REVIEWS IN Aquaculture

Reviews in Aquaculture, 1–17 doi: 10.1111/raq.12501

Fish welfare in offshore salmon aquaculture

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Received 25 December 2019; accepted 18 August 2020.

Abstract

To accommodate further growth in the Atlantic salmon aquaculture industry, new production sites may well be established at more exposed locations along the coast or even offshore. Here, fish will encounter strong currents and powerful waves, which are avoided at traditional sheltered locations. Exposed locations offer several advantages and necessitate new technological advancements. However, the most crucial question is whether Atlantic salmon are able to thrive in these more extreme environments. In this review, we describe how strong water currents affect the physiology, behaviour and ultimately the welfare of the fish. If ambient current speeds exceed swimming capacities, fish become fatigued and get stuck on the cage wall leading to unacceptable welfare. The swimming capacity will depend on both the magnitude and duration of the current speeds encountered. Moreover, several environmental and biological factors modulate swimming capabilities, where temperature, body size and health status are particularly important to consider. A series of empirical studies are subsequently used to formulate welfare guidelines with regard to biological limits in exposed aquaculture. In addition, owing to the growing popularity of cleaner fish in salmon aquaculture, we also evaluate their usefulness at exposed sites. Overall, Atlantic salmon is a powerful sustained swimmer, and based on available site surveys of ocean currents, we conclude that the prospects for responsible farming at exposed sites looks promising. However, cleaner fish species such as lumpfish and ballan wrasse are poor swimmers and are therefore not recommended for deployment at exposed sites.

Key words: Atlantic salmon Salmo salar, Ballan wrasse Labrus bergylta, critical swimming speed, exposed aquaculture, Lumpfish Cyclopterus lumpus, water currents, waves.

Introduction

In the latter half of the twentieth century, global aquaculture production increased dramatically from >1 million tonnes in 1950 to 16 million tonnes in 1990 and 80 million tonnes in 2017 (FAO 2011; FAO, 2019a). In contrast to this, global fisheries capture stagnated in the late 1980s owing to overexploitation of wild stocks and has stayed at a similar level since. As a consequence of these opposing growth trends, the year 2014 marked a significant turning point where more than half of the fish and shellfish consumed by humans came from aquaculture (FAO 2016). Since commercial fisheries are exploiting wild stocks to and beyond their limit, while the human population is growing more rapidly than ever, aquaculture and the continuous development towards sustainable practices will only become more important in the future.

One of the most successful species in modern aquaculture is the Atlantic salmon *Salmo salar* (L. 1758). It is easy to handle, grows fast, has a high commercial market value and is flexible in adapting to various farm environments (Heen *et al*. 1993). Furthermore, the commercial fishery of this species is almost non-existent owing to historic overfishing and extensive habitat damage (Heen *et al*. 1993; Knapp *et al*. 2007). After smoltification, on-growing Atlantic salmon are farmed in sea cages along the coast in Northern Europe, North America, Chile and Tasmania. Global harvest has steadily increased from 0.2 million tonnes in 1990 and remained above 2 million tonnes since 2012 (FAO, 2019b).

Salmon farms have traditionally been located within the fjords and along the coastline sheltered from extreme weather conditions. However, various environmental concerns are now making it difficult to expand production further. For instance, in Norway, the largest producer of Atlantic salmon, new farming permissions are restricted for traditional sites as long as key issues with negative environmental impacts are not solved or managed better. Hence, to meet the ambitions of continuous growth in the salmon industry, new alternative aquaculture sites are needed.

One possible solution to accommodate further growth is to move salmon sea cages to more exposed locations (Bjelland *et al.* 2015; Gentry *et al.* 2017). Exposed locations do not currently have a strict definition, but are generally understood as farm sites located more remotely off the coast and even offshore. These sites are characterized by occasionally experiencing rough weather conditions, strong water currents and powerful waves. In addition, some inshore areas are also characterized by periods of strong water currents, for instance owing to tidal forces encountering obstacles and narrow passages, and can therefore also be categorized as exposed locations.

The potential advantages with exposed aquaculture are many and include higher water quality owing to better flow conditions to remove and dilute waste products, stable vertical temperature, oxygen and salinity conditions within the sea cage to increase production capacity, and less interferences with other human activities in coastal areas (Holmer 2010; Bjelland *et al.* 2015). Presumably, risks of pathogen transmission between sites will also be reduced due to greater hydrographic distances.

Moving salmon production to more exposed locations also creates many new challenges associated with technology, infrastructure and work routines due to the increased risks of extreme weather conditions combined with geographical remoteness (Loverich & Gace 1997; Fredheim & Langan 2009; Bjelland *et al* 2015). As an example, farm structures need to be able to endure stormy weather and sea cages need to be enforced to avoid severe net deformations during periods with strong current conditions (Lader *et al.* 2008; Klebert *et al.* 2015; Gansel *et al.* 2018). To overcome these challenges, the salmon industry is investing extensively in research and developing technology adapted for aquaculture in exposed locations. However, the most important factor to consider when evaluating the feasibility of moving salmon production to exposed locations is whether the fish actually will be able to thrive and grow in these new and more extreme environments. In other words, we need to ensure that fish can be farmed in a responsible way so that fish welfare does not become compromised.

Similar to other vertebrates, fish are sentient beings with high cognitive capabilities (Branson 2008; Noble *et al.,* 2018). In Norway and most other Western countries, fish and other vertebrate species are therefore protected by animal welfare legislations (e.g. Webster 2001; Norwegian Ministry of Agriculture & Food, 2009). Some degree of suffering is inevitable in any production cycle and it can be difficult to agree upon what should be considered acceptable animal welfare in aquaculture. Furthermore, owing to increased consumer awareness, fish welfare in conjunction with environmental sustainability of salmon aquaculture is frequently discussed by the public. In recent years, this has led to more focus on fish welfare in the salmon industry (Noble *et al.,* 2018). However, prioritizing fish welfare should also promote the production potential since a healthy fish reared in an optimal environment will have better appetite and growth, and is more likely to survive a full production cycle compared to one that is stressed, sick or wounded.

When new farm concepts, new treatment methods and other new technologies are being implemented in aquaculture, it is imperative to investigate potential risks for poor fish welfare. This is especially true for exposed aquaculture operations since these represent a new frontier in fish farming. Moreover, standard routine operations at sheltered locations such as feeding, transportation and parasite treatments will be more complicated at exposed locations and likely impose additional welfare challenges. However, the most pressing concern with moving production to more exposed sites is how periods with strong water currents and powerful waves impact the fish.

The purpose of this review is to describe how environmental conditions that may be encountered at offshore aquaculture sites affect the physiology, behaviour and ultimately the welfare of Atlantic salmon. Our main focus will be on the effects of water currents of varying magnitudes and durations, and how to define water current thresholds based on the expected impact on fish welfare. Moreover, since deployment of cleaner fish in salmon cages to control sea lice infestations has become a widespread strategy (Powell *et al.,* 2017), we will also evaluate their suitability at exposed sites. We will then discuss site surveys of potential aquaculture sites and evaluate exposed conditions from a fish welfare perspective. Finally, we will briefly evaluate the impact of waves and highlight possible technological solutions to reduce risks of poor welfare.

