Vol. 14: 219–227, 2022
https://doi.org/10.3354/aei00439

AQUACULTURE ENVIRONMENT INTERACTIONS
Aquacult Environ Interact

Published September 15

OPINION PIECE

Recognising trade-offs between welfare and environmental outcomes in aquaculture will enable good decisions

Georgia Macaulay, Luke T. Barrett, Tim Dempster*

Sustainable Aquaculture Laboratory — Temperate and Tropical (SALTT), School of BioSciences, University of Melbourne, Victoria 3010, Australia

ABSTRACT: As aquaculture expands, ensuring the sustainability of practices requires a focus on minimising environmental effects. At the same time, where fish are cultured, their welfare needs to be secured to ensure compliance with legislation and gain social acceptance of farming practices. However, clear conflicts exist between protecting the environment and protecting welfare where either environmental or welfare outcomes are traded off against each other. We document 5 cases in aquaculture where environmental sustainability and welfare principles are antagonistic. If knowledge or management of environmental sustainability or welfare is weak in a specific setting, the best outcome may not be achieved. We contend that identifying conflicts between desired environmental and welfare outcomes as early as possible will allow for knowledge-based consideration of trade-offs using the best available evidence. Further, where different departments of regulators are responsible for different outcomes, targeted collaboration focused on identifying conflicts should reduce instances of unconscious trade-offs. Reducing conflicts between the 2 goals of good welfare and environmental protection should promote both ecologically and ethically sustainable aquaculture.

KEY WORDS: Environmental effect · Ethics · Fish farm · Fish welfare · Management

INTRODUCTION

Aquaculture continues to grow rapidly, with demand for finfish driving much of this growth (Costello et al. 2020), resulting in concomitant environmental impacts (Primavera 2006, De Silva 2012). In commercial aquaculture, profitability and economic sustainability are the primary goals. However, for aquaculture to be a sustainable sector, industries must strike a balance between supplying farmed fish and the environmental consequences of doing so. Ethical concerns for the welfare of cultured fish in intensive farming systems have emerged (Bovenkerk & Meijboom 2020). The term 'fish welfare' was rarely used in aquaculture or fisheries research prior to the year 2000, yet from 2009–2019 it was included in approximately 5000 research articles and reports (Kristiansen & Bracke 2020). As our understanding of fish cognition grows, so do societal expectations of acceptable fish welfare.

Increasing public awareness of issues within finfish aquaculture can motivate the industry to improve, while governments can require compliance with legislation that reflects societal expectations (Stien et al.

---

*Corresponding author: dempster@unimelb.edu.au

Publisher: Inter-Research · www.int-res.com

2020a). Companies that demonstrate high environmental and animal welfare standards have an advantage in marketplaces where consumers are willing to pay a premium for farmed fish with eco-labels (Gray et al. 2021) or animal welfare certifications (Miranda-de la Lama et al. 2019). Moreover, good fish welfare improves production efficiency via increased survival and, because appetite is impacted by stress, more rapid and efficient growth (Huntingford & Kadri 2014). Within the context of fish farming, efficiency also reduces direct and indirect environmental impacts of aquaculture by minimising feed requirements and subsequent waste.

Although fish welfare and environmental sustainability are closely aligned goals, 'pinch points' remain where either environmental sustainability or fish welfare is sacrificed in favour of the other. Bergh (2007, p. 163) stated that 'there is a fundamental conflict of interest between the concern for the environment and the concern for animal welfare', arguing that the strict legislation on antibacterial use in Atlantic salmon *Salmo salar* aquaculture in Norway prioritized reduction in environmental impacts over fish welfare. Moreover, different groups of people typically research the welfare of farmed fish and the environmental impact of fish farming, which can create a disconnect between the two. Likewise, different management agencies may be responsible for regulation in these two disparate areas. Further, certain jurisdictions may have strong regulations for one and weaker regulations for the other. One or combinations of these circumstances within an industry can create fertile ground for the accidental initiation of negative trade-offs. Trade-offs can also arise between welfare outcomes and between environmental outcomes, which can further complicate decision making.

The purpose of this paper is not to advocate for animal welfare over environmental impacts or vice versa, but rather to emphasize that conflicts between the 2 goals exist and should be identified as early as possible. Once recognized, the pros and cons for welfare and environmental outcomes in aquaculture can be considered with the best available evidence on a case-by-case basis. This will assist to achieve environmentally sustainable production that also prioritizes good animal welfare, or if a trade-off is necessary, for good decisions to be made by managers with eyes wide open. We (1) highlight 5 cases where environmental sustainability and animal welfare principles are antagonistic and (2) encourage discussion about potential strategies to reduce the severity of such trade-offs.

CASE 1: SELECTING FOR PRODUCTION EFFICIENCY CAN TRADE OFF AGAINST WELFARE

The early stages of a fish farming industry involve both incidental and deliberate trait selection to make cultured fish more suited to farm life than their wild counterparts. This process generally correlates positively with welfare since breeding fish that are less susceptible to stress brings benefits for both fish and farmer. Later, trait selection can be iteratively fine-tuned to decrease production costs, increase product quality, fulfil consumer preferences, and increase disease resistance (Gjedrem & Baranski 2010). For example, feed conversion ratios are much better in selectively bred fish (Talbot & Hole 1994), which is advantageous for resource use efficiency, benefitting the environment. However, traits that are commercially or ecologically desirable do not always align with animal health or welfare (Rauw et al. 1998). For example, Saraiva et al. (2018) considered the welfare consequences of selecting for fast growth and production performance in aquaculture, as fast-growing fish are often more aggressive. Another example of the welfare consequences when selecting for good performance is the development of triploid stock.

