Received: 12 November 2020 | Revised: 3 March 2021 | Accepted: 16 May 2021

DOI: 10.1111/raq.12587

REVIEWS IN Aquaculture

REVIEW

# Submerged cage aquaculture of marine fish: A review of the biological challenges and opportunities

**Michael Sievers**[1,2] | **Øyvind Korsøen**[1,3] | **Fletcher Warren-Myers**[4] | **Frode Oppedal**[1] | **Georgia Macaulay**[4] | **Ole Folkedal**[1] | **Tim Dempster**[4]

[1]Institute of Marine Research, Matre Aquaculture Research Station, Matredal, Norway

[2]Australian Rivers Institute–Coast & Estuaries, School of Environment and Science, Griffith University, Gold Coast, Queensland, Australia

[3]CageEye AS, Førde, Norway

[4]School of BioSciences, University of Melbourne, Melbourne, Victoria, Australia

**Correspondence**
Frode Oppedal, Institute of Marine Research, Matre Aquaculture Research Station, 5984 Matredal, Norway.
Email: frodeo@hi.no

**Funding information**
Norges Forskningsråd, Grant/Award Number: 267800

## Abstract

Surface-based cages are the dominant production technology for the marine finfish aquaculture industry. However, issues such as extreme weather events, poor environmental conditions, interactions with parasites, and conflicts with other coastal users are problematic for surface-based aquaculture. Submerged cages may reduce many of these problems and commercial interest in their use has increased. However, a broad synthesis of research into the effects of submerged culture on fish is lacking. Here, we review the current status of submerged fish farming worldwide, outline the biological challenges that fish with fundamentally different buoyancy control physiologies face in submerged culture, and discuss production benefits and problems that might arise from submerged fish farming. Our findings suggest that fish with closed swim bladders, and fish without swim bladders, may be well-suited to submerged culture. However, for fish with open swim bladders, such as salmonids, submergence is more complex as they require access to surface air to refill their swim bladders and maintain buoyancy. Growth and welfare of open swim bladder fish can be compromised by submergence for long periods due to complications with buoyancy regulation, but the recent addition of underwater air domes to submerged cages can alleviate this issue. Despite this advance, a greater understanding of how to couple advantageous environmental conditions with submerged culture to improve fish growth and welfare over the commercial production cycle is required if submerged cages are to become a viable alternative to surface-based cage aquaculture.

KEYWORDS
buoyancy, fish farming, fish welfare, mariculture, sea-cages, swimming behaviour

## 1 | INTRODUCTION

Industrial marine fish farming is a relatively young phenomenon but has grown to be a major industry in many regions of the world, producing some 6.6 million tons of fish per year.[1] The standard production units, sea-cage fish farms, are variations on a common theme,floating, surface-based structures holding large nets which contain thousands to hundreds of thousands of fish. The genesis of this technology came from the first Atlantic salmon farms in the 1960s and 1970s in Norway and Scotland, where nylon trawl nets were hung from wooden or polyethylene pipe structures.[2,3] Although more archaic forms of caged aquaculture have long been practised elsewhere, such as Asia,[4] shifts

[The copyright line for this article was changed on 29 June 2021 after original online publication]

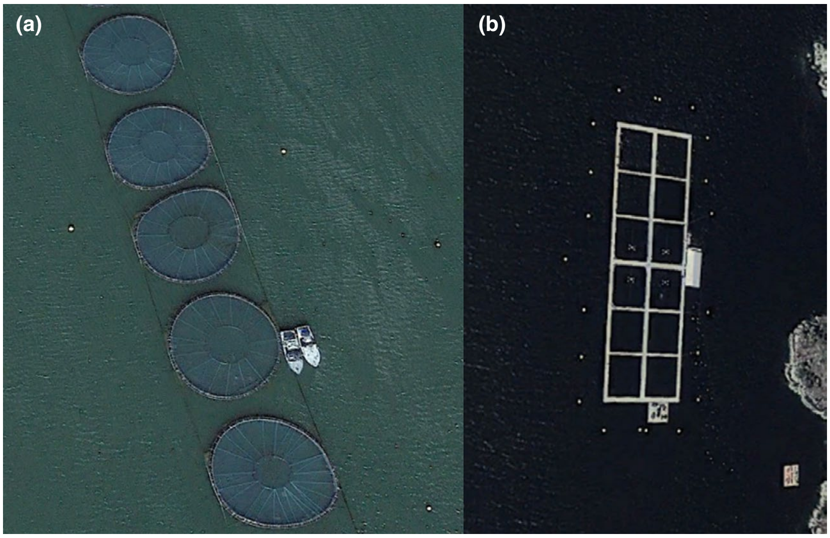

**FIGURE 1** Aerial view of surface-based cages to farm marine fish. (a) Circular plastic ring type farm; (b) steel platform farm. Photos from Google Earth

**TABLE 1** Hazards, depth of influence (the experience of the hazard within a pen), estimated duration of unsuitable surface conditions, the production problems caused for finish aquaculture in sea-cages, and example source references

| Hazards | Depth of influence (m) | Duration | Production problem | Source |
|---|---|---|---|---|
| Storm | 0–10 | Hours-weeks | Cage and or net rupture and subsequent escapes | 7,8 |
| Current/net deformation | 0–20 | Hours-weeks | Net deformations leading to excessive crowding of fish | 105 |
| Ice | Surface structures | Hours-days | Cage damage leading to escapes | 106 |
| Algal bloom | 0–20 | Days-weeks | Fish mortality and sub-lethal effects on welfare | 107,108 |
| Jellyfish bloom | 0–10 | Hours-weeks | Fish mortality and sub-lethal effects on welfare | 109,110 |
| Parasitic lice larvae *L. salmonis* on salmonids | 0–5 | Persistent | Infestation, leading to reduce growth when severe, and lethal and sub-lethal effects due to treatments | 111 |
| Parasitic lice larvae *C. rogercresseyi* on salmonids | 0–10 | Persistent | Infestation, leading to reduce growth when severe, and lethal and sub-lethal effects due to treatments | 112 |
| Parasitic skin fluke *N. girellae* on farmed kingfish | 0–5 | Persistent | | 12 |
| Amoebic gill disease | 0–5 | Weeks | Reduced gill health | 13 |
| Tapeworms (*Eubothrium* sp.) | 0–10 | Weeks | Growth reduction | 10 |
| Reduced oxygen | Variable | Hours-weeks | Loss of appetite, reduced growth rates | 113 |
| Unsuitable temperature | 0-10[a] | Hours-weeks | Loss of appetite, reduced growth rates | 114 |
| High aluminium levels | 0–2 | Days-weeks | | 115 |
| Biofouling | 0-10[a] | Summer, autumn | Low oxygen levels when severe; poor water quality after cleaning of cages | 103,116 |

[a] Variable, but usually greatest in surface waters.

to commercial-scale marine cages didn't occur here until the late 1970s – the early 1980s.[5] Stepwise innovation of this technology has generated the modern, highly engineered structures which dominate production today, with nets hung from either steel platforms or circular plastic rings (Figure 1). Most major commercial marine finfish aquaculture operations worldwide have adopted this production system because it is proven to be effective and comes production-ready 'off the shelf'.

Despite their widespread use, a range of issues are associated with surface-based production, including net deformations and cage breakdowns from storms which can lead to escape events, parasites and diseases, algal and jellyfish blooms, and the presence of less-than-optimal culture conditions such as high temperatures, low oxygen levels and contaminants from freshwater inputs (see Table 1 for a full list of problems). Further, several commercially important species such as sea bream (*Sparus aurata*), Atlantic cod (*Gadus morhua*) and cobia (*Rachycentron canadum*) are benthopelagic or benthic in nature, so production in surface sea cages may not provide ideal conditions. The production inefficiencies caused by these problems can be substantial, and the broader environmental costs of parasite transmission to wild stocks[6] and escaped fish from net breakdowns[7,8] create much of the controversy surrounding the industry and erode its public perception.

Culture in submerged cages, whether temporary or permanent, could alleviate the extent or severity of many of these problems. Deeper environments typically have more stable temperatures and salinities, largely avoid the full impact of storms, and are less favoured by the infectious stage of problematic parasites.[9-13] The adoption of submerged cages may also unlock new areas for production where surface-based sea-cage technologies are inappropriate due to surface wind and waves, or by social constraints such as space conflicts with other coastal users.[14]

Perhaps due to the dominance of surface-based sea-cages in the marketplace, the question of whether alternate marine production units, such as submerged cages, provide production advantages remains largely unanswered for most marine species. In addition, a range of biological and technical challenges associated with submerged culture (Table 1) have proven difficult to solve thus far, except for some species with physiologies more accepting of long-term submergence (e.g. cobia). As a result, submerged culture as a commercial method is still very much in its infancy. There are few sufficiently replicated trials that have assessed the effects of submerged culture on key production and welfare parameters, and most trials rely on data from one or few submerged cages with no or few control cages (i.e. traditional surface cages; Table 2). Such experimental designs provide minimal power to detect effects, and results generated are largely inadequate to properly assess whether submerged culture provides production advantages or disadvantages. Still, the small but growing body of literature (Figure 2) provides critical knowledge to further the development and application of submerged culture. The technological challenges of submerged culture, such as cage and mooring design, have been discussed elsewhere.[2] Instead, here we: (1) provide an overview of the current status of submerged culture worldwide; (2) outline the biological challenges that different fish species with fundamentally different buoyancy control physiologies face in submerged culture; and (3) focus on the behavioural, physiological, biological and environmental considerations and challenges. By bringing together this knowledge base and recommending avenues for future research, this review aims to help guide future industry development and support the research effort.

