



REVIEW

Aquaculture and eelgrass *Zostera marina* interactions in temperate ecosystems

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ABSTRACT: This paper reviews the impacts of shellfish and finfish aquaculture on eelgrass *Zostera marina*, the most widely distributed seagrass species in the northern hemisphere. Shellfish aquaculture can have positive, neutral, and negative effects on eelgrass. Positive interactions can be generated by the filtering activity of cultured bivalves, which may improve water quality and reduce epiphyte loads, and shellfish biodeposits may provide more nutrients to eelgrass and other vegetation. However, negative responses are more commonly reported and can be caused by shading and sedimentation. These negative effects tend to occur directly under and immediately surrounding shellfish farms and rapidly diminish with increasing distance. In contrast to shellfish aquaculture, only one field study has investigated the effects of finfish aquaculture on eelgrass in a temperate setting, and the results were inconclusive. However, many studies have investigated the effects of Mediterranean finfish farms on 2 other species of seagrass (*Posidonia oceanica* and *Cymodocea nodosa*). These studies reported clear negative interactions, which have been linked to increased nutrient concentrations, sulphides, sedimentation, epiphyte loads, and grazing pressure. It is unknown if these studies are relevant for finfish aquaculture in temperate regions due to differences in environmental conditions, and because the studies focused on different species of seagrass. Thus, further study in a temperate setting is warranted. We conclude by highlighting key research gaps that could help regulators establish unambiguous operational and siting guidelines that minimize the potential for negative interactions between aquaculture and eelgrass.

KEY WORDS: Seagrass · Shellfish · Finfish · Sedimentation · Shading · Nitrogen · Eutrophication

1. INTRODUCTION

Global aquaculture production has doubled approximately every decade since 1950 (FAO 2020). Consequently, aquaculture now provides over half the fish and shellfish consumed around the world (FAO 2021). Despite growing interest in developing aquaculture further offshore (Holmer 2010, Buck & Langan 2017, Froehlich et al. 2017), most marine

and estuarine aquaculture occurs in coastal waters near to shore (Campbell & Pauly 2013, Gentry et al. 2017). Thus, as aquaculture continues to expand, there is increasing potential for the industry to overlap and interact with seagrass and other coastal habitats (reviewed by Larkum et al. 2006).

Research on aquaculture–environment interactions is highly multi-disciplinary and of substantial

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interest to scientists, aquaculturists, regulators, environmentalists, fishermen, and a wide range of other stakeholders. To help inform such a diverse audience, this paper reviews the potential effects of marine aquaculture on eelgrass *Zostera marina*, the most widely distributed seagrass species in the northern hemisphere (Green & Short 2003, den Hartog & Kuo 2006). We then highlight key research gaps and priorities for future research.

1.1. Eelgrass distribution

Eelgrass is the most common seagrass species in the USA and Canada (Moore & Short 2006). On the west coast, eelgrass ranges from the Gulf of California to Alaska, and on the east coast, from North Carolina to the Arctic coast of northern Quebec (Fig. 1). In Europe, eelgrass occurs throughout the Northeast Atlantic, the Baltic Sea, and much of the Mediterranean Sea (Borum & Greve 2004, Schubert et al. 2015). It is also present in some parts of East Asia, including Korea, Japan, northern China, and western Russia (Shin & Choi 1998).

1.2. Ecological significance of eelgrass

Seagrasses are often described as ‘ecosystem engineers’ for their ability to modify their physical,

chemical, and biological environment (Jones et al. 1997, Bos et al. 2007). Seagrass meadows slow the movement of water currents and waves, protecting shorelines from erosion and promoting the settlement of suspended sediments (Ondiviela et al. 2014). Their roots and rhizomes can also trap sediments, preventing their resuspension, which can improve water clarity and allow for more light to penetrate to deeper depths (Folkard 2005, Koch et al. 2006, Carr et al. 2010). In addition to trapping sediments, seagrass beds can also trap detritus and other organic matter (reviewed by Bedulli et al. 2020), which can boost sediment microbial activity (Gacia & Duarte 2001, Marbà et al. 2006a, Tarquinio et al. 2019) and influence the cycling of carbon, nitrogen, sulphur, phosphorus, and oxygen (Marbà et al. 2006a, Mateo et al. 2006, Romero et al. 2006, Liu et al. 2018).

