

On modelling behaviour, development, stress and wellbeing in Atlantic salmon

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Abstract

The Atlantic salmon *Salmo salar* is a teleost fish, a multicellular animal with emotion-based body control through genes, sensing, nerves, hormones, cognition and behaviour. Its development and ecological role spans from being a prey in the egg and fry stages in freshwater systems to a piscivore predator in oceans. For humans, salmon represents a prestigious catch in rivers, an indicator species for ecosystem health and a valuable aquaculture stock. At present, most Atlantic salmon live in intensive aquaculture facilities and in the wild they live in river systems that are anthropogenically changed. There is thus increasing mismatches between its current situation and the environmental conditions that a salmon is evolved to expect. This mismatch leads to developmental errors, stress, lack of wellbeing and high mortality, which both industries and river managers aim to avoid. One way to understand better the constraints of the natural biology of salmon is to build a digital twin of the fish, and here we argue that such a model should resolve the mechanisms which underlie decision-making and development.

Therefore, we consider what it is like to be a salmon, and what knowledge is needed to model cognition, emotion, behaviour, development and welfare from the salmon’s perspective. Our focus is agent-based and subjective: how the fish experiences itself and its surroundings and thereby exerts control of its priorities. A salmon’s abilities to experience and prioritize result from the species’ evolutionary history and deep phylogeny, as well as from its own genetic and historical uniqueness. Its decisions are emotional and based on calculations in the nervous system of its future prospects, where motivations also are partly derived from its adaptive hormone systems. With this perspective, a digital twin of the Atlantic salmon can prove useful for to reduce or avoid developmental errors,

stress and lack of wellbeing in aquaculture. It can also inform managers of salmon river systems to adopt solutions to the natural biology of the salmon.

It is important to know what a salmon is experiencing

In 2022 and in Norway alone, almost 100 million Atlantic salmon and rainbow trout died prematurely in intensive aquaculture (Sommerset & al 2023). Stress is a major contributor to this mortality (Iversen & al 2005, Svendsen & al 2021). Another is diseases, which we will not cover in this paper. One set of stressful factors are well-intended treatments and procedures in the facilities, another set is the mismatch between the conditions in the fish farm and and what the salmon is evolved to expect. The aim of this paper is to build a basis that can be developed into models of Atlantic salmon development, physiology and behaviour. We first address why new models based on a deeper understanding of a salmon are needed. Then we describe the possible life-history choices confronting a young salmon in natural and aquaculture environments. Thereafter we stepwise build the decision machinery in a salmon: we use an evolutionary perspective to show the gradual emergence of its cognitive system, and finally we discuss how decision-making, stress and wellbeing can be considered in models that incorporate the experiences of a salmon.

A deep need for fundamental salmon digital twin models

The Atlantic salmon *Salmo salar* has a natural distribution in the North Atlantic Ocean and in thousands of rivers on both sides of it (Lennox & al 2021). Most of these populations, throughout this vast area, are considered to be at risk (WWF 2001, ICES 2022). For maybe more than a thousand years, causes of the decline in these populations have predominantly been anthropogenic, such as damming, hydropower, pollution, overfishing and physical changes in the rivers (Lenders & al 2016). More recently, reduced survival in the ocean driven by climate change and impacts by aquaculture through genetic introgression and collateral effects of disease have worsened the situation (Vollset & al 2022, 2023). Several mitigation measures have been instigated to counter the many declines, often through attempts at population restocking and restoration (reviewed in Lennox & al 2021). These reviewers 'advise to avoid restoration as much as possible by protecting and managing existing populations and when restoration is necessary, problems should be identified and addressed in partnership with river users' (p. 3480). Thus, the advice to managers is to consider how it is to be a salmon in the river rather than to attempt to engineer the aquatic world of the salmon from a human perspective.

Today, most Atlantic salmon live in captivity (FAO 2023) (as do also most of the world's non-human mammals, Greenspoon & al 2023) and make up a multibillion-dollar seafood industry. This industry faces many of the same challenges as in its early days 40 years ago with respect to robustness, early unwanted maturation, and mortality (REF). About one in five salmon in Norwegian aquaculture die prematurely. In 2022, thus summed to 92 million premature deaths (Sommerset & al 2023), with stress as a major factor (Iversen & al 2005, Svendsen & al 2021).

We think that some of the challenges in aquaculture management could be addressed by modelling tools that address biological processes of ontogeny, development and life-stage transitions as well as of stress and wellbeing. There are many situations both for natural populations and in aquaculture where a model that represents the inner life of the Atlantic salmon would be valuable. There is push for digital twins (Tao & al 2019) for precision fish farming (Antonucci & Costa 2020, Le Gall & al 2021) in salmon aquaculture (Føre & al 2018), as for precision livestock farming of land animals (Berckmans 2017). Precision fish farming aims to improve the economics of aquaculture, but also to reduce its environmental footprint. But a salmon, another teleost and many other animals cannot be understood from the current conditions alone, for instance in an experiment, since the response of each individual will vary (e.g., Gomes & al 2023) depending on its own motivations, which again depend on its own experiences and its own expectations to the future. Therefore, a model of such an animal should not be called a twin if it does not aim to understand the animal from its own

perspective.

A digital twin model of the Atlantic salmon in aquaculture should aim to address its capacity for experience in its life stages and give indications of the salmon’s experiences related to stress and wellbeing (Budaev & al 2020). Also outside of aquaculture, such as in local ecological management, models of what researchers and managers can expect that salmon may come to experience, can be of high practical value in considerations of its space use, growth, and survival (Edelblutte & al 2023). Yet, there are no high-quality models or school of models for salmon development, physiology, and behaviour, nor of stress and wellbeing. There are also no published high-quality models that combine these aspects for other fish species, either, nor are there models of the foundation for experience, stress and wellbeing in any other animal in the meat industries (Collins & Part 2013, Budaev & al 2020, Neethirajan 2021, Colditz 2023) or in nature conservation. Before such models are coded, one need to have a better understanding of the animal. Below we will discuss the basis for this understanding that will lead up to concepts for digital twin models of the Atlantic salmon.

Why should we care about the experience?

As we will show in this paper, the behaviour of an Atlantic salmon or another teleost is controlled by its experience of itself and of its surroundings. Experience is the key to a salmon’s own perspective of what it is like to live in a river, in the ocean or in an aquaculture facility, what to expect of the future, and how to prepare for it. If we can understand this experience (Fig. 1), we may be able to improve both nature and aquaculture management.

Keeping animals captive in aquaculture facilities, brings responsibilities for their welfare (Farm Animal Welfare Council 2009, Bovenkerk & Meijboom 2020, Van de Vis & al 2020, Cooper & al 2023). The wellbeing of a fish is informed by predictions based on its experiences (Kristiansen & Fernö 2020). Indeed, public concern for animal welfare and environmental impact is growing and influence the perception of amplified risk and poor fish welfare in many customers (Ankamah-Yeboah & al 2019, Pulcini & al 2020, Rickard & al 2020). Therefore, welfare in aquaculture has also become of interest for governments (Gismervik & al 2020).

Domestication changes the experiences of the fish and then their life histories. Conflicts between their naturally evolved expectations and the environmental and physiological conditions in the intensive facility is an important contributor to challenges in the industry, such as early, and unwanted, sexual maturity (Duncan & al 1999, Pino Martinez & al 2023).

Experience is highly relevant to ecology and nature conservation, as it impacts growth and survival for a wide variety of animals (but not all). The ecological range of humanity includes where we have emotional and thus behavioural impact on individuals. These impacts can cascade into populations and communities (Brown & al 1999, Gaynor & al 2019, Suraci & al 2019).

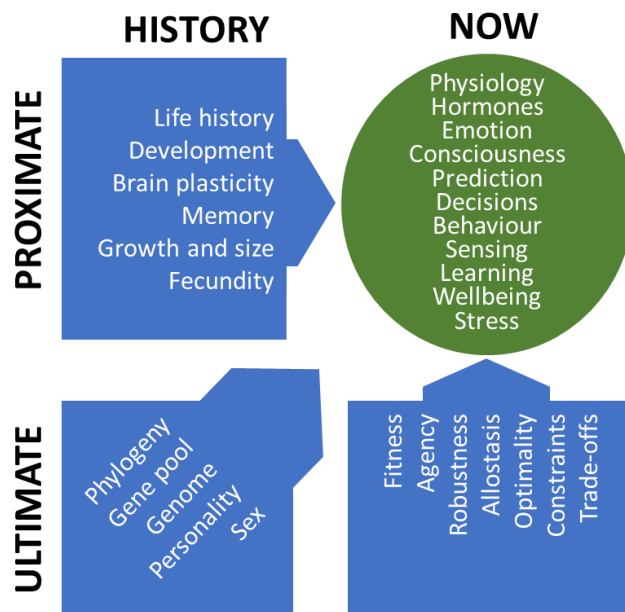


Fig. 1. Experience. All of Tinbergen’s (1963) four questions on behaviour—as organized by Nesse (2013) in the 2x2 table—impact each other directly and indirectly. All there is to be a salmon is found in the green circle (proximate and now). The processes and mechanisms in this circle contribute to or result from a salmon’s own experience. The three other quadrants inform the researcher on evolutionary and developmental processes that has led to—and constrain—a salmon’s current ability to experience.

Decisions: developmental and behavioural

Decisions are a recurring theme throughout the paper. We use the same word for two phenomena that are quite different but related: behaviour and development. They are both informed by the animal's interpretation of sensory information from the body and the environment, but they follow different pathways in the organism. Developmental decisions lead to changes in hormone profiles, such as an emphasis of gonadal rather than somatic growth. Behavioural decisions are cognitive and are triggered and executed through changes in the emotional state of the animal. However, the propensity for some of these emotional states and behavioural options can be impacted by the hormonal profile of the animal in its current developmental stage.

What is it like for an Atlantic salmon to be an Atlantic salmon?

There is immense variation in the life-history of Atlantic salmon, both within and between populations and regions (Fleming 1988, 1996, Klemetsen & al 2003, Good & Davidson 2016, Mobley & al 2021). As we will show later, this variation is possible since modularity and degeneracy (see **Box 1**) in the behavioural architecture hugely simplify local evolution of signals, thresholds and responses. Further, this evolution of developmental and behavioural flexibility is adaptive for anadromous life cycles in variable environments (Thorpe & al 1998, Mangel & Satterthwaite 2008).

To be an egg, alevin, fry, parr, smolt, and adult Atlantic salmon are widely different, and we cannot here discuss these scenarios. We will focus on how the perspective of subjective experience can be helpful for understanding the parr/smolt transformation, and then discuss stress and wellbeing, which cannot be understood from other perspectives than from inside the body.