Triploid fish possess an extra set of chromosomes, typically induced by temperature- and pressure-shocking eggs (Fraser et al. 2012). The resulting fish are sterile — a desirable trait in aquaculture, as maturity negatively affects growth, flesh quality, and feed utilisation in several species (Taranger et al. 2010) and can increase aggression (Iversen et al. 2016). Moreover, sterile farmed fish escapees cannot breed with wild conspecifics, and fish species that breed within sea-cages will not produce gametes that lead to 'escape by spawning' (Somarakis et al. 2013), making triploids ecologically beneficial (Jonsson & Jonsson 2011). However, triploids of several farmed species (cod, tilapia, carps) have higher instances of skeletal deformities (Fraser et al. 2012) and are less robust to hypoxia, high temperatures, and disease (Scott et al. 2015). Recently, after extensive, full-scale testing in multiple industrial salmon farms, the Norwegian government halted the production of triploid salmon due to welfare concerns, which included lower survival, higher incidences of emaciation, and poorer product quality compared to diploid fish (Madaro et al. 2021). This decision prioritised the welfare of farmed fish over the ecological consequences of escaped fertile farmed fish (Karlsson et al. 2016, Glover et al. 2017, Wacker et al. 2021), highlighting a clear trade-off that has been appropriately considered.

CASE 2: FEEDS WITH REDUCED WILD FISH CONTENT MAY BENEFIT WILD FISH POPULATIONS, BUT CAN CREATE CHALLENGES FOR FARMED FISH WELFARE

Using wild-caught fish to create feed for farmed fish is criticised on sustainability grounds (Naylor & Burke 2005, Deutsch et al. 2007, Shannon & Waller 2021). Considerable improvements in feed-delivery technology and greater incorporation of alternative nutritional sources (e.g. animal by-products and plants) have occurred in the past 2 decades (Naylor et al. 2021). This transition, driven by sustainability and economics, has had complex effects on farmed fish health and welfare (Gesto et al. 2021).

Providing the correct nutrition for fish is paramount for maintaining health, growth, and immune system function (Hixson 2014). The current suite of cultured finfish species spans a range of trophic levels with differing nutritional requirements. For marine fish farming, moving away from marine-derived, fish-oil-based diets creates challenges for feed quality, most notably in obtaining polyunsaturated fatty acids (Sprague et al. 2017). Aquaculture feeds low in fish oil and high in vegetable oil affect growth rate and immune and stress responses in a range of farmed species (Lu et al. 2019, Mu et al. 2020, Serradell et al. 2020, Gesto et al. 2021). The high cost of marine-derived proteins (e.g. fishmeal) has led to widespread replacement using terrestrial sources such as soy and offal (Rana et al. 2009). These proteins are often included at very high rates to maximise growth rates, but it remains challenging to replicate the amino acid profile of marine proteins. This has effects on fish health (Zhang et al. 2018), while high protein inclusion, together with a suboptimal amino acid profile, can lead to more severe benthic impacts as excess amino acids are excreted (Bureau et al. 2002, Teodósio et al. 2020). Efforts to create feeds that rely on minimal amounts of wild-caught fish but still provide adequate nutrition are ongoing and essential to increasing aquaculture sustainability.

Sustainable feed composition can be complemented by sophisticated feeding technology and an understanding of fish appetite. Modifying feeding schedules on-farm is one method to reduce waste, by feeding when fish are hungry and stopping when they are satiated (e.g. Bjordal et al. 1993, Juell et al. 1994). Appetite-led feeding may also be beneficial for welfare, as intensively cultured fish have little control over what they eat and when, despite known fluctuations in appetite with time of day and environmental conditions (Juell et al. 1993, Mallekh et al. 1998). Giving fish greater control over meal duration reduces competition for food and aggressive behaviours (Noble et al. 2008). Precision feeding management coupled with nutritious feeds that rely as little as possible on wild-caught fish should balance environmental sustainability and fish welfare.

