REVIEW

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

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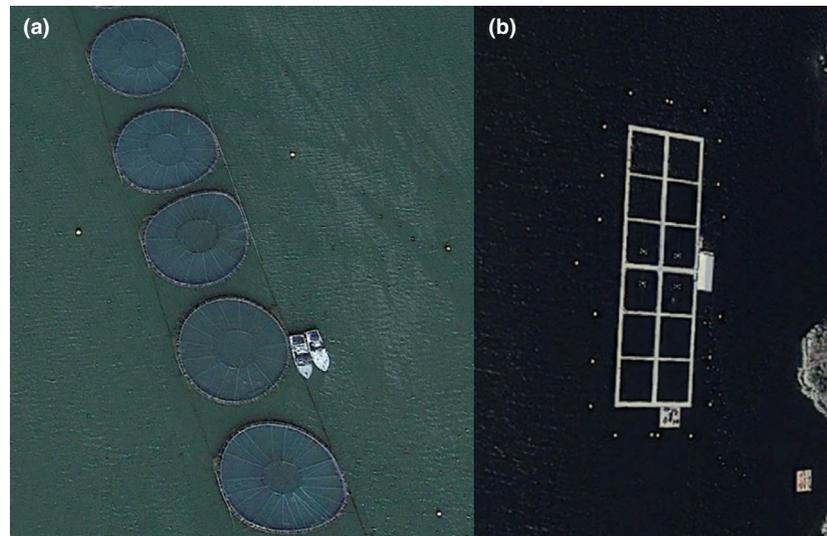
FIGURE 1 Aerial view of surface-based cages to farm marine fish. (a) Circular plastic ring type farm; (b) steel platform farm. Photos from Google Earth

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 bentho-pelagic 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 m³	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
Pacific bluefin tuna (*Thunnus orientalis*)	0.02	2	1	10	2–4	4 h	Japan		12
	15,000	1		1	2–24	2 days	Japan	30–60	121
Almaco jack (*Seriola rivoliana*)	3000	8	0	–	10–25	–	Hawaii	10–50	122
Pacific threadfin (*Polydactylus sexfilis*)	3000			–	10–25	–	Hawaii		123
	3000			–	10–25	–	Hawaii	10–50	123

TABLE 2 (Continued)

	Cage size m³	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

aThat 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.
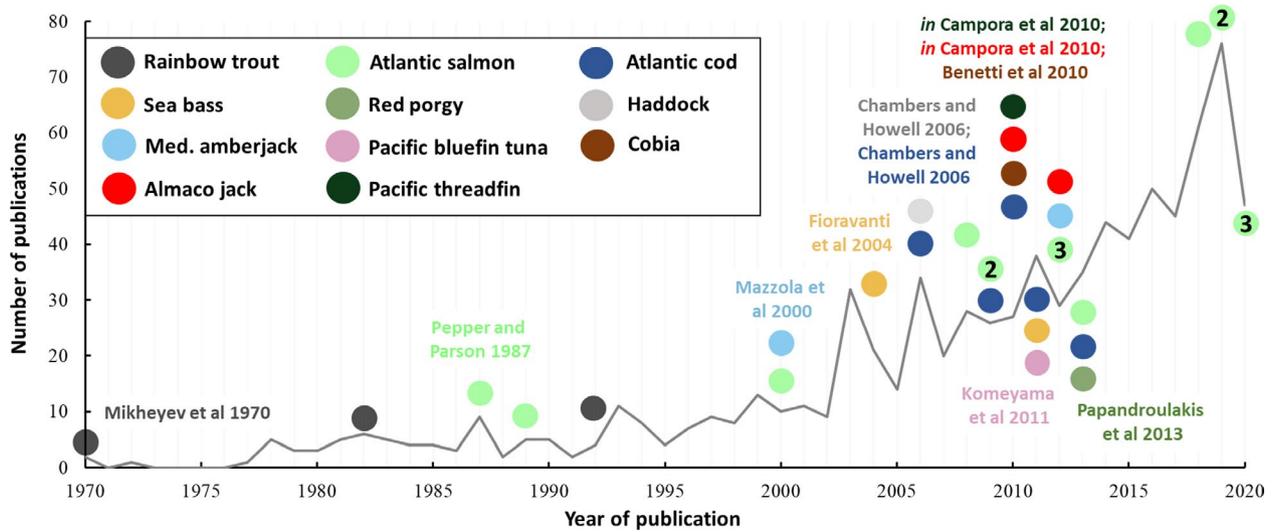
FIGURE 2 Relative research effort over time on submerged cage finfish aquaculture, measured by the number of journal articles published in each year (Web of Science: 'submerged or submergence or submersible) AND (aquaculture OR mariculture OR "fish farm*"'). Dots represent studies presenting empirical 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 re-filling.[48] This explains the lack of knowledge surrounding the basic
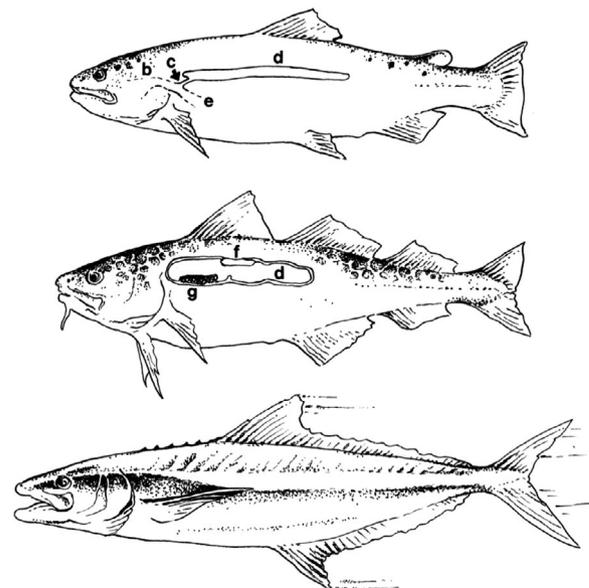