Phylogeny and ontogeny: smoltification or sexual maturation?

The family Salmonidae evolved at least 88 million years ago through a tetraploidization process (Allendorf & Thorgard 1984). The genus *Salmo* is the Atlantic branch of the extant salmonid family (McPhail & al 1997).

The evolution of agency in Atlantic salmon has led to sex difference in ontogeny (Fleming 1988, Mobley & al 2021). In females, production of descendants depends on egg production and survival, access to breeding territories and nest quality. In males, the reproductive success is largely determined by access to egg-laying females. This means that while growth is fundamental to female reproductive success, it needs not be so in males, as males have an alternative life history of remaining in the river and reproduce at a small size (Thorpe & al 1988). This decision is made at the parr stage, who may develop into a smolt and leave the river for the ocean or remain and sexually mature as a dwarf (Thorpe & al 1988). Similar breeding systems exist among its relatives in the subfamily Salmoninae, but early male maturity is more common in Atlantic salmon than in other Salmoninae species, and the size range of mature males is also largest in Atlantic salmon (Fleming 1988).

While many animals must prepare for seasonality, the extra challenge of being anadromous is to be prepared for the seasonal windows of opportunity for upstream and downstream migration in the river. With different ecological conditions in rivers, these individual choices have population consequences (Railsback & al 2014). The windows for life-history decisions in Atlantic salmon are evolutionarily adapted over millions of years (Stearley & Smith 1993). The neurotransmitters and the emotion systems that underlie these decisions, are even older than the first fishes (Andersen & al 2016).

Annually, as long as the parr remains in the river, it may meet four decision events involving an upcoming ontogenetic shift (**Fig. 2**):

(1) In late autumn, a parr that has not entered smoltification may initiate the gonadal maturation process. This sexual maturation is a life-history option that is top-down initiated with the activation of the brain-pituitary-gonad hormonal axis (Schulz & al 2010, Taranger & al 2010) in response to

several external and internal factors (Good & Davidson 2016, Pino Martinez & al 2023). This decision leads to changes in resource allocation from somatic growth to investment in reproduction and results in lower survival (Mobley & al 2021). Although parr maturation thus reduces the probability of smolting the next year, experimental studies indicate that these processes are decoupled (Mobley & al 2021).

(2A) In the spring a parr can inhibit gonadal maturation. This inhibition may lead towards smoltification and migration to the ocean next year. Inhibition of this maturation process is controlled by the photoperiod in the spring combined with the physiology of the parr (its lipid level and rate of change) and its genetics (an inherited threshold for maturation, Thorpe & al 1998, Bromage & al 2001).

(2B) Absence of this inhibition will initiate the process which will lead to sexual maturity in the river the year after.

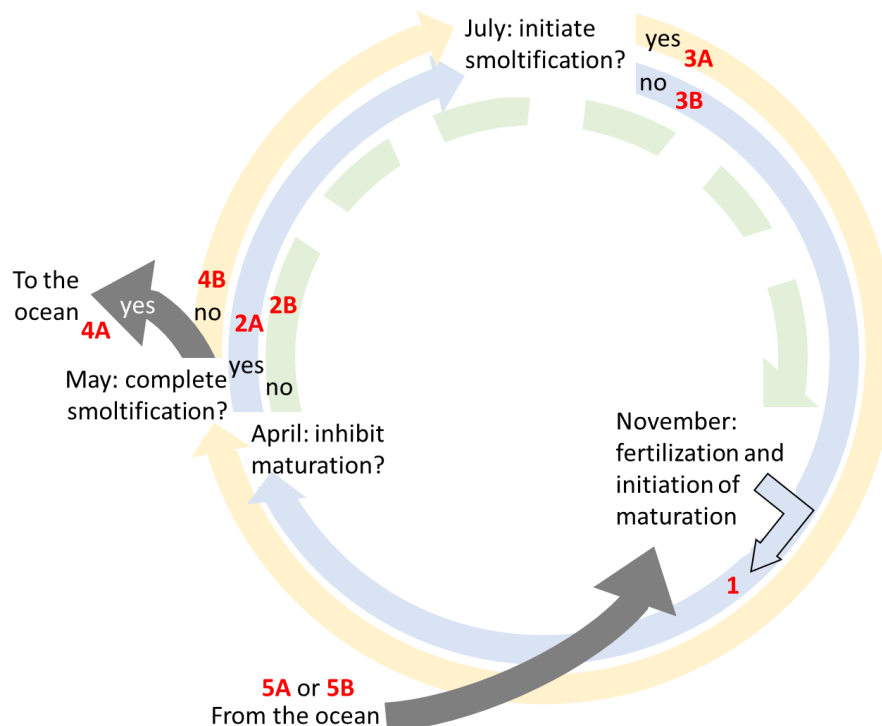


Fig. 2 Life-history decisions of Atlantic salmon parr in the river. Red numbers explained in the text. Green dotted line takes one and a half year. Months are indications of season as timing will vary with local conditions. Modified from Thorpe & al. (1988).

(3A) If maturation was inhibited in the spring (#2a, above), the parr may in the summer respond to photoperiod and temperature and initiate smoltification. These reliable cues trigger production of melatonin (the time-keeping hormone) and a complex interplay between growth hormone and thyroid hormones (Nisembaum & al 2020).

(3B) Alternatively, if the physiological condition in the summer does not match the requirements for this ontogenetic change, the fish will remain in the river for at least another year. It will then enter anorexia during winter and prepare for new maturation or smoltification matches next year (Thorpe & al 1982, Metcalfe & Thorpe 1992). In late autumn, it will then again (#1, above) check for initiation of gonadal maturation.

(4A) Smoltification will result in the fish migrating to the ocean the next spring. Yet, the smoltification process can also be reversed, where the fish after desmoltification (4B) remains in the river, maybe until a decision for resmoltification is done (Fraser & al 2019, Mobley & al 2021).

(5A) The normal behaviour for the smolt after leaving the river, is to acclimatize for a short time in the estuary, then head out to the ocean, and return to spawn after one or more years (Fleming

1988).

(5B) However, with the benign conditions in intensive aquaculture, some of the young salmon in the sea phase, then called 1 sea-winter grilse, make a developmental decision of starting sexual maturation rather than continued somatic growth (McClure & al 2007, Davidson & al 2016, Pino Martinez & al 2023).

These processes and mechanism are evolutionarily adapted for keeping young individuals in Atlantic salmon populations inside one of several possible windows of favourable environmental and physiological conditions for high reproductive output, either as 'dwarfs' which mature in the river or as returning large salmon after one or more years in the ocean (Fleming 1988). Now, most Atlantic salmon live in intensive aquaculture facilities (FAO 2023). Here, early maturation of male 0+ parr, 1 sea-winter grilse and postsmolts is a common problem, since growth is maximized by continuous light without seasonality (Duncan & al 1999, Ebbesson & al 2007, Stefansson & al 2007), constant high temperature (at least in RAS facilities), and unlimited access to high energy feed (Pino Martinez & al 2023).

Such differences in experience between a young salmon in the natural or intensive habitat have led to situations in aquaculture not encountered and solved in the Atlantic salmon evolution of robust Darwinian agents. Although early sexual maturation (#2B, above) and smoltification (#3A, above) have been considered in developmental conflict (Thorpe 1994, Good & Davidson 2016), they can now occur simultaneously in response to the same photoperiod cue in intensive aquaculture (Fjelldal & al 2011, 2018, Pino Martinez & al 2023).

We have not answered the question in the heading, yet. How does a parr, a young salmon in the river who has never seen or heard of the ocean, nor considered mating, navigate the complexity of sensory information to make behavioural and developmental decisions (Fig. 2), and how can we make models that capture this complexity, also when the fish makes 'mistakes?' To enable an answer to what it is for an Atlantic salmon to be an Atlantic salmon, we will build the decision machinery of a teleost fish from its evolutionary beginning.

What is it like to be an animal and a teleost fish?

- Use elements from Lars Chittka chapter 11

The difference between *being someone* rather than only *doing something* is the ability to experience (Locke 1690, Hume 1748, Lamarck 1809, Ginsburg & Jablonka 2019). This ability has evolved and thus comes in many grades and types (Feinberg & Mallatt 2016, Ginsburg & Jablonka 2019, Godfrey-Smith 2020, Seth 2021). Here we will summarize the basic structures and mechanisms underlying the experience of a teleost fish (central concepts explained in Box 1) which have emerged during evolution (Fig. 1) before we return to the Atlantic salmon. But we have to start with a disclaimer: the science of consciousness is soft, with many competing overall integrative perspectives (e.g., Baars 1988, Tononi & Edelman 1998, Godfrey-Smith 2016, Ginsburg & Jablonka 2019, Seth 2021). This means that most or all of the experts we cite below would have written a salmon story with their unique emphasis. This disclaimer does not mean that consciousness science is a mess, rather, that there is reason to expect better unifications of what it is to be a salmon in the years to come. We are sure these stories will contain agency, experience, emotion, attention, prediction and learning.

To be agentic

An often-cited maxim is that 'Nothing in biology makes sense except in the light of evolution' (Dobzhansky 1973). For an organism, this 'sense' comes from agency, and in all other ways that biology makes sense, it is based on organismic agency. To be an agent means to work towards a goal, which is a natural consequence of reproduction with inheritance under natural selection (Darwin 1859): Genes that contribute to more surviving offspring will gradually accumulate in the gene pool and the population will then be better adapted to its environment. After some time, the individuals

will have inherited traits that make them live *as if* to maximize expected reproductive rate (Lotka 1925, Sibly 1989). This is the gradual and never-ending adaptive natural selection. Agency is thus as old as life itself (Newman 2022) or older (Kauffman 2007).

Agentic beings are characterized by integrity, self-maintenance, and autonomous functioning (Varela & al 1974, Ruiz-Mirazo & al 2004, Friston & al 2010, van Hateren 2013, Seth & Tsakiris 2018). The robustness of an agent is its ability to remain in or return to a window of favourable states for future reproduction (Kitano 2004, Fernandez-Leon 2011a, b). In most animals, robustness mechanisms are predictive, not just reactive, and afford allostasis, which ensures homeostasis throughout change (Sterling & Eyer 1988, Sterling 2012, Schulkin & Sterling 2019). Sensing the outer world facilitates robustness, as it allows an agent to control its body (Seth 2021) towards an agentic goal. Minimizing the uncertainty of the sensory systems allows an agent, from bacteria to highly complex organisms, to reach and remain in a state that keeps it on track to future reproduction (Friston & al 2010).