CASE 3: ENVIRONMENTAL REGULATION SOMETIMES PROHIBITS FARMS FROM BEING SITED WHERE FISH WELFARE WILL BE MAXIMISED

New fish farm proposals must navigate barriers put up by environmental protection legislation, local regulations, competing industries, and negative public perception. As a result, some farmers are initiating sites that are more weather-exposed to avoid competing for sheltered, inshore space (Moe Føre et al. 2022), though there is little evidence to suggest many farms are moving more offshore (e.g. salmon farms; McIntosh et al. 2022). While the capital expenditure required is greater than for inshore farming, exposed farming provides greater dispersal of waste by deeper water and/or stronger currents compared to inshore farming (Holmer 2010) and reduced disease transmission risk, as farms can be sited farther apart and away from coastal features that aggregate infective particles (Lyngstad et al. 2011, Samsing et al. 2021, McIntosh et al. 2022). More stable water parameters throughout the year and higher dissolved oxygen concentrations could also improve fish welfare and growth in exposed locations (Dempster et al. 2016, Remen et al. 2016, Burke et al. 2021). However, extreme weather conditions and greater travel distances may affect the ability of farmers to conduct basic husbandry tasks. Welfare benefits of exposed aquaculture could also be offset if currents or waves exceed the tolerances of farmed fish. Sustained strong currents force fish to spend energy on continuous swimming, which precludes other voluntary behaviours and limits growth (Johansson et al. 2014). In severe cases, fish will fatigue and eventually be pressed against the net wall, resulting in significant injuries and distress (Hvas et al. 2021). Effects of current/wave exposure on welfare will be species-dependent: strong swimmers may thrive (e.g. thunnids and carangids), while many demersal species will depend on the provision of sheltered microhabitats (Hvas et al. 2021). Finally, exposed farms tend to consist of fewer, larger rigid cages that are more robust to severe weather but can impact welfare, especially in leeward cages (McIntosh et al. 2022). For example, Havfarm 1 is a new exposed sea-cage technology, consisting of a single row of 6 large and closely spaced cages on a swing mooring. The Norwegian government recently rejected an application to convert the research license the farm was initiated with for testing and development to a permanent biomass license, citing excessive mortality (25%) in some cages within the farm (Directorate of Fisheries 2021).

Conflicts regarding farm siting are not restricted to mariculture. For example, while the majority of farmed seabream *Sparus aurata* L. are produced in sea-cages in Europe, seabream production also occurs in land-based systems (Matos et al. 2017). There is some evidence that seabream farmed in different systems have different welfare outcomes. For instance, seabream from semi-intensive, land-based pond systems may experience better welfare compared to those reared in intensive sea-cage or raceway systems (Roncarati et al. 2006). However, future development of land-based seabream production may be limited by conflicts with competing land uses, such as tourism or coastal protection areas (Oca et al. 2002).

CASE 4: LAND-BASED FARMING REDUCES DISEASE TRANSMISSION AND WASTE EXPORT BUT PRESENTS NEW WELFARE CHALLENGES

Similar to exposed farming, land-based farming aims to avoid the environmental impacts and disease risks associated with coastal sea-cage fish farming. While land-based fish benefit from decreased exposure to the elements, poor welfare conditions can still arise (Davidson et al. 2017). Most notably, the high capital expenditure required to establish land-based farms means that fish are commonly stocked at high densities to offset expenses. This can lead to chronic stress and aggression (Bagni et al. 2007), and because oxygenation and waste removal must be done actively, system failures can lead to mass mortalities within minutes, especially in recirculating aquaculture systems (RASs) (Fornshell & Hinshaw 2008). For example, approximately 500 000 Atlantic salmon were lost in a Florida RAS facility due to filter issues which caused poor water quality (FishSite 2021). In a separate incident, a fire that broke out at an RAS facility in Denmark caused all fish to be lost (FishFarmingExpert 2021). Land-based environments may not be compatible with the behaviours of certain species. For example, northern bluefin tuna *Thunnus thynnus* frequently collide with tank walls, causing high mortality in the grow-out phase of juveniles and young adults (Miyashita et al. 2000), while various farmed fishes develop deformities through chronic 'walling' behaviour (Cobcroft & Battaglene 2009, Cobcroft & Battaglene 2013). Some of these issues are exacerbated by low levels of domestication (e.g. tuna), although even the most domesticated species with the greatest number of generations of selective breeding, Atlantic salmon, are prone to deformities in land-based systems (Robinson et al. 2021).

CASE 5: DISEASE CONTROL CAN TRADE OFF THE WELFARE OF FARMED AND WILD FISH

Most Atlantic salmon farming occurs in sea-cages that are open to the environment. The abundance and density of farmed hosts provide ideal conditions for sea lice (Caligidae), which reduce the welfare of farmed salmon and export larvae back into adjacent ecosystems (Dempster et al. 2021) and are considered a major threat to wild salmonid populations in the Northern Hemisphere (Krkošek et al. 2013, Vollset et al. 2018). To limit impacts on both farmed and wild salmon, regulators in most jurisdictions require salmon farmers to manage louse densities by prevention, treatment, or early harvest. While heavy infestations impact the welfare of farmed fish, so do most delousing treatment options (Overton et al. 2019), and farmed salmon are deloused far more frequently than would be required to safeguard their immediate welfare (Stien et al. 2020a).

Chemotherapeutants, delivered via feed additives or bathing, were the predominant delousing treatment until the late 2000s when evidence of treatment-resistance emerged (Aaen et al. 2015, Coates et al. 2021). Together with a pre-existing aversion to chemical use among consumers and environmental advocates, this motivated a recent and rapid transition to alternative treatments (Overton et al. 2019), predominantly mechanical removal by water jets and/or scrubbing, thermal removal by exposure to water of up to 34°C for short periods, and biological control by invertivorous cleaner fish.