Swimming behaviour in the sea cage environment

Inside net cages at sheltered locations, Atlantic salmon will normally swim in a circular pattern forming schools (Johansson *et al.,* 2007). This behaviour is thought to be a result of individual fish actively avoiding collisions with each other and the cage wall (Føre *et al.* 2009). In these low water currents, the fish can choose their own swimming speeds independent of the environment, which is termed the voluntary or preferred swimming speed. The observed voluntary swimming speeds of Atlantic salmon in sea cages generally vary from 0.3 to 0.9 body lengths s^{-1}, but can be as high as 2.8 body lengths s^{-1} in some conditions

(Sutterlin *et al.* 1979; Juell 1995; Dempster *et al.* 2009; Oppedal *et al.* 2019). These variations can be ascribed to a range of factors such as size differences, as smaller fish tend to swim at higher relative swimming speeds (Remen *et al.* 2016a; Hvas *et al.* 2018a). Fish may also swim faster to maintain buoyancy prior to refilling of the swim bladder (Glaropolous *et al.* 2019), while fish tends to swim slower at night (Oppedal *et al.* 2001; Hansen *et al.* 2017).

The constant swimming of Atlantic salmon in sea cages has been associated with the migratory nature of this species (Sutterlin *et al.* 1979). In open ocean studies, the observed migratory cruising speeds of wild salmonids tend to be around 1 body lengths s^{-1} (Weihs 1973; Drenner *et al.* 2012). Theoretically, the optimal migratory cruising speed will be when the gross cost of transport (CoT) is minimized, as this will allow the fish to travel the greatest distance while using the least amount of energy. By using swim tunnel respirometers, the CoT at a range of swimming speeds can be measured systematically (Brett 1964), and for Atlantic salmon post-smolts, the minimum CoT is generally around 1.5 body lengths s^{-1} (Hvas & Oppedal 2017; Hvas *et al.* 2017a). Hence, the migratory swimming speeds of salmonids seem to be within a similar range or perhaps slightly lower than their minimum CoT.

When moving away from sheltered sites, water current velocities through sea cages may occasionally exceed the preferred swimming speed of Atlantic salmon. How this affects the group dynamics and swimming behaviours have been observed at an exposed location at the Faroe Islands (Johansson *et al.* 2014) and experimentally assessed with large-scale push cages in a Norwegian fjord (Hvas *et al.* 2017b). In both studies, it was found that when the ambient current speed exceeded the preferred swimming speed of the fish, circular cruising behaviour was changed to standing on the current with no forward movement, swimming at a speed dictated by the environment. Hence, as the current speed increased, the group structure gradually changed from only circular swimming to a mixture of circular swimming with some individuals standing on the current, and eventually at higher current speeds, all the fish would stand on the current maintaining a fixed position (Johansson *et al.* 2014; Hvas *et al.* 2017b; Fig. 1).

It can be argued that conditions that force the fish to swim at speeds dictated by the environment rather than at their preferred cruising speed provide poor welfare since it violates the freedom to express normal behaviour (Brambell 1965; Norwegian Ministry of Agriculture & Food, 2009). The magnitude of this concern will depend on the durations of strong current exposure, where persistent chronic conditions lasting days or even weeks could be considered unacceptable from a welfare perspective. However, shorter periods (hours) with current conditions above the preferred swimming speed would likely have negligible effects on fish welfare. For instance, the disruption of circular group swimming observed at an exposed location at the Faroe Islands was fairly brief and, moreover, demonstrated a high flexibility of the fish to adapt adequately to sudden changes in the sea cage environment (Johansson *et al.* 2014). Brief swim challenges and variation in the farm environment could even be considered good welfare, as it provides a form of enrichment for the fish.

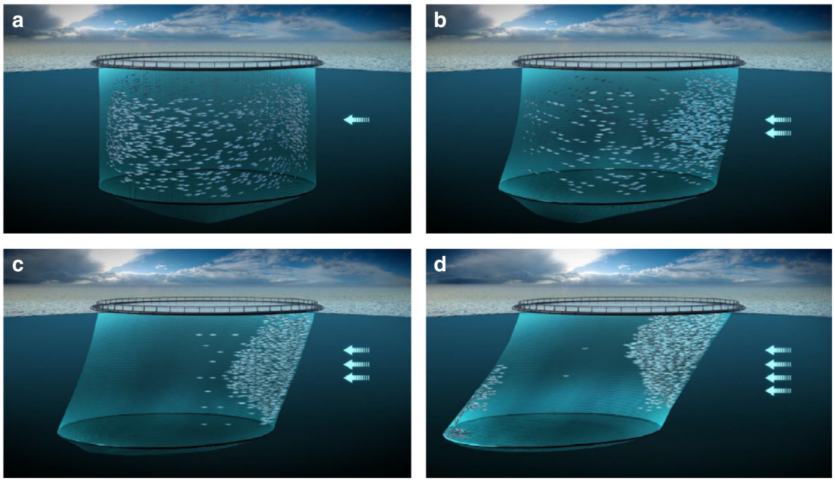

Figure 1 Atlantic salmon group structure in sea cages in response to increasing current velocities. At low currents, the fish adopt a circular structure swimming at their preferred speed (a). Once currents start to exceed the preferred speed of some of the fish, they will abolish circular swimming and stand on the current instead (b). At higher current speeds, all fish will eventually be standing on the current swimming at speeds dictated by the environment (c). When the current speed exceeds the swimming capacity of individual fish, they will become fatigued and get pushed back onto the downstream wall of the net (d).

If current speeds increase further, the swimming gait of the fish will change from being mostly steady to a greater reliance on burst and glide swimming. This transition in swimming behaviour marks the recruitment of fast white muscle fibres fuelled by anaerobic metabolism (Bone *et al.* 1978; Wilson & Egginton 1994). Remaining group patterns will become disorganized, and owing to the anaerobic component, the fish will become exhausted if maintained for too long in such conditions (see Swimming capacity).

Growth in relation to water currents

Ensuring high growth rates and efficient feed conversion rates are crucial for any aquaculture practice. To achieve this, it is necessary to provide an adequate environment for the fish. For instance, moderate hypoxia or suboptimal water temperatures will reduce the appetite and growth of Atlantic salmon (Remen *et al.* 2016b; Sambraus *et al.* 2018).

Persisting strong water currents will most likely also affect growth performance. When salmonids are swimming at high speeds, the blood flow is redistributed in systemic circulation to favour working muscles while blood flow to the liver, spleen and stomach is decreased (Randall & Daxboeck 1982). Continuous fast swimming is therefore likely to inhibit digestion and growth (Farrell *et al.* 2001). Moreover, if a substantial amount of energy is required to fuel increased swimming requirements in exposed sea cages, feed conversion rates should go down as less energy from the feed will be diverted towards growth.

To assess the effect of constant water currents on growth performance, a recent study maintained Atlantic salmon post-smolts in raceways at various swimming speeds for 6 weeks (Solstorm *et al.* 2015). Here, current speeds of 1.5 body lengths s^{-1} caused a significant reduction in growth compared to lower swimming speeds, although the reduction was modest with only a 5% lower weight gain. Similar results have also been reported for adult rainbow trout *Oncorhynchus mykiss* (Walbaum 1792), where fish maintained above 1 body lengths s^{-1} showed reduced growth compared to fish maintained at lower speeds (Farrell *et al.* 1991). As would be expected, chronic exposure to water currents above a certain threshold will have a negative effect on growth and feed conversion rates owing to the increased energetic demand from constant swimming. However, it should be noted that moderate aerobic swimming also has been reported to stimulate growth and improve feed conversion under experimental conditions in various aquaculture species (Davison & Herbert 2013; Palstra *et al.* 2015). However, a recent review on this topic concluded that it remains to be explicitly demonstrated whether swimming exercise actually promote growth, except through behavioural modifications (McKenzie *et al.* 2020). Hence, considering the voluntary swimming behaviour of Atlantic salmon in net cages where they spend the majority of their time actively cruising or balancing on the current regardless of environmental conditions (e.g. Oppedal *et al.* 2011; Hvas *et al.* 2017b), any benefits associated with moderate aerobic swimming exercises are likely obtained by default in this species under most production regimes.