The hormone systems constitute major agentic regulators of physiology and behaviour in fish and most other animals. Some hormone systems adjust agentic priorities through the ontogenetic life stages (e.g., Lorenz & Gäde 2009, McCormick 2009), others have shorter effects on keeping the animal within a favourable state in robustness terms, such as by influencing appetite (Rønnestad & al 2017, Deal & Volkoff 2020, Kalanathan & al 2020), stress (Chrousos 2009, Braithwaite & Ebbesson 2014) and fear (Davis & al 2001, Braida & al 2012). Most models of hormones, physiology and behaviour consider the short-term hormonal responses to current conditions, but there are also models where the hormone system is key in the continuous updating of agentic priorities through life and across situations (Husak & al 2009, Weidner & al 2020, Jensen & al 2021).

Atlantic salmon has been under artificial selection in aquaculture for more than 50 years and 20 generations (Besnier & al 2021) and this has led to genetic modifications in some hormonal systems (Fleming & al 2002, Bull & al 2022). These modifications have mostly impacted physiological and behavioural systems, leading to faster growth (Glover & al 2009, Solberg & al 2013), higher stress tolerance (Solberg & al 2013) and reduction in fear (Houde & al 2010, Debes & Hutchings 2014, Solberg & al 2020). In addition, changes in agentic control of development through the parr/smolt stage shift is also observed (Harvey & al 2018).

The Darwinian fitness of an agent is ultimately about maximizing reproductive rate (Lotka 1925, Sibly 1989). A century ago, Alfred Lotka himself commented that 'What guides a human being, for example in the selection of his activities, are his tastes, his desires, his pleasures and pains, actual or prospective' (Lotka 1925, p. 352). Even a half century before him, Darwin's younger friend George John Romanes (1883, p. 20) wrote that 'agents that are able to *choose* their actions are agents that are able to *feel* the stimuli which determine the choice' (italics by Romanes).

To have emotions

All animals are agentic, but not all animals have emotions (Barron & Klein 2016). The first theories of emotion (Darwin 1872, Izard 1977, Panksepp 2007) focused on physiological changes as inherent to emotional states and outlined a limited set of emotions as being basic, including fear, anger, joy and sadness, based on which several high-level emotions can be developed. Appraisal theories of emotion (Wundt 1897, Russell 1980, Barrett & Russell 2015) argue that emotions must include associated cognitive interpretations of these physiological changes. Yet another ingredient of emotions is the subjective feeling that an individual experiences. We shall focus on how emotions work, that is, how they have emerged and evolved, and how they change. We will continue with a definition of emotion as a (basic or cognitively interpreted) centralized state of the organism, which is triggered by stimuli and yields a range of physiological responses (Anderson & Adolphs 2014).

How emotions work: An emotion is a bodily system with strong neural integration of sensing, cognition, and response. It was termed a 'survival circuit' (Fig. 3) by LeDoux (1996, 2000, 2012). If the circuit needs to detect and respond to danger, for example, it must ensure a very rapid integration. If, instead, the circuit needs to avoid hunger, it will focus the organism on food search. In brief, the

survival circuit can bring an animal to a full-body emotional state which LeDoux (2012) calls the 'global organismic state', whose role is to successfully address challenges via agentic coordination of the brain and the entire body by activating cognitive, physiological, and behavioural mechanisms.

If several survival circuits are activated at the same time, there will be competition between their neurobiological states in the brain to determine which one of them will control the body's cognitive, physiological, and behavioural responses (LeDoux 2012, Giske & al 2013). Emotion can thus drive the organism towards expressing a single, important agentic challenge that may cause the brain to produce an adaptive bodily response.

How emotions evolve and adapt: The fundamental building blocks of emotions are shared across phylogenies (Anderson & Adolphs 2014). Indeed, the selection for improved agent robustness and associated genetic evolution in animals have benefitted from two system-architecture properties, namely modularity and degeneracy.

Box 1. Definition of concepts

Agency: the ability of an autonomous entity of adaptive, goal-directed behaviour.

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

Allostatic load: the strain on the body accumulating under chronic or repeated stress.

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

Awareness: a cognitive state that results in the representation of an environmental or an internal object as a whole so as to create a one-to-one mapping between this object and its subjective representation.

Broadcast: widespread communication in the brain.

Consciousness (basic): the capacity to have subjective experience.

Controlled hallucination: a prediction made by the brain, a perceptual best guess constrained and improved by experience.

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

Efference: lead outward from a part of the body, especially from the brain or spinal cord

Experience: a subjective process by which an agent awarley perceives its external and internal environment.

Emotional state: a centralized state of the organism, which is triggered by stimuli and yields a range of physiological responses.

Free energy: the quantity which approximates sensoric entropy (uncertainty).

Global organismic state (GOS): the organism's current emotional state in terms of the specific survival circuit that is dominant.

Global workspace: the currently active, subjectively experienced working memory.

Modularity: the independence and interchangeability of components in an architecture.

Neuronal response: the interpretation in the brain of the strength of a sensory signal.

Phenomenology: the investigation and description of phenomena as consciously experienced.

Prediction error: the difference between the predicted state of the body or the environment and that the later interpretation of the same by the sensory system as consequence of the action.

Prediction machine: also called beast machine; a view of the organism as a computational machine that makes decisions and selects actions based on its own predictions about the future states of itself and its environment.

Re-entrance: the brain's reuse of its emotional circuitry to simulate in the body an imagined experience: the state it expects following a behavioural option.

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

Sentience: the capacity to experience subjective feelings.

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

Subjective internal model (SIM): an internal representation or a model of an aspect of itself or the environment currently held in the brain of the organism, available in broadcast in the global workspace.

Survival circuit: an evolutionarily conserved and highly integrated neural pathway that responds to a specific class of stimuli and controls a specific set of neurobiological, physiological, and behavioural responses.

Modularity refers to the serial structure of the architecture as from top to bottom on the left-hand side in Fig. 3. This architecture is modular because each component can be replaced by an alternative while keeping the rest intact (Chen & Crilly 2014). Modularity can be selected for as it increases evolvability (Wagner 1996, Wagner & Altenberg 1996, Clune & al 2013) and simplifies evolution of complexity.

Degeneracy is the ability of structurally different components in an organism to perform the same function so that failure or absence of an important component is offset by compensatory adjustments elsewhere in the system (Chen & Crilly 2014). Degeneracy describes parallel structures in an architecture that

ensures that a goal can be reached via independent routes. An example from our own work (Giske & al 2013) is that appetite can be evoked either by sensing food or by sensing that others feed, or yet again by afferent signals from the digestive system or from the energy status of the body (Fig. 3, right-hand side). Degeneracy facilitates evolvability since these pathways may have different selection pressures (Whitacre 2010, Chen & Crilly 2014). It also facilitates robustness in an organism since the same functions (e.g., hunger-reducing behaviour in Fig. 3) can be executed from different stimuli (e.g. stomach fullness, food availability and energy stores).

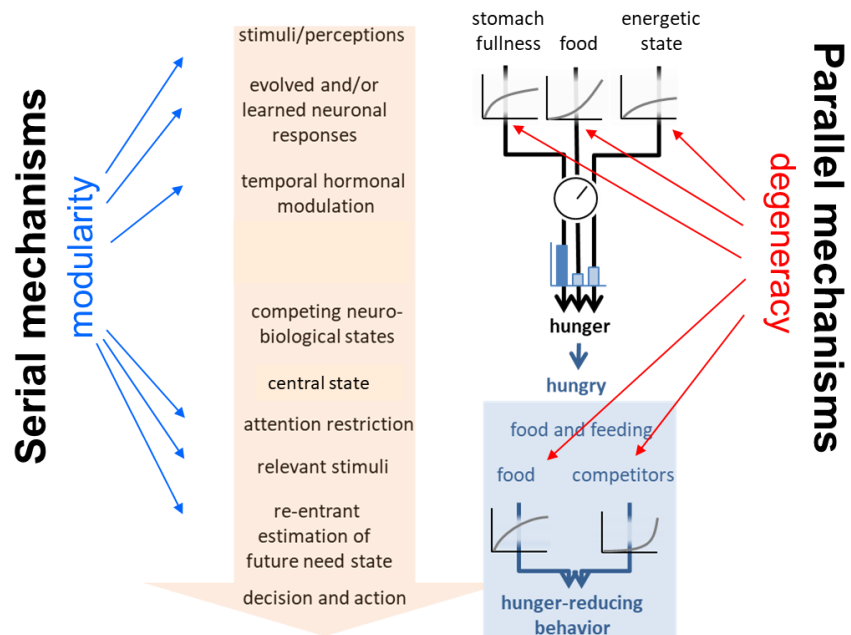


Fig. 3. The survival circuit. It is an integrated pathway between perception and reaction, here shown for to hunger and then to feeding. The emotional state, which is called central state in this figure, is called global organismic state by LeDoux (2012). Mutations and natural selection can, due to modularity (a series of modules that stepwise convert and scale the perception to an internal, central state in the brain), modify this chain by changing one component, e.g., the hormonal modulation, while keeping all else intact. Due to degeneracy (several independent and parallel functions that all can give the same brain state), it is relatively easy to modify the factors that will initiate the emotion or the reaction. Most animals will have many survival circuits serving different priorities and behaviours and competing through their neurobiological states for control of the body (Budaev & al 2019).

On the evolutionary and phylogenetic time scales, modularity and degeneracy thus facilitated evolution of robust, complex agents (Kitano 2004, Fernandez-Leon 2011b). On the time scale of a growing and surviving organism, emotions were among the first stabilizing tools for organismic robustness.

To have broadcast enables integration in working memory and gives subjective experience

We have mentioned that several emotion systems can compete for control over the body in winner-takes-it-all between neurobiological states (e.g., hunger versus fear). Having such emotions is necessary but not sufficient for subjective experience (Godfrey-Smith 2016). Subjective experience emerges in animals that can exchange information across emotion systems and with other brain regions (Godfrey-Smith 2016) in the brain's working memory. Then, an emotion is not an independent sensor-based machine but participates in generating a whole that is more than its

constituent parts.

This exchange in the brain's working memory is called broadcast and has been likened with a localised piece of emotion-related information 'becoming famous in the brain' (Shanahan 2012). Broadcast becomes global if it covers several aspects of the sensory and emotional system of an animal (Baars 1988). Godfrey-Smith (2016) argues that, for an animal to have subjective experience of what happens in the body, it is necessary to have broadcast in the global workspace of the brain (Baars 1988, Dehaene 2014), which means in the shared working memory.