Each of these alternatives carries severe animal welfare costs, meaning that more than ever, the welfare of fish in sea-cages trades off against the welfare and conservation of wild salmonids. Thermal and mechanical treatments cause more injuries and mortalities than chemotherapeutants (Sviland Walde et al. 2021), largely because their effects are less targeted. Affected salmon are now subjected to harsh conditions in the process of removing lice, i.e. extreme temperatures during thermal treatments (Nilsson et al. 2019, Moltumyr et al. 2022) and mechanical forces during mechanical treatments. Concurrently, around 60 million cleaner fish are stocked into Atlantic salmon sea-cages annually to remove lice without injuring salmon (Powell et al. 2018). However, the evidence base for their efficacy at the commercial scale is limited (Overton et al. 2020), and farmers using cleaner fish typically also employ thermal and mechanical methods (Barrett et al. 2020b). Meanwhile, cleaner fish themselves are vulnerable to disease and other drivers of poor welfare and mortality in sea-cages (Stien et al. 2020b). The welfare burden that was previously borne by farmed salmon alone has been partly shifted to cleaner fishes, animals that in theory — and law — have the same rights as salmon.

MOVING FORWARD: BALANCING WELFARE AND ENVIRONMENTAL PROTECTION

The priorities of fish welfare and environmental protection are often antagonistic in finfish aquaculture. Stien et al. (2020a, p. 9) considered the morality of 'weigh[ing] animal suffering against economic costs and other interests and values', suggesting that fish welfare is not always given top priority in aquaculture. Advances in environmentally sustainable practices in aquaculture are often implemented without considering the impacts on fish welfare and vice versa. Trade-offs between welfare and the environment are therefore likely not conscious. Bringing about greater balance to environmental and fish welfare protection in aquaculture requires careful consideration of the relative importance that (1) technological advances, (2) changing management practices, and (3) regulatory mandates will have in buffering or overcoming each trade-off.

Technological advancements

New farming environments and technologies continue to emerge as aquaculture expands and diversifies. With each new farming system, a new husbandry learning curve begins. These are specific to the characteristics of the system and the behavioural and physical responses of the farmed fish within it. New learning curves invariably lead to novel welfare challenges that must be mitigated, as evident in exposed aquaculture (Case 3), land-based aquaculture (Case 4), and disease management (Case 5). Advances in technology can help overcome these welfare challenges, such as the novel parasite prevention technologies emerging in salmon aquaculture. As discussed in Case 5, delousing methods will likely never be welfare-friendly, but lice must be controlled to protect both wild and farmed fish. However, preventative technologies that reduce initial infections and reduce the need for controls can help mitigate welfare challenges. Open sea-cages with plankton mesh or tarpaulin 'skirts' or 'snorkels' that cover the top ~10 m of the cage (where infective lice are most abundant) can reduce lice infestations by 55–75% on average (Geitung et al. 2019, Barrett et al. 2020a). These cages are considered welfare-friendly, provided that dissolved oxygen is monitored (Stien et al. 2018) and salmon are not held too deep (Macaulay et al. 2020).

Changing management practices

We contend that considering both the environmental and welfare consequences of husbandry practices in aquaculture will help alleviate pinch points. An example of a major paradigm shift in aquaculture management is through the development and application of fish vaccines. Finfish industries that have not yet created vaccines rely on antimicrobial compounds to treat infected fish, with loss of anti-microbials to the environment a cause of anti-microbial resistance (Lulijwa et al. 2020). Vaccines promote fish health by inhibiting infections and reducing the need for antimicrobial treatments and their loss to the environment. A major decline in the use of antibacterial agents in the Norwegian salmon aquaculture industry has been directly attributed to the development of effective vaccines (Lillehaug et al. 2003). Immunised farmed populations held in a production setting open to the wider environment are also less likely to cause disease spillback to wild populations. Although vaccination can be stressful for fish (Brudeseth et al. 2013), these negatives are outweighed by the benefits of being protected against highly contagious diseases with severe symptoms.

Regulation and legislation

Effective regulation is needed to safeguard both the environment and fish welfare within industrial aquaculture. However, in some jurisdictions, animal welfare and environmental protection are overseen by different government bodies in line with separate pieces of legislation. Similarly, research groups often focus on either animal welfare or environmental issues, seldom both. Recommendations and eventual decisions are therefore often made from a single perspective, and this likely exacerbates trade-offs between the environment and animal welfare in aquaculture. Moreover, fish protection regulations are relatively young compared to environmental protection regulations and both vary greatly depending on country. For example, Gismervik et al. (2020, p. 2396) compared the regulation of chicken farming to that of salmon farming in Norway and found that 'the regulation of salmon farming is more complex, has potentially conflicting aims and uses less positive welfare phrasings.' Giménez-Candela et al. (2020, p. 111) investigated how well the EU welfare legislation protects the welfare of farmed fish, finding ''farmed' fishes are currently only protected by the very basic and general principles laid down in secondary EU legislation which leave room for interpretation and are partly not applicable or even contradictory to the welfare of fishes'. The authors state this is largely because EU animal protection laws are created for land farm animals. Where there are shortfalls in fish welfare regulation, the onus falls on aquaculture companies to create their own codes of practice to safeguard fish welfare. However, moves to boost legal protection of fish welfare in aquaculture and fisheries are ongoing. For example, the European Platform on Animal Welfare has adopted a set of guidelines for fish farming (EU Platform on Animal Welfare 2020). As aquaculture continues to expand, complex ecological and ethical issues will continue to emerge. Cross-department collaboration between policymakers from welfare and environmental groups is needed to promote conscious discussion around the intertwined welfare–environment trade-offs. More conversation will generate the best possible outcomes for the 2 closely aligned goals of ethical and ecologically sustainable aquaculture.

