assessment based on needs and supported by expert opinion. *Neth. J. Agric. Sci.* 47, 307–322. <https://doi.org/10.18174/njas.v47i3.468>.
- Braithwaite, V.A., Salvanes, A.G.V., 2005. Environmental variability in the early rearing environment generates behaviourally flexible cod: implications for rehabilitating wild populations. *Proc. R. Soc. B-Biol. Sci.* 272, 1107–1113. <https://doi.org/10.1098/rspb.2005.3062>.
- Bratland, S., Stien, L.H., Braithwaite, V.A., Juell, J.-E., Folkedal, O., Nilsson, J., Oppedal, F., Fosseidengen, J.E., Kristiansen, T.S., 2010. From fright to anticipation: using aversive light stimuli to investigate reward conditioning in large groups of Atlantic salmon (*Salmo salar*). *Aquac. Int.* 18, 991–1001. <https://doi.org/10.1007/s10499-009-9317-8>.
- Britton, A., Shipley, M.J., 2010. Bored to death? *Int. J. Epidemiol.* 39, 370–371. <https://doi.org/10.1093/ije/dyp404>.
- Brown, C., 2023. *Fishes: from social learning to culture*. In: Kendal, R., Tehrani, J., Kendal, J. (Eds.), *The Oxford Handbook of Cultural Evolution*. Oxford University Press.
- Browning, H., 2023. Improving welfare assessment in aquaculture. *Front. Vet. Sci.* 10, 1060720. <https://doi.org/10.3389/fvets.2023.1060720>.
- Bubic, A., Von Cramon, D.Y., Schubotz, R.I., 2010. Prediction, cognition and the brain. *Front. Hum. Neurosci.* 4, 25. <https://doi.org/10.3389/fnhum.2010.00025>.
- Budaev, S., Cusimano, G., Rønnestad, I., 2024. Fishmet: A Digital Twin framework for appetite, feeding decisions and growth in salmonid fish. *SSRN Sch. Pap.* <https://doi.org/10.2139/ssrn.4883821>.
- Budaev, S., Dumitru, M.L., Enberg, K., Handeland, S.O., Higginson, A.D., Kristiansen, T.S., Opdal, A.F., Railsback, S.F., Rønnestad, I., Vollset, K.W., Mangel, M., Giske, J., 2024. Premises for a digital twin of the Atlantic salmon in its world: agency, robustness, subjectivity and prediction. *Aquac., Fish. Fish.* 4, e153. <https://doi.org/10.1002/aff2.153>.
- Budaev, S., Giske, J., Eliassen, S., 2018. AHA: A general cognitive architecture for Darwinian agents. *Biol. Inspired Cogn. Archit.* 25, 51–57. <https://doi.org/10.1016/j.bica.2018.07.009>.
- Budaev, S., Jørgensen, C., Mangel, M., Eliassen, S., Giske, J., 2019. Decision-making from the animal perspective: bridging ecology and subjective cognition. *Front. Ecol. Evol.* 7, 14. <https://doi.org/10.3389/fevo.2019.00164>.
- Budaev, S., Kristiansen, T.S., Giske, J., Eliassen, S., 2020. Computational animal welfare: towards cognitive architecture models of animal sentience, emotion and wellbeing. *R. Soc. Open Sci.* 7, 201886. <https://doi.org/10.1098/rsos.201886>.
- Burn, C.C., 2017. Bestial boredom: a biological perspective on animal boredom and suggestions for its scientific investigation. *Anim. Behav.* 130, 141–151. <https://doi.org/10.1016/j.anbehav.2017.06.006>.
- Burns, J.G., Saravanan, A., Rodd, F.H., 2009. Rearing environment affects the brain size of guppies: lab-reared guppies have smaller brains than wild-caught guppies. *Ethology* 115, 122–133. <https://doi.org/10.1111/j.1439-0310.2008.01585.x>.
- Busia, L., Griggio, M., 2020. The dawn of social bonds: what is the role of shared experiences in non-human animals? *Biol. Lett.* 16. <https://doi.org/10.1098/rsbl.2020.0201>.
- Cabanac, M., 1979. Sensory pleasure. *Q. Rev. Biol.* 54, 1–29. <https://doi.org/10.1086/410981>.
- Cabanac, M., 1992. Pleasure - the common currency. *Journal of Theoretical Biology* 155, 173–200. [https://doi.org/10.1016/s0022-5193\(05\)80594-6](https://doi.org/10.1016/s0022-5193(05)80594-6).
- Campbell, J.H., Dixon, B., Whitehouse, L.M., 2021. The intersection of stress, sex and immunity in fishes. *Immunogenetics* 73, 111–129. <https://doi.org/10.1007/s00251-020-01194-2>.
- Chalupka, K., Eberhardt, F., Perona, P., 2017. Causal feature learning: an overview. *Behaviormetrika* 44, 137–164. <https://doi.org/10.1007/s41237-016-0008-2>.
- Chatziantoniou, A., Papandroulakis, N., Stavrakidis-Zachou, O., Spondylidis, S., Taskaris, S., Topouzelis, K., 2023. Aquasafe: a remote sensing, web-based platform for the support of precision fish farming. *Appl. Sci.* 13, 6122. <https://doi.org/10.3390/app13106122>.
- Chen, C.-C., Crilly, N., 2014. Modularity, redundancy and degeneracy: cross-domain perspectives on key design principles. In: *IEEE International Systems Conference Proceedings*, 2014. IEEE.
- Cheng, K., 2021. Learning in Cnidaria: A systematic review. *Learn. Behav.* 49, 175–189. <https://doi.org/10.3758/s13420-020-00452-3>.
- Chittka, L., 2022. *The mind of a bee*. Princeton University Press.
- Ciliberti, R., Alfano, L., Petralia, P., 2023. Ethics in aquaculture: animal welfare and environmental sustainability. *J. Prev. Med. Hyg.* 64, E443–E447. <https://doi.org/10.15167/2421-4248/jpmh2023.64.4.3136>.