Other positive effects may be gained from maintaining Atlantic salmon at elevated swimming speeds. For instance, growth during moderate current conditions is associated with a greater increase in muscle mass and protein content, whereas growth in low current conditions is associated with a greater degree of lipid deposition (Houlihan & Laurent 1987; Solstorm *et al.* 2015). Atlantic salmon reared under rougher conditions with frequent exercise challenges could therefore, in theory, yield a leaner and perhaps a higher quality product in some markets. In addition, a recurring issue in salmonid aquaculture is precocious sexual maturation, since resources then are directed towards gonad development at the expense of somatic growth which leads to a poorer product and economic losses (Good & Davidson 2016. Interestingly, increased swimming requirements have been shown to inhibit maturation by focusing energetic strategies on migration rather than sexual development (Palstra *et al.* 2010; Waldrop *et al.* 2018). Hence, this may provide an additional benefit when producing Atlantic salmon in more exposed conditions. Increased exercise requirements in the sea cage environment may also provide health benefits by improving the cardiovascular system. As such, effects of exercise in salmonids includes larger ventricles, increased cardiac output and improved maximum metabolic rates and swimming capacities (Pearson *et al*, 1990; Farrell *et al.* 1990, 1991; Gallaugher *et al.* 2001; McKenzie *et al.* 2012). Consequently, the fish will then have a larger aerobic capacity at their disposal, which should render them more robust in coping with other stressors encountered in aquaculture settings while still maintaining good appetite and growth. For instance, a higher aerobic capacity may increase recovery rates from acute stressors (Milligan *et al.* 2000) and improve disease resistance (Castro *et al.* 2011).

Swimming capacity

While higher water currents in exposed sea cages may reduce growth performance (Solstorm *et al.* 2015) and compromise fish welfare by restricting voluntary behaviours (Johansson *et al.* 2014), a greater concern is if the ambient current speeds become so strong that it exceeds the swimming capacity of the fish. If this occurs, the fish will eventually reach physiological fatigue where locomotory control is lost, forcing them to be stuck on the rear cage wall. Getting stuck on the rear wall is likely to result in significant collision damage and injury. Moreover, physiological fatigue is associated with a massive metabolic acidosis caused by lactate build-up from anaerobic metabolism, high cortisol levels induced by the acute stress response, depletion of glycogen stores and a large disturbance in osmotic and ionic balance between intra- and extracellular body compartments (Wood 1991; Kieffer 2000). Hyperactivity and fatigue may even kill salmonids, presumably due to the severity of the associated acid-base disturbance (Black 1958; Wood *et al.* 1983). Hence, having Atlantic salmon fatiguing in exposed sea cages will result in unacceptable animal welfare. Generally, fish should never be farmed in an environment where ambient current conditions exceed their swimming capacity.

Swimming capacities of fish can be assessed in different ways. The most widely used concept in the literature of fish physiology is the critical swimming speed (U_{crit}) (Brett 1964; Plaut 2001). The U_{crit} is a measurement of the maximum prolonged swimming speed and is obtained in laboratory trials by using swim tunnel systems, which are specially designed ‘treadmills’ for fish. This method allows researchers to systematically quantify what current conditions fish are able to handle, while also obtaining important supplementary measurements such as metabolic rates and blood parameters (Hvas & Oppedal 2019a).

For aquaculture management, the nature of current conditions at farm sites must be evaluated to assess the relevance of various measurements of swimming performance. Specifically, the magnitude, duration and frequency of strong current events are all important to consider when defining the swimming limits of the fish. For this purpose, the U_{crit} represents the swimming capacity at an acute time scale (minutes), as longer durations result in fatigue since anaerobic metabolism will be required to endure water current conditions of this magnitude. As a welfare indicator, the U_{crit} thereby provides a suitable starting point when establishing guidelines for exposed aquaculture since peak current speeds above U_{crit} will be unacceptable (Remen *et al.* 2016a).

Most often, current conditions through sea cages are unlikely to mimic the incremental and systematic nature of a standard U_{crit} test protocol, and more importantly, strong current conditions may persist for much longer periods than a typical U_{crit} test interval (15–30 min). Measurements of U_{crit} may therefore provide little insight into the swimming capacities of fish that are forced to swim for several hours. It is therefore also relevant to define the sustained swimming capacity of Atlantic salmon. The sustained swimming capacity is here understood as the maximum swimming speed that can be maintained solely through aerobic metabolism and therefore do not result in fatigue (Beamish 1978). Physiologically, this means that propulsion is achieved strictly through recruitment of the thin layer of slow red muscle fibres on the lateral sides, while fast white muscle fibres remain inactive (Hudson 1973; Wilson & Egginton 1994). Furthermore, homeostasis should be maintained with no accumulation of lactate, depletion of glycogen stores or other respiratory or osmotic disturbances.

In general, salmonids are athletic fish and have high sustained swimming capacities, reflecting their migratory nature. In traditional U_{crit} tests, aerobic metabolism predominates at swimming speeds of up to 70–90% of the U_{crit} (Jones 1982; Burgetz *et al.* 1998; Beddow & McKinley 1999). In contrast, other groups of fish such as cyprinids may only sustain 30–50% of their U_{crit} aerobically (Jones 1982). To infer the sustained swimming capacity of fish, most studies have used indirect methods such as measurements of intramuscular lactate production (Burgetz *et al.* 1998) and electromyography (Wilson & Egginton 1994; Beddow & McKinley 1999) to establish the point of white muscle fibre recruitment in short term U_{crit} test protocols. Recently, a more practical assessment of the sustained swimming capacity of Atlantic salmon post-smolts was made, where fish were allowed to swim for up to 4 h at sub-U_{crit} speeds (Hvas & Oppedal 2017). Here, it was demonstrated that Atlantic salmon are able to sustain at least 80% of their U_{crit} for 4 h, corroborating previous indirect assessments (Hvas & Oppedal 2017). Hence, a threshold of 80% U_{crit} may be used as a welfare indicator to represent the estimated sustained swimming capacity with regards to strong current events at exposed aquaculture sites.

The cause of fatigue in U_{crit} tests is the inability to supply sufficient amount of metabolites within a short amount of time. However, strictly aerobically fuelled swimming may also eventually result in fatigue owing to depletion of metabolite supply. Similar to marathon runners, fish may therefore eventually ‘hit the wall’ even though they are swimming within their aerobic limit. As such, the sustained swimming capacity of Atlantic salmon described here is only a welfare guideline for strong current conditions of a limited duration (hours). Lower threshold values should therefore be used for chronic current conditions that persists for days or even weeks.