Denton & al (2009) points out that each of these emotion systems will detect signals in the body that needs to be addressed (as in a survival circuit, Fig. 3), and with global workspace these systems get integrated across the brain. Thus, the resulting emotion-driven state is a unified experience across sensory modalities (e.g. as a minnow combines the size, colour, movement and smell of a pike to be aspects of one predator). Further, the broadcast links this unified experience with brain areas for sensing, motivation, motor control, memory, and action selection (Chittka 2022). Hence, with broadcast, a new way of being an animal emerged.

A teleost fish has a wide spectrum of senses (von der Emde & al 2004, Brown 2015, Tigert & Porteus 2022) which can communicate with each other in the brain. Mathis & al (1996) demonstrated that fish have the ability to combine sensory and cognitive modalities. By presenting a naïve and an experienced minnow to the smell of a pike, the naïve minnow learned, by observing the fright response of the experienced conspecific, to associate the unknown smell with danger. Thus, by the courtesy of broadcast, the naïve minnow connected the smell to an emotion through visual social learning and used the smell to establish a (poor, but) multidimensional cognitive model of the unseen but dangerous animal with that smell.

So where in the brains of teleost fish do the broadcast occur? One key seems to be the optic tectum in the midbrain. It is the major visual centre in the fish brain (Woodruff 2017, Kotschal & Kotschal 2020). Nerve cells from the retina creates a model—a visual representation of the outer world—in the optic tectum (Meek 1983, Vanegas & Ito 1983, Nevin & al 2010, Feinberg & Mallatt 2016). Into this model, other interneurons provide modulation by excitation or inhibition so that the fish can focus its attention (Nevin & al 2010, Kardamakisa & al 2015).

To have attention

Because the working memory has low capacity, attention serves an important role in focusing the experience and reduce storage (Myers & al 2017). Attention is possible for animals with the capacity to have a central emotional state (a global organismic state, sensu LeDoux 2012), coming out of competition between survival circuits in the global workspace (top of Fig. 4). Emotion with attention thus contributes to robustness of the organism by temporarily narrowing its interests (Mendl 1999). Attention improves the sensory resolution of what is concentrated on, thus it helps 'the beast machine' (Seth & Tsakiris 2018) to reduce uncertainty of its interpretation of sensory information (Feldman & Friston 2010). The cost of attention is lower sensitivity to other stimuli (Lima & Bednekoff 1999, Dukas & Kamil 2000, Purser & Radford 2011, Miller & al 2012).

Attention can be graded (Dehaene & al 2006). It is low in absence of strong signals (Whyte & Smith 2020) or in absence of high affect in any neurobiological state in activated survival circuits (bottom of Fig. 4). It can also be graded due to conflicting priorities. Such, a stickleback can dynamically balance hunger and fear (Milinski & Heller 1978, Heller & Milinski 1979) through a gradual regulation of its attention towards prey and predators (Milinski 1985).

To be predictive

Broadcast gives the possibility for a unified experience in an organism, so that it can determine what is urgent and what must wait. But broadcast itself does not find or determine solutions. This is why prediction ability is adaptive. Prediction gives an extra dimension to attention which is now also used to narrow what needs to be predicted (top row of Fig. 4). Even single-celled bacteria can utilize a

gradient of nutrient concentrations to move to a better place (Macnab & Koshland 1972), and this can be seen as behaviour based on prediction. However, we will here restrict the term to an animal with a cognitive model of itself and its surroundings, so that it can make cognition-based expectations to the future.

The cognitive ability to predict in animals may have started with the ability to predict what will happen to the body if the animal contracts its muscles (Angel 1976, Chittka 2022). The efference copy is an internal signal that communicates the near-future consequences of an animal's own actions into internal models of the body and the surroundings, so the animal will not be surprised by the effects of its change of position. Then it can understand which new sensory interpretations are caused by some external force and not by itself (Miall & Wolpert 1996). This allows the animal to become afraid if 'something' seems to become bigger because it is moving towards the animal, but not if 'something' seems larger because the animal is moving towards it (Chittka 2022). Thus, the animal predicts what its senses soon will report about the external world. A cognitive capacity to model the body itself has also evolved, since, in the words of early cyberneticians, 'every good regulator of a system must be a model of that system' (Conant & Ashby 1970).

From this, we see that there are three kinds of predictions taking place. 1) the efference copy of the neural signal, 2) the neural signals from the body, and 3) the neural signals from sensing the outer world. Rather than a pike sending a clear message to a minnow 'I am a pike heading towards you', the minnow brain takes in a variety of sensory signals and then forms a hypothesis (Gregory 1980) about what likely causes these signals. Thereafter, other models in the minnow brain will predict what happens next. In many animals, this ability to model the body and the outer world has thus extended to a level where behaviour is executed on basis of simulated predictions (Seth & Tsakiris 2018), without waiting for the sensory confirmation. Cues from the external and internal worlds are captured, communicated through the nervous system and interpreted via Bayesian models (Parr & al 2018) of what could have caused these signals (Seth 2013, Seth & Tsakiris 2018), and then compared with model expectations from the 'prediction machine' (Bubic & al 2010) in the brain. According to the Bayesian brain framework (Friston & al 2017), the cognitive challenge for the minnow above is the fundamental task of minimizing sensory uncertainty, which is quantified as the information-theoretic 'free energy' (Ramstead & al 2018). One of the strongest benefits of this prediction, both in terms of immediate robustness and long-term reproductive output, is that prediction enables the animal to initiate the activation of relevant internal resources before they are needed (Soylu 2016).

Sensing reveals prediction errors

First, prediction in the form of efference copying took away the surprises the agent's own behaviour could have caused in the sensory system. Then, with more advanced predictions, the role of the sensory system became to report on surprises, which are now called prediction errors (Bubic & al 2010). In animals with sensing and emotion, but without prediction, action starts with sensing, as in Fig. 3. With the predictive brain, the emotion and the resulting action come from the animal's subjective internal models (SIMs) of itself and of the outer world (Godfrey-Smith 2016) in what Seth (2021) calls 'controlled hallucinations.' Sensing, which performs the control in the hallucination, now becomes confirmation of these expectations or a source for learning. Rather than the linear model of Fig. 3, we arrive in a repeating loop (Fig. 4).

Prediction facilitates learning through prediction error (surprises): new knowledge can appear when the observation does not match the expectation (Bubic & al 2010, Adams & al 2013, Clark 2013). Introducing error by bias or by ignoring information often allows the agent to make better adaptive decisions under uncertainty (Glimcher 2003, Hutchinson & Gigerenzer 2005, Johnson & al 2013).

Future planning: re-entrant simulation of expected emotional state

The ability to make predictions is essentially an internal simulation of what might be and is the basic component of complex cognitive capacities (Hesslow 2012, Seth 2013, Soylu 2016). To aid in the planning of behavioural responses to stimuli, the cognitive process also utilizes information from the

ancient emotion system through re-entrance (Crump & al 2020). Re-entrance means that the brain can reuse its emotional circuitry to simulate in the body an imagined experience: the emotional state that it expects after a behaviour it considers executing (Fig. 4). Animals without re-entry can still negotiate urgent bodily needs through the competition between survival circuits. With re-entrance, a new chapter in cognitive evolution and animal behaviour started: future planning (Edelman 1978). Re-entrance is one of the most crucial computational mechanisms of sensory recognition, goal-directed decision-making, behaviour (Wang 2008, Kim & al 2017, Tang & al 2018), and complex forms of cognition (Edelman & al 2011). We illustrate the force of prediction with a quote from the philosopher Karl Popper (1978). He imagined that natural selection may well have favoured organisms that could try out behavioural options before they were executed. He then imagined that only our own species could take the next leap: “Let our conjectures, our theories die in our stead” (p. 354). This is a nice illustration of the fitness value of controlled hallucinations, but this substitutionary death did not start with people. It started with animals with re-entrant prediction. Countless animal lives have been saved. Others have been lost.

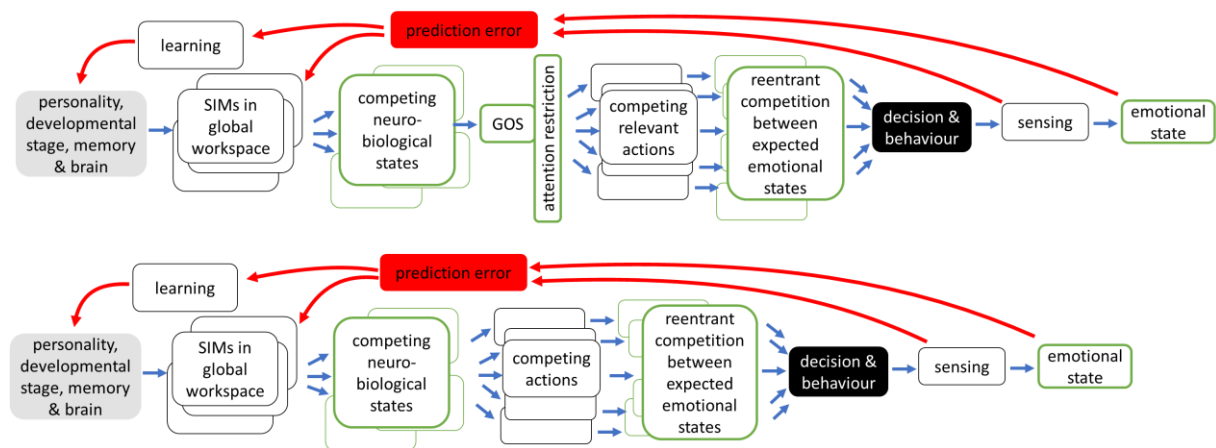


Fig. 4. Decision-making. The full process, including global workspace with subjective internal models (SIMs), emotional state (here: GOS, the global organismic state), re-entrant prediction, sensing, behaviour, prediction error and learning, is called ‘the beast machine’ by Seth & Tsakiris (2018) and ‘the prediction machine’ by Bubic & al (2010). In the top row, a GOS emerges from the competition between neurobiological states from activated survival circuits, with attention restriction to evaluate options relevant for this GOS. Below, either no survival circuit was activated, or the arousal of activated survival circuits were too weak to establish a GOS. In this situation the salmon can attend to many tasks, but with lower efficiency than above. These two alternatives represent extremes, and the fish can be in a state in between these.