- Clayton, N.S., Dickinson, A., 1998. Episodic-like memory during cache recovery by scrub jays. *Nature* 395, 272–274. <https://doi.org/10.1038/26216>.
- Clune, J., Mouret, J.B., Lipson, H., 2013. The evolutionary origins of modularity. *Proc. R. Soc. B-Biol. Sci.* 280. <https://doi.org/10.1098/rspb.2012.2863>.
- Colditz, I.G., 2023. A biological integrity framework for describing animal welfare and wellbeing. *Anim. Prod. Sci.* 63, 423–440. <https://doi.org/10.1071/AN22285>.
- Collins, L.M., Part, C.E., 2013. Modelling farm animal welfare. *Animals* 3, 416–441. <https://doi.org/10.3390/ani3020416>.
- Cooper, K., Breakey, H., Lewis, M., Marshallsay, R., Naraniecki, A., Sampford, C., 2023. Aquaculture ethics: a systematic quantitative review and critical analysis of aquaculture ethics scholarship. *Fish Fish.* 24, 321–338. <https://doi.org/10.1111/faf.12729>.
- Coveney, P.V., Dougherty, E.R., Highfield, R.R., 2016. Big data need big theory too. *Philos. Trans. R. Soc. A-Math. Phys. Eng. Sci.* 374. <https://doi.org/10.1098/rsta.2016.0153>.
- Crête-Lafrenière, A., Weir, L.K., Bernatchez, L., 2012. Framing the Salmonidae family phylogenetic portrait: A more complete picture from increased taxon sampling. *PLoS One* 7. <https://doi.org/10.1371/journal.pone.0046662>.
- Croft, D.P., James, R., Thomas, P.O.R., Hathaway, C., Mawdsley, D., Laland, K.N., Krause, J., 2006. Social structure and co-operative interactions in a wild population of guppies (*Poecilia reticulata*). *Behav. Ecol. Sociobiol.* 59, 644–650. <https://doi.org/10.1007/s00265-005-0091-y>.
- Crump, A., Bethell, E.J., Earley, R., Lee, V.E., Mendl, M., Oldham, L., Turner, S.P., Arnott, G., 2020. Emotion in animal contests. *Proc. R. Soc. Biol. Sci. Ser. B* 287, 1–9. <https://doi.org/10.1098/rspb.2020.1715>.
- Damasio, A., 1999. *The feeling of what happens. Body and emotion in the making of consciousness*. Harcourt Brace, New York, p. 385.
- Damasio, A., 2003. Mental self: The person within. *Nature* 423 (227). <https://doi.org/10.1038/423227a>.
- Dawkins, M.S., 2023. Farm animal welfare: Beyond "natural" behavior. *Sci. (N. Y., N. Y.)* 379, 326–328. <https://doi.org/10.1126/science.ade5437>.
- de Boer, J., Aiking, H., 2022. Considering how farm animal welfare concerns may contribute to more sustainable diets. *Appetite* 168. <https://doi.org/10.1016/j.appet.2021.105786>.
- Dehaene, S., Kerszberg, M., Changeux, J.-P., 1998. A neuronal model of a global workspace in effortful cognitive tasks. *Proc. Natl. Acad. Sci. USA* 95, 14529–14534. <https://doi.org/10.1073/pnas.95.24.14529>.
- Del Giudice, M., 2023. A general motivational architecture for human and animal personality. *Neurosci. Biobehav. Rev.* 144. <https://doi.org/10.1016/j.neubiorev.2022.104967>.
- Del Giudice, M., Ellis, B.J., Shirliff, E.A., 2011. The Adaptive Calibration Model of stress responsivity. *Neurosci. Biobehav. Rev.* 35, 1562–1592. <https://doi.org/10.1016/j.neubiorev.2010.11.007>.
- Dumitru, M.L., Opdal, A.M.F., 2024. Beyond the mosaic model of brain evolution: Rearing environment defines local and global plasticity. *Ann. N. Y. Acad. Sci.* 1542, 58–66. <https://doi.org/10.1111/nyas.15267>.
- Duncan, N., Mitchell, D., Bromage, N., 1999. Post-smolt growth and maturation of out-of-season 0+ Atlantic salmon (*Salmo salar*) reared under different photoperiods. *Aquaculture* 177, 61–71. [https://doi.org/10.1016/s0044-8486\(99\)00069-1](https://doi.org/10.1016/s0044-8486(99)00069-1).
- Dunlap, K.D., 2016. Fish neurogenesis in context: assessing environmental influences on brain plasticity within a highly labile physiology and morphology. *Brain Behav. Evol.* 87, 156–166. <https://doi.org/10.1159/000446907>.
- Dyer, J., Bishop, N.G., Felekis, Y., Zennaro, F.M., Calinescu, A., Damoulas, T., Wooldridge, M.J., 2024. Interventionally consistent surrogates for complex simulation models. *Thirty-Eighth Annu. Conf. Neural Inf. Process. Syst.*
- Eastwood, J.D., Frischen, A., Fenske, M.J., Smilek, D., 2012. The unengaged mind: Defining boredom in terms of attention. *Perspect. Psychol. Sci.* 7, 482–495. <https://doi.org/10.1177/1745691612456044>.
- Ebbesson, L.O.E., Braithwaite, V.A., 2012. Environmental effects on fish neural plasticity and cognition. *J. Fish. Biol.* 81, 2151–2174. <https://doi.org/10.1111/j.1095-8649.2012.03486.x>.
- Eguiraun, H., Casquero, O., Sørensen, A.J., Martinez, I., 2018. Reducing the number of individuals to monitor shoaling fish systems - application of the Shannon entropy to construct a biological warning system model. *Front. Physiol.* 9. <https://doi.org/10.3389/fphys.2018.00493>.