Acknowledgements. The authors thank members of the SALTT lab for comments on the manuscript and 3 anonymous reviewers for their thoughtful feedback that improved the quality of the manuscript.

LITERATURE CITED

Aaen SM, Helgesen KO, Bakke MJ, Kaur K, Horsberg TE (2015) Drug resistance in sea lice: a threat to salmonid aquaculture. Trends Parasitol 31:72–81

Bagni M, Civitareale C, Priori A, Ballerini A, Finoia M, Brambilla G, Marino G (2007) Pre-slaughter crowding stress and killing procedures affecting quality and welfare in sea bass (*Dicentrarchus labrax*) and sea bream (*Sparus aurata*). Aquaculture 263:52–60

Barrett LT, Oppedal F, Robinson N, Dempster T (2020a) Prevention not cure: a review of methods to avoid sea lice infestations in salmon aquaculture. Rev Aquacult 12: 2527–2543

Barrett LT, Overton K, Stien LH, Oppedal F, Dempster T (2020b) Effect of cleaner fish on sea lice in Norwegian salmon aquaculture: a national scale data analysis. Int J Parasitol 50:787–796

Bergh Ø (2007) The dual myths of the healthy wild fish and the unhealthy farmed fish. Dis Aquat Org 75:159–164

Bjordal Å, Juell J, Lindem T, Fernö A (1993) Hydroacoustic monitoring and feeding control in cage rearing of Atlantic salmon (*Salmo salar* L.). In: Reinersten H, Dahle LA, Jørgensen L, Tvinnereim K (eds) Fish farming technology. AA Balkema, Rotterdam, p 203–208

Bovenkerk B, Meijboom F (2020) Ethics and the welfare of fish. In: Kristiansen TS, Fernö A, Pavlidis MA, van de Vis H (eds) The welfare of fish. Springer International Publishing, Cham, p 19–42

Brudeseth BE, Wiulsrød R, Fredriksen BN, Lindmo K and others (2013) Status and future perspectives of vaccines for industrialised fin-fish farming. Fish Shellfish Immunol 35:1759–1768

Bureau DP, Kaushik S, Cho CY (2002) Bioenergetics. In: Halver JE, Hardy RW (eds) Fish nutrition. Academic Press, San Diego, CA, p 1–59

Burke M, Grant J, Filgueira R, Stone T (2021) Oceanographic processes control dissolved oxygen variability at a commercial Atlantic salmon farm: application of a real-time sensor network. Aquaculture 533:736143

Coates A, Phillips BL, Bui S, Oppedal F, Robinson NA, Dempster T (2021) Evolution of salmon lice in response to management strategies: a review. Rev Aquacult 13: 1397–1422

Cobcroft JM, Battaglene SC (2009) Jaw malformation in striped trumpeter *Latris lineata* larvae linked to walling behaviour and tank colour. Aquaculture 289:274–282

Cobcroft JM, Battaglene SC (2013) Skeletal malformations in Australian marine finfish hatcheries. Aquaculture 396–399:51–58

Costello C, Cao L, Gelcich S, Cisneros-Mata MÁ and others (2020) The future of food from the sea. Nature 588: 95–100

Davidson J, Good C, Williams C, Summerfelt ST (2017) Evaluating the chronic effects of nitrate on the health and performance of post-smolt Atlantic salmon *Salmo salar* in freshwater recirculation aquaculture systems. Aquacult Eng 79:1–8

De Silva SS (2012) Aquaculture: a newly emergent food production sector—and perspectives of its impacts on biodiversity and conservation. Biodivers Conserv 21: 3187–3220

Dempster T, Wright D, Oppedal F (2016) Identifying the nature, extent and duration of critical production periods for Atlantic salmon in Macquarie Harbour, Tasmania, during summer. Fisheries Research and Development Corporation (FRDC) report. University of Melbourne, Parkville

Dempster T, Overton K, Bui S, Stien LH and others (2021) Farmed salmonids drive the abundance, ecology and evolution of parasitic salmon lice in Norway. Aquacult Environ Interact 13:237–248

Deutsch L, Gräslund S, Folke C, Troell M, Huitric M, Kautsky N, Lebel L (2007) Feeding aquaculture growth through globalization: exploitation of marine ecosystems for fishmeal. Glob Environ Change 17: 238–249

Directorate of Fisheries (2021) Rejection of application for conversion of development permits. www.fiskeridir.no/Akvakultur/Nyheter/2021/avslag-pa-soknad-om-konvertering-av-utviklingstillatelser (accessed 18 March 2022)

EU Platform on Animal Welfare (2020) Guidelines on water quality and handling for the welfare of farmed vertebrate fish. https://food.ec.europa.eu/system/files/2022-07/aw_platform_plat-conc_guide_farmed-fish_en.pdf

