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Biofouling in marine aquaculture: a review of recent research and developments

Jana Bannister[a], Michael Sievers[b], Flora Bush[a] and Nina Bloecher[c]

[a]Institute for Marine and Antarctic Studies, University of Tasmania, Hobart, Tasmania, Australia; [b]Australian Rivers Institute - Coast and Estuaries, Griffith University, Gold Coast, Queensland, Australia; [c]SINTEF Ocean, Trondheim, Norway

ABSTRACT

Biofouling in marine aquaculture is one of the main barriers to efficient and sustainable production. Owing to the growth of aquaculture globally, it is pertinent to update previous reviews to inform management and guide future research. Here, the authors highlight recent research and developments on the impacts, prevention and control of biofouling in shellfish, finfish and seaweed aquaculture, and the significant gaps that still exist in aquaculturalists' capacity to manage it. Antifouling methods are being explored and developed; these are centred on harnessing naturally occurring antifouling properties, culturing fouling-resistant genotypes, and improving farming strategies by adopting more sensitive and informative monitoring and modelling capabilities together with novel cleaning equipment. While no simple, quick-fix solutions to biofouling management in existing aquaculture industry situations have been developed, the expectation is that effective methods are likely to evolve as aquaculture develops into emerging culture scenarios, which will undoubtedly influence the path for future solutions.

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Introduction

In 2016, global aquaculture production was 110.2 million tonnes (US$243.5 billion), including 54.1 million tonnes of finfish (US$138.5 billion), 17.1 million tonnes of molluscs (US$29.2 billion) and 30.1 million tonnes of aquatic plants (US$11.7 billion) (FAO 2018). Despite annual growth rates of global aquaculture slowing to an average of 5.8% during the period 2000–2016, aquaculture continues to grow faster than other major food production sectors (FAO 2018). More specifically, marine shellfish aquaculture has expanded substantially over the last few decades, with Asia dominating production and accounting for >90% of global tonnage (FAO 2018). Supped oysters (*Crassostrea* spp.) and the Japanese carpet shell (*Ruditapes philippinarum*; a clam) account for more than half of global production (FAO 2018). Finfish aquaculture has increased its volume by >70% over the last decade and freshwater fish, most of them cyprinids, make up 86%. Salmonids, including Atlantic salmon (*Salmo salar*), which are predominantly featured in the scientific literature on biofouling in finfish aquaculture and its management, account for 43% of non-freshwater aquaculture (FAO 2018). Finally, aquatic plants are harvested globally for direct human consumption, and for the production of thickening agents for pharmaceutical and cosmetics, and dried ingredients for animal feed, fertilisers and other products (FAO 2018). Global aquatic plant production has tripled from 10.1 million tonnes in 2000 to 30.1 million tonnes in 2016 (FAO 2002, 2018) with the increased production of the tropical seaweeds *Kappaphycus alvarezii* and *Eucheuma* spp. in Indonesia (as raw material for carrageenan extraction) being the major contributor to this growth (FAO 2018).

Biofouling in marine aquaculture is one of the main barriers to efficient and sustainable production (Dürr and Watson 2010). It is the settlement and development of unwanted aquatic species on natural and artificial surfaces, and plagues shellfish, finfish and seaweed culture globally. The direct economic costs of managing biofouling in the aquaculture industry are estimated to be 5–10% of production costs (Lane and Willemsen 2004). However, the cost of biofouling often varies considerably between aquaculture locations, species and companies, as farmers use differing management approaches and cost

CONTACT Jana Bannister jana.bannister@utas.edu.au
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accounting (Iversen et al. 2016). Furthermore, many of the indirect impacts remain largely unassessed, so the overall economic cost of biofouling in marine aquaculture is still uncertain but is likely to be significantly underestimated (Fitridge et al. 2012).

The aim of this review article is to present and discuss recent research and developments on the impacts, prevention and control of biofouling in marine aquaculture, and thereby update the seminal review article by Fitridge et al. (2012). In addition to marine shellfish and finfish aquaculture, the authors also include a comprehensive evaluation of epiphytism/biofouling in seaweed aquaculture, as this industry has grown significantly over recent years.

The impact of biofouling on shellfish aquaculture

A wide variety of biofouling organisms are associated with shellfish aquaculture globally (Table S1 Supplemental material). The impacts of these species growing on shellfish and farm infrastructure can be partitioned into three broad categories: (1) increased weight, (2) physical damage, and (3) reductions to shellfish fitness. These impacts, along with the cost of biofouling management, can culminate in substantially reduced farm productivity.

Increased weight

Biofouling adds considerable weight to both stock and culture equipment, causing stock detachment in longline culture and increasing the costs associated with buoyancy and anchoring systems (see Fitridge et al. 2012 and references within). Relative to finfish and seaweed culture, the impacts of increases to weight to shellfish culture are less frequently quantified, so impacts to productivity are comparatively unknown.

Physical damage

Boring organisms, such as clionid sponges and polychaete worms from the genus *Polydora*, can penetrate shellfish, causing blisters, cavities and tunnels (Sato-Okoshi and Abe 2013; Carroll et al. 2015). This causes disrupted shell and hinge formation and results in brittle, thin shells that are susceptible to parasites, disease and predation (see Fitridge et al. 2012 and references within). Several other calcareous fouling species settle on shellfish and do not cause direct damage to the shellfish but do affect aesthetics and often lead to the product being devalued or discarded, with considerable financial losses to affected farms (Campbell and Kelly 2002).