For moderate to strong current conditions on longer time scales, a suitable welfare indicator is the preferred swimming speed of Atlantic salmon. When the preferred swimming speed is exceeded, the behavioural freedom is compromised and excess energy will be used on continuous swimming that eventually may reduce growth performance (see Swimming behaviour in the sea cage environment and Growth in relation to water current). Hence, three different swimming capacity thresholds have now been identified (U_{crit}, sustained, preferred), which provide a framework to establish welfare guidelines for exposed aquaculture under different current exposure regimes (summarized in Table 1).

Table 1 Different swimming capacities as welfare indicators in exposed aquaculture

Welfare indicator	Speed	Duration	Consequence
U_{crit}	Extreme	Minutes	Fatigue, injuries, death
Sustained	High	Hours	Fatigue, injuries, death
Preferred	Moderate	Days/ Weeks	Involuntary behaviour, reduced growth

The critical swimming speed (U_{crit}) is the maximum acute limit. Sustained swimming is the maximum speed that does not result in immediate fatigue and can be maintained for several hours. The preferred or voluntary swimming speed in sea cages resembles the optimum cost of transport of migrating salmonids. The relevance of each welfare indicator depends on the magnitude and duration of current speeds in the farm environment. The consequences of exceeding these limits are summarized in the table.

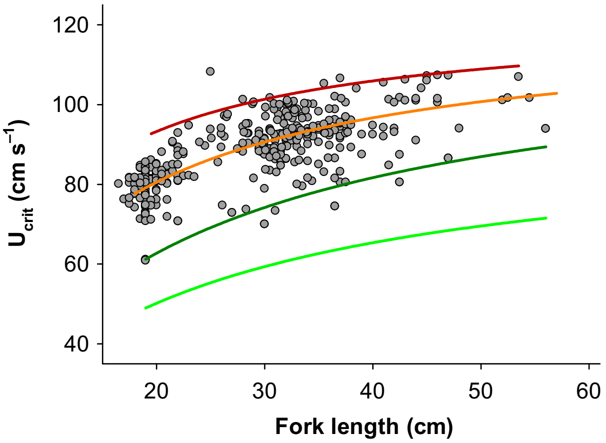

Figure 2 How welfare guidelines based on the critical swimming speed (U_{crit}) can be derived. The figure consists of a scatterplot that shows the U_{crit} of individual Atlantic salmon measured at 13–14°C versus their fork length (grey dots). These data were gathered from previous studies that all used the same swim tunnel setup (Remen *et al.* 2016a; Hvas & Oppedal 2017; Hvas *et al.* 2017a, 2017c, 2018b). On top of this plot, first order inverse regression lines are shown that represents the average U_{crit} (orange), the best and worst swimmers (red and green, respectively), and the 80% U_{crit} level of the worst swimmers as a conservative estimate of the sustained swimming capacity (light green). — Best swimmers; — Average U_{crit}; — Worst swimmers; — 80% U_{crit} worst swimmers

Swimming performance of Atlantic salmon in relation to biological and environmental factors

Since the maximum swimming capacity of fish depends on both the magnitude and duration of the swim challenge encountered, it would be overly simplistic to provide one static threshold value for maximum allowable current speeds in exposed sea cages. Formulating welfare guidelines regarding acceptable current conditions becomes even more complex when considering the range of biological and environmental factors that are known to modulate swimming capabilities.

One major factor in determining the maximum swimming speed of fish is their size. Swimming speeds can either be expressed on a relative scale as body lengths s^{-1} or on absolute scales such as metre s^{-1}. Smaller fish are generally able to attain higher relative swimming speeds while larger fish are able to swim faster in absolute units (Brett 1965; Hvas *et al.* 2018a). Most often, swimming performances of fish are reported in relative units, but since our purpose is to describe the impacts of current speeds in the ambient sea cage environment, it is here more appropriate to focus on absolute units.

Atlantic salmon post-smolts are typically transferred to sea cages when they have a fork length of 20–25 cm and will remain there until they have reached harvest size (65–80 cm). However, owing to larger fish having a higher absolute swimming capacity, a valid strategy for exposed aquaculture could be to postpone the sea cage phase since smaller fish will be less robust to handle rougher conditions. The U_{crit} of individual Atlantic salmon at a range of sizes representing the sea cage growth phase is shown in Figure 2. On average, the U_{crit} of smaller Atlantic salmon of 20 cm in fork length is ~75 cm s^{-1}, while larger fish of 40 cm in fork length have a U_{crit} of ~95 cm s^{-1}. However, it is evident on Figure 2 that there are substantial individual variations in swimming performance where some fish are good swimmers and others are poor swimmers. This variation affects how specific welfare guidelines should be derived which is discussed further in Defining welfare guidelines for water currents.

Another major factor in determining swimming abilities of fish is water temperature. Fish are poikilothermic animals meaning that their body temperature is similar to the temperature in the environment, and since temperature affects all physiological functions, different species have adapted a thermal niche in which they can function optimally (Scholander *et al.* 1953; Fry 1971; Beamish 1981). The combined effect of temperature and size on U_{crit} is summarized in Figure 3. The swimming capacity of Atlantic salmon is highest between 13 and 18°C. At either thermal extreme, the U_{crit} decreases, and this decrease is most notable at very low temperatures (Hvas *et al.* 2017a). Stormy weather conditions in winter and early spring when water temperatures are lowest will therefore pose a greater risk in exposed aquaculture. However, higher temperatures will overall be of greater concern as Atlantic salmon are unable to survive longer periods at 23°C (Hvas *et al.* 2017a), while appetite and growth already start to decline at 18–19°C (Handeland *et al.* 2008; Kullgren *et al.* 2013). Note that all the data previously shown in Figure 2 were obtained at 13–14°C, which is within the optimal range for

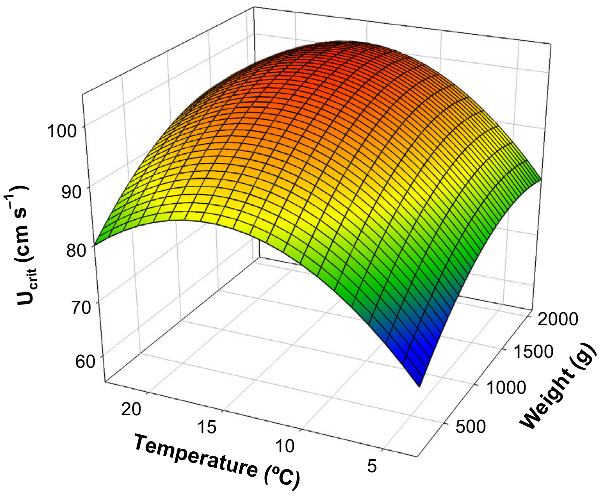

Figure 3 The critical swimming speed (U_{crit}) of Atlantic salmon at different sizes and temperatures. Larger fish are able to swim faster while both thermal extremes reduce swimming performance. The figure is based on a dynamic paraboloid fit ($f = 52.2020 + 0.0203 \times x + 4.0963 \times y - 6.1904 \times 10^{-6} \times x^2 - 0.1331 \times y^2$, $R^2 = 0.5156$) using 390 U_{crit} measurements from novel fish. Data were gathered from previous studies that all used the same swim tunnel setup (Remen *et al.* 2016a; Hvas & Oppedal 2017; Hvas *et al.* 2017a, 2017c).

growth of Atlantic salmon post-smolts (Handeland *et al.* 2008).