- Eliassen, S., Andersen, B.S., Jørgensen, C., Giske, J., 2016. From sensing to emergent adaptations: modelling the proximate architecture of decision-making. *Ecol. Model.* 326, 90–100. <https://doi.org/10.1016/j.ecolmodel.2015.09.001>.
- Elkan, C., 2001. *The foundations of cost-sensitive learning. International joint conference on artificial intelligence*. Lawrence Erlbaum Associates Ltd.
- Elwood, R.W., 2021. Potential pain in fish and decapods: Similar experimental approaches and similar results. *Front. Vet. Sci.* 8. <https://doi.org/10.3389/fvets.2021.631151>.
- FAO, 2023. Atlantic Salmon, *Salmo salar* Linnaeus, 1758 [online], FAO.

- Farm Animal Welfare Council, 2009. Farm animal welfare in Great Britain: Past, present and future. Farm Animal Welfare Council.
- Farnsworth, K.D., Elwood, R.W., 2023. Why it hurts: with freedom comes the biological need for pain. *Anim. Cogn.* 26, 1259–1275. <https://doi.org/10.1007/s10071-023-01773-2>.
- Feinberg, T.E., Mallatt, J., 2013. The evolutionary and genetic origins of consciousness in the Cambrian Period over 500 million years ago. *Front. Psychol.* 4, 667. <https://doi.org/10.3389/fpsyg.2013.00667>.
- Feinberg, T.E., Mallatt, J.M., 2016. *The ancient origins of consciousness: How the brain created experience*. MIT Press.
- Feldman, H., Friston, K.J., 2010. Attention, uncertainty, and free-energy. *Front. Hum. Neurosci.* 4. <https://doi.org/10.3389/fnhum.2010.00215>.
- Fernandez-Leon, J.A., 2011a. Evolving cognitive-behavioural dependencies in situated agents for behavioural robustness. *Biosystems* 106, 94–110. <https://doi.org/10.1016/j.biosystems.2011.07.003>.
- Fernandez-Leon, J.A., 2011b. Evolving experience-dependent robust behaviour in embodied agents. *Biosystems* 103, 45–56. <https://doi.org/10.1016/j.biosystems.2010.09.010>.
- Folkedal, O., Fernö, A., Nederlof, M.A.J., Fosseidengen, J.E., Cerqueira, M., Olsen, R.E., Nilsson, J., 2017. Habituation and conditioning in gilthead sea bream (*Sparus aurata*): Effects of aversive stimuli, reward and social hierarchies. *Aquac. Res.* 49, 335–340. <https://doi.org/10.1111/are.13463>.
- Folkedal, O., Stien, L.H., Torgersen, T., Oppedal, E., Olsen, R.E., Fosseidengen, J.E., Braithwaite, V.A., Kristiansen, T.S., 2012. Food anticipatory behaviour as an indicator of stress response and recovery in Atlantic salmon post-smolt after exposure to acute temperature fluctuation. *Physiol. Behav.* 105, 350–356. <https://doi.org/10.1016/j.physbeh.2011.08.008>.
- Folkedal, O., Torgersen, T., Nilsson, J., Oppedal, F., 2010. Habituation rate and capacity of Atlantic salmon (*Salmo salar*) parr to sudden transitions from darkness to light. *Aquaculture* 307, 170–172. <https://doi.org/10.1016/j.aquaculture.2010.06.001>.
- Folkedal, O., Torgersen, T., Olsen, R.E., Fernö, A., Nilsson, J., Oppedal, F., Stien, L.H., Kristiansen, T.S., 2012. Duration of effects of acute environmental changes on food anticipatory behaviour, feed intake, oxygen consumption, and cortisol release in Atlantic salmon parr. *Physiol. Behav.* 105, 283–291. <https://doi.org/10.1016/j.physbeh.2011.07.015>.
- Føre, M., Frank, K., Norton, T., Svendsen, E., Alfredsen, J.A., Dempster, T., Eguiraun, H., Watson, W., Stahl, A., Sunde, L.M., Schellewald, C., Skoien, K.R., Alver, M.O., Berckmans, D., 2018. Precision fish farming: A new framework to improve production in aquaculture. *Biosyst. Eng.* 173, 176–193. <https://doi.org/10.1016/j.biosystemseng.2017.10.014>.
- Friston, K.J., Daunizeau, J., Kilner, J., Kiebel, S.J., 2010. Action and behavior: a free-energy formulation. *Biol. Cybern.* 102, 227–260. <https://doi.org/10.1007/s00422-010-0364-z>.
- Friston, K.J., Rosch, R., Parr, T., Price, C., Bowman, H., 2017. Deep temporal models and active inference. *Neurosci. Biobehav. Rev.* 77, 388–402. <https://doi.org/10.1016/j.neubiorev.2017.04.009>.
- Gaffney, L.P., Lavery, J.M., 2022. Research before policy: identifying gaps in salmonid welfare research that require further study to inform evidence-based aquaculture guidelines in Canada. *Front. Vet. Sci.* 8, 768558. <https://doi.org/10.3389/fvets.2021.768558>.
- Gans, C., Northcutt, R.G., 1983. Neural crest and the origin of vertebrates: A new head. *Science* 220, 268–273. <https://doi.org/10.1126/science.220.4594.268>.
- Garcia, J., Fernandez, F., 2015. A comprehensive survey on safe reinforcement learning. *J. Mach. Learn. Res.* 16, 1437–1480.
- Ginsburg, S., Jablonka, E., 2010. The evolution of associative learning: A factor in the Cambrian explosion. *J. Theor. Biol.* 266, 11–20. <https://doi.org/10.1016/j.jtbi.2010.06.017>.
- Ginsburg, S. and Jablonka, E. 2019. The evolution of the sensitive soul: learning and the origins of consciousness. MIT Press.
- Giske, J., Budaev, S., Eliassen, S., Higginson, A.D., Jørgensen, C., Mangel, M., 2025. Vertebrate decision making leads to the interdependence of behaviour and wellbeing. *Anim. Behav.* <https://doi.org/10.1016/j.anbehav.2025.123101>.