## 2 | THE STATUS OF SUBMERGED CAGE AQUACULTURE

Submerging cultured fish has occurred since at least the 1970s, with early experiments on rainbow trout[15] and more comprehensive trials in the 1980s with Atlantic salmon.[16,17] These were largely either short-term submergence or shallow depths (Table 2) and were often attempts to avoid temporary hazardous surface conditions (e.g. extreme winter surface cooling). In the last decade, there has been a considerable surge in research into submerged culture (Figure 2). To date, at least 11 finfish species that have been produced, largely experimentally, in submerged cages of various sizes, at different depths, and over various submergence durations (Table 2; it is probable that additional species have been trialled, but published research on these is not available or were not identified).

Several species appear to cope and grow well in submerged cages, yet few species have been produced at truly commercial scales in submerged cages. Collaboration between industry and research to develop a submerged culture in Costa Rica has resulted in the successful start-up of a submerged culture industry for cobia, now produced at commercial scales.[18-22] These cobia sustain high growth rates when reared in submerged cages[19] with relatively low ecological impacts on the surrounding environment.[22] Almaco jack (*Seriola rivoliana*) are also produced commercially in submerged cages in countries such as Puerto Rico, the Bahamas and Hawaii[19] (www.bofish.com/farm/mariculture/). Seabass and seabream in the Mediterranean have also been produced in commercial submersible cages,[23] and experiments with the submergence of these species showed comparable growth rates with surface culture.[24]

There has been considerable and growing research interest into the submerged culture of several species that have not yet been produced at full commercial scale. Commercial-scale proof-of-concept testing occurred in the early 2000s for Atlantic cod,[25,26] primarily in response to concerns over limited coastal sites available for production in several countries. Experiments are promising, with submerged Atlantic cod on the east coast of the US[25-27] and in Norway[28,29] had production parameters similar to those from surface-based sea-cages. Furthermore, amberjack (*Seriola dumerili*) and red porgy (*Pagrus pagrus*) have also been shown to experience good growth rates when submerged compared to wild fish and surface-reared fish, respectively,[30,31] but we are unaware of commercial-scale efforts.

Worldwide, interest in commercial submerged Atlantic salmon farming is growing, with farms deployed or under development in New Zealand, China, Chile and Scotland. This has been spurred by a rapid development towards commercial-scale production. For instance, in response to a Norwegian government scheme to support new technological concepts to tackle the aquaculture industry's environmental challenges, several companies proposed submerged cages in their successful applications. These include Norway Royal Salmon's Arctic Offshore Farming cage concept and Akva Group's Atlantis Subsea Farming concept. Despite the high interest, the submerged culture of salmonids has had limited success. While small-scale trials with submerged cages in freshwater settings demonstrate they can be used to overwinter salmon beneath surface ice,[17] a range of studies at industry-scale demonstrate mixed results on submergence as a viable production method. Salmonids grow poorly when held in submerged cages for longer than a month in the on-growing phase in seawater.[32,33] Even when continuous lighting reduced some of the negative side effects of submergence, growth rates were still

**TABLE 2** Research on finfish production within submerged cages, including species information, level of replication, production parameters and location. Research identified using the search terms outlined in Figure 2 and bibliographies of those papers

| | Cage size m$^3$ | Sub cage no. | Control cage no. | Fish per cage | Depth (top-bottom; m) | Duration | Region/Sea | Preferred depth (m) | References |
|---|---|---|---|---|---|---|---|---|---|
| Open swim bladder (physostomous) | | | | | | | | | |
| Rainbow trout (*Oncorhynchus mykiss*) | – | – | – | – | – | – | Russia | 0–50 | 15 |
| | 32 | | | 182 | 30–32 | 60 days | Norway | | 55 |
| | – | – | – | – | – | – | Russia | | 117 |
| Atlantic salmon (*Salmo salar*) | 21 | 2 | 0 | 250 | 1.5–6 | 180 days | New Hampshire US | 0–50 | 17 |
| | | 1 | 0 | | | 9–15 days | U.K. | | 16 |
| | 450 | | | 2000 | 10–18 | 90 days | Norway | | 118 |
| | 1600 | 2 | 2 | 500 | 4–15 | 17 days | Norway | | 35 |
| | 1600 | 2 | 2 | 4000 | 4–15 | 22 days | Norway | | 36 |
| | 2000 | 3 | 3 | 3500 | 10–25 | 42 days | Norway | | 32 |
| | 1600 | 2 | 2 | 3800 | 4–14 | 22 days | Norway | | 33 |
| | 2000 | 3 | 3 | 2300 | 10–24 | 24 days | Norway | | 33 |
| | 175 | 1 | 0 | 15 | 10–17 | 14 days | Norway | | 53 |
| | 272 | 1 | 0 | 10 | 1–10 | 19 h | Norway | | 119 |
| | 2000 | 3 | 3 | 823–916 | 10–24 | 42 days | Norway | | 34 |
| | 175 | 4 | 0 | 200–300 | 1–8 | 44 h | Norway | | 120 |
| | 2000 | 3 | 3 | 1700 | 10–24 | 56 days[a] | Norway | | 37 |
| | 2880 | 3 | 0 | 10,000 | 10–30 | 35–49 days | Norway | | 38 |
| | 1728 | 3 | 3 | 3359–6700 | 15–27 | 365 days | Norway | | Warren-Myers et al. *in prep* |
| | 100 | 6 | 3 | 1000 | 4–7 | 22 days | Norway | | 45 |
| Closed swim bladder (physoclistous) | | | | | | | | | |
| Sea bass (*Dicentrarchus labrax*) | 2000 | 2 | 2 | 75,000 | 5–15 | 12 months | Mediterranean | 10–50 | 24 |
| | | 2 | 6 | | | >12 months | Mediterranean | | 98 |
| Red porgy (*Pagrus pagrus*) | 636 | 1 | 1 | 3000 | 35–45 | 4 months | Mediterranean | 40–100 | 31 |
| Mediterranean amberjack (*Seriola dumerili*) | 75 | 2 | 0 | 800 | 10–15 | 4 months | Mediterranean | 10–50 | 30 |
| | 0.02 | 2 | 1 | 10 | 2–4 | 4 h | Japan | | 12 |
| Pacific bluefin tuna (*Thunnus orientalis*) | 15,000 | | | 1 | 2–24 | 2 days | Japan | 30–60 | 121 |
| Almaco jack (*Seriola rivoliana*) | 3000 | 8 | 0 | – | 10–25 | – | Hawaii | 10–50 | 122 |
| | 3000 | | | – | 10–25 | – | Hawaii | | 123 |
| Pacific threadfin (*Polydactylus sexfilis*) | 3000 | | | – | 10–25 | – | Hawaii | 10–50 | 123 |

(Continues)

**TABLE 2** (Continued)

| | Cage size $m^3$ | Sub cage no. | Control cage no. | Fish per cage | Depth (top-bottom; m) | Duration | Region/Sea | Preferred depth (m) | References |
|---|---|---|---|---|---|---|---|---|---|
| Atlantic cod (*Gadus morhua*) | 3000 | 1 | 0 | 30000 | 12–18 | 17 months | New Hampshire US | 10–400 | [25] |
| | 3000 | 1 | 0 | 50000 | 15–30.5 | 5 months | New Hampshire US | | [26,27] |
| | 175 | 4 | 0 | 400 | 20–27 | 14 months | Norway | | [29] |
| | 175 | 1 | 0 | 100 | Various | <7 days | Norway | | [28] |
| Haddock (*Melanogrammus aeglefinus*) | 600 | 1 | 0 | 3000 | 12–21 | 17 months | New Hampshire US | 50–400 | [25] |
| No swim bladder | | | | | | | | | |
| Cobia (*Rachycentron canadum*) | 2700 | 2 | 0 | 8000 | 10–25 m | 12 months | Puerto Rico | 10–50 | [19] |

[a]That fish were provided surface access weekly during submergence.

lower relative to surface cages.[34] In contrast, shorter-term submergence for periods less than 21 days appear to have relatively little effect on growth rates[35-37] and have been promoted as an effective way to avoid temporary negative surface events such as storms.[36] However, integrating an air dome into the ceiling of a submerged cage to enable salmonids to refill their swim bladders underwater[38] led to sustained good growth rates over submergence periods up to 7 weeks. Since this trial, 18,000 salmon have been grown from 0.2 kg to harvest size (~5 kg) in three submerged cages fitted with air domes for a full sea production cycle of 14 months (Warren-Myers et al. *in review*. Growth rates of salmon were poorer (harvest weight; submerged fish 3.3 ± 0.2 kg, control fish 6.2 ± 0.3 kg; mean ± SE than in co-located standard surface-based cages due to persistent unfavourable environmental conditions experienced at the deeper depths the submerged fish were held in (Warren-Myers et al. unpubl. data.)

## 3 | THE BIOLOGICAL OUTCOMES, CONSIDERATIONS AND CHALLENGES OF SUBMERGED FISH FARMING

One of the main biological considerations surrounding the adoption and success of submerged cages is centred around fish buoyancy regulation. Swim bladders make up 3%–6% of the body volume in marine fish species, and reduce the metabolic cost of maintaining buoyancy by around 90% compared to hydrodynamic compensation alone.[39] Buoyancy problems can arise in multiple ways in submerged cages, with swim bladders becoming either too full or too empty, dependent upon the physiological system a fish species possesses to fill and empty their swim bladder. Swim bladder anatomy and mechanisms for regulating volume differ among species.[40] Fish can be classified by whether their swim bladder has a conjunction via the mouth cavity (physostome, Greek *physa* = bladder, *stoma* = mouth) or not (physoclist; Greek *kleistos* =closed), while other fish have no swim bladder at all (Figure 3). These fundamentally different buoyancy control physiologies require careful consideration when attempting to culture fish in submerged cages.