Reductions to shellfish fitness

One of the most important impacts from biofouling in shellfish aquaculture is the reduction in shellfish fitness (ie survival, growth, condition and weight). These reductions are typically attributed to direct competition for food, oxygen and other resources, or indirectly, *via* smothering or interfering with proper valve functioning (Lodeiros and Himmelman 1996; Pit and Southgate 2003; Woods et al. 2012). In an empirical study, Sievers et al. (2013) added biofouling to experimental mussel lines and found clear evidence of commercially relevant reductions in growth and flesh weights in mussels (*Mytilus galloprovincialis*) fouled by the widespread tunicates *Ciona intestinalis* and *Styela clava* and the hydroid *Ectopleura crocea*. However, in general, scant evidence exists in the literature to confirm fitness reductions (Sievers et al. 2017). Much of the evidence comes from observational studies, where initial differences between fouled and unfouled stock such as health, size and antifouling (AF) capacity may confound observed patterns. For example, slower growing stock may be more susceptible to the settlement of fouling on shells, potentially leading to erroneous conclusions that fouling reduces growth where fouled and unfouled stock are compared. Despite a general lack of empirical evidence, considerable observational and anecdotal evidence (eg Daigle and Herbinger 2009; Fitridge and Keough 2013) strongly suggests that biofouling can impact cultured shellfish fitness and thus warrants considerable attention from the industry.

Farm productivity

The aforementioned impacts coupled with the substantial cost of removal has spurred considerable interest in quantifying the total impact of biofouling on farm productivity. For example, based on impacts to yield and seed-stock supply, fouling within green-lipped mussel farms by *M. galloprovincialis* was estimated to cost the New Zealand industry US$16.4 million per year, representing ~10% of the industry's value (Forrest and Atalah 2017). In the same region, the direct and combined economic impacts of two key biofoulers (the tunicate *Styela clava* and the polychaete *Sabella spallanzanii*) were estimated at NZ$26.4 million over a 24-year period (the timeframe at which models predict total farm infestation would occur [Soliman and Inglis 2018]). Similar estimates from around the world (eg Adams et al. 2011) mean that biofouling prevention and treatment are critical areas of research and that suitable AF methods are pertinent to efficient production within the shellfish industry.

The control of biofouling in shellfish aquaculture

The diverse impacts from biofouling drive persistent, resource intensive control efforts across the shellfish industry. Husbandry strategies to reduce the impact of biofouling involve preventing the development of fouling and treating fouled stock and infrastructure (Fitridge et al. 2012; Sievers et al. 2017) with the most effective biofouling management strategies incorporating aspects of both.

Prevention

Preventing harmful organisms from affecting aquaculture offers considerable advantages over treatments (Bui et al. 2019). A greater focus on avoiding biofouling will yield production benefits by reducing both the direct impacts of fouling organisms, and the frequency and intensity of treatments. In locations with predictable seasonal fouling patterns, spatial and temporal avoidance of biofouling may be feasible (Bullard et al. 2013; Sievers et al. 2014; Holthuis et al. 2015), and considerable recent effort has gone into monitoring biofouling development at farms around the world (eg Carraro et al. 2012; Antoniadou et al. 2013; Watts et al. 2015; Casso et al. 2018; das Chagas et al. 2018). Modelling biofouling settlement and development is also paving the way for sophisticated avoidance strategies. For example, computer modelling of mussel spat-fall in New Zealand, together with the creation of a readily accessible interactive application, has allowed farmers to actively avoid mussel fouling by informing when and where to deploy lines (Atalah, Rabel, et al. 2016; Atalah et al. 2017). In addition to using monitoring and modelling data to avoid culturing stock in specific locations during times of heavy fouling by particularly harmful species, these data can lead to more effective decisions on the timing of spat collection, and also inform when AF treatments and husbandry strategies that incidentally remove fouling, such as re-socking and grading, should occur (Cyr et al. 2007; Sievers et al. 2014).

Alternative preventative measures include strategic selection of rope types or culture methods, applying AF shell coatings, and culturing fouling resistant genotypes. For example, Sievers et al. (2019) examined both spat collection and biofouling accumulation rates on seven different rope types, noting substantial and consistent variability amongst ropes, with clear advantages of selecting particular types in long-line mussel culture. Modifying stocking densities can also influence fouling rates (Dunham and Marshall 2012), and the surface wettability and microtopography of spat collectors has been altered to both enhance spat settlement and reduce fouling loads (Carl et al. 2012; Vucko et al. 2013). Finally, selective breeding of fouling resistant stock holds potential as a future preventative measure. In New Zealand, the fouling resistant properties of genetic variants of Greenshell™ mussels (*Perna calaniculus*) are being investigated, with efforts extending beyond pilot-scale trials to large-scale intensive efforts (Camara and Symonds 2014).

Treatment

Despite the clear advantages of prevention, some biofouling will inevitably develop. On-site treatment methods which remove biofouling effectively, cheaply, easily and with minimal environmental impact are needed. Since Fitridge et al. (2012), several treatment methods have been tested experimentally and used commercially with varying levels of success, including manual removal (Li et al. 2018), exposure to air (Hillock and Costello 2013; Hopkins et al. 2016), freshwater (Fletcher et al. 2013), heat (Sievers et al. 2019), organic acids and bases (Rolheiser et al. 2012), pressure washing (Davidson et al. 2012), applying silicone release coatings (Tettelbach et al. 2014), adding a culture medium (a substratum within suspended bag culture that physically dislodges biofouling) (Dunham and Marshall 2012; Marshall and Dunham 2013), and employing biocontrol (Atalah et al. 2014; Sterling et al. 2016).