- Giske, J., Eliassen, S., Fiksen, Ø., Jakobsen, P.J., Aksnes, D.L., Jørgensen, C., Mangel, M., 2013. Effects of the emotion system on adaptive behavior. *Am. Nat.* 182, 689–703. <https://doi.org/10.1086/673533>.
- Giske, J., Eliassen, S., Fiksen, Ø., Jakobsen, P.J., Aksnes, D.L., Mangel, M., Jørgensen, C., 2014. The emotion system promotes diversity and evolvability. *Proc. Biol. Sci. / R. Soc.* 281, 20141096. <https://doi.org/10.1098/rspb.2014.1096>.
- Giske, J., Huse, G., Fiksen, Ø., 1998. Modelling spatial dynamics of fish. *Rev. Fish. Biol.* 8, 57–91. <https://doi.org/10.1023/A:1008864517488>.
- Gismervik, K., Torud, B., Kristiansen, T.S., Osmundsen, T., Størkersen, K.V., Medaas, C., Lien, M.E., Stien, L.H., 2020. Comparison of Norwegian health and welfare regulatory frameworks in salmon and chicken production. *Rev. Aquac.* 12, 2396–2410. <https://doi.org/10.1111/raq.12440>.
- Godfrey-Smith, P., 2017. Animal evolution and the origins of experience. In: Smith, D. (Ed.), *How biology shapes philosophy: New foundations for naturalism*. Cambridge University Press.
- Godfrey-Smith, P. 2020. Metazoa: Animal life and the birth of the mind. Farrar, Straus and Giroux.
- Godfrey-Smith, P. 2024. Living on Earth - Life, Consciousness and the Making of the Natural World, William Collins.
- Gonda, A., Herczeg, G., Merila, J., 2009. Habitat-dependent and -independent plastic responses to social environment in the nine-spined stickleback (*Pungitius pungitius*) brain. *Proc. R. Soc. B-Biol. Sci.* 276, 2085–2092. <https://doi.org/10.1098/rspb.2009.0026>.
- Greenspoon, L., Krieger, E., Sender, R., Rosenberg, Y., Bar-On, Y.M., Moran, U., Antman, T., Meiri, S., Roll, U., Noor, E., Milo, R., 2023. The global biomass of wild mammals. *Proc. Natl. Acad. Sci. USA* 120, e2204892120. <https://doi.org/10.1073/pnas.2204892120>.
- Grimm, H., Biller-Andorno, N., Buch, T., Dahlhoff, M., Davies, G., Cederroth, C.R., Maissen, O., Lukas, W., Passini, E., Tornqvist, E., Olsson, I.A.S., Sandstrom, J., 2023. Advancing the 3Rs: innovation, implementation, ethics and society. *Front. Vet. Sci.* 10, 1185706. <https://doi.org/10.3389/fvets.2023.1185706>.
- Grimm, V., Railsback, S.F., 2013. *Individual-based modeling and ecology*. Princeton university press.
- Gygax, L., 2017. Wanting, liking and welfare: The role of affective states in proximate control of behaviour in vertebrates. *Ethology* 123, 689–704. <https://doi.org/10.1111/eth.12655>.
- Hawkins, P., Dennison, N., Goodman, G., Hetherington, S., Llywelyn-Jones, S., Ryder, K., Smith, A.J., 2011. Guidance on the severity classification of scientific procedures involving fish: report of a Working Group appointed by the Norwegian Consensus-Platform for the Replacement, Reduction and Refinement of animal experiments (Norecopa). *Lab. Anim.* 45, 219–224. <https://doi.org/10.1258/la.2011.010181>.
- Heathcote, R.J.P., Darden, S.K., Franks, D.W., Ramnarine, I.W., Croft, D.P., 2017. Fear of predation drives stable and differentiated social relationships in guppies. *Sci. Rep.* 7, 41679. <https://doi.org/10.1038/srep41679>.
- Huse, G., Giske, J., 1998. Ecology in Mare Pentium: an individual-based spatio-temporal model for fish with adapted behaviour. *Fish. Res.* 37, 163–178. [https://doi.org/10.1016/s0165-7836\(98\)00134-9](https://doi.org/10.1016/s0165-7836(98)00134-9).
- Jablonka, E., Ginsburg, S., 2022. Learning and the evolution of conscious agents. *Biosemiotics* 15, 401–437. <https://doi.org/10.1007/s12304-022-09501-y>.
- Johansson, D., Ruohonen, K., Juell, J.E., Oppedal, F., 2009. Swimming depth and thermal history of individual Atlantic salmon (*Salmo salar* L.) in production cages under different ambient temperature conditions. *Aquaculture* 290, 296–303. <https://doi.org/10.1016/j.aquaculture.2009.02.022>.
- Jonsson, B., Jonsson, N., 2006. Cultured Atlantic salmon in nature: a review of their ecology and interaction with wild fish. *ICES J. Mar. Sci.* 63, 1162–1181. <https://doi.org/10.1016/j.jicesjms.2006.03.004>.
- Jonsson, B., Jonsson, N., 2014. Early environment influences later performance in fishes. *J. Fish. Biol.* 85, 151–188. <https://doi.org/10.1111/jfb.12432>.
- Karin, O., Alon, U., 2022. The dopamine circuit as a reward-taxi navigation system. *PLoS Comput. Biol.* 18, e1010340. <https://doi.org/10.1371/journal.pcbi.1010340>.
- Kauffman, S., 2007. Question 1: Origin of life and the living state. *Orig. Life Evol. Biospheres* 37, 315–322. <https://doi.org/10.1007/s11084-007-9093-2>.
- Kitano, H., 2004. Biological robustness. *Nat. Rev. Genet.* 5, 826–837. <https://doi.org/10.1038/nrg1471>.