### 3.1 | Physostomous fish

### 3.1.1 | Swim bladder, buoyancy and maximum neutral buoyancy depth

The swim bladder in physostomous species is connected to the oesophagus via a short pneumatic duct.[41] Physostomes need to refill their swim bladder periodically by snapping and swallowing air during ‘porpoising’ rolls or jumps out of the water.[42] For all physostomes, achieving neutral buoyancy reduces the energetic cost of horizontal swimming and sustaining vertical position in the water column.[39] The maximum depth at which physostomous fish attain neutral buoyancy is likely an important influence of swimming depth behaviour.

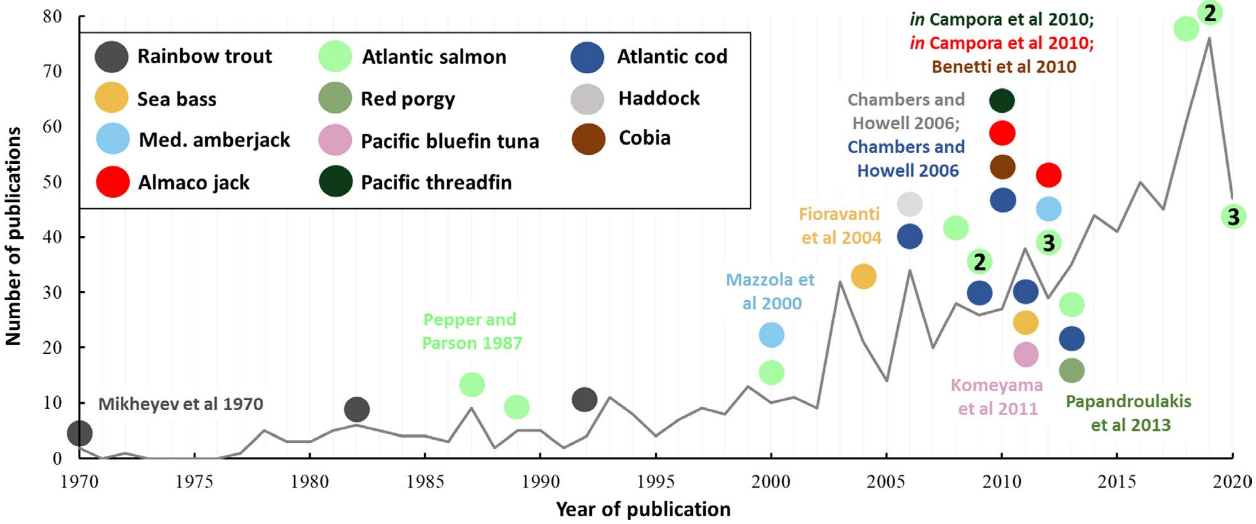

FIGURE 2 Relative research effort over time on submerged cage finfish aquaculture, measured by the number of journal articles published in each year (Web of Science: 'submerged or submergence or submersible) AND (aquaculture OR mariculture OR "fish farm*"'). Dots represent studies presenting empirical evidence of the outcomes of submerged culture (details in Table 2), with references provided for the first published evidence of submerged culture for each fish species. Numbers within dots represent number of studies for that year (if >1)

For example, wild Atlantic salmon spend >80% of their time in the upper 10 m of the ocean,[43] which may in part be explained by their ability to fill their swim bladder at the surface and achieve neutral buoyancy at shallow depths, but not deeper. Forcing physostomous fish to swim deeper than the maximum depth at which they are neutrally buoyant results in negative buoyancy. Therefore, determining this depth threshold is important for farmed fish that will be forcibly submerged. The extent to which a fish can fill their swim bladder will influence this neutral buoyancy depth limit.

Using an increased excess mass test (IEMT),[44] estimated the maximum neutral buoyancy depth (MNBD) of juvenile Chinook salmon (*Oncorhynchus tshawytscha*) to be a median of 6.7 m in freshwater. In the IEMT, the maximum swim bladder volume is calculated. The excess mass is surgically added to the fish and incrementally increased. The fish must compensate for this added mass via gulping air at the surface. Mass is added until the fish can no longer achieve neutral buoyancy at which point the test is terminated and MNBD can be calculated. Recent application of this method to a farmed strain of Atlantic salmon indicates their MNBD is <20 m in seawater, irrespective of fish size.[45] This does not, however, mean that above 20 m depth is optimal for salmon. Fish can swim (of which they do day and night) and generate lift (even though we do not know exactly how much). Optimal depth is therefore somewhat deeper. Optimal depth is where the "optimal" growth conditions are, which vary with location, season and latitude. In the wild, fish occasionally dive into deep water down to 500–1200 m.[46,47] When air domes (see below for discussion) are applied at depth, MNBD will be shifted deeper, which opens up a new depth range within which salmon can be neutrally buoyant.

Until recently, buoyancy has not been considered in salmon aquaculture as surface-based cages allow full surface access for refilling.[48] This explains the lack of knowledge surrounding the basic limits of salmon buoyancy to date. Dependent on lipid content,[49] life history stage [50,51] and factors influencing swim bladder volume, buoyancy in fish is dynamic over time. Therefore, understanding how neutral buoyancy limits change across species and life stages is essential to determine the suitability of submerged cages at different stages during production. The few examples that exist of

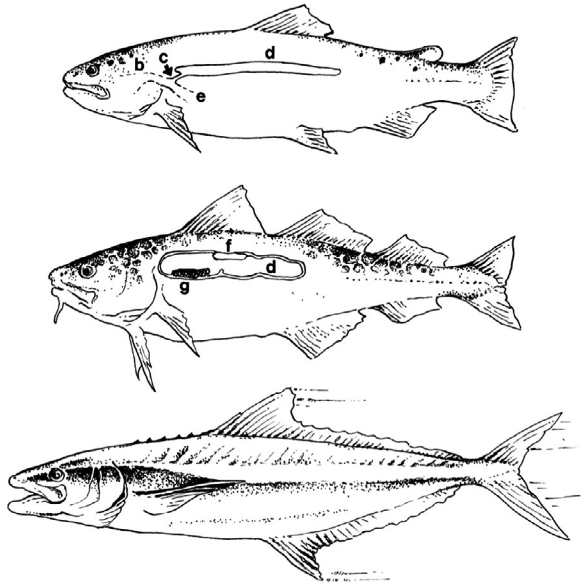

FIGURE 3 Schematic diagram of different swim bladder types: (1) physostomous (salmon), (2) physostome (cod) and (3) fish without swim bladder (cobia); b = buccal cavity, c = pneumatic duct, d = swim bladder, e = oseouphagus into stomach, f = oval, g = *rete mirabile* (gas gland). Drawings by Stein Mortensen, Institute of Marine Research, Norway

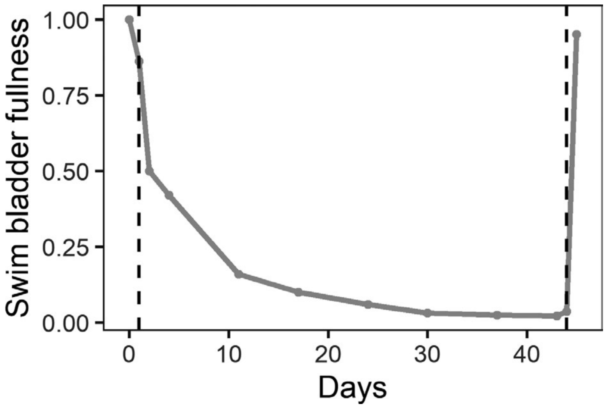

**FIGURE 4** Gas content in swim bladder of salmonids before, during and after submergence (data from Sievers et al.[34]). Fish are submerged at day 1 (left dashed vertical line), after which gas quickly begins to diffuse out until the swim bladder slowly becomes empty after ~3 weeks (subject to a suite of additional factors). Following re-surfacing (right dashed vertical line), salmonids rapidly re-fill their swim bladders

mapping swim bladder volumes during forced submergence reveal that Atlantic salmon swim bladders emptied over ~3 weeks, largely irrespective of the submergence depth tested (Figure 4).[32,34,36]

Buoyancy challenges for physostomous fish in submerged culture, however, may not be insurmountable. Novel techniques and technologies built into submerged cages now allow fish access to air and provide the ability to refill their swim bladders via gulping. Short, repeated submergence periods with intermittent lifting to access the surface and allow fish to refill their swim bladders is effective at reducing the negative impacts of forced submergence in Atlantic salmon.[35,37] However, this solution may not suit all submerged farm operations for logistical reasons. A recent technological advance added an underwater air dome to submerged cages to allow fish to access air at depth.[38,53] The addition of an air dome allows salmonids to refill their swim bladder while submerged and to regulate their buoyancy, which results in the fish maintaining normal balance. This solution to buoyancy regulation now means the industry is one step closer to the successful submerged culture of physostomous species. Commercial-scale testing of air dome technology in submerged cages is in progress (Warren-Myers et al. unpubl. data) and will reveal if farmers can take advantage of optimal environmental conditions for production within the water column.