An interesting avenue of continued research which may prove useful for many cultured species involves combining multiple treatments. This approach has considerable appeal as (1) it may be more effective against a broader range of fouling species; (2) treatments will be effective using lower chemical concentrations or temperatures when applied simultaneously (safer for farmers and the environment); and (3) the effective exposure times are likely to be shorter. For example, recent evidence suggests that combining heat and acid treatments is more effective against numerous fouling species at lower intensities than either in isolation (Sievers et al. 2019). Strategic timing of treatment application also offers considerable benefits over a random or intermittent approach. For instance, cost–benefit analysis of high pressure washing to remove the tunicate *Ciona intestinalis* found that beginning treatment when tunicates were small was most effective, and that three to four repeat treatments produced the greatest increase to overall farm profitability (Davidson et al. 2012).

In general, specific treatment methods are often tailored for the species cultured (eg oysters, mussels, scallops), the culture method (eg longline, trays, lanterns) and the composition of the fouling community. It is thus difficult to provide general guidelines for biofouling management within shellfish culture. Furthermore, although often effective at removing fouling, many current and previous treatment methods have little benefit for shellfish fitness or farm productivity, and at times can be more detrimental to cultured shellfish than biofouling (Sievers et al. 2017). For example, although the addition of culture media reduced biofouling by 70%, it also significantly reduced shellfish fitness due to the media limiting access to fresh seawater and food (Marshall and Dunham 2013). These issues have spurred considerable research into novel AF methods since Fitridge et al. (2012).

Novel antifouling control technologies

Natural compounds that inhibit larval metamorphosis may be useful antifoulants in shellfish aquaculture (Cahill et al. 2012; Cahill, Burritt, et al. 2013; Moodie et al. 2017). These products typically have a contact active mode of action, whereby they are effective while remaining bound within a stable matrix, so effects are limited to coated surfaces (Cahill and Kuhajek 2014). Although these compounds are suggested to have little environmental impact, be applicable to both farm infrastructure and shellfish, and reduce biofouling (Cahill, Heasman, et al. 2013), the present authors are not aware of any commercial-scale trials to test the effectiveness or feasibility of this method. Other natural compounds, such as extracts from shellfish periostracum, exhibit strong AF properties and can be designed for commercial use. For example, periostracum dichloromethane extracts containing oleamide reduce algal spore settlement (Kang et al. 2016), and crude periostracum extracts inhibit the attachment of barnacles, diatoms and marine bacteria (Bers et al. 2006). Shellfish periostraca and biogenically derived microtopographies present a non-toxic, environmentally friendly substratum to prevent the settlement and attachment of a range of fouling organisms. However, many of the tested topographies that reduce biofouling settlement are species-specific and thus not particularly useful as a broad AF treatment (Bers and Wahl 2004; Magin et al. 2010; Scardino and de Nys 2011; Vucko et al. 2013). Furthermore, developing suitable methods to apply these types of compounds to shellfish is a major challenge. Coating shellfish with an AF formulation may be unviable from a logistical, fiscal, or consumer perspective. However, with additional research these products may become – at a minimum – a useful future tool for the shellfish aquaculture industry to protect infrastructure from biofouling.

An emerging strategy currently being tested to combat non-indigenous biofouling species *via* biosecurity incursion responses is encapsulation, whereby fouled structures are wrapped in material (eg PVC pallet wrapping), denying the organisms oxygen, nutrients and light (Roche et al. 2015; Atalah, Brook, et al. 2016). Toxic compounds also build up and contribute to high mortality rates of biofoulers (Coutts and Forrest 2007; Vaquer-Sunyer and Duarte 2010). Empirical evidence also suggests that combining encapsulation with chemical dosing using acetic acid may greatly reduce effective treatment times (Forrest et al. 2007; Denny 2008). Encapsulation was largely developed for use on boat hulls, pontoons and piles (see Atalah, Brook, et al. 2016 and references within), and is unlikely to be appropriate for use directly on shellfish (eg wrapping mussel lines). As with coatings, encapsulation may, however, be a viable option for removing biofouling from infrastructure such as mooring lines, buoys and trays.

The long-term genetic improvement of broodstock through selective breeding offers several advantages for the shellfish industry, including a potential means to combat biofouling (Camara and Symonds 2014; Hollenbeck and Johnston 2018). Selective breeding of Greenshell™ mussel and Pacific Oyster genetic variants have begun to improve farm productivity and overall profit yields, with indications that these variants accumulate hard-bodied biofoulers at lower rates (Camara and Symonds 2014). Ultimately, the practicality and efficacy of genetic improvements, and indeed all novel AF methods, need to be rigorously evaluated, with particular attention given to how such treatments affect stock fitness and farm productivity.

The impact of biofouling on finfish aquaculture

There are four main concerns regarding the growth of biofouling organisms on fish cages and infrastructure in finfish aquaculture: (1) modified hydrodynamics in and around the cage affecting water quality and the cage's volume and stability; (2) increased disease risk due to biofoulers and associated pathogens; (3) behavioural impacts to cleaner fish used as biological control against sea lice; and (4) reservoirs for non-indigenous species.

Modified hydrodynamics

The occlusion of nets by biofouling restricts water exchange, which reduces oxygen levels, waste flushing and cage volumes, and increases the effective stocking densities, impacting fish health and welfare (reviewed in Fitridge et al. 2012). In addition, biofouling can increase the hydrodynamic load on nets up to 10-fold (Bi et al. 2018), deforming cages and adding strain to moorings. Impacts differ with species composition (Gansel et al. 2015, 2017) and organism size (Lader et al. 2015), and percentage net-aperture occlusion is a good predictor of flow reduction and drag increase associated with biofouling (Gansel et al. 2015; Bi and Xu 2018).