- Klopf, A., 1983. *The hedonistic neuron. A theory of memory, learning, and intelligence*. Hemisphere Publishing Corporation, p. 140.
- Korte, S.M., Koolhaas, J.M., Wingfield, J.C., McEwen, B.S., 2005. The Darwinian concept of stress: benefits of allostasis and costs of allostatic load and the trade-offs in health and disease. *Neurosci. Biobehav. Rev.* 29, 3–38. <https://doi.org/10.1016/j.neubiorev.2004.08.009>.
- Korte, S.M., Olivier, B., Koolhaas, J.M., 2007. A new animal welfare concept based on allostasis. *Physiol. Behav.* 92, 422–428. <https://doi.org/10.1016/j.physbeh.2006.10.018>.
- Lai, F., Rønnestad, I., Budaev, S., Balseiro, P., Gelebart, V., Pedrosa, C., Stevnebo, A., Haugarvoll, E., Korsøen, Ø.J., Tangen, K.L., Folkedal, O., Handeland, S., 2024. Freshwater history influences farmed Atlantic salmon (*Salmo salar*) performance in seawater. *Aquaculture* 586, 740750. <https://doi.org/10.1016/j.aquaculture.2024.740750>.
- LeDoux, J.E., 2000. Emotion circuits in the brain. *Annu. Rev. Neurosci.* 23, 155–184. <https://doi.org/10.1146/annurev.neuro.23.1.155>.
- LeDoux, J., 2012. Rethinking the emotional brain. *Neuron* 73, 653–676. <https://doi.org/10.1016/j.neuron.2012.02.004>.
- Lennox, R.J., Alexandre, C.M., Almeida, P.R., Bailey, K.M., Barlaup, B.T., Boe, K., Breukelaar, A., Erkinaro, J., Forseth, T., Gabrielsen, S.E., Halfyard, E., Hanssen, E.M., Karlsson, S., Koch, S., Koed, A., Langaker, R.M., Lo, H., Lucas, M.C., Mahlum, S., Perrier, C., Pulg, U., Sheehan, T., Skoglund, H., Svenning, M., Thorstad, E.B., Velle, G., Whoriskey, F.G., Vollset, K.W., 2021. The quest for successful Atlantic salmon restoration: perspectives, priorities, and maxims. *ICES J. Mar. Sci.* 78, 3479–3497. <https://doi.org/10.1093/icesjms/fsab201>.
- Low, P., Panksepp, J., Reiss, D., Edelman, D., Van Swinderen, B., Koch, C., 2012. The Cambridge declaration on consciousness. *Fr. Crick Meml. Conf. (Cambridge, UK)*.
- Madaro, A., Kristiansen, T.S., Pavlidis, M.A., 2020. How fish cope with stress? In: Kristiansen, T.S., Fernö, A., Pavlidis, M.A., van de Vis, H. (Eds.), *The Welfare of Fish*. Springer.
- Måløy, H., 2020. EchoBERT: A transformer-based approach for behavior detection in echograms. *IEEE Access* 8, 218372–218385. <https://doi.org/10.1109/access.2020.3042337>.
- Martin, M., Sadlo, G., Stew, G., 2006. The phenomenon of boredom. *Qual. Res. Psychol.* 3, 193–211. <https://doi.org/10.1191/1478088706qrp0660a>.
- Martinez, E.P., Balseiro, P., Stefansson, S.O., Kaneko, N., Norberg, B., Fleming, M.S., Imslad, A.K.D., Handeland, S.O., 2023. Interaction of temperature and feed ration on male postsmolt maturation of Atlantic salmon (*Salmo salar* L.). *Aquaculture* 562, 738877. <https://doi.org/10.1016/j.aquaculture.2022.738877>.
- McEwen, B.S., 1998. Protective and damaging effects of stress mediators. *N. Engl. J. Med.* 338, 171–179. <https://doi.org/10.1056/nejm199801153380307>.
- McEwen, B.S., Bowles, N.P., Gray, J.D., Hill, M.N., Hunter, R.G., Karatsoreos, I.N., Nasca, C., 2015. Mechanisms of stress in the brain. *Nat. Neurosci.* 18, 1353–1363. <https://doi.org/10.1038/nn.4086>.

- McNamara, J.M., Houston, A.I., 1986. The common currency for behavioral decisions. *Am. Nat.* 127, 358–378. <https://doi.org/10.1086/284489>.
- McNamara, J.M., Houston, A.I., 2009. Integrating function and mechanism. *Trends in Ecology & Evolution* 24, 670–675. <https://doi.org/10.1016/j.tree.2009.05.011>.
- Meagher, R.K., 2019. Is boredom an animal welfare concern? *Anim. Welf.* 28, 21–32. <https://doi.org/10.1016/j.jahp.2019.05.001>.
- Mellor, D.J., Beausoleil, N.J., Littlewood, K.E., McLean, A.N., McGreevy, P.D., Jones, B., Wilkins, C., 2020. The 2020 five domains model: including human-animal interactions in assessments of animal welfare. *Animals* 10. <https://doi.org/10.3390/ani10101870>.
- Mendl, M., 1999. Performing under pressure: stress and cognitive function. *Appl. Anim. Behav. Sci.* 65, 221–244. [https://doi.org/10.1016/S0168-1591\(99\)00088-X](https://doi.org/10.1016/S0168-1591(99)00088-X).
- Mendl, M., Paul, E.S., 2020. Animal affect and decision-making. *Neurosci. Biobehav. Rev.* 112, 144–163. <https://doi.org/10.1016/j.neubiorev.2020.01.025>.
- Mes, D., van Os, R., Gorissen, M., Ebbesson, L.O.E., Finstad, B., Mayer, I., Vindas, M.A., 2019. Effects of environmental enrichment on forebrain neural plasticity and survival success of stocked Atlantic salmon. *J. Exp. Biol.* 222. <https://doi.org/10.1242/jeb.212258>.
- Mitchell, M., 1998. *An introduction to genetic algorithms*. MIT press.