FishFarmingExpert (2021) 'All fish lost' in blaze at Atlantic Sapphire Denmark. www.fishfarmingexpert.com/article/atlantic-sapphire-loses-all-in-fish-in-blaze-at-danish-site/ (accessed 9 May 2022)

FishSite (2021) Atlantic Sapphire report all fish lost after fire. https://thefishsite.com/articles/atlantic-sapphire-report-all-fish-lost-after-fire (accessed on 9 May 2022)

Fornshell G, Hinshaw JM (2008) Better management practices for flow-through aquaculture systems. In: Tucker CS, Hargreaves JA (eds) Environmental best management practices for aquaculture. John Wiley & Sons, Ames, IO, p 331–388

Fraser TW, Fjelldal PG, Hansen T, Mayer I (2012) Welfare considerations of triploid fish. Rev Fish Sci 20:192–211

Geitung L, Oppedal F, Stien LH, Dempster T, Karlsbakk E, Nola V, Wright DW (2019) Snorkel sea-cage technology decreases salmon louse infestation by 75% in a full-cycle commercial test. Int J Parasitol 49: 843–846

Gesto M, Madsen L, Andersen NR, El Kertaoui N, Kestemont P, Jokumsen A, Lund I (2021) Early performance, stress- and disease-sensitivity in rainbow trout fry (*Oncorhynchus mykiss*) after total dietary replacement of fish oil with rapeseed oil. Effects of EPA and DHA supplementation. Aquaculture 536:736446

Giménez-Candela M, Saraiva JL, Bauer H (2020) The legal protection of farmed fish in Europe — analysing the range of EU legislation and the impact of international animal welfare standards for the fishes in European aquaculture. Derecho Animal 11:1

Gismervik K, Tørud B, Kristiansen TS, Osmundsen T and others (2020) Comparison of Norwegian health and welfare regulatory frameworks in salmon and chicken production. Rev Aquacult 12:2396–2410

Gjedrem T, Baranski M (2010) Selective breeding in aquaculture: an introduction. Springer Science & Business Media, Dordrecht

Glover KA, Solberg MF, McGinnity P, Hindar K and others (2017) Half a century of genetic interaction between farmed and wild Atlantic salmon: status of knowledge and unanswered questions. Fish Fish 18:890–927

Gray M, Barbour N, Campbell B, Robillard AJ, Todd-Rodriguez A, Xiao H, Plough L (2021) Ecolabels can improve public perception and farm profits for shellfish aquaculture. Aquacult Environ Interact 13:13–20

Hixson SM (2014) Fish nutrition and current issues in aquaculture: the balance in providing safe and nutritious seafood, in an environmentally sustainable manner. J Aquac Res Dev 5:3

Holmer M (2010) Environmental issues of fish farming in offshore waters: perspectives, concerns and research needs. Aquacult Environ Interact 1:57–70

Huntingford FA, Kadri S (2014) Defining, assessing and promoting the welfare of farmed fish. Rev Sci Tech 33: 233–244

Hvas M, Folkedal O, Oppedal F (2021) Fish welfare in offshore salmon aquaculture. Rev Aquacult 13:836–852

Iversen M, Myhr AI, Wargelius A (2016) Approaches for delaying sexual maturation in salmon and their possible ecological and ethical implications. J Appl Aquacult 28: 330–369

Johansson D, Laursen F, Fernö A, Fosseidengen JE and others (2014) The interaction between water currents and salmon swimming behaviour in sea cages. PLOS ONE 9: e97635

Jonsson B, Jonsson N (2011) Farmed Atlantic salmon in nature. In: Ecology of Atlantic salmon and brown trout. Springer, Dordrecht, p 517–566

Juell J, Furevik D, Bjordal Å (1993) Demand feeding in salmon farming by hydroacoustic food detection. Aquacult Eng 12:155–167

Juell JE, Fernö A, Furevik D, Huse I (1994) Influence of hunger level and food availability on the spatial distribution of Atlantic salmon, *Salmo salar* L., in sea cages. Aquacult Res 25:439–451

Karlsson S, Diserud OH, Fiske P, Hindar K (2016) Widespread genetic introgression of escaped farmed Atlantic salmon in wild salmon populations. ICES J Mar Sci 73: 2488–2498

Kristiansen T, Bracke BMB (2020) A brief look into the origins of fish welfare science. In: Kristiansen TS, Fernö A, Pavlidis MA, van de Vis H (eds) The welfare of fish. Springer International Publishing, Cham, p 19–42

Krkošek M, Revie CW, Gargan PG, Skilbrei OT, Finstad B, Todd CD (2013) Impact of parasites on salmon recruitment in the Northeast Atlantic Ocean. Proc R Soc B 280: 20122359

Lillehaug A, Lunestad BT, Grave K (2003) Epidemiology of bacterial diseases in Norwegian aquaculture a description based on antibiotic prescription data for the ten-year period 1991 to 2000. Dis Aquat Org 53:115–125