Biofouling and associated pathogens

Direct contact with cnidarian biofouling can be harmful to the fish, as organisms bearing nematocysts (stinging cells), such as the hydroid *Ectopleura larynx* and the anemone *Anthothoe albocincta*, have the potential to cause gill and skin damage (Baxter et al. 2012; Wybourne 2013; Bloecher, Powell, et al. 2018). In addition, biofouling poses a health risk to cultured fish as it can facilitate and amplify the presence of pathogens by harbouring viral, bacterial, and parasitic organisms that cause various diseases (reviewed in Fitridge et al. 2012). Resuspended faeces of the mussel *Mytilus edulis* containing the bacterium *Vibrio anquillarum* can infect cod with vibriosis in nearby cages and cause mortalities (Pietrak et al. 2012). This issue is also concerning for integrated multi trophic aquaculture (IMTA) sites where fish and shellfish are intentionally cultured in close vicinity. Vibriosis bacteria have also been found in biofilms on cage nets in Malaysia, where their abundance correlated with outbreaks of the disease (Albert and Ransangan 2013). The parasitic amoeba responsible for amoebic gill disease (AGD) in Atlantic salmon, *Paramoeba perurans*, is associated with several key biofouling organisms during acute AGD outbreaks, including hydroids, bryozoans, tunicates, and molluscs (Hellebø et al. 2017). Although the amoeba's reservoir between outbreaks is still unknown, biofouling organisms could act as reinfection agents for recently treated or uninfected fish in nearby cages. Finally, other parasites, such as blood flukes (*Cardicola* spp.) that infect bluefin tuna in Japan, can be found growing on ropes, floats, and frames around cages where their intermediate hosts, terebellid polychaetes, live in balanid shells (Shirakashi and Hirano 2015; Sugihara et al. 2015).

Effects on cleaner fish

Cleaner fish, such as lumpfish (*Cyclopterus lumpus*) and ballan wrasse (*Labrus bergylta*), are increasingly used for biological control of sea lice in salmon farming (Powell et al. 2018). They are opportunistic, omnivorous feeders, targeting multiple food sources and switching their choice of prey organisms to what becomes available in their environment (Deady et al. 1995; Kvenseth 1996; Imsland et al. 2015; Eliasen et al. 2018). As their prey includes biofoulers, such as seaweeds, crustaceans, hydrozoans and mussels (Deady et al. 1995; Imsland et al. 2015; Eliasen et al. 2018), they can effectively reduce biofouling on cage nets (Kvenseth 1996). Consequently, to encourage lice feeding behaviour, farmers were recommended to keep nets free of biofouling (Deady et al. 1995; Kvenseth 1996; Powell et al. 2018). However, recent research has found the presence of biofouling to have a positive effect on the prevalence of sea lice in lumpfish stomachs, possibly because of a more active foraging behaviour of the lumpfish, or the provision of a sheltered environment resulting in better lumpfish welfare (Eliasen et al. 2018). Furthermore, cleaning cage nets to remove biofouling does not affect the behaviour (depth distribution, activity and habitat use) of lumpfish and ballan wrasse (Leclercq et al. 2018). Based on these findings, the salmon producer HiddenFjord on the Faroe Islands reduced the frequency of net cleaning to allow biofouling to accumulate for the benefit of cleaner fish, reporting positive results (E. Patursson, HiddenFjord, pers. comm.). In Norway and Scotland, however, regular net cleaning remains the norm.

Non-indigenous species reservoir

Fish farm biofouling communities can act as reservoirs for non-indigenous species (NIS) that can affect fish health, while farming practices can result in their range expansion, with potential ecological impacts (Table S2; Mineur et al. 2012; Simkanin et al. 2012).

For example, the movement of infrastructure into new areas increases the risk of spreading harmful algal blooms (HABs) when biofouling includes certain tunicates (eg *Didemnum vexillum* and *Molgula manhattensis*) (Rosa et al. 2013). HABs reduce fish welfare and can even cause mass mortality in caged fish with considerable economic consequences (Rensel and Whyte 2003; Cook et al. 2012). In some jurisdictions where the presence of NIS is of significant environmental concern, more stringent biofouling management and waste disposal practices are required (Rosa et al. 2013), with the presence of NIS resulting in stricter controls and potential removal of the site. However, from an operational farm perspective, biofouling by NIS is no more harmful to finfish culture than fouling by native species unless they have a faster growth rate, greater biomass or introduce additional health risks to cultured species than compared to their native counterparts, and thus the presence of NIS does not necessarily increase the need for additional biofouling management practices. To the best of the authors' knowledge, no studies exploring the economic implications of NIS *vs* native biofouling communities on fish aquaculture have been published.

The control of biofouling in finfish aquaculture

The management of biofouling in finfish aquaculture is an increasingly important issue for regulators as the impacts of different control methods become realised (Sim-Smith and Forsythe 2013; Floerl et al. 2016; Scianni et al. 2017). While the use of antifoulants is generally declining, the onset of other biofouling management techniques (eg *in situ* cleaning) with different environmental implications has spurred the development of aquaculture biofouling best management practices. This development has been largely industry-led and, in some jurisdictions, statutory aquaculture biofouling regulation has not yet been established. Table S3 summarises the current statutory and recommended best management practices for select countries.

Net cleaning and exchange

In situ net cleaning is one of the most common methods to manage biofouling on fish cage nets (Floerl et al. 2016). The technology, based on a rig equipped with rotating discs that expel high pressure water through nozzles, is moving towards remote operation and autonomy by attaching rigs to remotely operated vehicles or equipping them with crawl belts (eg 'RONC' by MPI, 'NCL-LX' by Yanmar) or propulsion units (eg 'FNC8' by AKVAgroup, 'Manta' by Stranda Prolog, 'Stealth Cleaner' by Ocein). Alternative systems apply suction parallel to (and potentially independent of) high-pressure cleaning (eg 'MIC2.0' by PFG group), while others rely on cavitation-based systems (eg Cavitator Underwater Surface Cleaners).