- Moghadam, H.K., Johnsen, H., Robinson, N., Andersen, O., Jørgensen, E.H., Johnsen, H. K., Baehr, V.J., Tveiten, H., 2017. Impacts of early life stress on the methylome and transcriptome of Atlantic salmon. *Sci. Rep.* 7. <https://doi.org/10.1038/s41598-017-05222-2>.
- Mustapha, U.F., Alhassan, A.W., Jiang, D.N., Li, G.L., 2021. Sustainable aquaculture development: a review on the roles of cloud computing, internet of things and artificial intelligence (CIA). *Rev. Aquac.* 13, 2076–2091. <https://doi.org/10.1111/raq.12559>.
- Näslund, J., Rosengren, M., Johnsson, J.I., 2019. Fish density, but not environmental enrichment, affects the size of cerebellum in the brain of juvenile hatchery-reared Atlantic salmon. *Environ. Biol. Fishes* 102, 705–712. <https://doi.org/10.1007/s10641-019-00864-9>.
- Neethirajan, S., 2021. The use of artificial intelligence in assessing affective states in livestock. *Front. Vet. Sci.* 8. <https://doi.org/10.3389/fvets.2021.715261>.
- Nista, N.A., Jannuzzi, C.A.S.C., Falsarella, O.M., Benedicto, S.C.D., 2020. Society and sustainable development: animal rights in sustainability discourse. *Ambient. Soc.* 23, e02782. <https://doi.org/10.1590/1809-4422asoc20180278r2vu202014ao>.
- Overton, K., Dempster, T., Oppedal, F., Kristiansen, T.S., Gismervik, K., Stien, L.H., 2019. Salmon lice treatments and salmon mortality in Norwegian aquaculture: a review. *Rev. Aquac.* 11, 1398–1417. <https://doi.org/10.1111/raq.12299>.
- Peters, A., McEwen, B.S., Friston, K., 2017. Uncertainty and stress: why it causes diseases and how it is mastered by the brain. *Prog. Neurobiol.* 156, 164–188. <https://doi.org/10.1016/j.pneurobio.2017.05.004>.
- Pettersen, J.M., Bracke, M.B.M., Midtlyng, P.J., Folkedal, O., Stien, L.H., Steffenak, H., Kristiansen, T.S., 2014. Salmon welfare index model 2.0: an extended model for overall welfare assessment of caged Atlantic salmon, based on a review of selected welfare indicators and intended for fish health professionals. *Rev. Aquac.* 6, 162–179. <https://doi.org/10.1111/raq.12039>.
- Pielke Jr, R.A., 2007. *The honest broker: making sense of science in policy and politics*. Cambridge University Press.
- Pipia, S., 2020. Emergence of global animal law as a separate branch of international law. *Anim. Nat. Resour. Law Rev.* 16, 171–192. <https://msujanrl.org/previous-volumes/>.
- Pulcin, D., Franceschini, S., Buttazzoni, L., Giannetti, C., Capocioni, F., 2020. Consumer preferences for farmed seafood: An Italian case study. *J. Aquat. Food Prod. Technol.* 29, 445–460. <https://doi.org/10.1080/10498850.2020.1749201>.
- Rasheed, A., San, O., Kvamsdal, T., 2020. Digital Twin: values, challenges and enablers from a modeling perspective. *IEEE Access* 8, 21980–22012. <https://doi.org/10.1109/ACCESS.2020.2970143>.
- Reichstein, M., Benson, V., Camps-Valls, G., Boran, H., Fearnley, C., Kornhuber, K., Rahaman, N., Schölkopf, B., Tarraga, J.M. and Vinuesa, R. 2024. Early warning of complex climate risk with integrated artificial intelligence. doi: 10.21203/rs.3.rs-4248340/v1.
- Reid, C.R., 2023. Thoughts from the forest floor: a review of cognition in the slime mould *Physarum polycephalum*. *Anim. Cogn.* <https://doi.org/10.1007/s10071-023-01782-1>.
- Rickard, L.N., Britwum, K., Noblet, C.L., Evans, K.S., 2020. Factory-made or farm fresh? Measuring US support for aquaculture as a food technology. *Mar. Policy* 115, 103858. <https://doi.org/10.1016/j.marpol.2020.103858>.
- Rose, P.E., Nash, S.M., Riley, L.M., 2017. To pace or not to pace? A review of what abnormal repetitive behavior tells us about zoo animal management. *J. Vet. Behav. -Clin. Appl. Res.* 20, 11–21. <https://doi.org/10.1016/j.jveb.2017.02.007>.
- Rosengren, M., Kvingedal, E., Näslund, J., Johnsson, J.I., Sundell, K., 2017. Born to be wild: effects of rearing density and environmental enrichment on stress, welfare, and smolt migration in hatchery-reared Atlantic salmon. *Can. J. Fish. Aquat. Sci.* 74, 396–405. <https://doi.org/10.1139/cjfas-2015-0515>.
- Röller, D.C., Kim, K., De Agros, M., Jordan, A., Galizia, C.G., Shamble, P.S., 2022. Regularly occurring bouts of retinal movements suggest an REM sleep-like state in jumping spiders. *Proc. Natl. Acad. Sci. USA* 119, e2204754119. <https://doi.org/10.1073/pnas.2204754119>.
- Royer, E., Pastres, R., 2023. Data assimilation as a key step towards the implementation of an efficient management of dissolved oxygen in land-based aquaculture. *Aquac. Int.* 31, 1287–1301. <https://doi.org/10.1007/s10499-022-01028-w>.
- Ruiz-Mirazo, K., Pereto, J., Moreno, A., 2004. A universal definition of life: Autonomy and open-ended evolution. *Orig. Life Evol. Biospheres* 34, 323–346. <https://doi.org/10.1023/B:ORIG.0000016440.53346.dv>.
- Russell, W.M.S., Burch, R.L., 1959. *The principles of humane experimental technique*. Methuen.