Learning

We have now presented an evolutionary pathway for increased robustness, with emotion systems in global broadcast as the marker of the transition to animals with subjective experience (Godfrey-Smith 2016). But this path is not the only way to explain this emergence. Ginsburg & Jablonka (2019) shows how the evolution of the nervous system is linked to gradual improvements in learning abilities, from sensitization (a decrease in the threshold to elicit a response) and habituation (an increase in the threshold), to early associative learning (reinforcement of associations between non-complex stimuli and stereotypical behaviours) and in some branches of the animal tree of life, to ‘universal associative learning’ (learning of novel behaviours from novel combinations of stimuli). Universal associative learning represents a critical juncture in evolution because it involves both flexibility in combining a rich repertoire of stimuli and actions, as well as reflectivity, which is an organism’s ability to continue learning based on previous learning outcomes. (Ginsburg & Jablonka 2019). They therefore define the ability for universal (unlimited) associative learning as the best transition marker to organisms with basic consciousness, and they find this ability is arthropods and vertebrates (from the Cambrian) and in some molluscs (250 million years later).

While this focus on learning emphasises some other drivers for the evolution towards consciousness

than Baars, Edelman, Tononi, Seth, Godfrey-Smith and others do, Ginsburg & Jablonka (2019) shows that emotion, global workspace, prediction, attention, and the other building blocks we have mentioned above, also are needed for universal associative learning. Associative learning contributes to core functions of consciousness, including global activity levels, accessibility of information, binding, selection, plasticity and attention, agency, values, goals, and emotions (also see Dehaene & al 1998).

Learning in fish

The capacity for learning is well-studied in fish (Kelley & Magurran 2003, Brown & al 2011, Griffiths & Ward 2011, Ebbesson & Braithwaite 2012, Bshary & al 2014, Brown 2015, 2023).

Many studies have shown examples of universal associative learning in teleosts, and we show only a few. The archerfish can rapidly learn to complete an alternative forced-choice test and select the conditioned stimulus when faced with four stimuli (Newport & al 2014). Mosquitofish can learn to distinguish between 100 and 200 objects with the same ease as between 4 and 8 (Agrillo & al 2010). The weakly electric fish *Gnathonemus petersii* is capable of recognize objects across its visual and electric senses (Schumacher & al 2016). This recognition of objects across different sensory modalities, as also mentioned for minnows learning to fear pikes above (Mathis & al 1996), shows the exchange of information in broadcast, which is central to associative learning.

Social learning and culture are also important in fish (Brown & Laland 2011, Brown 2023, Wilson & Giske ms). When learning from each other, members of the group factor in both context and social identity. For example, the young learn from their parents, and socially lower-ranked members learn from dominant members (Nicol 2006). Like other behavioural traits, learning is shaped by evolutionary forces (Wilson & Giske ms) and by ecological context, hence animals are better prepared to learn some types of associations over others (Krause 2015).

Although fish brains are small compared to land vertebrates, they have much higher rates of brain cell proliferation and neurogenesis during adulthood than most land vertebrates (Zupanc 2006). This entails that all parts of the fish brain continue to develop and produce new neurons throughout adulthood. Importantly, the rates and location of these processes are greatly influenced by the evolutionary history of a population (Kruska 2005, Gonda & al 2012), and by the social and environmental experiences of a fish (Marchetti & Nevitt 2003, Lema & al 2005, Kihlslinger & Nevitt 2006, von Krogh & al 2010). This high level of cell proliferation and its environmental responsiveness suggest that experiences and learning may be particularly important for behavioural plasticity in fish (Ebbesson & Braithwaite 2012, Dunlap 2016). Both absence of and presence of experience can change brain anatomy, emotional responses and fish behaviour (Braithwaite & Salvanes 2005, Kihlslinger & al 2006, Burns & al 2009, von Krogh & al 2010, Salvanes & al 2013, Mes & al 2019, Näslund & al 2019, Nilsen & al 2023). From this follows that past experiences are substantial to the fish (Balcombe 2016), and that its current and future experiences depend on its past experiences (Jonsson & Jonsson 2014).

Basic consciousness

Animals with emotions that are interconnected in broadcast in the global workspace fulfil Godfrey-Smith's (2016) criteria for having subjective experience. Being predictive with re-entrant simulations of expected emotional gain or loss in each alternative action (Fig. 4) further improves the subjective experience. Such animals also pass Ginsburg & Jablonka (2019)'s transition marker 'universal associative learning' to organisms with basic consciousness.

There are many classifications of consciousness (Morin 2006). Each posits a basic form that consists of a direct awareness of the world without higher-order afterthoughts. This basic level has been termed phenomenal (Block 1995), core (Parvizi & Damasio 2001, Panksepp 2008), primary (Edelman 2003), and 'I' (Christoff & al 2011) consciousness. Thus, at its most basic level, consciousness is the

same as the capacity to have subjective experience (Morin 2006). Also, according to integrated information theory of consciousness (IIT), conscious experience emerges when various pieces of information become integrated and are no longer non-interdependent subsets of phenomenal distinctions (Tononi & Edelman 1998). The central emotional state is a 'unified experience', which is one of the basic axioms of IIT (Tononi & al 2016). This basic level of consciousness is also equated with sentience - the capacity to experience subjective feelings (Allen & Trestman 2020). To a certain degree, basic consciousness, sentience and subjective experience are interchangeable concepts (Ginsburg & Jablonka 2019).

Sentience in vertebrates seems to have emerged when the hindbrain, midbrain and diencephalic nuclei first evolved (Panksepp 2005, Merker 2007, Damasio 2010, Feinberg & Mallatt 2013, 2016, Woodruff 2017). While these researchers disagree on several issues, they agree that at least minimal sentience is possible without a neocortex, and that the optic tectum is central for the generation of sentience.

In humans, subjective experience is produced in the midbrain by an integrated efference simulation of the body's movement in the environment (Merker 2005, 2007). In vertebrates, information about the animal's resource budgeting needs (allostasis), its external environment, and its own movement are processed in different parts of the midbrain, and these subjective internal models are combined to create a model complex that links the needs of the animal with its understanding of the environment (Merker 2007). This combined neural model complex fulfils Godfrey-Smith's (2016) criterion for subjective experience by joining needs and prediction into a global workspace (Baars 1988). This enables a vertebrate to use integrated models to organise its behaviour (McHaffie & al 2005, Merker 2007).

Consciousness in fish

Ginsburg & Jablonka (2019) find universal associative learning in teleosts, which is their marker for basic consciousness. With the dual conditions for subjective experience, hence basic consciousness, as (i) emotions (ii) in global broadcast, Godfrey-Smith (2016, p. 64) wrote 'I regard fish as likely to undergo some forms of subjective experience.' This doubt is unnecessary (Brown 2015, Dunlap 2016, Woodruff 2017). Brown (2023) points out that cognitive abilities of fish are not much different from tetrapods (Brown & al 2011, Vila-Pouca & Brown 2017, Sneddon & Brown 2020, Salena & al 2021) or even primates (Bshary & al 2002).

Many studies show that fish use basic consciousness in agentic priorities. One example is the gradual switch in attention from only food to both food and predators with decreasing hunger in sticklebacks (Milinski & Heller 1978, Heller & Milinski 1979, Milinski 1985), another is short-term lack of attention towards predators when female crucian carps are preparing for mating (Lastein & al 2008). Ashley & al (2009) found that noxiously stimulated rainbow trout did not show antipredator responses, indicating that the pain avoidance survival circuit dominated over the predator avoidance circuit. In the cichlid *Neolamprologus furcifer*, females providing maternal care not only switch attention to predators, but selectively focuses on high-threat carnivorous intruders while limiting attention to other threats (Satoh & al 2021). In the same species, Hotta & al (2019) found that individuals concentrate on the face colouration for recognition of other individuals, which only makes sense if their attitude or behaviour towards another may depend on it.

The cleaner wrasse has even passed the mirror test (Kohda & al 2019, 2022), which is taken as evidence of not only awareness, but of self-awareness (REF). This is one level up from basic consciousness. Only a few mammal species, such as chimpanzees, elephants and dolphins, as well as one bird species have been considered self-aware (McCallum 2019), while other researchers consider that only great apes have passed this test (Gallup & Anderson 2020).

The agentic evolution of improved robustness by sensing, emotions, broadcast and prediction, and thus to subjective experience and basic consciousness, gives us a foundation for thinking about the components of experience in an Atlantic salmon (or in another teleost). But only to the *components*,

as the actions of an agent with subjective experience can only be understood from the inside of the animal, since they are based on subjective experiences, and they are private to the experiencing animal (Budaev & al 2020, **REFs**).

Thus, humans can only infer what it now feels like to be an individual fish based on its behaviour and our general understanding of the mechanisms that generate subjective experience. In the process, we assume that the stakes are largely the same, i.e. fitness-maximizing agency, as well as promoting subjective preferences and making counterintuitive choices in line with individual differences. Based on this assumption, consciousness in fish can be defined as a series of subjective experiences and associated emotional states, which have been regulated during evolution but nevertheless vary among individuals. Furthermore, private conscious experience can change the motivation in individuals (Cleeremans & Tallon-Baudry 2022), such that an Atlantic salmon parr may choose to start smolting out of season despite suboptimal growth prospects (Duncan & al 1999).

Decision-making

Decision-making in such animals as described here, sits between subjective experience and Darwinian agency, and depends on personality, learning, sensing, emotion, and prediction through controlled hallucination (Fig. 4). However, while the theory of evolution will place genetic contribution to future generations as the ultimate source of motivation (Lotka 1925, Sibly 1989), the proximate motivation system of such animals is driven by emotion (Cabanac 1992, Loewenstein & Lerner 2003, Mendl & Paul 2020). The emotion system has evolved to become ‘the common currency’ (McFarland & Sibly 1975, McCleery 1978) by which survival circuits representing the animal’s widely differing needs can be compared and prioritized (Cabanac 1992).

The controlled hallucination in what Seth & Tsakiris (2018) calls ‘the beast machine’ must answer three questions in emotional terms; 1) what is the current situation?, 2) what is the best response? and 3) was the response correct?

Question 1 is answered in competition between activated survival circuits, which produce neurobiological states in the active workspace of the brain (Fig. 4). If no survival circuit is actively pressing, the fish will be able to weakly attend to many types of sensory information (bottom of Fig. 4). It may then eat, move about, follow the others and look for danger at the same time. But if one survival circuit dominates (top of Fig. 4), it will set the fish in a global organismal state (GOS, LeDoux 2012), which is an emotional state where attention immediately sharpens the senses to improve the quality of the most relevant sensory information (Feldman & Friston 2010).

Question 2. With this focussed attention, the fish enters the response phase of its now dominant survival circuit (LeDoux 2012). To answer question 2, it will use its sharpened information in the hallucinating (Seth 2021) re-entrant prediction (Soylu 2016) of how alternative behavioural options would feel like (Fig. 4), so that the fish can choose the option that most likely would decrease its current suffering or increase its current pleasure (Cabanac 1992, Budaev & al 2019). For this process, utilization of readily available information on internal states can be more efficient than near-optimal Bayesian learning (Higginson & al 2018).