Net cleaning or net exchange is often conducted *ad hoc*, determined by biofouling accumulation rates and requirements of the cultured species and/or statutory requirements. While this can be as seldom as once a year, in some cultures more frequent biofouling control is required. Further, in many salmon farms in Norway and Scotland concern over cleaner fish performance has led to considerable increases in cleaning frequency within the last decade (Guenther et al. 2010; Bloecher et al. 2015), now commonly fixed at fortnightly intervals (Bloecher et al. 2015). During the main biofouling season, intervals may even be reduced to as little as five days, especially for nets without antifouling coatings (SINTEF Ocean, unpublished data). For coated nets, increased net cleaning frequency leads to abrasion of the AF coating, considerably reducing the life-time of the coating (SINTEF Ocean, unpublished data) and contributing to the release of harmful AF products into the environment (Skarbøvik et al. 2017).

Other farm infrastructure such as mooring lines and chains, walkways and buoys are cleaned at much lower frequencies, occasionally only following the grow-out phase. Therefore, biofouling accumulation on these structures can be considerable (Bloecher et al. 2015) and may act as a reservoir for pathogens (Sugihara et al. 2014; Shirakashi and Hirano 2015), likely exacerbating biofouling recruitment to cage nets (Bloecher et al. 2015).

Net cleaning can also facilitate the spread of NIS by fracturing colonial species (Hopkins et al. 2011; Aldred and Clare 2014; Floerl et al. 2016) and triggering the simultaneous release of gametes, causing rapid recolonization (Carl et al. 2011; Floerl et al. 2016). Furthermore, the release of cleaning waste containing fragments of biofouling organisms and, potentially, particles of abraded copper coating, can severely impact fish health. Salmon farmers report agitated behaviour and reduced appetite during net cleaning and have observed gill and skin disorders afterwards. Upon contact, cnidarian biofoulers expel nematocysts that can penetrate fish skin and deliver poison (Helmholz et al. 2010; Cegolon et al. 2013), even after fragmentation following pressure-washing (Bloecher, Floerl, et al. 2018). For example, the hydroid *Ectopleura larynx* causes gill injuries in Atlantic salmon (Baxter et al. 2012; Bloecher, Powell, et al. 2018), and white-striped anemones *Anthothoe albocincta* are suspected to cause skin damage in Chinook salmon (Wybourne 2013). Management methods for other issues (eg parasitic sea lice) can further exacerbate these impacts. For example, lice skirts (Stien et al. 2018) can trap cleaning waste within cages, leading to greater interaction and risk of stinging by nematocysts.

Finally, *in situ* cleaning without waste retention can release large volumes of organic material into the surrounding environment, exacerbating existing issues around the build of organic matter below salmon farms (Sim-Smith and Forsythe 2013; Floerl et al. 2016). For this reason, *in situ* cleaning has been discontinued in New Brunswick and Nova Scotia in areas where the benthic environment is anoxic or hypoxic. While *in situ* cleaning is still conducted in New Zealand, Sim-Smith and Forsythe (2013) recommend that it should not be used at sites with low flow due to concerns for the benthic environment (see Table S1).

Net materials and treatments

While salmon farmers in Australia and New Zealand have recently abandoned biocidal antifoulants due to environmental concerns (Floerl et al. 2016, Table S3), their use is common elsewhere. Copper continues to be the main active biocide (Guardiola et al. 2012; Makridis et al. 2018), with Norway's salmon industry using ~1,250 t of copper for AF coatings annually (Skarbøvik et al. 2017). Copper coatings protect nylon nets from fouling for up to seven months at sea (Edwards et al. 2015) and can result in better growth and feed conversion rates in seabass compared to those in unprotected nylon nets (Yigit et al. 2018). However, if biofouling pressure is high, coatings may fail after only eight weeks at sea (Bloecher, Floerl, et al. 2018). Furthermore, ~85% of the copper on Norwegian farms is released into the sea because of leaching and abrasive net cleaning (Skarbøvik et al. 2017). While copper accumulation in marketable tissue of cultured fish does not exceed food safety standards (Cotou et al. 2012; Nikolaou et al. 2014; Kalantzi et al. 2016), impacts on the fish (Azizishirazi et al. 2015) and non-target organisms (Fitridge et al. 2012; Guardiola et al. 2012) have been reported.

Alternative biocides termed 'booster biocides' can be added to enhance the efficacy of copper coatings (Guardiola et al. 2012; Amara et al. 2018), or can be used as the main active ingredient, offering alternatives to traditional coatings based on cuprous oxide. The most commonly used 'booster biocide' compounds in net coatings include copper pyrithione, zinc pyrithione, and tralopyril ('Econea') (Bloecher, Floerl, et al. 2018). In a comparative study, only copper pyrithione-based coatings performed similar to conventional copper coating (Bloecher, Floerl, et al. 2018). While booster biocides are often marketed as environmentally friendly alternatives to conventional copper coatings, there are still environmental concerns regarding their toxicity. Copper pyrithione, for example, reduced salmonid gill health in laboratory assays (Borg and Trombetta 2010) and impacted non-target organisms (Bao et al. 2011; Oliveira et al. 2014; Oliveira et al. 2016; Amara et al. 2018).

Another alternative to traditional copper coatings is copper alloy metal (CAM) nets. CAM nets are able to prevent most biofouling (Chambers et al. 2012) and offer higher form stability in strong currents due to reduced drag (Tsukrov et al. 2011). Growth and feed conversion rates in CAM nets are equal to or better than in nylon net pens treated with conventional copper coating (Chambers et al. 2012; Yigit et al. 2018). In comparison to conventional copper coatings, leaching rates are higher during the first six months at sea before they reach similar levels (Kalantzi et al. 2016). It is assumed, however, that the reduced frequency of cleaning required for CAM nets will result in an overall lower leaching rate for a growing season (Kalantzi et al. 2016).