Farmed Atlantic salmon may suffer from a series of health issues, and depending on the severity, swimming capabilities are likely to be negatively affected. So far, the swimming performance of Atlantic salmon infested with the salmon lice (*Lepeophtheirus salmonis*) and the gill amoeba *Paramoeba perurans* have been studied (Bui *et al.* 2016; Hvas *et al.* 2017c). Pathophysiological effects of other commonly encountered diseases, parasites and other health issues in Atlantic salmon aquaculture have not yet been documented.

Controlling salmon lice (*Lepeophtheirus salmonis*) infestations remain the biggest challenge in Atlantic salmon aquaculture (Costello 2006; Brooker *et al.* 2018). This issue will most certainly also affect offshore farm sites. Interestingly, the impact of various life stages of the salmon lice had negligible effects on the U_{crit} of small Atlantic salmon post-smolts, but this was likely because only low to moderate infestation levels were assessed (Bui *et al.* 2016). Salmon lice attach to the skin of the fish where they feed on mucus and blood (Costello 2006). Hence, they do not interfere with functions directly involved with swimming, and any potential impacts on more severely affected fish will therefore likely be caused by other factors such as increased cost of osmoregulation and anaemia.

The amoeba *P. perurans* is the aetiological agent of amoebic gill disease which has become a growing problem in recent years globally (Oldham *et al.* 2016). In contrast to salmon lice, *P. perurans* was found to cause a substantial reduction in the swimming capacity of Atlantic salmon (Hvas *et al.* 2017c). In this study, fish with pronounced amoebic gill disease had a U_{crit} of 77.7 cm s^{-1} while healthy fish had a U_{crit} of 93.3 cm s^{-1}, where the size of both groups was ~340 g in weight and ~31.5 cm in fork length. Differences in swimming performance could be explained by a drastic reduction in maximum oxygen uptake rates caused by reduced functional surface areas of the gills in infected fish (Hvas *et al.* 2017c).

The impact on swimming capabilities of other diseases and parasites will depend on their pathological nature. For instance, any disease that affects components of the cardiorespiratory system such as heart function, haematology and gas exchange is likely to assert a direct negative effect on swimming capabilities. Negative effects would also be expected when the locomotory system is involved, whether by reduced muscle functionality, vertebrae deformities or damages to fins. In the case of diseases and parasites that target other organs and tissues not directly related to swimming, such as the salmon lice (Bui *et al.* 2016), negative effects on swimming abilities will most likely first be observed when the general health of the fish has severely deteriorated.

The digestive state of the fish may also impact swimming capacity. For instance, the U_{crit} of rainbow trout (*Oncorhynchus mykiss*) fed to satiation was reduced by 15% compared to fasted counterparts (Alsop & Wood 1997). Hence, rainbow trout were unable to divert their full aerobic capacity to swimming because of the metabolic burden associated with digestion. Similar results would be expected for Atlantic salmon as both species are salmonids with comparable physiologies. Consequently, when rough weather conditions are being forecasted at exposed aquaculture sites, a management strategy could be to stop feeding 1–2 days beforehand to better prepare the fish for an imminent swim challenge.

Salinity and oxygen levels are two important environmental factors that can fluctuate substantially in Atlantic salmon sea cages, both over time and with depth within the sea cage (Oppedal *et al.* 2011). With regard to salinity, there was no difference in the U_{crit} between Atlantic salmon post-smolts acclimated to either freshwater, brackish water or seawater, which highlights the remarkably physiological flexibility of this species (Hvas *et al.* 2018b). With regard to oxygen levels, moderate hypoxia of 50–55% saturation reduced the U_{crit} of Atlantic salmon post-smolts of 3 different size classes owing to a reduced maximum rate of oxygen uptake (Oldham *et al.* 2019). However, considering conditions at exposed sites, these two parameters are expected to have limited relevance. Off the coast or offshore salinity will be uniform with depth as well as over time, and hypoxia is associated with insufficient water exchange which is the opposite situation of a strong current event where fast swimming is required. However, it should be noted that in some of the largest offshore cages presently being planned (diameter >160 m, 45 m deep, up to 3 million salmon, 510 000 m^3) the oxygen may be depleted simply due to the biomass of fish the water has to flow through. In present larger cages (Ø = 240 m), hypoxic conditions are considerably more common compared to standard cages (Ø = 160 m) (Oldham *et al.* 2018).

Other potentially important factors to consider are genetics and the acclimation history of the fish. For instance, considering the apparent individual variation in U_{crit} of farmed Atlantic salmon (Fig. 2), it may be possible to select for swimming traits and establish a line of fish more suited for exposed aquaculture. Moreover, conditioning fish by systematically giving them various swim challenges prior to sea cage transfer could also improve their swimming capacities (e.g. Anttila *et al.* 2014; Robinson *et al.* 2017). The question then is how big of an improvement in swimming traits that actually can be achieved either through genetic selection or through phenotypic plasticity. Nevertheless, both are worthy of future studies.

Cleaner fish

A rapidly growing strategy to manage salmon lice infestations is the use of cleaner fish as biological control agents in sea cages, since they can be effective in removing lice from Atlantic salmon and are considered to be more cost-effective and less harmful compared to other treatment methods (Liu & Bjelland 2014; Imsland *et al.* 2018). The most popular cleaner fish species is the lumpfish (*Cyclopterus lumpus*), since it is easy to culture and remains active during winter temperatures (Powell *et al.* 2017). However, several species of temperate wrasses are also deployed, and of these, only the ballan wrasse (*Labrus bergylta*) is currently being cultured for the purpose of cleaner fish deployment (Norwegian Directorate of Fisheries, 2018).

All cleaner fish are protected by the same animal welfare legislations that apply to Atlantic salmon in Norway and most other western countries (Branson 2008; Norwegian Ministry of Agriculture & Food, 2009). However, in contrast to Atlantic salmon, cleaner fish have no commercial value as food and are solely used for parasite control. Cleaner fish welfare has therefore typically been ignored despite of many anecdotal reports of very high unaccounted mortality rates in sea cages.

The cause of poor welfare and mortalities in aquaculture can often be ascribed to inadequate environmental conditions. Cleaner fish differ fundamentally from Atlantic salmon in physiological adaptations, and their environmental requirements and thresholds will therefore be different. For instance, the lumpfish is a cold water species and cannot survive longer periods at 18°C (Hvas *et al.* 2018a), while this temperature maximizes the swimming performance and aerobic scope of Atlantic salmon (Hvas *et al.* 2017a). On the other hand, the ballan wrasse is a warm water species that thrives at 25°C (Yuen *et al.* 2019), which is a lethal temperature for Atlantic salmon. Cleaner fish species also responds differently than Atlantic salmon to stress and hypoxia (Hvas *et al.* 2018a; Hvas & Oppedal 2019b), further corroborating that farm environments suitable for Atlantic salmon may not necessarily allow cleaner fish to thrive, which ultimately will defeat their purpose as biological control agents.