- Ruxton, G.D., Beauchamp, G., 2008. The application of genetic algorithms in behavioural ecology, illustrated with a model of anti-predator vigilance. *J. Theor. Biol.* 250, 435–448. <https://doi.org/10.1016/j.jtbi.2007.10.022>.
- Salvanes, A.G.V., Moberg, O., Braithwaite, V.A., 2007. Effects of early experience on group behaviour in fish. *Anim. Behav.* 74, 805–811. <https://doi.org/10.1016/j.anbehav.2007.02.007>.
- Salvanes, A.G.V., Moberg, O., Ebbesson, L.O.E., Nilsen, T.O., Jensen, K.H., Braithwaite, V.A., 2013. Environmental enrichment promotes neural plasticity and cognitive ability in fish. *Proc. R. Soc. B-Biol. Sci.* 280, 20131331. <https://doi.org/10.1098/rspb.2013.1331>.
- Schilthuis, M., 2018. *Darwin comes to town: How the urban jungle drives evolution*. Picador.
- Schölkopf, B., Locatello, F., Bauer, S., Ke, N.R., Kalchbrenner, N., Goyal, A., Bengio, Y., 2021. Toward causal representation learning. *Proc. IEEE* 109, 612–634. <https://doi.org/10.1109/jproc.2021.3058954>.
- Schultz, W., 2024. A dopamine mechanism for reward maximization. *Proc. Natl. Acad. Sci.* 121, e2316658121. <https://doi.org/10.1073/pnas.2316658121>.
- Segner, H., Reiser, S., Ruane, N., Rösch, R., Steinhagen, D. and Vehanen, T. 2019. Welfare of fishes in aquaculture. FAO Fisheries and Aquaculture Circular No. C1189, Budapest: FAO.
- Seth, A., 2021. *Being you: A new science of consciousness*. Penguin.
- Shapouri, S., Sharifi, A., Folkedal, O., Fraser, T.W.K., Vindas, M.A., 2024. Behavioral and neurophysiological effects of buspirone in healthy and depression-like state juvenile salmon. *Front. Behav. Neurosci.* 18, 1285413. <https://doi.org/10.3389/fnbeh.2024.1285413>.
- Sloman, K.A., Bouyoucos, I.A., Brooks, E.J., Sneddon, L.U., 2019. Ethical considerations in fish research. *J. Fish. Biol.* 94, 556–577. <https://doi.org/10.1111/jfb.13946>.
- Solås, M.R., Skoglund, H., Salvanes, A.G.V., 2019. Can structural enrichment reduce predation mortality and increase recaptures of hatchery-reared Atlantic salmon *Salmo salar* L. fry released into the wild? *J. Fish. Biol.* 95, 575–588. <https://doi.org/10.1111/jfb.14004>.
- Sommeret, I., Wiik-Nielsen, J., Moldal, T., Oliveria, V., JC, S., Haukaas, A. and Brun, E. 2024. Fiskehelse rapporten 2023, Veterinærinstituttets rapportserie, Veterinærinstituttet, Oslo.
- Sommeret, I., Wiik-Nielsen, J., Oliveira, V., Moldal, T., Bornø, G., Haukaas, A. and Brun, E. 2023. Fiskehelse rapporten 2022, Veterinærinstituttets rapportserie.
- Soylu, F., 2016. An embodied approach to understanding: making sense of the world through simulated bodily activity. *Front. Psychol.* 7, 1914. <https://doi.org/10.3389/fpsyg.2016.01914>.
- Spruijt, B.M., van den Bos, R., Pijlman, F.T.A., 2001. A concept of welfare based on reward evaluating mechanisms in the brain: anticipatory behaviour as an indicator for the state of reward systems. *Appl. Anim. Behav. Sci.* 72, 145–171. [https://doi.org/10.1016/S0168-1591\(00\)00204-5](https://doi.org/10.1016/S0168-1591(00)00204-5).
- Sterling, P., 2012. Allostasis: a model of predictive regulation. *Physiol. Behav.* 106, 5–15. <https://doi.org/10.1016/j.physbeh.2011.06.004>.
- Stien, L.H., Bracke, M.B.M., Folkedal, O., Nilsson, J., Oppedal, F., Torgersen, T., Kittilsen, S., Midtlyng, P.J., Vindas, M.A., Øverli, Ø., Kristiansen, T.S., 2013. Salmon welfare index model (SWIM 1.0): a semantic model for overall welfare assessment of caged Atlantic salmon: review of the selected welfare indicators and model presentation. *Rev. Aquac.* 5, 33–57. <https://doi.org/10.1111/j.1753-5131.2012.01083.x>.
- Strand, D.A., Utne-Palm, A.C., Jakobsen, P.J., Braithwaite, V.A., Jensen, K.H., Salvanes, A.G.V., 2010. Enrichment promotes learning in fish. *Mar. Ecol. Prog. Ser.* 412, 273–282. <https://doi.org/10.3354/meps08682>.
- Sumida, B.H., Houston, A.I., McNamara, J.M., Hamilton, W.D., 1990. Genetic algorithms and evolution. *J. Theor. Biol.* 147, 59–84. [https://doi.org/10.1016/S0022-5193\(05\)80252-8](https://doi.org/10.1016/S0022-5193(05)80252-8).
- Taborsky, B., English, S., Fawcett, T.W., Kuijper, B., Leimar, O., McNamara, J.M., Ruuskanen, S., Sandi, C., 2021. Towards an evolutionary theory of stress responses. *Trends Ecol. Evol.* 36, 39–48. <https://doi.org/10.1016/j.tree.2020.09.003>.
- Taborsky, B., Kuijper, B., Fawcett, T.W., English, S., Leimar, O., McNamara, J.M., Ruuskanen, S., 2022. An evolutionary perspective on stress responses, damage and repair. *Horm. Behav.* 142, 105180. <https://doi.org/10.1016/j.yhbeh.2022.105180>.