### 3.1.2 | Swimming behaviours

Tilted swimming with an upwards angle of attack (i.e. head up, tail down) provides lift[52,54] and is symptomatic of physostomous fish subjected to long-term submergence without access to air as seen in Fig 5.[32,34] Tilted swimming can be problematic as it gradually leads to exhaustion and loads the muscles in the tail region to such a degree that some vertebrae can become compressed (i.e. lordosis,[16,17,55] leading to vertebral overload and deformation.[32] Continuous, artificial lighting during submergence can reduce tilted swimming angle, alleviating vertebral deformities.[34] In smaller salmon (<500 g), tilted swimming did not occur under short-term (17–21 days) submergence.[35,36] Submerged physostomous fish also swim 1.3–3.4 times faster than normal.[32,34,36,37] Tilted swimming behaviour and faster swimming speeds in submerged cages allow fish to generate lift and compensate for negative buoyancy due to underinflated swim bladders. The addition of air domes to submerged cages has largely resolved these behaviour issues by allowing fish to freely access air whenever needed.[38]

Swimming depths of farmed salmonids are driven by both environmental gradients (e.g. temperature and light) in the water column, and internal motivations such as hunger levels (see review by Oppedal et al.[48] Salmonids are typically fed at the surface, with fish moving up into shallow depths when feed enters a cage. The diurnal vertical migration patterns of Atlantic salmon in standard surface cages are similar to those in submerged cages,[32,35,36] but submerged fish exhibit greater vertical space use during the day.[33,36] Based on the currently available evidence, there appear to be few issues associated with depth-related swimming behaviour of fish in submerged cages.

### 3.1.3 | Growth and welfare

Achieving comparable fish growth and welfare is essential if submerged culture is to become a viable alternative to surface-based cage production. Based on the published research on physostomous fishes (mainly salmonids), comparable growth has not been achieved for a full production cycle, although most research has been short-term (i.e. <56 days; Table 2). Short-term periods of submergence (7–22 days) of Atlantic salmon, without access to air, generally has no negative effect on growth or welfare,[36,37] but this may be due to the submergence period not being long enough for the acute effects of negative buoyancy to result in a measurable reduction in growth. One short-term submergence trial reported lower SGRs in submerged fish, but this was likely due to lower temperatures in submerged compared to surface cages.[35] Submergence for longer periods (>40 days) without access to air, led to sub-optimal growth rates and some fin and snout erosion.[32,34]

The recent addition of air domes to submerged cages to resolve fish buoyancy issues resulted in a submergence trial run for ~40 days reporting no negative effect on growth or welfare on salmon.[38] However, salmon submerged for a full production cycle in cages fitted with air domes had lower growth rates and poorer welfare scores for snout and eye condition, likely due to periods of colder temperatures experienced from summer through autumn and low oxygen levels in winter/spring at depth (Warren-Myers et al. unpubl. data). Ensuring salmon experience their preferred environmental conditions is central to achieving optimal growth in sea-cages.[48] Hence, whilst issues around buoyancy may have been resolved, ensuring submerged fish are grown under environmental conditions optimal for growth and welfare remains a challenge. Ongoing trials

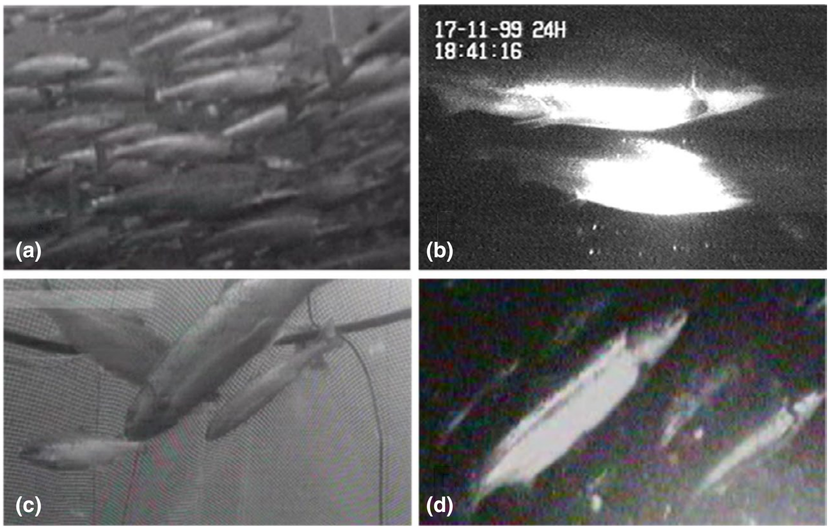

**FIGURE 5** Salmon in a surface based sea-cage at daytime schooling at ~0.6 BL/s (a), at night slow, dispersed distribution in a slightly tilted head-down position (b), positively buoyant salmon 2 h after re-filling of swim bladder from an artificial air filled dome at 10 m depth after being kept submerged without air for 7 days (c) and, negatively buoyant salmon swimming in tilted head-up angle at ~36° after 41 days of submergence below 10 m depth (d); fish size 3.5–5.0 kg, from Korsøen et al.[33] and Korsøen et al.[53]

are testing if air-dome fitted cages and flexible submergence depth matching the best environment through the seasons can solve the issues (F. Oppedal, personal comment). Other trials are testing if air-bubbling can be used by the physostome fish for swim bladder refilling (O. Folkedal, personal comment).

## 3.2 | Physoclistous fish

### 3.2.1 | Swim bladder and buoyancy

Like physostomous fish, physoclistous fish also fill their swim bladder by swallowing air, but only when larvae.[56,57] During development, the connection between the swim bladder and gut disappears, resulting in a closed swim bladder disconnected from the external environment (Figure 3).[41,56] Instead of swallowing air, gas is secreted into and resorbed from the swim bladder by diffusion with the bloodstream.[58,59] Although this allows physoclistous fish to swim and often maintain neutral buoyancy at great depths, rapid ascension and the resultant gas expansion can rupture the swim bladder, sometimes leading to death.[60-62] Consequently, this group of fishes have restricted free vertical ranges (FVR) and in the wild ascend slowly to avoid injury or becoming too buoyant.[63,64] To partially counteract this shortcoming, some physoclistous fish such as samson fish (*Seriola hippos*) and silver trevally (*Pseudocaranx georgianus*) have evolved the ability to release excess air from expanding swim bladders during ascent through a specialised vent near the back of the mouth.[56] However, most cultured physoclists, such as Atlantic cod, sea bass, red porgy, amberjack and haddock, have not evolved this unique anatomical structure. Consequently, issues with submerged culture generally centre around the rapidity of cage submergence and re-surfacing, with similar impacts as barotrauma exhibited by fish caught in deep waters by fishers.[65,66]

The impact of a sudden ascent for physoclistous fish depends on the degree of pressure reduction. If the vertical distance is within the FVR and the fish can retain behavioural control (e.g. by downward swimming), any stress will likely be short-term and diminish as gas is released from the swim bladder *via* the oval organ and reabsorptive capillary network. Extending beyond the FVR will lead to an uncontrolled and highly stressful experience, where the lift force of the expanding swim bladder will accelerate the movement of fish towards the surface, creating a negative feedback buoyancy loop. If a fish is unable to swim forcefully downward to a depth where swim bladder pressure is safe, it will quickly surface with an overinflated swim bladder and may experience symptoms of barotrauma, which can be lethal.[67] If rapid surfacing causes a pressure reduction greater than approximately 70%, a cod's swim bladder can rupture[68] and gas releases out the anal opening.[60] This bursting mechanism functions as a safety valve preventing a total loss of buoyancy control, with some individuals able to recover under optimal conditions.[60] Whether recovery would occur under commercial settings, however, is unclear. Other physoclists, such as red snapper (*Lutjanus campechanus*, Poey 1860), do not have this safety valve and the expanding gas in their swimming bladder following rapid changes in pressure often causes catastrophic decompression, which everts the stomach and bulges the eyes, leading to mortality.[61] The lifting of submerged cages with physoclistous fish must therefore be done slowly to reduce stress and limit mortality. Since sea-caged cod voluntarily ascend to depths representing a maximum of 40% pressure reduction, raising submerged cages would ideally involve lifting stages each representing a 40% pressure reduction or less with a pause of at least 10 h between each lift.[28] The vertical distance that represents a 40% pressure reduction depends on the starting depth, for example, 30 to 14, 20 to 8, 14 to 4, 10 to 2 and 7 to 0 m (see Figure 1 in Korsøen et al.[28]).

Pressure reductions from lifting are not the only issue with submerging physoclists; submerge too deep too quickly, and these fish cannot adjust their buoyancy quickly enough by pumping air into the swim bladder. This creates negative buoyancy until the fish can compensate, which can drive unsatisfactory crowding towards the bottom of cages with negative consequences for welfare. For example, Korsøen et al.[28] witnessed this phenomenon when cod were rapidly submerged in cages equivalent to pressure increases of 100%–200%, and higher than their FVR of 50%. Under these circumstances, more than half of the cod rested on the net-bottom after 1.5 h at low temperature and after 4 h at high temperature, and appetite was reduced for several days.[28] Therefore, as with cage lifting, cage lowering should be done slowly, with the FVR in mind to avoid these problems.

Future research should attempt to quantify swim bladder gas resorption rates for other physoclistous species that might be suited to aquaculture, as they likely differ from cod, and thus, differ in their tolerance to submergence and surfacing speeds.

### 3.2.2 | Swimming behaviours

The vertical movements of wild physoclistous fish are thought to depend on temperature, depth, season and ontogenetic stage.[63,69,70,71] Cultured Atlantic cod distribute shallower than wild cod, particularly wild males (~40 m depth compared to farmed fish (~20–30 m)).[71] Further, when submerged, swimming speeds (1.3–2.3 times) and tail beat frequencies (1.4–2.3 times) increase immediately, and fish swim with an average 30-degree head-up swimming angle.[28] However, cod return to normal swimming angles after 16–60 h.[28] Although comparative research on swimming behaviours of submerged physoclists is scarce, there is no evidence suggesting compromised production as a result of altered swimming behaviours under submerged conditions.