To evaluate the feasibility of cleaner fish deployment at exposed aquaculture sites, we have compared the U_{crit} of Atlantic salmon to lumpfish and ballan wrasse at a range of sizes in Figure 4. Here, it is strikingly obvious that Atlantic salmon have a much higher swimming capacity than both cleaner fish species. Considering morphological and ecological differences, this is not surprising. Low U_{crit} in lumpfish can be explained by its globiform body shape and poorly developed tail musculature (Hvas *et al.* 2018a). Ballan wrasse and other wrasse species are labriform swimmers, which mean that they rely primarily on their pectoral fins for propulsion. This style of swimming is good for precision and fine-scale manoeuvrability in rocky and algal reef habitats, but is ill-suited for prolonged high speed swimming (Webb 1984; Walker & Westneat 1997, 2002). As such, neither cleaner fish species are built for prolonged high speed swimming like salmonids. Furthermore, the

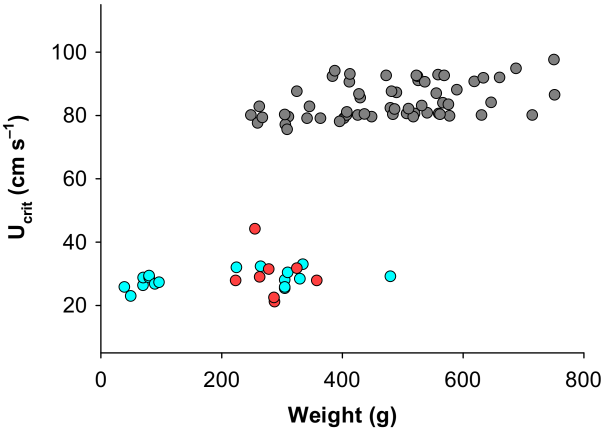

Figure 4 The critical swimming speed (U_{crit}) of Atlantic salmon, lumpfish and ballan wrasse versus size. Atlantic salmon and lumpfish data were obtained at 8 and 9°C, respectively. However, the U_{crit} of ballan wrasse was measured at 25°C because this species was reluctant to swim continuously for prolonged periods at lower temperatures, which is a requirement for proper U_{crit} estimates (Modified from Hvas *et al.* 2017b, 2018a; Yuen *et al.* 2019). ● Atlantic salmon; ○ Lumpfish; ● Ballan wrasse.

sizes of cleaner fish typically deployed in sea cages are substantially smaller than growing Atlantic salmon. This means that cleaner fish are further disadvantaged when comparing swimming capacities on absolute scales. Therefore, cleaner fish are much more likely to struggle at aquaculture sites prone to rougher current conditions.

Defining welfare guidelines for water currents

For management of fish welfare at exposed aquaculture sites, it will be necessary to formulate guidelines for allowable current speeds based on the swimming capabilities of the fish being farmed.

As we have seen in Swimming performance of Atlantic salmon in relation to biological and environmental factors, several environmental and biological factors can be expected to modulate swimming performance of Atlantic salmon to some extent. Of these, the two key factors that should be considered first for management purposes are fish size and water temperature, since they both assert substantial and predictable effects on swimming capacities (Remen *et al.* 2016; Hvas *et al.* 2017a; Fig. 3). Health status must also be considered where any issues may be assumed to impose some negative effects on swimming capabilities.

Most of our knowledge on Atlantic salmon swimming performance in relation to environmental and biological factors is based on U_{crit} measurements. However, the incremental nature of the U_{crit} test may not represent sea cage conditions, and U_{crit} merely indicates how fast Atlantic salmon are able to swim for a limited time before reaching fatigue. We have therefore identified two other indicators of swimming capacity, sustained and preferred, to represent swimming on longer time scales (summarized in Table 1). Hence, to formulate reasonable welfare guidelines we must consider the biological status of the fish, environmental parameters and the duration of strong current events.

An attempt to show how welfare guidelines for maximum allowable current speeds in salmon sea cages could be defined is presented in Figure 2. Here, regression lines are plotted to show the general effect of size on U_{crit}. In addition, regression lines were also made for the best and worst swimmers in each 5 cm length interval to illustrate individual variation. Taking individual variation into account is a crucial point, since all fish within a given stock should be able to thrive in their environment. Any welfare guideline should therefore be based on conservative estimates. In the case of Figure 2, the regression line representing the weakest swimmers then define the maximum allowable current conditions at 13–14°C for farmed Atlantic salmon.

For strong current exposure that lasts several hours, sustained swimming capacity should be used instead of the U_{crit} as a welfare threshold (Table 1). It has been established that Atlantic salmon are able to sustain at least 80% of their U_{crit} for minimum 4 hours (Hvas & Oppedal 2017). A regression line representing 80% of the U_{crit} of the weakest swimmers has therefore also been included on Figure 2 to provide a conservative estimate of the sustained swimming capacity.

In the case of chronic current conditions lasting days or weeks, the recommended speed limit is even lower than suggested in Figure 2. Here, it will be more appropriate to use the preferred swimming speed, since currents above this threshold compromises the natural behaviour of Atlantic salmon and may decrease growth performance (Johansson *et al.* 2014; Solstorm *et al.* 2015). The preferred swimming speed of caged Atlantic salmon resembles migratory swimming speeds of wild counter parts, which theoretically should correspond to their minimum CoT (see Swimming behaviour in the sea cage environment). The minimum CoT is approximately 60% of the U_{crit} in Atlantic salmon post-smolts (Hvas & Oppedal 2017). As a welfare guideline, chronic current conditions at exposed sites should therefore not exceed 60% of the U_{crit}.

To formulate nuanced welfare guidelines, it is evident that different levels of swimming capacities and behaviours need to be considered, as well as the interactive effects of biological and environmental factors. With this in mind and based on a series of empirical studies over the recent years, we have now established a good knowledge base from which welfare guidelines can be derived. However, more studies would certainly still be useful, especially on the pathological effects of various common diseases and parasites in Atlantic salmon aquaculture.

Site surveys

So far, the swimming capabilities and behaviours of Atlantic salmon and two species of cleaner fish have been discussed to provide a nuanced assessment of the magnitude and duration of water currents that can be allowed without causing unacceptable fish welfare at exposed locations. An important question that now remains is: What are current conditions actually like at locations that are considered exposed, and based on the knowledge presented here, is it feasible to farm salmon in these environments?

In a field study at an exposed salmon farm in the Faroe Islands, current speeds in the centre of sea cages peaked at 40 cm s^{-1}, while reference measurements in the adjacent marine environment experienced peak currents of 70 cm s^{-1} over a 3 day period in February (Johansson *et al.* 2014). These levels of current exposures were sufficient to disrupt the circular schooling structure and force the salmon to stand on the current.

At another Faroe Island, salmon farm peak current speeds through sea cages were reported to be 60 cm s^{-1} during 3 weeks of persisting stormy weather in December and January. Unfortunately, these conditions caused mass mortalities of Atlantic salmon and the decision was therefore made to terminate the remaining stock prematurely. However, the infrastructure of the farm site was able to handle the weather conditions (IntraFish 2017).

In a recent study, ocean current data were collected using acoustic Doppler current profilers at five exposed sites along the Norwegian coast over a minimum period of 5 months (Jónsdóttir *et al.* 2019). At the most exposed location surveyed, peak current speeds were 113 cm s^{-1}, and periods of up to 5 h with current speeds above 60 cm s^{-1} were observed.

In Figure 5, the temporal distribution of different current magnitudes at the most exposed location surveyed by Jónsdóttir *et al.* (2019) is presented. Here it can be seen that for the majority of time, current speeds were weak (less than 20 cm s^{-1}). However, current speeds between 20 to 40 cm s^{-1} occurred for a substantial amount of time. Such magnitudes will pose a significant challenge for cleaner fish (Fig. 4), but should be below the preferred swimming threshold of Atlantic salmon. Events of very strong currents that approached the U_{crit} of Atlantic salmon (above 60 cm s^{-1}) were infrequent. However, regardless how rare they might be, extreme events must be considered in risk assessments owing to their potential catastrophic consequences (Fig. 1d).