In addition to their positive influence on sediment stability, organic content, and water clarity, eelgrass meadows are often associated with diverse communities of benthic invertebrates and macroalgae (Orth 1973, 1977, Joseph et al. 2012, Schmidt et al. 2012, Wong 2018, Wong & Kay 2019). These diverse communities can provide greater feeding opportunities for a wide range of other species, partially explaining why organisms inhabiting eelgrass beds often exhibit faster rates of growth (Tupper & Boutilier 1995, 1997, Heck et al. 2003, Renkawitz et al. 2011). Additionally, as eelgrass canopies can hinder the visual

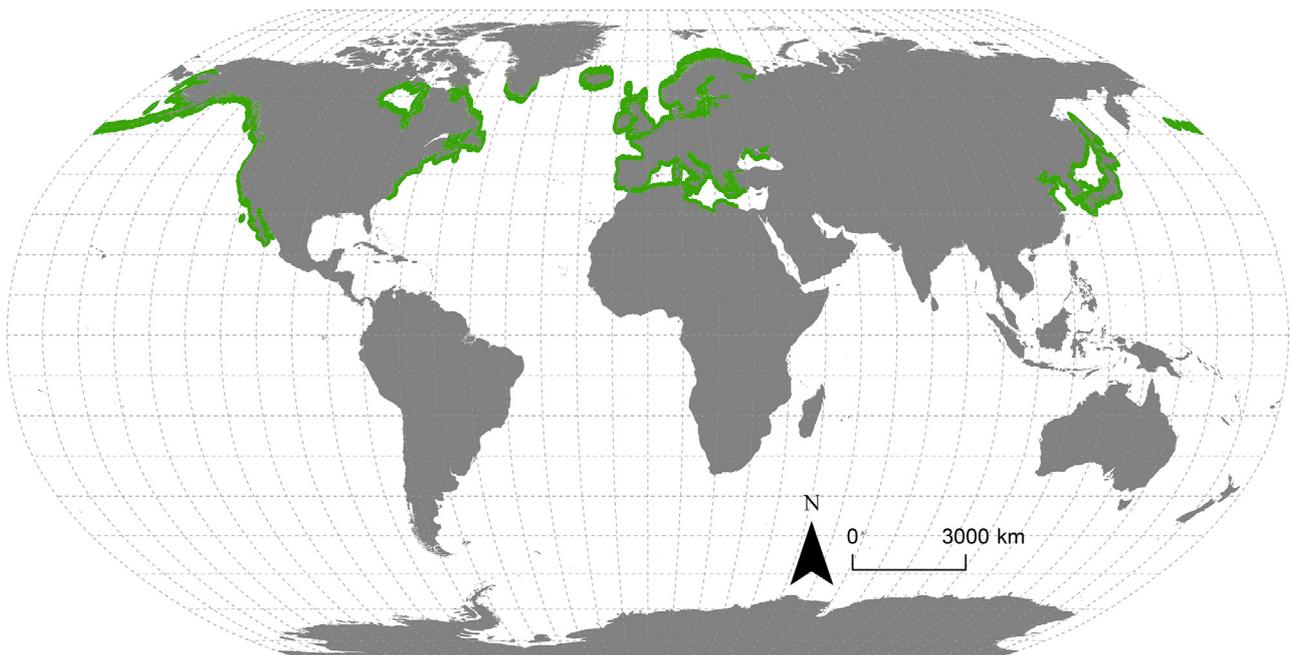


Fig. 1. Global distribution of eelgrass (green shading). Data obtained from IUCN Red List of Threatened Species (2021)

and swimming capabilities of predators, they can provide protection from predation (e.g. Joseph et al. 2006, 2012, Heck et al. 2008, Gorman et al. 2009, Renkawitz et al. 2011, Schein et al. 2012, Peters et al. 2015, Park & Kwak 2018) and serve as nursery habitat for a diversity of fish, crustaceans, and molluscs (Joseph et al. 2006, 2012, Heck et al. 2008, Renkawitz et al. 2011, Schein et al. 2012, Peters et al. 2015, Park & Kwak 2018). Many of these species are of commercial importance (Heck et al. 2003, Laurel et al. 2003, Gillanders 2006, Fonseca & Uhrin 2009, Bertelli & Unsworth 2014, 2018, McCain et al. 2016) and often occur in higher densities within eelgrass beds compared to other vegetated and non-vegetated habitats (e.g. Hosack et al. 2006, Gorman et al. 2009, Kim et al. 2009, Park et al. 2020).