Question 3 is answered after the behaviour is executed. If the prediction was wrong, the prediction error will lead to belief updating that will control the hallucination (Fig. 4) to improve the next behavioural step (Seth 2021).

In addition to exploiting its own experiences, the fish brain takes advantage of experience in other individuals through social learning (Brown 2023, Wilson & Giske ms).

On top of this, individuals in the same fish population differ in decision-making and behavioural tendencies due to genetically influenced life-history strategies (Braun & al 2016, Erkinaro & al 2018) and personalities (Budaev 1997a,b, 1999, Budaev & Brown 2011, Conrad & al 2011). Personality variation can come from frequency-dependent selection of agency (Maynard Smith & Price 1973, McNamara & Leimar 2020) but will also emerge as a necessary by-product of degeneracy in the

behavioural architecture (Giske & al 2014) and of sexual reproduction in diploids. These inherited differences will in turn lead to different subjective experiences in the individuals, as they are sensitive to different kinds of information, may have been in different places, and may have been exposed to different episodes of social learning (Cote & al 2010).

Stress and wellbeing in fish

By expanding the subjective experience from emotions in global workspace to also include the capacity for prediction, opportunities to learn from prediction error arise (Bubic & al 2010, Adams & al 2013, Clark 2013). However, while these new gifts from evolvability allowed for the origin of sentient animals, it came with an added curse of stress and the potential for the experience of poor wellbeing. Stress therefore becomes an important factor, and it is a major cause of mortality for salmon in aquaculture (Iversen & al 2005, Svendsen & al 2021). Uncertainty about the future, including the consequences of the animal's own choices (Fig. 4), is recognized as the main stress mechanism (Peters & al 2017).

To survive and reproduce, animals benefit from efficient strategies to reduce uncertainties about their environment and the results of their actions. Thus, adaptive strategies including the capacity for stress emerged during evolution. However, stress has not received much attention in behavioural ecology, which has hampered the integrated understanding of its evolutionary history, mechanisms and adaptive value.

Stress is often defined as a non-specific physiological, behavioural, or cognitive state as well as the response of the organism to cope with real or anticipated challenges that may disturb its functioning (Koolhaas & al 2011, Schreck & al 2016, Peters & al 2017, Broom & Johnson 2019). While stress is an agentic robustness mechanism in animal evolution (Korte & al 2005, Del Giudice & al 2018, Taborsky & al 2021) and an integral part of life in most species, repeated acute or prolonged stress can be detrimental for health and survival (Broom & Johnson 2019, Dawkins 2019, Kristiansen & al 2020). Stress also involves complex cognitive processes that provide for the animal's ability to predict environmental challenges and choose adaptive behavioural response. Environmental uncertainty and uncontrollability are the most essential causal factors of stress (Koolhaas & al 2011, Peters & al 2017, Del Giudice & al 2018).

The most advanced integral framework for analysing stress is linked with the robustness mechanism of allostasis (Sterling & Eyer 1988, McEwen & Wingfield 2010). In allostasis, the organism predicts its near-future fitness-related needs and adjusts its hormones, physiology, attention and behaviour to prepare for the anticipated future. The nervous system, brain and cognition are crucial components of the organism's architecture for prediction (Peters & al 2017, Schulkin & al 2019). But the hormone system is also very important (McEwen & Wingfield 2010) and provides an adaptive control system (Weidner & al 2020) with very simple mechanisms for predictive adjustments (Jensen & al 2021). The nervous and endocrine systems are of course closely interdependent. The body can be controlled via slow chemical signals if speed is not urgent but global broadcast is necessary, or by fast nervous system signalling to manage rapid response.

Fish show well developed stress responses at the affective, cognitive (Vindas & al 2014, Rey & al 2015, Madaro & al 2016, Golla & al 2020), behavioural (Folkedal & al 2012, White & al 2017, Nilsson & al 2019, Thomson & al 2020), neuroendocrine and immunological levels (Tort 2011, Vindas & al 2014, Madaro & al 2015, Schreck & al 2016, Campbell & al 2021). Stress response in fish involves homologous brain regions with mammals (Silva & al 2015), including shared pain and stress pathways (de Abreu & al 2022). Fish (mostly zebrafish) has become a major animal model for the study of stress and depression in neuropsychiatry (Cachat & al 2011, Fonseka & al 2016, de Abreu & al 2022).

Some studies indicate that stress experiences in early life can help the salmon grow and cope with stress later in life (Vindas & al 2016, Moghadam & al 2017). Madaro & al (2020) frames this as improvements in robustness via allostasis, where repeated challenging experiences improve the individual's ability to cope with the next (Korte & al 2007), for instance with a weaker stress response

that enables the fish to attend to other goals (Fig. 4). Stress management in salmon is thus linked to learning and probably to the high capacity for brain change in fish. In this sense, repeated stress is better than a new kind of stress.

If we assume that fish are able to subjectively experience positive and negative emotional states, they may experience either suffering or pleasure (Mendl & al 2009). Wellbeing is the state of the individual as it copes with its environment through mechanisms such as physiology, behaviour, feelings and pathological responses (Broom 2001). To have capacity for experiencing stress (Wingfield 2013 a,b) and variation in the experience of wellbeing is a tool (Spruijt & al 2001) that result from the agentic evolution of keeping an organism within a window of robust states that are compatible with (future) reproduction (Fernandez-Leon 2011a,b).

While stress is an ancient, evolved capacity, animal welfare is a concept still under rapid evolution in human culture. Good physical health, such as absence of disease, injury, hunger, and thirst, are seen as basic components of animal welfare, such as in The Five Freedoms (Farm Animal Welfare Council 2009), the Five Domains (Mellor & al 2020), and in the Four Principles of EU's Welfare Quality Assessment. Lately, there has also been a strong focus on the species' natural behaviour (e.g. Bracke & Hopster 2006). However, natural behaviour does not in itself imply good welfare nor wellbeing (Dawkins 2023), as is obvious for any field biologist. Rather, we can use the perspective of subjective experience. Then, a fish will be in a state of positive welfare as long as it remains in a window of rewarding (as opposed to punishing) global organismic states. This means that the allostatic controlled hallucinations (Seth 2021) of the fish should contain positive alternatives (Fig. 4). Whether those alternatives existed in the ancestral environment or not is not important for wellbeing. Further, it is helpful to minimize the uncertainty of the sensory systems (Friston & al 2010) and in the predictions, so the fish can avoid stress. In this respect, there may be more wellbeing in regular and familiar events than in many natural events. Further, such robustness in cognition and wellbeing may also facilitate physiological robustness.

Modelling the Atlantic salmon's behaviour

Now we have described both the components of cognition and decision-making in a teleost fish and the life history alternatives that an Atlantic salmon parr needs to navigate. So now we ask if this young fish can be represented by a digital twin.

Differences between proximate-predictive and optimal behaviour

- Make a para on the need for emotion/prediction/experience in salmon behaviour. Natural salmon behaviour also based on environmental complexity-> learning-> brain development.

Models of optimal animal behaviour, such as in life-history theory (REF), game theory (REF) and state-dependent life history theory (REF) are based on maximization of a fitness criterion which is directly or indirectly derived from the Euler-Lotka equation (Lotka 1925). Then, for each time step, the optimal solution is the trade-off between opposing forces (e.g., food, predation risk, temperature) that will contribute maximally to this fitness criterion.

Most of these ultimate (fitness-seeking) approaches can also be said to be predictive. This is most obvious in state-dependent life history theory (REF), where the solution to the optimal decision at time t is found by backwards iterations from a future time horizon. Thus, the optimal behaviour considers future fitness effects of the decision alternatives. The proximate-predictive approach of the prediction machine (REF) or beast machine (REF) does not consider fitness effects of the actions, but emotional effects. In this case, the hormone systems, emotions, sensing, etc, are robustness mechanisms that tries to keep the animal on a trajectory that will lead to high fitness, but this fitness criterion is not represented in the model.

An animal which is placed centrally in the window of favourable states for future reproduction

(Kitano 2004, Fernandez-Leon 2011a, b) can, without pressure, make behavioural considerations that resemble those done in optimization models. Without the need for focussed attention, it can consider a wide range of sensory impressions of relevance to several survival circuits and make a choice that considers two or more of these (Fig. 4, bottom). However, an animal in a less favourable state (Fig. 4, top), for instance because of elevated predation risk, will narrow its attention accordingly. The proximate prediction is short-sighted, but the whole physiological, hormonal, sensoric, and cognitive machinery is fine-tuned in adaptive evolution by those who, with this and earlier body architectures, have produced each new generation.

Parr-smolt dynamics

As shown above (Fig. 2), the evolved life history of Atlantic salmon contains many decisions in the parr phase in the river, either towards sexual maturation in the river, growth followed by smoltification, or anorectic delay during winter (Thorpe & al 1998), with even more possibilities for state-dependent decision reversals (Mobley & al 2021). Thus, this species has evolved to many adapted robust phenotypes that depends on subjective experience and bodily interpretations of how these conditions will unwind into the future. We illustrate this modelling challenge in **Fig. 5**.

For an Atlantic salmon parr, the decision to prepare for the next developmental stage depends on both the physiological state of the parr and the state of the environment. Hence, the young salmon faces both behavioural and developmental decisions that are made from the controlled hallucinations in its brain, that in turn are based on its subjective interpretations of the sensory information. Therefore, the short-term decision-making as a competition between survival circuits to determine the global organismic state needs to be seen within a slower competition over the developmental stage of the organism (Fig. 4). These developmental decisions utilize the broadcast in the brain to combine signals from the external environment and from the body in its prediction of the future, where the evolution of adaptive fine-tuning has been simplified by modularity and degeneracy. This prediction, however, is not behavioural and emotional, but it leads to a hormonal cascade that changes developmental, physiological and behavioural priorities (Fig. 2).

These developmental priorities include gonadal development rather than somatic growth under parr sexual maturation, anorexia under delayed smoltification, or emphasis on somatic growth in the preparation for upcoming smoltification (Fig. 2). The developmental decision (Fig. 5, top) thus impacts behavioural decisions (Fig. 5, bottom) through hormonal regulation. On top of this, the unnaturally generous conditions in intensive aquaculture have greatly increased number of possible decisions (Duncan & al 1999, Pino Martinez & al 2023). This adds confusion, as the far-from-ancestral environment in intensive aquaculture generates mismatches between the proximate cues and the evolved assumptions of correlation to the future. Some parr individuals take evolutionarily rational choices to sexually mature, others take seemingly irrational choices not seen in wild salmon (Duncan & al 1999, Pino Martinez & al 2023). Their future predictions in the evolved developmental programs do not match current artificial conditions.