FIGURE 3 Schematic diagram of different swim bladder types: (1) physostomous (salmon), (2) physostome (cod) and (3) fish without swim bladder (cobia); b = buccal cavity, c = pneumatic duct, d = swim bladder, e = oseouphagus into stomach, f = oval, g = *rete mirabile* (gas gland). Drawings by Stein Mortensen,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

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
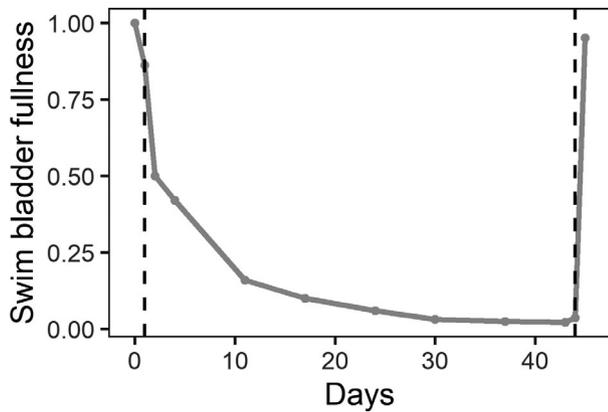
FIGURE 4 Gas content in swim bladder of salmonids before, during and after submergence (data from Sievers et al.[34]). Fish are submerged at day 1 (left dashed vertical line), after which gas quickly begins to diffuse out until the swim bladder slowly becomes empty after ~3 weeks (subject to a suite 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
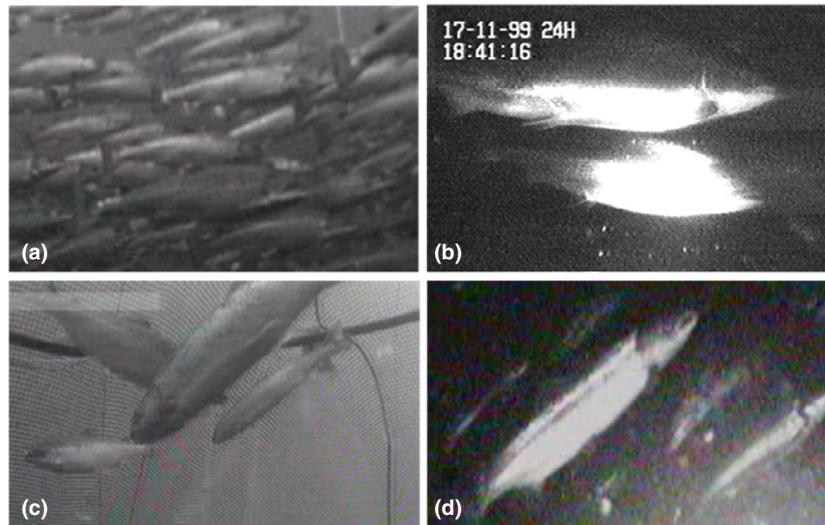
FIGURE 5 Salmon in a surface based sea-cage at daytime schooling at ~0.6 BL/s (a), at night slow, dispersed distribution in a slightly tilted head-down position (b), positively buoyant salmon 2 h after re-filling of swim bladder from an artificial air filled dome at 10 m depth after being kept submerged 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.

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CONFLICT OF INTEREST

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