Eelgrass beds can also benefit terrestrial species, as their associated communities form an important dietary component for many migratory bird species around the world (Tubbs & Tubbs 1983, Nienhuis & Groenendijk 1986, Ganter 2000, Seymour et al. 2002, Balsby et al. 2017). Lastly, eelgrass detritus can wash up on the shore in large quantities, providing food and habitat to terrestrial invertebrates, birds, and mammals (reviewed by Mateo et al. 2006, Heck et al. 2008).

1.3. Protection and recognition in policy and legislation

In recognition of their ecological significance, eelgrass beds are protected by, or referenced within, many national and international policies, legislation, and regulations. In the USA, eelgrass is protected under the federal Clean Water Act (EPA 2021) and a range of federal and state-wide legislation including the Magnuson-Stevens Fishery Conservation and Management Act (reviewed by Neckles et al. 2005, Sherman & DeBruyckere 2018). In Canada, eelgrass is protected by the federal Fisheries Act (Revised Statutes of Canada 1985) through a prohibition on the harmful alteration, disruption, or destruction of fish habitat. In Europe, eelgrass is of conservation importance under the Convention for the Protection of the Marine Environment of the North-East Atlantic (OSPAR Convention; www.ospar.org) and is a protected 'Annex I Habitat' under the European Union (EU) Habitats Directive (Council Directive 92/43/EEC). On a national level, eelgrass is listed as a 'priority marine feature' in Scotland (NatureScot 2020) and a 'priority habitat' under the UK Biodiversity Action Plan (JNCC 2007). In South Korea, eelgrass is

listed as a 'marine organism under protection' (reviewed by Lee et al. 2016).

1.4. Factors influencing eelgrass declines

Like all species of seagrass (Waycott et al. 2009, Unsworth et al. 2019), eelgrass has declined throughout much of its range over the last century for a variety of reasons (de Jonge et al. 1996, Tamaki et al. 2002, Orth et al. 2010, Costello & Kenworthy 2011, Jorgensen & Bekkby 2013, Boström et al. 2014, Eriander et al. 2016, Krause-Jensen et al. 2021). Eelgrass survival and habitat suitability are influenced by a wide range of chemical, biological, and physical parameters (Table 1). Thus, a multitude of interacting factors have been implicated in the global decline of eelgrass, including sedimentation, shading, eutrophication, disease, species invasions, and disturbance from boating and fishing activity (reviewed by Moore & Short 2006, Howarth et al. 2021). Of these impacts, those most likely to be exacerbated by aquaculture (i.e. shading, sedimentation, and eutrophication) are reviewed below.

1.4.1. Shading and sedimentation

Eelgrass, like all plants, requires light to photosynthesize sugars and other carbohydrates necessary for respiration and growth. Consequently, light availability is one of the most important factors controlling seagrass growth and survival (Dennison & Alberte 1985, Duarte et al. 2006, Thom et al. 2008, Schmidt et al. 2012). Many sources of natural and human disturbance can reduce light availability, including shading from coastal infrastructure, eutrophication (see Section 1.4.2), and sedimentation/sediment resuspension from storms, river discharge, and coastal construction (Unsworth et al. 2017, Glasby & West 2018).