Lu KL, Rahimnejad S, Ji ZL, Zhang CX, Wang L, Song K (2019) Comparative analysis of vertebral transcriptome in Japanese seabass (*Lateolabrax japonicus*) fed diets with varying phosphorus/calcium levels. Comp Biochem Physiol A Mol Integr Physiol 230:49–55

Lulijwa R, Rupia EJ, Alfaro AC (2020) Antibiotic use in aquaculture, policies and regulation, health and environmental risks: a review of the top 15 major producers. Rev Aquacult 12:640–663

Lyngstad TM, Hjortaas MJ, Kristoffersen AB, Markussen T, Karlsen ET, Jonassen CM, Jansen PA (2011) Use of molecular epidemiology to trace transmission pathways for infectious salmon anaemia virus (ISAV) in Norwegian salmon farming. Epidemics 3:1–11

Macaulay G, Wright D, Oppedal F, Dempster T (2020) Buoyancy matters: establishing the maximum neutral buoyancy depth of Atlantic salmon. Aquaculture 519:734925

Madaro A, Kjøglum S, Hansen T, Fjelldal PG, Stien LH (2021) A comparison of triploid and diploid Atlantic salmon (*Salmo salar*) performance and welfare under commercial farming conditions in Norway. J Appl Aquacult, doi:10.1080/10454438.2021.1916671

Mallekh R, Lagardère JP, Bégout Anras ML, Lafaye JY (1998) Variability in appetite of turbot, *Scophthalmus maximus* under intensive rearing conditions: the role of environmental factors. Aquaculture 165:123–138

Matos E, Dias J, Dinis MT, Silva TS (2017) Sustainability vs. quality in gilthead seabream (*Sparus aurata* L.) farming: Are trade-offs inevitable? Rev Aquacult 9:388–409

McIntosh P, Barrett LT, Warren-Myers F, Coates A and others (2022) Supersizing salmon farms in the coastal zone: a global analysis of changes in farm technology and location from 2005 to 2020. Aquaculture 553:738046

Miranda-de la Lama GC, Estévez-Moreno LX, Villarroel M, Rayas-Amor AA, María GA, Sepúlveda WS (2019) Consumer attitudes toward animal welfare-friendly products and willingness to pay: exploration of Mexican market segments. J Appl Anim Welf Sci 22:13–25

Miyashita S, Sawada Y, Hattori N, Nakatsukasa H, Okada T, Murata O, Kumai H (2000) Mortality of northern bluefin tuna *Thunnus thynnus* due to trauma caused by collision during growout culture. J World Aquacult Soc 31: 632–639

Moe Føre H, Thorvaldsen T, Osmundsen TC, Asche F, Tveterås R, Fagertun JT, Bjelland HV (2022) Technological innovations promoting sustainable salmon (*Salmo salar*) aquaculture in Norway. Aquacult Rep 24:101115

Moltumyr L, Nilsson J, Madaro A, Seternes T, Winger FA, Rønnestad I, Stien LH (2022) Long-term welfare effects of repeated warm water treatments on Atlantic salmon (*Salmo salar*). Aquaculture 548:737670

Mu H, Wei C, Xu W, Gao W, Zhang W, Mai K (2020) Effects of replacement of dietary fish oil by rapeseed oil on growth performance, anti-oxidative capacity and inflammatory response in large yellow croaker *Larimichthys crocea.* Aquacult Rep 16:100251

Naylor R, Burke M (2005) Aquaculture and ocean resources: raising tigers of the sea. Annu Rev Environ Resour 30: 185–218

Naylor RL, Hardy RW, Buschmann AH, Bush SR and others (2021) A 20-year retrospective review of global aquaculture. Nature 591:551–563

Nilsson J, Moltumyr L, Madaro A, Kristiansen TS and others (2019) Sudden exposure to warm water causes instant behavioural responses indicative of nociception or pain in Atlantic salmon. Vet Anim Sci 8:100076

Noble C, Kadri S, Mitchell DF, Huntingford FA (2008) Growth, production and fin damage in cage-held 0+ Atlantic salmon pre-smolts (*Salmo salar* L.) fed either a) on-demand, or b) to a fixed satiation–restriction regime: data from a commercial farm. Aquaculture 275: 163–168

Oca J, Reig L, Flos R (2002) Is land-based sea bream production a feasible activity on the northwest Mediterranean coast? Analysis of production costs. Aquacult Int 10: 29–41

Overton K, Dempster T, Oppedal F, Kristiansen TS, Gismervik K, Stien LH (2019) Salmon lice treatments and salmon mortality in Norwegian aquaculture: a review. Rev Aquacult 11:1398–1417

Overton K, Barrett LT, Oppedal F, Kristiansen TS, Dempster T (2020) Sea lice removal by cleaner fish in salmon aquaculture: a review of the evidence base. Aquacult Environ Interact 12:31–44

Powell A, Treasurer JW, Pooley CL, Keay AJ, Lloyd R, Imsland AK, Garcia de Leaniz C (2018) Use of lumpfish for sea-lice control in salmon farming: challenges and opportunities. Rev Aquacult 10:683–702

Primavera JH (2006) Overcoming the impacts of aquaculture on the coastal zone. Ocean Coast Manage 49: 531–545