If a digital salmon model shall guide managers to steer the parr in the wanted trajectory, it must resolve such questions. Then it is not enough to be agentic, it also needs representation of the hormone systems, emotions, sensing and physiology, thus the foundations of subjective experience that a parr uses in its decision-making.

Accounting for subjective experience is important for modelling some aspects of both farmed and wild salmon. Model representation of experience is key to understand the salmon's own perspective of stress and welfare, and it may also be necessary to understand conflicts that occur in salmon aquaculture with respect to ontogenetic stage shifts. While no model can resolve the complexity of a salmon nor of a single-celled organism, there are many possible ways to simplify the natural salmon into a digital model, with different degrees of complexity. However, any digital twin in biology fails if it is not agentic.

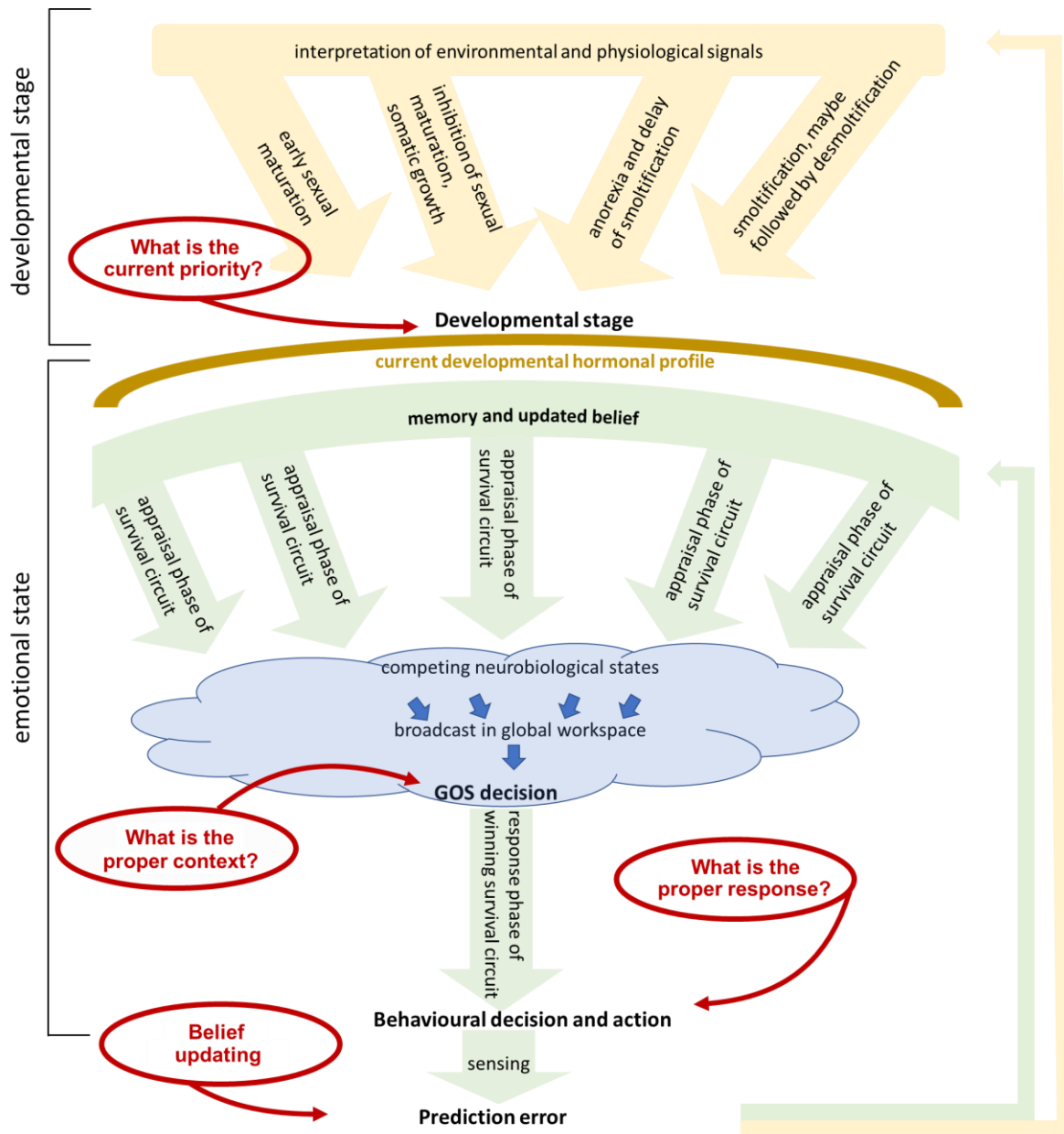


Fig. 5. Parr development and behaviour. Decision-making in the emotional system (bottom half) is embedded in the developmental processes which modify its agentic profile through life-history defining hormone systems (top half). There is a continuity in the subjective internal models (SIMs) of controlled hallucinations in the global workspace (blue). These SIMs are continuously challenged by activated survival circuits, either already present in memory or from prediction error from new sensory information. This leads to a competition between neurobiological states where the winner defines the central emotional state (the global organismic state, GOS) with attention, prediction, and response, which again may lead to learning and updating of the appraisal phase of survival circuits via prediction error. The alternative, with no clearly defined GOS, is also possible (Fig. 4) but not shown here.

The most fundamental description of a salmon is that it is agentic, where agency is Darwinian and has evolved through success in survival and reproduction. Robustness of this agency did early lead to evolution of hormone systems and emotion systems, and to sensing for their support. Learning, and the associated memory also came early, until universal associative learning (Ginsburg & Jablonka 2019) was established. Further, a salmon is what Seth & Tsakiris (2018) calls a 'beast machine' and Bubic & al (2010) a 'prediction machine', where decisions are made out of expectations to the future (Friston & al 2010, Soylu 2016, Budaev & al 2019, Seth 2021), and not only from what has happened in the past. This applies for setting both emotional state and developmental stage, and thus for emotional and hormonal control of the organism. Therefore, the bioenergetic machinery of its digital

twin should be 'by-demand' as opposed to 'feed-forward' which is used in most biological models. In by-demand bioenergetics, the agent has a goal-driven control system that translates situational fitness incentives into allostatic physiological responses that prime the phenotype to fulfil the goal (Weidner & al 2020).

There are many ways to do this. Even the Euler-Lotka equation (Lotka 1925) is agentic (maximizing reproductive rate) and forward-looking (full life cycle that repeats in identical generations), but it is not situational, and the solution is objective and the same for all individuals. We should aim higher and make the goal function dependent on the ecological context and the physiological state of the agent, like salmon do. An excellent pathway to achieve this aim, is through state-dependent life-history theory (Houston & McNamara 1999, Clark & Mangel 2000). This has been used by Thorpe & al (1998) and Mangel & Satterthwaite (2008) to model ontogenetic stage shifts in salmon, and by Weidner & (2020) and Jensen & al (2021) to model hormonal control of growth in fish. Another viable route come from 'state- and prediction-based theory' developed by Railsback & Harvey (2020) for use in simulation models. This is a forward-running agent-based (Grimm & Railsback 2013) approach that captures important aspects of dynamic future planning in the behavioural decisions. This method can then also work under all sorts of spatial and temporal variation. A third option is to use a genetic algorithm (Holland 1975) to evolve the artificial gene pool of a population that adapts to a variable environment (e.g., Giske & al 1998, Huse & Giske 1998, Recknagel 2001, Bond & Kamil 2002, Wood & Ackland 2007). It is important to maintain a diversity of methods, since each method simply the biological organism differently.

We advocate an algorithmic approach to the building of the digital salmon. This approach is effectively a conversion of verbal, graphical or mathematical descriptions of a process or mechanism into a computer algorithm that can run in a simulation. These algorithms are then merged into a digital salmon that also can run in simulations. One example is the algorithmic simulation model of a survival circuit (Giske & al 2013) based on the verbal and graphical model of LeDoux (2000, 2012). We posit that explanation is not sufficient until the different causal parts are combined into an algorithm that can run. Then, the best way to test a theory is to (a) implement it into a computer model and (b) demonstrate that it can work, producing the patterns that agree with the observed biological data. This follows the famous motto set forward by Nobel laureate Richard Feynman: *"What I cannot create I do not understand"* (Way 2017).

Towards the digital salmon, one can stepwise increase the number and quality of process and mechanism algorithms. Using the forward-running agent-based approach (Grimm & Railsback 2013), all aspects discussed so far can be considered: agency, robustness, sensing, development, hormones, emotion, attention, prediction, learning, and more. While a model cannot capture a given animal's private subjective experience, we think that the distribution of subjective experiences in a group of animals can be modelled with some accuracy. Some of this is already done (Giske & al 2013, 2014, Andersen & al 2016, Eliassen & al 2016, Budaev & al 2018), but not for salmon, and not at the precision level needed for nature management or industry.

Since the natural salmon is a product of frequency-dependent selection and local adaptation in the gene pool, its digital twin should also be an array of individual variation. Natural salmon populations have genetic constraints, life-history strategies, sex, personalities and variation in physiological states and experiences. Further, ecological differences between wild populations, and the rapid artificial adaptation in aquaculture, imply that there will be need for several digital salmon populations.

In want of measured parameters, artificial evolution of the digital salmon by a genetic algorithm may be necessary (Huse & Giske 1998, Strand & al 2003, Giske & al 2013). This evolutionary process is much simplified in the simulation laboratory through modularity and degeneracy in the decision architecture (Fig. 3). We can then specify the environment with the types of variation that are likely in the relevant evolutionary and ecological time frame (Giske & al 2014). We think that once artificial evolution in a model like this has arrived at a quasi-stable genetic diversity underlying the behavioural architecture (Giske & al 2014), it can be used (and refined) for models of stress and

welfare, nature management, and aquaculture management. Evolved adaptive parameters should gradually be replaced with formulations based on observations, when possible.

Robustness, stress and welfare in salmon aquaculture

To model the stress and wellbeing of an animal is at least one notch harder than to model its developmental transitions or its short-term behaviour (Budaev & al 2020, Edelblutte & al 2023). Development and behaviour are closely related to agency and fitness, while stress occurs when this relationship is weak or absent. This makes the argument for a high-quality digital twin much stronger but also set some extra constraints on the construction. The digital twin to be used for studying stress and wellbeing should, or must, be a forward-running simulation as in individual-based or agent-based modelling (REF). Only when we have a robust naturally reacting and behaving digital twin, can we expose it to stressful situations.