Generally, lower light availability can reduce eelgrass biomass, growth, leaf size, shoot density, photosynthesis, and survival. Experimental field manipulations by Burke et al. (1996) showed that shading eelgrass for 3 wk led to reductions of 40–51% in tissue sugar concentration, 34% in leaf biomass, 27% in shoot density, and 23% in root and rhizome biomass. Similar field manipulations were conducted by Wong et al. (2020) and yielded comparable results. Such negative responses tend to get stronger with longer durations of light reduction (Ralph et al. 2006). For example, a laboratory study conducted by Ber-

Table 1. Overview of the key environmental parameters that can affect eelgrass distribution

Parameter	Thresholds	Source
Ammonium (NH ₄ ⁺)	Aquatic toxicity begins at 25 µM and mortality occurs at 125 µM	van Katwijk et al. (1997)
Current speeds	Can tolerate a range of 16–180 cm s ⁻¹	Fisheries and Oceans Canada (2009)
Dissolved oxygen (O ₂)	Minimum dissolved concentration of 2.02 mg O ₂ l ⁻¹	Fisheries and Oceans Canada (2009)
Hydrogen sulphide (H ₂ S)	Sediment toxicity begins at 100 µM and mortality occurs at 680 µM	Fisheries and Oceans Canada (2009), Dooley et al. (2013)
Light	Minimum light requirement: 11–34 % surface irradiance (SI) or 1.2–12.6 mol photons m ⁻² d ⁻¹	van Katwijk et al. (1997), Hauxwell et al. (2003), Eriander (2017), Bertelli & Unsworth (2018)
Nitrate (NO ₃ ⁻)	Aquatic toxicity effects begin at 35 µM and mortality occurs at ~250 µM	Burkholder et al. (1992)
Salinity	Optimal range: 20–26 ppt Tolerable range: 5–35 ppt	Fisheries and Oceans Canada (2009)
Sediment composition	Reported in sediments ranging in particle size, from mud to cobbles	Fisheries and Oceans Canada (2009)
Redox potential of sediment	Tolerable range for seagrasses in general: -175 to +300 mV	Marbà et al. (2006a)
Water temperature	Optimal range: 10–25°C Tolerable range: 0–35°C	Fisheries and Oceans Canada (2009)
Water depth	Euphotic zone. Maximum depth in Canada and USA is approximately 12 m, but often occurs between 1 and 7 m; can occur as deep as 15–30 m in very clear waters (e.g. in the Mediterranean Sea)	Borum & Greve (2004), Moore & Short (2006), Dahl et al. (2016), Murphy et al. (2021)

telli & Unsworth (2018) demonstrated that reducing light levels below 20 µmol photons m⁻² s⁻¹ resulted in significant reductions in eelgrass growth and photosynthetic performance after 7 d, a 41 % reduction in leaf size after 29 d, and shoot mortality within 4–6 wk. Burial under sediments can also affect seagrass by reducing the area of the plant available for photosynthesis. A field manipulation study by Mills & Fonseca (2003) showed that burying eelgrass to 25 % of its height for 24–28 d resulted in a 75 % mortality rate, while burying it to 50–75 % of its height increased mortality to 100 %, leading the authors to conclude that eelgrass has a low tolerance for burial under sediments.

1.4.2. Eutrophication and nitrogen toxicity

Effluents from point sources (e.g. aquaculture, pulp mills, wastewater treatment facilities) and non-point/diffuse sources (e.g. agriculture, urban run-off) can elevate nutrient loads in coastal waters and lead to eutrophication (Nixon 1995, Smith 2003, Howarth et al. 2019). The term ‘eutrophication’ describes a series of interlinked processes whereby elevated nutrient loads lead to an increase in plankton and

aquatic plants, resulting in reductions in oxygen and light availability. Thus, in addition to shading, burial, and sedimentation (as described earlier), eutrophication can also reduce the amount of light available to eelgrass by stimulating the growth of: (1) phytoplankton, which can reduce water clarity; (2) benthic macroalgae, which can compete with eelgrass for light and space; and (3) epiphytic algae and other organisms growing on the blades of eelgrass that obstruct light (Williams & Ruckelshaus 1993, Short et al. 1995, Hauxwell et al. 2001, 2003, McGlathery 2001, Fertig et al. 2013). For example, a survey of 12 estuaries in eastern Canada indicated that those with elevated nutrient levels supported almost double the biomass of phytoplankton, 40 times more epiphytic algae, and 670 times more opportunistic green macroalgae (Schmidt et al. 2012). Due to lower light availability, the eelgrass growing in these nutrient-enriched estuaries also exhibited significantly lower shoot density and above- and belowground biomass (Schmidt et al. 2017).