Most non-biocidal alternatives seal net surfaces under wax- or resin-based coatings. The aim is to reduce surface structure and texture to create a less favourable settlement surface in addition to increasing resilience to net cleaning (Swain and Shinjo 2014; Edwards et al. 2015; Baum et al. 2017). Alternative net materials such as HDPE ('Dyneema') or PET monofilaments ('Kikko net') are also used with similar intention. While this technology can delay the onset and reduce the accumulation of biofouling compared to regular, uncoated raschel-knitted nylon nets (Edwards et al. 2015; Baum et al. 2017), they do not outperform conventional copper coated nets (Edwards et al. 2015; Bloecher, Floerl, et al. 2018).

Biological control

While there are a range of invertebrate and fish species that feed on specific biofouling organisms and can theoretically be co-cultured in cages or on nets, not all biofoulers have natural predators suitable as biofouling control agents (reviewed in Fitridge et al. 2012; Madin and Ching 2015). Since the publication of Fitridge et al. (2012), no significant advances in the use of biological controls have been made and therefore their use in finfish aquaculture remains in the experimental stage.

Novel biofouling control technologies

Given the current reliance on copper for biofouling control, efforts have been put into developing methods to minimise the release of copper into the environment whilst maintaining the use of its AF properties (Liu et al. 2017). The combination of polymer coatings with embedded copper biocide has shown potential in deterring biofouling while limiting the release of copper on hard surfaces (Vucko, King, et al. 2014) and netting (Sato et al. 2012; Ashraf and Edwin 2016; Ashraf et al. 2017). Although many studies have explored the use of natural compounds (eg from plants, bacteria, fungi, algae and sponges) as antifoulants with varying success (reviewed in Almeida and Vasconcelos 2015), to date none are available for commercial application in finfish aquaculture.

As a biocide-free approach to biofouling prevention, manipulation of surface texture and wettability to create a less favourable settlement and adhesion surface has been explored (Scardino and de Nys 2011; Bloecher et al. 2013; Nir and Reches 2016). However, results highlight the limited use of this approach in finfish farming as different species are impacted by different textures (Vucko, Poole, et al. 2014) and deterrence of key pest species, such as hydroids, is ineffective (Bloecher et al. 2013).

Silicone-based fouling-release (FR) technologies have been trialled to develop environmentally benign coatings that reduce adhesion and improve the ability to clean nets (see references in Nurioglu et al. 2015, Pradhan et al. 2018, and Gevaux et al. 2019 for examples). Although these coatings provide little preventative benefit when applied to fish cage nets, silicon-based FR coatings offer the potential for improved biofouling control in conjunction with mechanical cleaning methods (Swain and Shinjo 2014; Edwards et al. 2015).

With regard to mechanical cleaning, recent trends have shifted towards preventing the development of mature biofouling communities by frequent disturbance using autonomous brush systems which continuously clean the net (eg 'HALO Net Maintenance System' by AquaRobotics, 'Netrobot' by Mørenot). However, as these systems are just entering the market, their efficacy has not yet been assessed independently.

While ambitions to develop environmentally benign AF materials and cleaning strategies remain, further developments are needed before existing alternatives compete with the biofouling management methods currently employed by the finfish aquaculture industry.

The impacts of biofouling in seaweed aquaculture

Biofouling exerts a range of negative impacts on the commercial production of seaweeds (Table S4). These can be categorised into three groups: (1) competition for light, space and dissolved nutrients; (2) physical damage; and (3) interference with seaweed culture infrastructure. The culmination of these can reduce the productivity of seaweed farms.

Competition for light, space and dissolved nutrients

Fouling species compete with cultured seaweed species for light, space and dissolved nutrients. Studies on the cultured red algae *Gracilaria chilensis* (Buschmann and Gómez 1993) and *Kappaphycus alvarezii* (Marroig and Reis 2016) show that biofouling significantly reduces levels of solar irradiance reaching cultured stock, leading to lower photosynthetic rates and photosynthetic efficiency than unfouled stock (Borlongan et al. 2016). Interestingly, higher chlorophyll-*a* and phycobilin content in heavily fouled stock suggests that some seaweeds can acclimatise to low-irradiance conditions (Borlongan et al. 2016). Furthermore, opportunistic benthic algae growing on cultured seaweed and farm infrastructure, such as cultivation ropes, raceways and rafts, directly compete with cultured seaweed for substratum, space, and dissolved nutrients, such as ammonia, nitrogen and inorganic carbon (Buschmann and Gómez 1993; Fletcher 1995; Veeragurunathan et al. 2015).

Physical damage

Biofouling adds considerable weight to cultured seaweeds, making them prone to breakage and dislodgement. Some fouling species, such as the encrusting bryozoans *Membranipora membranacea* and *Electra pilosa*, make the lamina of cultivated kelps brittle, which increases susceptibility to breakage (Førde et al.

2016). In addition, the presence of tunicates, predominantly *Ciona intestinalis*, and the hydroid *Obelia geniculata* can deteriorate the appearance and quality of cultured kelp blades (Park and Hwang 2012; Rolin et al. 2017). Furthermore, some epiphytic fouling species penetrate deep into the host cell tissues, causing disorganisation or even destruction of the host's cells close to the infection (Leonardi et al. 2006). Epiphytic red algae from the genus *Neosiphonia* (syn. *Polysiphonia*) can cause pit-like structures to form on cultured seaweeds, leading to future infections (Hurtado et al. 2006; Vairappan et al. 2008).