### 3.2.3 | Growth and welfare

Current evidence suggests that cultured, physoclistous fish have high growth and welfare under submerged conditions. For example, Atlantic cod submerged below 20 m for 14 months had very high survival (~99%), grew faster than estimated rates based on empirical models,[72] and had negligible problems during sexual maturation with or without artificial light.[29] Maricchiolo et al.[73] also documented similar growth rates of seabass between surface-based and submerged cages, with those reared in submerged cages also having lower stress levels (measured as higher haemolytic activity and lysozyme levels). Finally, red porgy in submerged cages displayed more natural skin colours and had lower skin melatonin content than in surface-based cages, indicative of more optimal rearing conditions.[31]

## 3.3 | Fish without swim bladder

Fish without swim bladders are always negatively buoyant, and cope by either continuous swimming and/or by utilising hydrodynamically efficient body shapes, and large fins and tails that generate lift with forward swimming (e.g. mackerel, tuna and cobia; Figure 3). There is no constraint with regards to vertical migration as no gas expansion or compression occurs. Consequently, these fish utilise a large depth range. Wild cobia, for example, freely swim anywhere within 100 m of the surface.[74] Cobia (and likely other species without swim bladders) do not suffer the same issues from long term submergence as physostomous and physoclistous fish, such as lacking surface access or rapid lifting of sea-cages. As such, submerged culture may be well suited to fish without swim bladders. Indeed, as mentioned, submerged cobia grew more rapidly than surface-reared cobia, suggesting submerged culture can provide a perfect match between low stress and optimal water quality.[19] In fact, cobia stocked in submerged cages are often observed spawning naturally, and several commercial submerged culture facilities are in operation.[75]

## 3.4 | Broader challenges and bottlenecks

There are a suite of broader challenges or bottlenecks for the commercial adoption of a submerged culture of finfish, that are more related to technological, social or financial factors rather than biological. Since these are still inherently related to the specific biology of the cultured species, we briefly discuss several of these here (also see Fredheim and Langan[2])For example, although submerged culture can alleviate poor surface conditions, at other times, surface conditions are superior to those at depth. Developing capacity to monitor environmental conditions and manipulate cage depths to access optimum conditions will overcome this issue and enable ‘dynamic submergence’ as a culture strategy. Consideration of the rapidity of these depth changes is of course important for physoclists in this process. Further, no serious commercial investment in submerged production – for Atlantic salmon for example – will occur until there is clear evidence that production metrics, and thus profitability, are uncompromised in submerged cages. This requires considerable investment in research and technological advancements that may alleviate current issues of submergence (e.g., air domes).

Finally, although primarily a technological consideration, feeding is the key element of successful submerged culture so we briefly address this here.[2] From a biological perspective, providing feed underwater could be less efficient than surface feeding if (i) fish do not descend below the feed entrance depth, (ii) the space below the feed entrance point is too limited, or (iii) there is insufficient horizontal spreading of feed throughout the cage, creating high-density feeding zones where scramble competition for the available feed leads to negative interactions for the fish. Typically, underwater feed is delivered using gravity alone or combined with a water pump at the cage (e.g. AKVAgroup subsea feeding in Bui et al.[76]) or the use of pumped water from a barge including the feed through pipes and final spreading using several outlets or a rotating pipe at the end using the water flow as force (e.g. Vard Aqua's Appetite Feed Control System).

## 4 | THE BENEFITS OF SUBMERGED CULTURE

### 4.1 | Optimisation of environmental conditions

Fish have optimal environmental conditions at which survival, growth and condition are maximised.[77,78] In some, but not all locations, deeper waters can provide more stable or appropriate temperatures for production, salinities and oxygen levels, as they are often below thermoclines and haloclines. Increased risk of poor oxygen availability, suboptimal growth and increased mortalities occurs at the higher end of surface temperatures for salmon (>12°C), which occur in several Atlantic salmon producing countries during summer and early autumn.[48,79,80,81,82,83] Conversely, during winter when surface water is coldest, growth rates slow. Submergence to find better temperatures may provide better growth performance during these times, and short-term periodic submergence can be a solution to avoid negative surface events such as heat waves, storms or swell. As an additional benefit, less frequent or severe damage to sea-cages from storms events will lessen the number of farmed fish escaping into the wild.[8]

### 4.2 | Reduced interaction with harmful organisms

Submergence can be an effective measure for parasite and disease control. Salmon lice (*Lepeophtheirus salmonis*), often regarded as the greatest threat for the sustainability, growth and social perception of much of the Atlantic salmon industry[11,84] distribute predominantly in surface layers,[9,85] so attracting or keeping fish deeper can lower infestation rates.[34,86,87] For example, the submergence of Atlantic salmon has resulted in periods of reduced salmon lice infestations of 72 to 96% compared to surface-reared fish[34]. Such reductions would almost certainly lead to long-term welfare benefits from the direct effects of infestation and reduced need for de-lousing procedures which can prove harmful.[88,89] Given the negative social implications of salmon lice, such reductions would also help enhance public perception of the industry. Other problematic lice species that plague finfish aquaculture in other countries, such as *Caligus elongatus and C. rogercresseyi*, are not as surface-oriented as salmon lice,[90] so submergence may not reduce infestations in locations affected by these lice species. However, Nilsen et al.[91] did find reduced lice numbers on fish reared in closed cages with water intake at 25 m depth. Tapeworm infestations (*Eubothrium* sp.) in salmon were reduced when a central barrier tube (snorkel) was added to standard cages to move salmon deeper, but retain surface access.[10] The reasoning for this was believed to be that the intermediate hosts of *Eubothrium*, night-time surface-dwelling calanoid copepods, were kept away and not preyed upon by the salmon.

Gill disorders arising from interactions with harmful organisms is another important health issue for sea-cage culture.[92,93] Amoebic gill disease, for example, is widespread and requires frequent and expensive treatments.[94] Skin flukes (*Neobenedenia girellae*) are problematic for the production of amberjack in Japan,[95] several mass mortality events of farmed salmon have been caused by blooms of gelatinous zooplankton,[96] and there is an increasing trend in the abundance of toxic phytoplankton species and areas affected compared to previous decades.[97] Many of these disease-causing organisms are more prevalent in surface layers,[13] so submergence will likely reduce interactions with and impacts to farmed fish. For example, infestations by skin flukes were reduced by submerging cages to 2 and 4 m depth,[12] while seabass in cages submerged below the thermocline exhibited lower infection rates from intestinal myxosporean parasites than fish in surface cages, as faecal transmission from seabirds were less likely.[98] As aquatic animal health is key to production success, future submerged cage trials should focus on documenting disease levels and making comparisons to surface-based cages.

The settlement of unwanted organisms, or biofouling, on sea-cages is a major production issue as it occludes nets, reducing oxygen and waste transfer in and out of cages, increases the weight on and drag of farm infrastructure, and can directly harm fish.[99,100] Since light intensity decreases rapidly with depth in seawater due to scattering and absorption, fouling algal species that require light for photosynthesis are less prevalent on structures deeper in the water column.[101] Other problematic fouling species, such as the hydroid *Ectopleura larynx* which can release stinging fragments when disturbed,[102] are often more abundant on the shallower portion of nets.[103] Submerged net cages may, thus, attract less biofouling overall, as well as less problematic fouling species.

### 4.3 | Unlocking new production areas

The adoption of submerged cages could unlock new areas for production where surface-based sea-cage technologies are inappropriate due to surface wind and waves, or due to space conflicts with other coastal users.[14] Further, given the growing interest in offshore aquaculture, submerged cages will likely be crucial to reduce expensive construction costs and avoid large swells and extreme offshore weather events such as hurricanes. Offshore production sites have the added advantage of greater waste dispersal leading to limited benthic impacts beneath below cages,[22] which can occur in nearshore, shallow water culture.[104]

## 5 | CONCLUSIONS AND FUTURE RESEARCH

Submerging aquaculture cages hold the promise of providing relief from periods of less than optimal environmental conditions, reducing fish interactions with harmful organisms, and unlocking new production areas devoid of conflict with other coastal users. However, not all fish species will be similarly suited to submerged culture, and a suite of key challenges and bottlenecks stand in the way of commercial production of several species. Based on the available evidence, fewer issues exist for the submerged culture of physoclists and fish without swim bladders. Finding optimal culture sites based on the biology of the species, focusing on streamlining operational techniques, and documenting behavioural and welfare responses to long-term submergence at commercial scales will ground-truth the projected benefits of submerged culture.

Physostomous fish present unique and complex challenges for submerged culture; recent advances have overcome many of these issues. Recent developments in technologies that allow fish to refill their swim bladders while submerged via an underwater air dome [38,53] means fish can be grown in submerged cages for a full production cycle. Concerted testing at industry scale is required to unlock the potential of submerged cages for salmonids and resolve remaining production and welfare issues. The use of dynamic submergence, where cage depth is manipulated to maintain fish in the most optimal conditions in the water column year-round may reduce some of these issues.

If submerged culture is to mature and fulfil its promise, research to empirically document production and environmental benefits, and issues surrounding fish welfare throughout the production cycle needs to lead the way. Robust, industry-scale experiments of new production technologies are difficult to conduct, but possible[76,88] and significant co-investment from government and industry is required to achieve them. Conducting meaningful scientific research will thus assist in ensuring the successful adoption of submerged culture, where possible. For physostomous fish, in particular, this requires a shift from the typically short-term, unreplicated, and uncontrolled trials found in the current literature (see Table 2), towards long-term (preferably over the full production cycle), replicated and controlled trials (e.g., Warren-Myers et al. *in prep*). Once these are established, the technological developments required to realise functioning submergence systems that integrate the myriad of procedures (e.g. net handling, feeding, sorting, harvesting, depth preference) required in modern aquaculture can follow.