- Tao, F., Xiao, B., Qi, Q.L., Cheng, J.F., Ji, P., 2022. Digital twin modeling. *J. Manuf. Syst.* 64, 372–389. <https://doi.org/10.1016/j.jmsy.2022.06.015>.
- Thompson, E., 2007. *Mind in Life: Biology, Phenomenol. Sci.*
- Tort, L., 2011. Stress and immune modulation in fish. *Dev. Comp. Immunol.* 35, 1366–1375. <https://doi.org/10.1016/j.dci.2011.07.002>.
- Trimmer, P.C., Houston, A.I., Marshall, J.A.R., Bogacz, R., Paul, E.S., Mendl, M.T., McNamara, J.M., 2008. Mammalian choices: combining fast-but-inaccurate and slow-but-accurate decision-making systems. *Proc. R. Soc. B-Biol. Sci.* 275, 2353–2361. <https://doi.org/10.1098/rspb.2008.0417>.
- United Nations, 1972. *Declaration of the United Nations conference on the human environment*.
- van de Vis, H., Kolarevic, J., Stien, L.H., Kristiansen, T.S., Gerritzen, M., van de Braak, K., Abbink, W., Sæther, B.-S., Noble, C., 2020. Welfare of farmed fish in different production systems and operations. In: Kristiansen, T.S., Fernø, A., Pavlidis, M.A., Van de Vis, H. (Eds.), *The welfare of fish*. Springer.
- VanderHorn, E., Mahadevan, S., 2021. Digital Twin: Generalization, characterization and implementation. *Decis. Support Syst.* 145, 113524. <https://doi.org/10.1016/j.dss.2021.113524>.
- Vindas, M.A., Folkedal, O., Kristiansen, T.S., Stien, L.H., Braastad, B.O., Mayer, I., Øverli, Ø., 2012. Omission of expected reward agitates Atlantic salmon (*Salmo salar*). *Anim. Cogn.* 15, 903–911. <https://doi.org/10.1007/s10071-012-0517-7>.

- Vindas, M.A., Helland-Riise, S.H., Nilsson, G.E., Øverli, Ø., 2019. Depression-like state behavioural outputs may confer beneficial outcomes in risky environments. *Sci. Rep.* 9, 3792. <https://doi.org/10.1038/s41598-019-40390-3>.
- Vindas, M.A., Johansen, I.B., Folkedal, O., Höglund, E., Gorissen, M., Flik, G., Kristiansen, T.S., Øverli, Ø., 2016. Brain serotonergic activation in growth-stunted farmed salmon: adaption versus pathology. *R. Soc. Open Sci.* 3, 160030. <https://doi.org/10.1098/rsos.160030>.
- Vindas, M.A., Madaro, A., Fraser, T.K., Höglund, E., Olsen, R.E., Øverli, Ø., Kristiansen, T.S., 2016. Coping with a changing environment: the effects of early life stress. *R. Soc. Open Sci.* 3, 160382. <https://doi.org/10.1098/rsos.160382>.
- Vindas, M.A., Sørensen, C., Johansen, I.B., Folkedal, O., Höglund, E., Khan, U.W., Stien, L.H., Kristiansen, T.S., Braastad, B.O., Øverli, Ø., 2014. Coping with unpredictability: dopaminergic and neurotrophic responses to omission of expected reward in Atlantic salmon (*Salmo salar* L.). *Plos One* 9, e85543. <https://doi.org/10.1371/journal.pone.0085543>.
- von der Emde, G., Mogdans, J., Kapoor, B.G., 2012. *The senses of fish: adaptations for the reception of natural stimuli*. Springer Science & Business Media.
- Wagner, G.P., 1996. Homologues, natural kinds and the evolution of modularity. *Am. Zool.* 36, 36–43. <https://doi.org/10.1093/icb/36.1.36>.
- Ward, R.H., Quinn, T.P., Dittman, A.H., Yopak, K.E., 2024. The effects of rearing environment on organization of the olfactory system and brain of juvenile sockeye salmon, *Oncorhynchus nerka*. *Integr. Comp. Biol.* 64, 92–106. <https://doi.org/10.1093/icb/icae002>.
- Way, M., 2017. "What I cannot create, I do not understand". *J. Cell Sci.* 130, 2941–2942. <https://doi.org/10.1242/jcs.209791>.
- Wickens, S.M., 2020. The health situation in Norwegian aquaculture 2018. Welfare concerns over the use of new technologies. *Anim. Welf.* 29, 114–116. <https://doi.org/10.1017/S0962728600011672>.
- Wingfield, J.C., 2013. The comparative biology of environmental stress: behavioural endocrinology and variation in ability to cope with novel, changing environments. *Anim. Behav.* 85, 1127–1133. <https://doi.org/10.1016/j.anbehav.2013.02.018>.
- Wingfield, J.C., Maney, D.L., Breuner, C.W., Jacobs, J.D., Lynn, S., Ramenofsky, M., Richardson, R.D., 1998. Ecological bases of hormone-behavior interactions: The "emergency life history stage". *Am. Zool.* 38, 191–206. <https://doi.org/10.1093/icb/38.1.191>.
- Zacks, O., Ginsburg, S., Jablonka, E., 2022. The futures of the past. The evolution of imaginative animals. *J. Conscious. Stud.* 29, 29–61. <https://doi.org/10.53765/20512201.29.3.029>.
- Zacks, O., Jablonka, E., 2023. The evolutionary origins of the Global Neuronal Workspace in vertebrates. *Neurosci. Conscious.* 2023, niad020. <https://doi.org/10.1093/nc/niad020>.
- Zupanc, G.K.H., 2006. Neurogenesis and neuronal regeneration in the adult fish brain. *J. Comp. Physiol. A -Neuroethol. Sens. Neural Behav. Physiol.* 192, 649–670. <https://doi.org/10.1007/s00359-006-0104-y>.