A digital twin which is evolved in a gene pool in a realistically complex and variable environment (e.g. Giske & al. 2013, 2014) can after this evolution be exposed to presumably stressful situations for digital experiments on stress and wellbeing. Thus, first evolution of a gene pool to a quasi-stable adaptive state, then simulation experiments in presumably stressful situations, such as vaccination, de-lousing or transportation.

However, the applicability goes far beyond stress, as a high-quality digital twin can be used to reduce the need for experimentation on live salmon in aquaculture research. This digital salmon twin will enable researchers to perform high-quality computational experiments on fish growth, health, stress, and mortality, to guide decision-making. This will save costs, time, and use of animals in experiments: *replacement* is the first of ‘the 3Rs’ in the Principles of Humane Experimental Technique (Flecknell 2002). The industry is in transition to semi-closed and recirculating systems, and to ever-larger facilities. It cannot afford to do large-scale experiments with facilities or operations, but computer experiments are cheap, fast, and non-invasive (Flecknell 2002). Thus, they must be reliable. The model can study one-factor change at the time and give predictions of the system based on a range of possible decisions.

As stress evolved to help the animal, why do salmon die of it? A key is that most salmon today find themselves in a situation not anticipated to be dealt with by its evolved robustness mechanisms. The salmon prediction machinery strives to anticipate the future in the many novel circumstances it finds itself, such as transportation, vaccination, and delousing, which they may consider as potentially outside the window that can lead to future reproduction. Further, the near-continuous presence of disease agents requires additional allocation of resources for defence, even for fish that is vaccinated against some of the major risks.

Allostatic regulation generally provides huge cost-efficient fitness benefits. However, allostatic costs can become disproportionately high if (a) there is an excessive prediction error in the estimation of the challenge, (b) the challenge exceeds the capacity or reserves of the organism, or (c) the challenge is chronic and will continue for a long time. Persistent activation of the allostatic mechanism will result in adverse effects on the health and wellbeing of the organism, known as allostatic load. Allostatic overload can be pathological and destructive (McEwen & Wingfield 2003, McEwen & al 2015). The ideas of predictive regulation and allostasis have been developed into a general physiological framework—the reactive scope model—that tries to specify divergent responses of the organism to different predictable and unpredictable challenges (Romero & al 2009). Predictable challenges result in predictive homeostatic responses of the various mediators (hormonal and behavioural), while sudden unpredictable challenges result in reactive homeostatic responses. However, when the challenge elicits a response that exceeds the predictive or reactive homeostatic range, the organism enters into a homeostatic overload or even homeostatic failure condition, which is chronic stress. Finally, if allostatic load is extreme and largely exceeds the capacity of the organism, the best adaptive response is to switch to the emergency life history stage and redirect energy to self-maintenance at the expense of growth, reproduction and all less-essential processes (Wingfield & al

1998). Thus, subjective experience and decision-making (Fig. 4) is a key issue of stress, uncertainty and prediction, as it involves what to expect about the future, how to prepare for it, and what to do about it.

As researchers and managers do not have access to the experience of another organism, stress and wellbeing indicators have focussed on behaviour and other observable phenomena (Stien & al 2020, Barreto & al 2021, Berlinghieri & al 2021). Here we have shown that by working through the organismic architectures that underly experience (Figs 1-5), it is possible to complement these observational methods by approaching the components of salmon cognition through simulation. If not for a particular individual, then for a group. Yet, also for agent-based models that are evolved by a genetic algorithm, analysis of stress will require that stressful events and situations have been encountered sufficiently often during the adaptive evolution simulation. This digital twin approach is compute intensive (Budaev & al 2020), and to develop dynamic state variable models (Houston & McNamara 1999, Clark & Mangel 2000) where the goal function is to bring the fish back into the window of favourable states, may also be a goal.

The most important insight from such models, may be to learn how to prevent stress from starting or escalating. This can be done by simulating a procedure or a situation and thus investigate the likelihood of stress emergence. Stress can emerge from several of the connections in Fig. 4. From left to right they are

Subjective internal model (SIM):

- Uncertainty in the interpretation of new types of sensory signals into the SIMs: what these signals represent, and what future consequence they may have for the salmon.
- Fish brains can change both due to new experiences and lack of experiences, thus fish can learn to cope with stressors.

Global organismic state (GOS):

- Simultaneous and lasting high activation of several survival circuits, leading to competition between several pressing needs among the neurobiological states, and problems in focussing on a GOS.

Re-entrant competition:

- All the available competing actions have bleak (or worse) future prospects in the re-entrant estimations of expected emotional states.
- Persistent activation of a costly GOS will result in allostatic load, with adverse effects on the health and wellbeing of the organism. Even higher activation can lead to potentially pathological and destructive allostatic overload.
- When the challenge elicits a response that the organism does not have resources to maintain, the organism enters a homeostatic overload or even homeostatic failure condition, which is chronic stress. If allostatic load is extreme and largely exceeds the capacity of the organism, the best adaptive robustness response is to switch to the emergency life history stage and redirect energy to self-maintenance.

Decision and behaviour:

- An activated GOS can lead to aggressive behaviour, which can be stressful for other fish, particularly smaller or subdominant individuals.

Sensing:

- Sensing after the behaviour is executed finds the animal in a poorer situation than expected, which means that the individual's world view is wrong.

Prediction and learning:

- Mismatch between expectations from the SIMs and the following sensing can lead to disappointment, and from there to aggression or depression.

- Frequent mismatch between the sensing and expectations from the SIMs after previous prediction error and learning increases the informational free energy in the sensory system and reduces the reliability of the controlled hallucinations.

To reduce stress-related mortality in salmon aquaculture, it may be possible to combine the learning capacity and the prediction machine (Fig. 4) to train salmon to expect an upcoming stressful event, such as delousing, vaccination, transportation etc. This training should be done with specific sensory signals not else observed in the facility (sound, light, etc). Thus, the fish can after learning enter the most relevant GOS and activate the most relevant internal resources (Soylu 2016), and, also through learning, it may know that it does not need to panic: it will survive and recover.

Discussion (more a collection of points than a flowing text)

Salmon aquaculture, like other intensive animal industries, has removed the farmed animal from its ancestral environment. Wild Atlantic salmon populations also live in anthropogenically changed environments. In these new situations, evolved robustness mechanisms (Kitano 2004, Fernandez-Leon 2011a,b) will still work to keep the animal inside the evolved window of states and stage shifts that may lead to reproduction (Thorpe & al 1998, Mangel & Satterthwaite 2008). The industries as well as nature managers will benefit from acknowledging these mechanisms and minimize uncertainty in the sensory environments (Friston & al 2010) that reduces stress and facilitates the wanted survival, growth and development.

A key to understand what it is for a salmon to be a salmon, is to understand its capacity for experience, as it has evolved during deep and recent phylogeny and develops during ontogeny. This perspective is again key to understand behaviour, physiology, development, stress and wellbeing of Atlantic salmon in natural and artificial environments.

The brain is a highly interconnected network of neurons and other cells, with ongoing efforts to recreate its entire complexity (Bassett & Sporns 2017, Einevoll & al 2019). In this tradition, artificial neural networks (ANN) have been used to mimic decision-making in animals (e.g. Mangel 1990, Huse & Giske 1998, Recknagel 2001, REFS). ANN, and the wider concept of artificial intelligence and machine learning may well turn out to be important tools in aquaculture management. We have followed another level of analysis: a growing understanding of bodily and cognitive systems such as hormones, sensing, emotions, learning, memory, prediction and decision opens for a focus on these phenomena and their major connections. We think the two approaches of mechanisms and machine learning may complement each other for salmon aquaculture and in wildlife management in the near future (Christin & al 2019).

Subjective experience is a first-person/animal phenomenon, which one cannot access for anybody else than oneself. Even if we cannot get inside the mind of a salmon and gain access to its own perspective, we can acknowledge it and even use its functional components in simulations of how it is to be a salmon. This is a novel approach, as many of the perspectives we have discussed in this paper have emerged or been refined in the last decade.

As we in the paper have journeyed in cognitive complexity from early life forms to teleost fish, we have also come close to answer Why?, What? and How? of basic consciousness, although much larger texts are needed (e.g., Ginsburg & Jablonka 2019). The 'why' comes out of agency and robustness and emerged to the first-person perspective and the needs of this self; the 'what' is a unified subjective experience in the brain; and the 'how' is by global workspace in working memory where activated emotions meet and learning follows from prediction errors, but another good answer is through the adaptive evolution of modular and degenerate cognitive architectures.

Brains have evolved to monitor the body and its environment and prepare the body for its future (Schulkin 2003, Sterling 2012, Glimcher 2016, Barrett 2017, 2020, Seth 2021). To do this, brains forecast the bodily sensations and emotions that an animal may experience if it carries out an action (Glimcher 2016, Barrett 2017, Crump & al 2020, Mendl & Paul 2020). Neuroscientists have therefore

started thinking of the brain as an evolved prediction machine (Bubic & al 2010, Clark 2015, Seth & Friston 2016, Seth & Tsakiris 2018). We think this perspective is useful for understanding Atlantic salmon, both for its development, growth and survival, and for its stress and wellbeing. We have therefore laid out the components needed for building a digital salmon with a prediction machine. Then one can model the fundamental mechanisms ('produce the phenotype') rather than deduce the phenotype from optimization.

The gene pool's adaptive evolution, combined with the individual's current future expectations, are key both for hormonal and neural control of the organism. The dynamic control of agentic priorities, including preparation for the expected future, is carried out through the hormone systems, which are genetically adapted and triggered by interoceptive sensing of the body and the exteroceptive sensing of the environment. The salmon's behaviour is elicited from hormone-influenced emotionally controlled hallucinations (Seth 2021) that link its experiences with its agency (Thorpe & al 1998, Mangel & Satterthwaite 2008). Some challenges in intensive aquaculture stem from construction of combinations of sensory signals that confuse the salmon to make wrong life-history decisions, while other signal combinations into the prediction machine lead to stress.

Theories of animal behaviour are often about the individuals' choices, such as diet selection, habitat selection and mate selection. Already in 1883, George John Romanes commented that choices are based on experienced feelings. Ultimate models based on fitness-maximization (Lotka 1925, Clark & Mangel 2000, McNamara & Leimar 2020) are excellent tools for understanding how agency leads to life histories and optimal behaviour, but when we aim to understand what has happened or will likely happen at the finer time scale or in situations that are uncommon in the ancestral environment, a proximate approach may capture the subjective experience of an animal and its estimations of the near-future (Edelblutte & al 2023).

Finally, we will point out that the five figures in this paper are also models. They are thinking tools for what it is to be a salmon or a quite different animal in the ocean, in a forest or in captivity.

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