Rana KJ, Siriwardena S, Hasan MR (2009) Impact of rising feed ingredient prices on aquafeeds and aquaculture production. FAO, Rome

Rauw W, Kanis E, Noordhuizen-Stassen E, Grommers F (1998) Undesirable side effects of selection for high production efficiency in farm animals: a review. Livest Prod Sci 56:15–33

Remen M, Sievers M, Torgersen T, Oppedal F (2016) The oxygen threshold for maximal feed intake of Atlantic salmon post-smolts is highly temperature dependent. Aquaculture 464:582–592

Robinson N, Karlsen C, Ytteborg E, Krasnov A, Gerwins J, Johnsen H, Kolarevic J (2021) Skin and bone development in Atlantic salmon (*Salmo salar*) influenced by hatchery environment. Aquaculture 544:737155

Roncarati A, Melotti P, Dees A, Mordenti O, Angellotti L (2006) Welfare status of cultured seabass (*Dicentrarchus labrax* L.) and seabream (*Sparus aurata* L.) assessed by blood parameters and tissue characteristics. J Appl Ichthyol 22:225–234

Samsing F, Rigby M, Tengesdal HK, Taylor RS and others (2021) Seawater transmission and infection dynamics of pilchard orthomyxovirus (POMV) in Atlantic salmon (*Salmo salar*). J Fish Dis 44:73–88

Saraiva JL, Castanheira MF, Arechavala-López P, Volstorf J, Studer BH (2018) Domestication and welfare in farmed fish. In: Teletchea F (ed) Animal domestication. IntechOpen, London, p 109–135

Scott MA, Dhillon RS, Schulte PM, Richards JG (2015) Physiology and performance of wild and domestic strains of diploid and triploid rainbow trout (*Oncorhynchus mykiss*) in response to environmental challenges. Can J Fish Aquat Sci 72:125–134

Serradell A, Torrecillas S, Makol A, Valdenegro V and others (2020) Prebiotics and phytogenics functional additives in low fish meal and fish oil based diets for European sea bass (*Dicentrarchus labrax*): effects on stress and immune responses. Fish Shellfish Immunol 100: 219–229

Shannon L, Waller L (2021) A cursory look at the fishmeal/oil industry from an ecosystem perspective. Front Ecol Evol 9:245

Somarakis S, Pavlidis M, Saapoglou C, Tsigenopoulos CS, Dempster T (2013) Evidence for 'escape through spawning' in large gilthead sea bream *Sparus aurata* reared in commercial sea-cages. Aquacult Environ Interact 3: 135–152

Sprague M, Betancor MB, Tocher DR (2017) Microbial and genetically engineered oils as replacements for fish oil in aquaculture feeds. Biotechnol Lett 39:1599–1609

Stien LH, Lind MB, Oppedal F, Wright DW, Seternes T (2018) Skirts on salmon production cages reduced salmon lice infestations without affecting fish welfare. Aquaculture 490:281–287

Stien LH, Tørud B, Gismervik K, Lien ME and others (2020a) Governing the welfare of Norwegian farmed salmon: three conflict cases. Mar Policy 117:103969

Stien LH, Størkersen KV, Gåsnes SK (2020b) Analysis of mortality data from survey on cleaner fish welfare. Report from the Norwegian Institute of Marine Research, Bergen. (in Norwegian). www.hi.no/en/hi/nettrapporter/rapport-fra-havforskningen-2020-6 (accessed 18 March 2022)

Sviland Walde C, Bang Jensen B, Pettersen JM, Stormoen M (2021) Estimating cage-level mortality distributions following different delousing treatments of Atlantic salmon (*Salmo salar*) in Norway. J Fish Dis 44: 899–912

Talbot C, Hole R (1994) Fish diets and the control of eutrophication resulting from aquaculture. J Appl Ichthyol 10:258–270

Taranger GL, Carrillo M, Schulz RW, Fontaine P and others (2010) Control of puberty in farmed fish. Gen Comp Endocrinol 165:483–515

Teodósio R, Engrola S, Colen R, Masagounder K, Aragão C (2020) Optimizing diets to decrease environmental impact of Nile tilapia (*Oreochromis niloticus*) production. Aquacult Nutr 26:422–431

Vollset KW, Dohoo I, Karlsen Ø, Halttunen E and others (2018) Disentangling the role of sea lice on the marine survival of Atlantic salmon. ICES J Mar Sci 75:50–60

Wacker S, Aronsen T, Karlsson S, Ugedal O and others (2021) Selection against individuals from genetic introgression of escaped farmed salmon in a natural population of Atlantic salmon. Evol Appl 14:1450–1460

Zhang C, Rahimnejad S, Wang Yr, Lu K, Song K, Wang L, Mai K (2018) Substituting fish meal with soybean meal in diets for Japanese seabass (*Lateolabrax japonicus*): effects on growth, digestive enzymes activity, gut histology, and expression of gut inflammatory and transporter genes. Aquaculture 483:173–182

Editorial responsibility: Pablo Arechavala-Lopez,
Esporles, Illes Balears, Spain
Reviewed by: K. Toledo-Guedes and 2 anonymous referees

Submitted: May 23, 2022
Accepted: July 12, 2022
Proofs received from author(s): September 6, 2022