Modelling water currents over larger offshore areas may also indicate where it will be most feasible to establish farm sites in the future. By using the NorKyst800 model that provides a horizontal resolution of 800 × 800 metre at 35 depth levels (Albretsen *et al.* 2011), this has recently been done for the entire Norwegian coast and out to the continental shelf and subsequently analysed with regard to the expected impact on Atlantic salmon welfare (Albretsen *et al.* 2019). In Figure 6, the outcome of this model is summarized and shows that some areas have potential for offshore aquaculture, while the environmental conditions elsewhere may be too extreme. Similar modelling methods could also be used in other salmon farming regions as preliminary assessments of potential aquaculture sites.

It should be noted that ocean current data in Jónsdóttir *et al.* (2019) and Albretsen *et al.* (2019) were derived from outside sea cages, and a substantial current damping is expected within sea cages owing to the net wall, while Atlantic salmon in trailing positions also are likely to experience even lower current speeds (Johansson *et al.* 2014; Hvas *et al.* 2017b). Hence, experienced environmental conditions by farmed fish within cages will be less severe than what is reported by Jónsdóttir *et al.* (2019) and similar ocean surveys. Going forward, technological solutions could further aid in mitigating current speeds through sea cages.

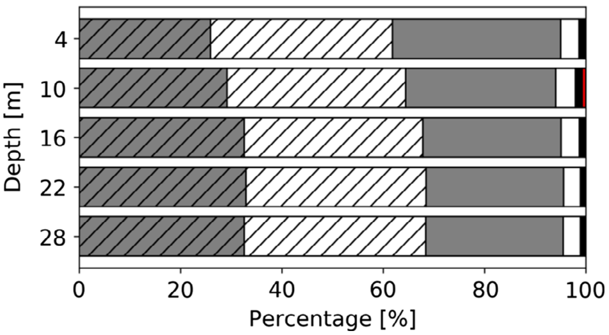

Figure 5 Current speed distribution at an exposed aquaculture site. Data were collected with an acoustic Doppler current profiler over a 5 month period including a winter season at a location in Frøya, Norway. All measurements were then allocated to categories based on conservative estimates of the impact on Atlantic salmon swimming behaviours (see legend). The figure shows the fractional duration of each current category at representative depth intervals over the entire measurement period and was modified from Jónsdóttir *et al.* (2019). ▨ Very week ($U \leq 10$ cm s^{-1}); ▧ Week ($10 < U \leq 20$ cm s^{-1}); ▩ Moderate ($20 < U \leq 40$ cm s^{-1}); ☐ Substanial ($40 < U \leq 50$ cm s^{-1}); ■ Strong ($50 < U \leq 60$ cm s^{-1}); 🟥 Very strong ($U > 60$ cm s^{-1}).

Currently, a strict definition of what constitute an exposed aquaculture site does not exist. However, in accordance with Norwegian law, site surveys that classify environmental conditions are required prior to establishing new aquaculture sites (Laksetildelingsforskriften 2004; NAS, 2009). Here, ambient current speeds need to be measured to ensure that weather conditions do not jeopardize the structural integrity of the farm. However, environmental impacts on fish welfare are currently considered in much less detail and only in general terms.

From the unfortunate events at a Faroe Island salmon farm, it was concluded that present infrastructure and technology were able to handle rough weather conditions that proved to be lethal for the fish (IntraFish 2017). Hence, it will be necessary to expand the present requirements for site surveys and subsequent criteria for their evaluation to include fish welfare considerations in much greater detail. The welfare guidelines presented in this review provide adequate and more precise thresholds that can be used for such evaluations.

Waves

Powerful waves are expected at offshore sites and their impact is likely to impose a serious challenge to many aquaculture operations (Bjelland *et al.* 2015; Faltinsen & Shen 2018). However, unlike water currents very little research has so far been made on the impact of waves on farmed fish. This is primarily due to the practical limitations with studying the interaction of waves and fish behaviour on scales that are relevant to commercial aquaculture.

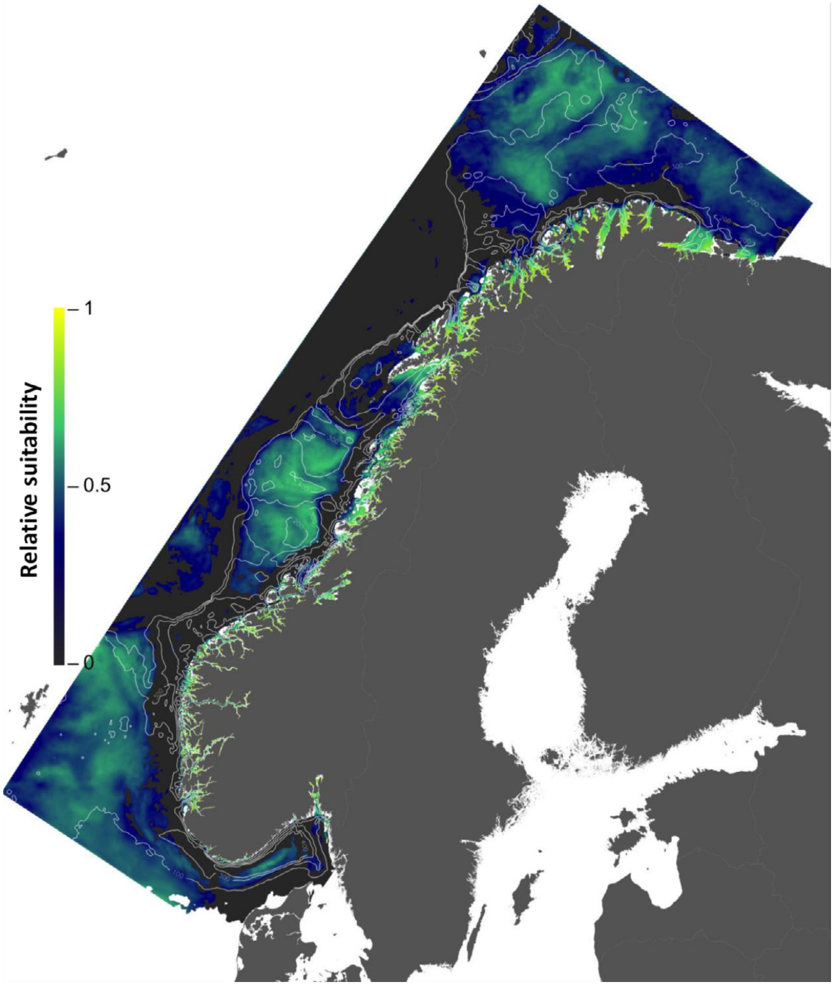

Figure 6 Relative suitability of Norwegian ocean areas for offshore aquaculture based on the water current tolerance of Atlantic salmon. Black represents areas that are not suitable for fish farming according to our present knowledge of Atlantic salmon swimming capabilities (e.g. average current speeds above 50 cm s^{-1}). The figure is based on modelled current data and their expected impact on Atlantic salmon welfare and is reproduced with permission from Albretsen *et al*. (2019).

An ocean wave is a periodic surface movement constrained to the upper most layer of the water column. They are generated by winds and can travel over large distances before they hit the shores. Waves can vary substantially in size from shallow ripples to several metres in height, and from few to many seconds in periodicity. Despite of large horizontal movements of energy, individual water particles are only subjected to limited movement in the direction of the wave, and instead, they mainly move in either ellipses or circular patterns, depending on the length of the wave (Kundu, 2016). The movement of water particles decays rapidly down the water column, meaning that their impact largely can be avoided by fish if they stay away from the surface layers.