Interference with seaweed culture infrastructure

Fouling organisms on ropes and rafts used to culture seaweeds can cause infrastructure to sink below the surface, requiring labour-intensive cleaning and leading to a loss of productivity (Marroig and Reis 2011, 2016). Biofouling on infrastructure can also cause environmental effects beyond geographic farm boundaries. For example, the recurring large-scale green tides in the Yellow Sea of China originated from the green alga *Ulva prolifera* that was scraped off rafts at *Pyropia* (syn. *Porphyra*) *yezoensis* farms in the Yellow Sea (Fan et al. 2015; Song et al. 2018). The decomposition of green tides can result in hypoxia and acidification, induce red tides and have long lasting effects on the coastal carbon cycle and ecosystem health (reviewed in Zhang et al. 2019).

Reduction in productivity, quality and commercial value

Similar to shellfish and finfish culture, the culmination of these negative impacts can lead to a loss in productivity of seaweed culture by decreasing growth rates and biomass and reducing the quality and commercial value of the end product (Kuschel and Buschmann 1991; Park and Hwang 2012; Bruhn et al. 2016; Førde et al. 2016; Marroig and Reis 2016). Although the impact of biofouling is consistently cited as a leading issue in seaweed aquaculture (Lüning and Pang 2003; Kim et al. 2017), the authors are unaware of any attempt to quantify the financial implications of productivity reductions or increases to time and labour costs.

The control of biofouling in seaweed aquaculture

The economic feasibility of seaweed aquaculture requires the control of various factors, including biofouling (Zuniga-Jara and Marin-Riffo 2016; Kim et al. 2017). Prevention, inhibition and treatment of biofouling on commercially cultivated seaweed species includes understanding and harnessing the natural antifouling defences of seaweeds, and strategic farm management and husbandry practices.

Prevention and inhibition

Strategic farm management and husbandry strategies can minimise the presence and impact of biofouling and optimise biomass yields. Like shellfish and finfish culture, farmers can choose to culture seaweed in areas less likely to develop harmful biofouling by considering levels of exposure and water movement, water temperature, cultivation period, timing of harvest, and through the choice of infrastructure materials, which all influence biofouling rates. Farming seaweed at exposed locations is one promising strategy, but it is highly species-specific. For example, exposed sites are linked with reduced levels of biofouling for the cultured kelps *Undaria pinnatifida*, *Saccharina latissima* and *Laminaria digitata* (Andersen et al. 2011; Peteiro and Freire 2013; Rolin et al. 2017) and increased water movement with less siltation is recommended for the cultivated red alga *Kappaphycus alvarezii* (Hurtado et al. 2006). In contrast, softer-bodied seaweeds such as the red alga *Gracilaria chilensis* may lose biomass when cultured at exposed locations (reviewed in Buck et al. 2018). However, cultivating seaweeds at exposed sites may also present other environmental challenges as severe storms can damage seaweeds and displace aquaculture structures, leading to reductions in biomass and farm productivity (Rolin et al. 2017).

Water temperature also influences the accumulation of fouling species. In general, it has been recommended that cultured seaweeds are harvested before sea temperatures rise in spring and summer to avoid the negative impacts of seasonal biofouling (Park and Hwang 2012; Ateweberhan et al. 2015; Marinho et al. 2015; Førde et al. 2016; Keesing et al. 2016).

In terms of infrastructure material, the efficacy of microtextured surfaces in deterring the settlement of specific fouling organisms has been increasingly studied, with mixed findings (reviewed in Scardino and de Nys 2011). For example, polyethylene tubes used in the culture of *Gracilaria* promoted the unwanted accumulation of *Giffordia* (Kuschel and Buschmann 1991), but treated bamboo poles used in the culture of *Pyropia yezoensis* inhibited the attachment and germination of green alga *Ulva prolifera* micro-propagules (Song et al. 2018). The use of such bamboo poles might therefore play a role in mitigating recurring large-scale green tides in the Yellow Sea caused by *U. prolifera* (Song et al. 2018).

Biological aspects of farm management and husbandry strategies to prevent and inhibit biofouling include the selection of seed stock and stocking density. The selection of clean and healthy seedlings that are free of epiphytes to initiate cultivation is strongly recommended to curb biofouling problems later in the cultivation cycle (Hurtado et al. 2006; Hayashi et al. 2010). Epiphytic biofouling can be controlled by growing seaweeds at high densities in rope cultures in the sea or in tank cultures on land (reviewed in Lüning and Pang 2003), although the efficacy of this method appears species-specific, with the culture density for some species such as *Gracilaria* sp. and the kelp *Alaria esculenta* not affecting the abundance, species richness or composition of fouling species (Kuschel and Buschmann 1991; Walls et al. 2017).

In addition, the role of surface-associated secondary metabolites as a chemical AF defence mechanism has been demonstrated for several seaweed species (reviewed in Jormalainen and Honkanen 2008; da Gama et al. 2014; Othmani et al. 2016; Pereira et al. 2017), including the cultivated red alga *Gracilaria vermiculophylla* (Wang et al. 2018) and the brown alga *Fucus vesiculosus* (Lachnit et al. 2013). These mechanisms could be enhanced by farmers by using Acadian Marine Plant Extract Powder (AMPEP), a commercial product derived from the brown alga *Ascophyllum nodosum* and used extensively to increase the productivity of agricultural and horticultural crops for over 30 years (Hurtado and Critchley 2013). More recently, AMPEP has been tested and used as a culture medium to propagate and cultivate the red seaweed *Kappaphycus alvarezii* (Hurtado et al. 2009; Hurtado et al. 2012; Hurtado and Critchley 2013; Marroig and Reis 2016) and mitigate various biotic and abiotic stressors including biofouling (reviewed in Hurtado and Critchley 2018). For example, dipping *K. alvarezii* seedlings in AMPEP solutions helps prevent the occurrence of epiphytic infections and epibiont biomass during their culture period (Borlongan et al. 2011; Marroig and Reis 2016). The use of AMPEP and alternative extracts to prevent and inhibit epiphytes is a promising method, which may lead to further studies on the mode of action and metabolic pathways (Hurtado and Critchley 2018) and to the broader adoption of this method in seaweed aquaculture.