## ACKNOWLEDGEMENTS

Funding was provided by the Research Council of Norway to the project "Environmental requirements and welfare indicators for new cage farming locations and systems" (Future Welfare; project no. 267800).

## CONFLICT OF INTEREST

The authors declare no conflict of interest.

## ORCID

*Michael Sievers* https://orcid.org/0000-0001-7162-1830
*Fletcher Warren-Myers* https://orcid.org/0000-0001-9451-2127
*Frode Oppedal* https://orcid.org/0000-0001-8625-0331
*Georgia Macaulay* https://orcid.org/0000-0001-6354-1283
*Ole Folkedal* https://orcid.org/0000-0001-6823-4143
*Tim Dempster* https://orcid.org/0000-0001-8041-426X

## REFERENCES

1. FAO. *The State of World Fisheries and Aquaculture 2020. Sustainability in Action*. Food and Agriculture Organization of the United Nations; 2020.
2. Fredheim A, Langan R. Advances in technology for off-shore and open ocean finfish aquaculture. In: Burnell, G & Allan, G, eds. *New Technologies in Aquaculture*. Sawston: Woodhead Publishing Series in Food Science, Technology and Nutrition; 2009:914–944.
3. Tilseth S, Hansen T, Møller D. Historical development of salmon culture. *Aquaculture*. 1991;98:1-9.
4. Bao-Tong H. Cage culture development and its role in aquaculture in China. *Aquacult Res*. 1994;25:305-310.
5. Chen J, Guang C, Xu H, et al. A review of cage and pen aquaculture: China. *FAO Fish Tech Pap*. 2007;498:53.
6. Costello MJ. How sea lice from salmon farms may cause wild salmonid declines in Europe and North America and be a threat to fishes elsewhere. *Proc R Soc Lond, Ser B: Biol Sci*. 2009;276:3385-3394.
7. Jackson D, Drumm A, McEvoy S, et al. A pan-European valuation of the extent, causes and cost of escape events from sea cage fish farming. *Aquaculture*. 2015;436:21-26.
8. Jensen Ø, Dempster T, Thorstad E, Uglem I, Fredheim A. Escapes of fishes from Norwegian sea-cage aquaculture: causes, consequences and prevention. *Aquacult Environ Interact*. 2010;1:71-83.
9. Crosbie T, Wright D, Oppedal F, Johnsen I, Samsing F, Dempster T. Effects of step salinity gradients on salmon lice larvae behaviour and dispersal. *Aquacult Environ Interactions*. 2019;11:181-190.
10. Geitung L, Wright DW, Stien LH, Oppedal F, Karlsbakk E. Tapeworm (*Eubothrium* sp.) infection decreased in lice barrier snorkel sea cages during commercial-scale study. *Aquaculture*. 2021;541:736774.
11. Heuch PA, Parsons A, Boxaspen K. Diel vertical migration: A possible host-finding mechanism in salmon louse (*Lepeophtheirus salmonis*) copepodids. *Can J Fish Aquat Sci*. 1995;52:681-689.
12. Shirakashi S, Hirano C, Ishitani H, Ishimaru K. Diurnal pattern of skin fluke infection in cultured amberjack, Seriola dumerili, at different water depths. *Aquaculture*. 2013;402:19-23.
13. Wright DW, Nowak B, Oppedal F, Bridle A, Dempster T. Depth distribution of the amoebic gill disease agent, *Neoparamoeba perurans*, in salmon sea-cages. *Aquacult Environ Interact*. 2015;7:67-74.
14. Dempster T, Sanchez-Jerez P. Aquaculture and coastal space management in Europe: an ecological perspective. In: Holmer, M, Black, K, Duarte, CM, Marbà, N, Karakassis, I, eds. *Aquaculture in the Ecosystem*. Dordrecht: Springer; 2008.
15. Mikheyev P, Meysner YV, Mikheyev V. The importance of contact with the air in the life of the rainbow trout. *J Ichthyol*. 1970;10:691-693.
16. Ablett RF, Marr CR, Roberts JD. Influence of chronic subsurface retention on swimming activity of Atlantic salmon (*Salmo salar*) in cold temperature conditions. *Aquacult Eng*. 1989;8:1-13.
17. Pepper VA, Parsons P. An experiment on aquaculture potential of Atlantic salmon *Salmo salar* L. kelts in Newfoundland Canada. *Aquac Fish Manage*. 1987;18:327-344.
18. Benetti DD, Benetti GI, Rivera JA, Sardenberg B, O'Hanlon B. Site selection criteria for open ocean aquaculture. *Mar Technol Soc J*. 2010a;44:22-35.
19. Benetti DD, O'Hanlon B, Rivera JA, Welch AW, Maxey C, Orhun MR. Growth rates of cobia (*Rachycentron canadum*) cultured in open ocean submerged cages in the Caribbean. *Aquaculture*. 2010b;302:195-201.
20. Benetti DD, Orhun MR, Sardenberg B, et al. Advances in hatchery and grow-out technology of cobia *Rachycentron canadum* (Linnaeus). *Aquac Res*. 2008a;39:701-711.
21. Benetti DD, Sardenberg B, Welch A, Hoenig R, Orhun MR, Zink I. Intensive larval husbandry and fingerling production of cobia *Rachycentron canadum*. *Aquaculture*. 2008b;281:22-27.