The sea cage structure from top to bottom will follow the movement of ocean waves. Therefore, central questions regarding offshore aquaculture are whether farmed fish exposed to powerful waves retains adequate behavioural control to avoid collision with each other and the cage wall, and how much excess energy the fish require in those situations. To our knowledge, there are presently only two available studies on this topic, where both were conducted at wave-exposed sites on the Faroe Islands (Dam 2015; Johannesen *et al.* 2020). In the first study, the group structure was disestablished by powerful waves with significant wave heights of 2–2.5 m, periods of ~14 s and vertical movements of 0.3–0.8 m. Furthermore, it seemed that during daytime, the fish would avoid the surface layers (Dam 2015). Similar observations were made by Johannesen *et al.* (2020) at a farm site with significant wave heights of up to 2.9 m, but with mostly wind driven short period waves of less than 14 s and low current speeds of less than

20 cm s^{-1}. In addition, fish tended to move away from the side of the cage during large waves, orienting their swimming direction along the wave rather than maintaining a position against the current (Johannesen *et al.* 2020). These behavioural responses were also seen in a miniature wave and current tank study, where waves caused 16 cm long salmon to swim in individually independent patterns rather than displaying organized group behaviours as when only water currents are present (He *et al.* 2018). Some of the fish also went to the bottom of the net possibly owing to them being uncomfortable in the wave zone. If Atlantic salmon actively chooses to move down the water column during periods of powerful waves, they will be able to avoid most of their impact. However, Atlantic salmon in sea cages are known to migrate towards the surface layers during night time (Oppedal *et al.* 2011). Accordingly, observations of diurnal fish behaviour at a wave-exposed site revealed a wider depth distribution of the fish at night where a part of the group occupied shallower waters (Johannesen *et al.* 2020). Whether such variation in diurnal depth preference can be an issue in exposed aquaculture is worthy of additional study.

The Faroe Islands are currently the forerunners of Atlantic salmon aquaculture in locations exposed to severe wave action. Here, significant wave heights of 5–6 m have been measured (Øystein Patursson, Fiskaaling, Faroe Islands, personal communication). Waves of such magnitude can pose a serious challenge to routine operations. For instance, it may not be possible to safely catch fish for inspection for longer time periods with prevailing bad weather (Dam 2015). Other handling procedures such as crowding, delousing and transportation will also become more difficult. One study has reported high stress levels and mortality rates during the first month in sea cages following well boat transport in waves of 3–5.5 m in height (Iversen *et al.* 2005). Another topic that has not been studied is how turbulent flow conditions impact the ability of the fish to eat food pellets. Hence, it is possible that alternative feeding strategies must be implemented such as deep feeding. Future research will hopefully shed more light on the impact of waves on fish welfare and production performance in offshore aquaculture.

Technological solutions

Compared with traditional sea cages, the ongoing development towards exposed and offshore salmon farming relies on larger rearing units and more rigid structures which minimizes cage deformation and vertical movement by current and wave forces (e.g. Ocean Farm 1, Salmar, Norway). In larger volumes and group sizes, the fish may express a wider range of group behaviours and may better benefit from specialized behaviour towards water currents and effectively avoid wave forces by positioning themselves in deeper water. Structural barriers which dampen currents and waves may be implemented for permanent use or as a periodic safety measure when the fish are small, or physiologically vulnerable by sickness or during and after handling operations such as delousing. Barriers can be implemented to cover a restricted part of the volume as seen with lice prevention skirts (Stien *et al.* 2012, 2018; Grøntvedt *et al.* 2018) or completely surrounding semi-closed sea cages (Nilsen *et al.* 2017). However, it is not known whether Atlantic salmon are effective in seeking out sheltered areas within the sea cage. Submergence of cages is another strategy which is considered very effective in escaping strong wave and current forces at the surface (e.g. Artic Offshore Farming, Norwegian Royal Salmon, Norway) and will by default also reduce sea lice infestation and eliminate icing on structures. However, submergence without air access for the salmon to refill their swim bladders is not feasible (Dempster *et al.* 2009; Korsøen *et al.* 2009), while repetitive submergence or submergence with an air dome may be used (Glaropolous *et al.,* 2019). However, such strategies currently need trials on commercial scale levels to prove whether this principle works for all individuals throughout a production cycle.

Cage designs for exposed aquaculture require novel methods for capture of fish, transport, harvest, feeding and delousing, as well as tailoring of fish and environment observation tools and methods. Such rethinking is certain to push biological knowledge frontiers of generic interest to salmon farming. For fish welfare safeguarding, documentation and improvement of farming structures and methods, especially with the high stakes of implementing novel offshore technology containing a vast number of fish, it is of utmost importance to record and understand the environment the fish acutely are exposed to and how they cope with it. Hence, recording of environmental gradients within the cage (current, wave height and period, temperature, light) will be necessary, while the spatial distribution and group swimming behaviour of the fish can be monitored with echo sounders and camera observations (e.g. Johannesen *et al.* 2020). Moreover, advances in bio-logging technologies may provide additional information about the physiology and behaviour on the individual level in the ambient farm environment (Brijs *et al.* 2018; Hvas *et al.* 2020).

Conclusion

Atlantic salmon is an athletic species with high sustained swimming capabilities, and as a eurythermal and euryhaline fish, it also displays an impressive flexibility to cope well in different environmental conditions. Based on a series of empirical studies on swimming performance in growing post-smolts in combination with site surveys of ocean currents, we believe that responsible Atlantic salmon farming that ensures acceptable welfare is possible at more exposed locations. However, popular cleaner fish species such as lumpfish and ballan wrasse are clearly unable to attain similar prolonged swimming speeds as Atlantic salmon. They are instead primarily adapted to precise fine-scale manoeuvrability. Cleaner fish are therefore not recommended for deployment at sites with occasional moderate to high current speeds.

We have obtained substantial knowledge on swimming behaviours and capacities in farmed Atlantic salmon in recent years that now have allowed us to define specific welfare guidelines with regard to ambient current speeds. Hopefully, these guidelines will be implemented by various authorities to ensure that good fish welfare is maintained as more exposed farm sites become established. However, some crucial knowledge gaps still exist. Most glaringly is the impact of waves that for practical reasons will need to be studied in field studies. Generally, more field observations of behaviour and welfare in exposed conditions are warranted, where new bio-logging technologies will be particularly useful. The pathophysiological effect of various diseases and parasites found in salmon aquaculture is another understudied area, especially when several pathogens are present simultaneously as well as their interaction with different environmental conditions.

It will undoubtedly be interesting to follow the evolution of exposed salmon aquaculture in the coming years as new advanced farm concepts and technological innovations are introduced. Although we must not forget that to successfully farm Atlantic salmon or other species in more extreme environments, biological considerations need to be at the core of decisions, where it is paramount to respect the physiological limits of the fish.

Competing interests

The authors declare no competing or financial conflicts of interests.

Author contributions

This work was conceived by all authors. M.H. wrote the first draft of the manuscript and arranged figures while all co-authors provided valuable feedback before approving the final version.

Funding

This study was funded by the Research Council of Norway through the Centre for Research-based Innovation in Aquaculture Technology, Exposed (237790) and Future Welfare (267800).

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