Treatment and mitigation

Seaweeds, particularly long-lived macroalgae species, have numerous natural defences that effectively remove biofouling, including blade abandonment and simultaneous rapid proliferation (Littler and Littler 1999), and periodic epidermal shedding (Filion-Myklebust and Norton 1981; Nylund and Pavia 2005; Yamamoto et al. 2013; Halat et al. 2015). For example, the commercially harvested brown alga *Ascophyllum nodosum* from the intertidal zone of Nova Scotia, Canada, sheds ~25% of its frond epidermis per week for at least nine months of the year to remove epiphytes, such as the host-specific red alga *Vertebrate lanosa* (syn. *Polysiphonia lanosa*) and the facultative brown algae *Elachista fucicola* and *Pylaiella littoralis* (Longtin et al. 2009; Halat et al. 2015). Combining knowledge of these natural defence mechanisms together with knowledge of the seasonal occurrence of biofouling could provide seaweed farmers with an increased capacity to limit biomass losses by harvesting at strategic times.

Strategic farm management and husbandry practices to control epiphytes include the exposure of desiccation-tolerant intertidal seaweed species, such as *Porphyra*, to air or the application of organic acids onto the cultivation nets to control the pH (Harrison and Hurd 2001; Kim et al. 2017). For seaweed species cultured in tanks, such as *Gracilaria*, epiphytes can also be controlled by nutrient pulsing, thereby starving the epiphytes of nitrogen between pulses, while not significantly affecting the growth of *Gracilaria* (reviewed in Harrison and Hurd 2001).

Biological control methods include encouraging grazing by herbivores, such as amphipods, isopods, and some fish species. The isopod *Paridotea reticulata* grazes on the epiphytic red alga *Ceramium diaphanum* growing on commercially farmed red alga *Gracilaria gracilis* (Anderson et al. 1998; Smit et al. 2003). However, the relationships between cultured seaweed, epiphytes and herbivores are dynamic, and the benefits of herbivores preferentially consuming epiphytes can be quickly overshadowed by negative effects of herbivores grazing on cultured seaweed when herbivore densities become too high and alternative food sources scarce (Shacklock and Doyle 1983; Smit et al. 2003; Cruz-Rivera and Friedlander 2011). In *Gracilaria* culture, isopod densities can be controlled by short-term freshwater exposure (Smit et al. 2003). Furthermore, in a food preference study with 11 fish species, the fish *Aphanius dispar* and *Tilapia zillii*, acclimatised to seawater, displayed selective feeding on epiphytes and were identified as good candidates to control epiphytes in the mass culture of *Gracilaria conferta* (Friedlander et al. 1996). Future efforts should focus on harnessing the utility of biological control agents within culture settings.

Finally, since biofouling on seaweed culture infrastructure can be a reservoir for epibionts, periodic manual removal of fouling organisms on infrastructure and/or cultured species occurs in some farming regions (Kuschel and Buschmann 1991; Hurtado et al. 2006; Marroig and Reis 2011; Liu et al. 2013). However, manual removal is labour-intensive, and the gains in productivity must be evaluated against the increases in labour costs (Kuschel and Buschmann 1991). Furthermore, for several cultured seaweeds, the logistics of removing epiphytes make this method almost impossible. For example, epiphytic filamentous red algae from the genus *Polysiphonia* penetrate the cells of commercially cultured *Kappaphycus* (Hurtado et al. 2006; Leonardi et al. 2006), making manual removal difficult without harming the stock.

Although seaweed aquaculture technologies have developed significantly over the last decades, simple, economically viable biofouling management solutions have not yet been realised. Further research in this area is required (Kim et al. 2017), including trials of promising methods at commercial scales to facilitate future implementation by the industry.

Conclusion and future directions

Although there have been considerable recent advances in knowledge of biofouling in aquaculture, there are still significant gaps in aquaculturalists' capacity to manage biofouling. Issues surrounding biofouling differ among shellfish, finfish and seaweed aquaculture industries, yet the direction of emerging biofouling management strategies are similar. These strategies aim to take advantage of improved scientific understanding and technological advances to develop robust and proactive preventative approaches. The use of monitoring and modelling to inform preventative management decisions (eg farm locations, timing of treatment, harvesting cycles) can reduce the cost of biofouling management and maximise the benefit of any subsequent control treatments. The most effective strategies are likely to include a combination of both prevention and treatment. Likewise, though successes have been identified at varying scales by applying methods in isolation, the combination of multiple treatments may enable more success in combating biofouling in aquaculture.

Future research will need to address the unresolved issues in existing aquaculture practice, in addition to broadening the scope to encompass a wider variety of culture species and habitats as the aquaculture industry moves into new culture scenarios (eg offshore aquaculture and closed culture systems). By understanding the settlement and development of biofouling in these environments, novel materials and/or AF coatings for infrastructure, and technological advances, such as equipment for more efficient monitoring, modelling and autonomous cleaning can be developed. Aquaculture may help feed the world into the future, but biofouling stands out as a clear barrier that needs to be overcome first.

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ORCID

Jana Bannister http://orcid.org/0000-0002-5281-7800
Michael Sievers http://orcid.org/0000-0001-7162-1830
Flora Bush http://orcid.org/0000-0003-0596-0601
Nina Bloecher http://orcid.org/0000-0002-8009-331X

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