22. Welch AW, Knapp AN, El Tourky S, Daughtery Z, Hitchcock G, Benetti D. The nutrient footprint of a submerged-cage offshore aquaculture facility located in the tropical Caribbean. *J World Aquacult Soc*. 2019;50:299-316.
23. Cardia F, Lovatelli A. A review of cage aquaculture: Mediterranean Sea. *FAO Fisheries Technical Paper*. 2007;498:159.
24. Maricchiolo G, Mirto S, Caruso G, et al. Welfare status of cage farmed European sea bass (*Dicentrarchus labrax*): A comparison between submerged and surface cages. *Aquaculture*. 2011;314:173-181.
25. Chambers MD, Howell WH. Preliminary information on cod and haddock production in submerged cages off the coast of New Hampshire, USA. *ICES J Mar Sci*. 2006;63:385-392.
26. Rillahan C, Chambers M, Howell WH, Watson WH III. A self-contained system for observing and quantifying the behavior of Atlantic cod, Gadus morhua, in an offshore aquaculture cage. *Aquaculture*. 2009;293:49-56.
27. Rillahan C, Chambers MD, Howell WH, Watson WH III. The behavior of cod (*Gadus morhua*) in an offshore aquaculture net pen. *Aquaculture*. 2011;310:361-368.
28. Korsøen OJ, Dempster T, Fosseidengen JE, Ferno A, Heegaard E, Kristiansen TS. Behavioural responses to pressure changes in cultured Atlantic cod (*Gadus morhua*): Defining practical limits for submerging and lifting sea-cages. *Aquaculture*. 2010;308: 106-115.
29. Korsøen OJ, Dempster T, Fosseidengen JE, et al. Towards cod without spawning: artificial continuous light in submerged sea-cages maintains growth and delays sexual maturation for farmed Atlantic cod *Gadus morhua*. *Aquacult Environ Interact*. 2013;3:245-255.
30. Mazzola A, Favaloro E, Sara G. Cultivation of the Mediterranean amberjack, *Seriola dumerili* (Risso, 1810), in submerged cages in the Western Mediterranean Sea. *Aquaculture*. 2000;181:257-268.
31. Papandroulakis N, Mesa-Rodriguez A, Anastasiadis P, Lisac D, Asderis M, Pavlidis M. Installation, operation and evaluation of a submerged cage at 45M depth in crete for the rearing of red porgy Pagrus pagrus. *Aquac Res*. 2013;44:1196-1205.
32. Korsøen OJ, Dempster T, Fjelldal PG, Oppedal F, Kristiansen TS. Long-term culture of Atlantic salmon (*Salmo salar* L.) in submerged cages during winter affects behaviour, growth and condition. *Aquaculture*. 2009;296:373-381.
33. Korsøen OJ, Dempster T, Oppedal F, Kristiansen TS. Individual variation in swimming depth and growth in Atlantic salmon (*Salmo salar* L.) subjected to submergence in sea-cages. *Aquaculture*. 2012a;334:142-151.
34. Sievers M, Korsøen Ø, Dempster T, et al. Growth and welfare of submerged Atlantic salmon under continuous lighting. *Aquacult Environ Interact*. 2018;10:501-510.
35. Dempster T, Juell J-E, Fosseidengen JE, Fredheim A, Lader P. Behaviour and growth of Atlantic salmon (*Salmo salar* L.) subjected to short-term submergence in commercial scale sea-cages. *Aquaculture*. 2008;276:103-111.
36. Dempster T, Korsoen O, Folkedal O, Juell J-E, Oppedal F. Submergence of Atlantic salmon (*Salmo salar* L.) in commercial scale sea-cages: a potential short-term solution to poor surface conditions. *Aquaculture*. 2009;288:254-263.
37. Glaropoulos A, Stien LH, Folkedal O, Dempster T, Oppedal F. Welfare, behaviour and feasibility of farming Atlantic salmon in submerged cages with weekly surface access to refill their swim bladders. *Aquaculture*. 2019;502:332-337.
38. Oppedal F, Folkedal O, Stien L, et al. Atlantic salmon cope in submerged cages when given access to an air dome that enables fish to maintain neutral buoyancy. *Aquaculture*. 2020;525:735286.
39. Alexander RM. Physical aspects of swimbladder function. *Biol Rev*. 1966;41:141-176.
40. Berenbrink M, Koldkjær P, Kepp O, Cossins AR. Evolution of oxygen secretion in fishes and the emergence of a complex physiological system. *Science*. 2005;307:1752-1757.
41. Fänge R. Gas exchange in fish swim bladder. *Rev Physiol Biochem Pharmacol*. 1983;97:111–158.
42. Furevik DM, Bjordal A, Huse I, Ferno A. Surface-activity of Atlantic salmon (*Salmo salar*) in net pens. *Aquaculture*. 1993;110:119-128.
43. Hedger RD, Rikardsen AH, Strøm JF, Righton DA, Thorstad EB, Næsje TF. Diving behaviour of Atlantic salmon at sea: effects of light regimes and temperature stratification. *Mar Ecol Prog Ser*. 2017;574:127-140.
44. Pflugrath, BD, Brown, RS & Carlson, TJ. Maximum neutral buoyancy depth of juvenile Chinook salmon: implications for survival during hydroturbine passage. *Trans Am Fish Soc*. 2012;141:520–525.
45. Macaulay G, Bui S, Oppedal F, Dempster T. Acclimating salmon as juveniles prepares them for a farmed life in sea-cages. *Aquaculture*. 2020;523:735227.
46. Einarsson SM, Guðjónsson S, Jónsson IR, Guðbrandsson J. Deep-diving of Atlantic salmon (*Salmo salar*) during their marine feeding migrations. *Environ Biol Fishes*. 2018;101:1707-1715.
47. Strøm JF, Thorstad EB, Hedger RD, Rikardsen AH. Revealing the full ocean migration of individual Atlantic salmon. *Anim Biotelem*. 2018;6:2.
48. Oppedal F, Dempster T, Stien LH. Environmental drivers of Atlantic salmon behaviour in sea-cages: A review. *Aquaculture*. 2011;311:1-18.
49. Folkedal O, Stien LH, Nilsson J, Torgersen T, Fosseidengen JE, Oppedal F. Sea caged Atlantic salmon display size-dependent swimming depth. *Aquat Living Resour*. 2012;25:143-149.
50. Coombs S, Boyra G, Rueda L, et al. Buoyancy measurements and vertical distribution of eggs of sardine (*Sardina pilchardus*) and anchovy (*Engraulis encrasicolus*). *Mar Biol*. 2004;145:959-970.
51. Weitkamp LA. Buoyancy regulation by hatchery and wild coho salmon during the transition from freshwater to marine environments. *Trans Am Fish Soc*. 2008;137:860-868.
52. Ona E. Physiological factors causing natural variations in acoustic target strength of fish. *J Mar Biol Assoc UK*. 1990;70:107-127.
53. Korsøen OJ, Fosseidengen JE, Kristiansen TS, Oppedal F, Bui S, Dempster T. Atlantic salmon (*Salmo salar* L.) in a submerged sea-cage adapt rapidly to re-fill their swim bladders in an underwater air filled dome. *Aquacult Eng*. 2012b;51:1-6.
54. Magnuson JJ. Hydrodynamics, morphology and behavior. In: Hoar WS, Randall DJ, eds. *Locomotion, Book 7*. San Diego, CA: Academic Press; 1979.
55. Fosseidengen J, Boge E, Huse I. A survey with rainbow trout and salmon in submersible cages. *Nor Fiskeoppdrett*. 1982;10:24-25.
56. Hughes JM, Rowland AJ, Stewart J, Gill HS. Discovery of a specialised anatomical structure in some physoclistous carangid fishes which permits rapid ascent without barotrauma. *Mar Biol*. 2016;163:169.
57. McCune AR, Carlson RL. Twenty ways to lose your bladder: common natural mutants in zebrafish and widespread convergence of swim bladder loss among teleost fishes. *Evol Dev*. 2004;6:246-259.
58. Ross L. The haemodynamics of gas resorption from the physoclist swimbladder: the structure and morphometrics of the oval in *Pollachim virens* (L). *J Fish Biol*. 1979;14:261-266.
59. Strand E, Jørgensen C, Huse G. Modelling buoyancy regulation in fishes with swimbladders: bioenergetics and behaviour. *Ecol Model*. 2005;185:309-327.
60. Midling KØ, Koren C, Humborstad O-B, Sæther B-S. Swimbladder healing in Atlantic cod (*Gadus morhua*), after decompression and rupture in capture-based aquaculture. *Mar Biol Res*. 2012;8:373-379.
61. Rummer JL, Bennett WA. Physiological effects of swim bladder overexpansion and catastrophic decompression on red snapper. *Trans Am Fish Soc*. 2005;134:1457-1470.
62. Tytler P, Blaxter J. Adaptation by cod and saithe to pressure changes. *Neth J Sea Res*. 1973;7:31-45.
63. Arnold G, Walker MG. Vertical movements of cod (*Gadus morhua* L.) in the open sea and the hydrostatic function of the swimbladder. *ICES J Mar Sci*. 1992;49:357-372.

64. Stewart J, Hughes JM. Swim bladder function and buoyancy control in pink snapper (*Pagrus auratus*) and mulloway (*Argyrosomus japonicus*). *Fish Physiol Biochem*. 2014;40:335-346.
65. Curtis JM, Johnson MW, Diamond SL, Stunz GW. Quantifying delayed mortality from barotrauma impairment in discarded red snapper using acoustic telemetry. *Mar Coast Fish*. 2015;7:434-449.
66. Gravel M-A, Cooke SJ. Severity of barotrauma influences the physiological status, postrelease behavior, and fate of tournament-caught smallmouth bass. *N Am J Fish Manage*. 2008;28:607-617.
67. Gitschlag GR, Renaud ML. Field experiments on survival rates of caged and released red snapper. *N Am J Fish Manage*. 1994;14:131-136.
68. Humborstad O-B, Mangor-Jensen A. Buoyancy adjustment after swimbladder puncture in cod *Gadus morhua*: an experimental study on the effect of rapid decompression in capture-based aquaculture. *Mar Biol Res*. 2013;9:383-393.
69. Godø OR, Michalsen K. Migratory behaviour of north-east Arctic cod, studied by use of data storage tags. *Fish Res*. 2000;48:127-140.
70. Hobson VJ, Righton D, Metcalfe JD, Hays GC. Vertical movements of North Sea cod. *Mar Ecol Prog Ser*. 2007;347:101-110.
71. Meager JJ, Skjæraasen JE, Fernö A, et al. Vertical dynamics and reproductive behaviour of farmed and wild Atlantic cod *Gadus morhua*. *Mar Ecol Prog Ser*. 2009;389:233-243.
72. Björnsson B, Steinarsson A, Árnason T. Growth model for Atlantic cod (*Gadus morhua*): effects of temperature and body weight on growth rate. *Aquaculture*. 2007;271:216-226.
73. Maricchiolo G, Caruso T, Caruso G, Genovese L, Mirto S. Rearing conditions and welfare in *Dicentrarchus labrax*: A comparison between submerged and surface cages. *Biol Mar Mediterr*. 2010;17:274-275.
74. Miao S, Jen CC, Huang CT, Hu S-H. Ecological and economic analysis for cobia *Rachycentron canadum* commercial cage culture in Taiwan. *Aquacult Int*. 2009;17:125-141.
75. Benetti DD, Orhun MR, Zink I, et al. Aquaculture of cobia (*Rachycentron canadum*) in the Americas and the Caribbean. In: Liao, IC, Leaño, EM, eds. *Cobia Aquaculture: Research, Development and Commercial Production*. Keelung: Asian Fisheries Society, The Fisheries Society of Taiwan, World Aquaculture Society, National Taiwan Ocean University; 2007.
76. Bui S, Stien LH, Nilsson J, Trengereid H, Oppedal F. Efficiency and welfare impact of long-term simultaneous in situ management strategies for salmon louse reduction in commercial sea cages. *Aquaculture*. 2020;520: 734934.
77. Remen M, Sievers M, Torgersen T, Oppedal F. The oxygen threshold for maximal feed intake of Atlantic salmon post-smolts is highly temperature-dependent. *Aquaculture*. 2016;464:582-592.
78. Sambraus F, Remen M, Olsen RE, et al. Changes in water temperature and oxygen: the effect of triploidy on performance and metabolism in large farmed Atlantic salmon. *Aquacult Environ Interact*. 2018;10:157-172.
79. Burke M, Grant J, Filgueira R, Stone T. Oceanographic processes control dissolved oxygen variability at a commercial Atlantic salmon farm: Application of a real-time sensor network. *Aquaculture*. In press. 533:736143.
80. Stehfest KM, Carter CG, McAllister JD, Ross JD, Semmens JM. Response of Atlantic salmon *Salmo salar* to temperature and dissolved oxygen extremes established using animal-borne environmental sensors. *Sci Rep*. 2017;7:1-10.
81. Stien LH, Lind MB, Oppedal F, Wright DW, Seternes T. Skirts on salmon production cages reduced salmon lice infestations without affecting fish welfare. *Aquaculture*. 2018;490:281-287.
82. Stien LH, Nilsson J, Hevroy EM, et al. Skirt around a salmon sea cage to reduce infestation of salmon lice resulted in low oxygen levels. *Aquacult Eng*. 2012;51:21-25.
83. Wade NM, Clark TD, Maynard BT, et al. Effects of an unprecedented summer heatwave on the growth performance, flesh colour and plasma biochemistry of marine cage-farmed Atlantic salmon (*Salmo salar*). *J Therm Biol*. 2019;80:64-74.
84. Costello MJ. Ecology of sea lice parasitic on farmed and wild fish. *Trends Parasitol*. 2006;22:475-483.
85. Crosbie T, Wright DW, Oppedal F, Dalvin S, Myksvoll MS, Dempster T. Impact of thermoclines on the vertical distribution of salmon lice larvae. *Aquacult Environ Interact*. 2020;12:1-10.
86. Bui S, Oppedal F, Sievers M, Dempster T. Behaviour in the toolbox to outsmart parasites and improve fish welfare in aquaculture. *Rev Aquacult*. 2019;11:168-186.
87. Hevroy EM, Boxaspen K, Oppedal F, Taranger GL, Holm JC. The effect of artificial light treatment and depth on the infestation of the sea louse *Lepeophtheirus salmonis* on Atlantic salmon (*Salmo salar* L.) culture. *Aquaculture*. 2003;220:1-14.
88. Geitung L, Oppedal F, Stien LH, et al. Snorkel sea-cage technology decreases salmon louse infestation by 75% in a full-cycle commercial test. *Int J Parasitol*. 2019;49:843-846.
89. Overton K, Dempster T, Oppedal F, Kristiansen TS, Gismervik K, Stien LH. Salmon lice treatments and salmon mortality in Norwegian aquaculture: a review. *Rev Aquacult*. 2019;11:1398-1417.
90. á Norði G, Simonsen K, Danielsen E, et al. Abundance and distribution of planktonic *Lepeophtheirus salmonis* and *Caligus elongatus* in a fish farming region in the Faroe Islands. *Aquacult Environ Interact*. 2015;7:15-27.
91. Nilsen A, Nielsen KV, Biering E, Bergheim A. Effective protection against sea lice during the production of Atlantic salmon in floating enclosures. *Aquaculture*. 2017;466:41-50.
92. Baxter EJ, Rodger HD, McAllen R, Doyle TK. Gill disorders in marine-farmed salmon: investigating the role of hydrozoan jellyfish. *Aquacult Environ Interact*. 2011;1:245-257.
93. Gunnarsson G, Karlsbakk E, Blindheim S, et al. Temporal changes in infections with some pathogens associated with gill disease in farmed Atlantic salmon (*Salmo salar* L). *Aquaculture*. 2017;468:126-134.
94. Oldham T, Rodger H, Nowak BF. Incidence and distribution of amoebic gill disease (AGD)—an epidemiological review. *Aquaculture*. 2016;457:35-42.
95. Hirazawa N, Takano R, Hagiwara H, Noguchi M, Narita M. The influence of different water temperatures on *Neobenedenia girellae* (Monogenea) infection, parasite growth, egg production and emerging second generation on amberjack *Seriola dumerili* (Carangidae) and the histopathological effect of this parasite on fish skin. *Aquaculture*. 2010;299:2-7.
96. Doyle TK, De Haas H, Cotton D, et al. Widespread occurrence of the jellyfish *Pelagia noctiluca* in Irish coastal and shelf waters. *J Plankton Res*. 2008;30:963-968.
97. Anderson DM, Burkholder JM, Cochlan WP, et al. Harmful algal blooms and eutrophication: examining linkages from selected coastal regions of the United States. *Harmful Algae*. 2008;8:39-53.
98. Fioravanti ML, Caffara M, Florio D, Gustinelli A, Marcer F. *Sphaerospora dicentrarchi* and *S. testicularis* (Myxozoa: Sphaerosporidae) in farmed European seabass (*Dicentrarchus labrax*) from Italy. *Folia Parasitol*. 2004;51:208-210.
99. Bannister J, Sievers M, Bush F, Bloecher N. Biofouling in marine aquaculture: a review of recent research and developments. *Biofouling*. 2019;35(6):631-648.
100. Fitridge I, Dempster T, Guenther J, de Nys R. The impact and control of biofouling in marine aquaculture: a review. *Biofouling*. 2012;28:649-669.
101. Sievers M, Dempster T, Fitridge I, Keough MJ. Monitoring biofouling communities could reduce impacts to mussel aquaculture by allowing synchronisation of husbandry techniques with peaks in settlement. *Biofouling*. 2014;30:203-212.
102. Baxter EJ, Sturt MM, Ruane NM, Doyle TK, McAllen R, Rodger HD. (2012) Biofouling of the hydroid *Ectopleura larynx* on aquaculture nets in Ireland: Implications for finfish health.

103. Guenther J, Misimi E, Sunde LM. The development of biofouling, particularly the hydroid *Ectopleura larynx*, on commercial salmon cage nets in Mid-Norway. *Aquaculture*. 2010;300:120-127.
104. Karakassis I, Tsapakis M, Hatziyanni E, Papadopoulou K-N, Plaiti W. Impact of cage farming of fish on the seabed in three Mediterranean coastal areas. *ICES J Mar Sci*. 2000;57:1462-1471.
105. Lader P, Dempster T, Fredheim A, Jensen Ø. Current induced net deformations in full-scale sea-cages for Atlantic salmon (*Salmo salar*). *Aquacult Eng*. 2008;38:52-65.
106. Jensen Ø. (2006) Assessment of technical requirements for floating fish farms—based on escape incidents. January 2006. Rep no SFH80 A 66056.
107. Díaz PA, Álvarez A, Varela D, et al. Impacts of harmful algal blooms on the aquaculture industry: Chile as a case study. *Perspect Phycol*. 2019;6(1-2):39-50.
108. Quiñones RA, Fuentes M, Montes RM, Soto D, León-Muñoz J. Environmental issues in Chilean salmon farming: a review. *Rev Aquacult*. 2019;11:375-402.
109. Bosch-Belmar M, Azzurro E, Pulis K, et al. Jellyfish blooms perception in Mediterranean finfish aquaculture. *Mar Policy*. 2017;76:1-7.
110. Kintner A, Brierley AS. Cryptic hydrozoan blooms pose risks to gill health in farmed North Atlantic salmon (*Salmo salar*). *J Mar Biol Assoc UK*. 2019;99:539-550.
111. Overton K, Dempster T, Oppedal F, Kristiansen TS, Gismervik K, Stien LH. Salmon lice treatments and salmon mortality in Norwegian aquaculture: a review. *Rev Aquacult*. 2018.
112. Molinet C, Cáceres M, Gonzalez MT, et al. Population dynamic of early stages of Caligus rogercresseyi in an embayment used for intensive salmon farms in Chilean inland seas. *Aquaculture*. 2011;312:62-71.
113. Solstorm D, Oldham T, Solstorm F, et al. Dissolved oxygen variability in a commercial sea-cage exposes farmed Atlantic salmon to growth limiting conditions. *Aquaculture*. 2018;486:122-129.
114. Johansson D, Ruohonen K, Kiessling A, et al. Effect of environmental factors on swimming depth preferences of Atlantic salmon (*Salmo salar* L.) and temporal and spatial variations in oxygen levels in sea cages at a fjord site. *Aquaculture*. 2006;254:594-605.
115. Bjerknes V, Fyllingen I, Holtet L, Teien HC, Rosseland BO, Kroglund F. Aluminium in acidic river water causes mortality of farmed Atlantic Salmon (*Salmo salar* L.) in Norwegian fjords. *Mar Chem*. 2003;83:169-174.
116. Braithwaite RA, Carrascosa MCC, McEvoy LA. Biofouling of salmon cage netting and the efficacy of a typical copper-based antifoulant. *Aquaculture*. 2007;262:219-226.
117. Bugrov LY. Rainbow trout breeding in the submersible cages used offshore oil platforms. *Aquaculture*. 1992;100:169.
118. Osland H, Sandvik J, Holm J, Heuch P, Bakke S. Studie av lakselus-påslag og tilvekst hos Atlantisk laks (*Salmo salar*) i nedsenkede merder. HSF-report, R-NR 4:01-22.
119. Bui S, Oppedal F, Korsøen ØJ, Dempster T. Modifying Atlantic salmon behaviour with light or feed stimuli may improve parasite control techniques. *Aquacult Environ Interact*. 2013;3:125-133.
120. Dempster T, Bui S, Overton K, Oppedal F. Jumping to treat sea lice: Harnessing salmon behaviour to enable surface-based chemotherapeutant application. *Aquaculture*. 2019;512: 734318.
121. Komeyama K, Kadota M, Torisawa S, Suzuki K, Tsuda Y, Takagi T. Measuring the swimming behaviour of a reared Pacific bluefin tuna in a submerged aquaculture net cage. *Aquat Living Resour*. 2011;24:99-105.
122. Sims NA. Kona Blue Water Farms case study: permiting, operations, marketing, environmental impacts, and impediments to expansion of global open ocean mariculture. Proc Technical workshop proceedings: Expanding mariculture farther offshore: technical, environmental, spatial, and governance challenges; 2013.
123. Campora, CE, Hokama, Y, Tamaru, CS, Aderson, B & Vincent, D. Evaluating the Risk of Ciguatera Fish Poisoning from Reef Fish Grown at Marine Aquaculture Facilities in Hawaii. *J World Aquacult Soc*. 2010;41:61–67.

**How to cite this article:** Sievers M, Korsøen Ø, Warren-Myers F, et al. Submerged cage aquaculture of marine fish: A review of the biological challenges and opportunities. *Rev Aquacult*. 2021;00:1–14. https://doi.org/10.1111/raq.12587

Author/s:
Sievers, M;Korsoen, O;Warren-Myers, F;Oppedal, F;Macaulay, G;Folkedal, O;Dempster, T

Title:
Submerged cage aquaculture of marine fish: A review of the biological challenges and opportunities

Date:
2021-06-22

Citation:
Sievers, M., Korsoen, O., Warren-Myers, F., Oppedal, F., Macaulay, G., Folkedal, O. & Dempster, T. (2021). Submerged cage aquaculture of marine fish: A review of the biological challenges and opportunities. REVIEWS IN AQUACULTURE, 14 (1), pp.106-119. https://doi.org/10.1111/raq.12587.