Higher biomasses of phytoplankton, epiphytic algae, and macroalgae can also result in larger quantities of detritus and organic matter settling on the seafloor. In oxygenated environments, bacteria decompose this organic matter through aerobic respiration.

However, excessive quantities of organic matter can cause bacteria to partially (hypoxia) or fully (anoxia) deplete oxygen, prompting bacteria to switch to anaerobic respiration, which can lead to the build-up of hydrogen sulphide (H_2S) and other sulphide compounds (Schmidt et al. 2012, Benson et al. 2013). Eelgrass is relatively tolerant to anoxia compared to other seagrass species, but low oxygen levels can reduce its metabolism and growth (Pregnall et al. 1984, Smith et al. 1988). Sulphides are potentially a greater concern, as they are toxic to seagrass and significantly affect eelgrass photosynthesis, metabolism, leaf size, and shoot height, which can lead to mortality (Carlson et al. 1994, Goodman et al. 1995, Terrados et al. 1999, Pedersen et al. 2004). For example, Dooley et al. (2013) observed that eelgrass seedlings were consistently killed when exposed to water H_2S concentrations above 680 μM . The degree to which sulphides impact eelgrass is strongly linked to oxygen concentrations both within the water column and sediment, as eelgrass can resist sulphides from entering their tissues provided their roots and rhizomes are supplied with sufficient levels of oxygen (Pedersen et al. 2004).

Lastly, effluents highly enriched in nitrate (NO_3^-) and ammonium (NH_4^+) can lead to nitrogen toxicity in seagrass. Burkholder et al. (1992) maintained eelgrass in elevated water NO_3^- concentrations of approximately 200–300 μM for 8 wk. This treatment caused eelgrass shoots to crumble, eventually resulting in their mortality (reviewed by Moore & Wetzel 2000). Likewise, van Katwijk et al. (1997) observed that water NH_4^+ concentrations of 25 μM adversely affected eelgrass, and that concentrations of 125 μM led to mortality within 2–5 wk. Interestingly, seagrasses are more tolerant to high nitrogen concentrations within the sediment than in the water column. For instance, Peralta et al. (2003) demonstrated that eelgrass could tolerate sediment NH_4^+ concentrations up to 30 mM, which is 1200 times higher than what it can tolerate in the water (van Katwijk et al. 1997). Nitrogen toxicity also depends on sediment type, as eelgrass has been shown to be less sensitive to NH_4^+ when growing in muddy sediments compared to sand (van Katwijk et al. 1997).

Overall, eutrophication is considered one of the most important drivers underlying the loss of seagrasses worldwide (Kenworthy et al. 2006, Walker et al. 2006). However, the effects of eutrophication on eelgrass are highly complex, as multiple mechanisms (e.g. light limitation, oxygen depletion, and nitrogen toxicity) can interact. These mechanisms can also be influenced by a range of other factors,

including sediment composition, light availability, temperature, oxygen concentration, and sediment redox potential (McGlathery 2001, Walker et al. 2006).

1.4.3. Multiple stressors

Eelgrass beds exist across a wide spectrum of human stressors including nutrient enrichment, species invasions, fishing, aquaculture, and coastal construction (e.g. Murphy et al. 2019). A growing number of studies have shown that multiple stressors can interact and that the effects of one can cause seagrass to become more sensitive to another (Blake & Duffy 2012, Brown et al. 2014, Stockbridge et al. 2020, Vieira et al. 2020, Krumhansl et al. 2021). For example, Krumhansl et al. (2021) found evidence that eelgrass beds in warmer waters were less tolerant of low light conditions. Conversely, some stressors have been shown to have no interactive effects, while others can reduce the sensitivity of seagrass to other stressors (Blake & Duffy 2010, York et al. 2013, Mvungi & Pillay 2019). For example, York et al. (2013) observed clear effects of light irradiance and temperature on the growth and health of *Zostera muelleri* in a laboratory setting, yet found no evidence of interactions between the two. Consequently, it can be very difficult to isolate or predict the effects of a single stressor on seagrass populations in a field-based setting.

2. SHELLFISH AQUACULTURE AND EELGRASS INTERACTIONS

2.1. Gear and methods

Shellfish aquaculture is an incredibly diverse industry encompassing a wide variety of species and culture/harvest methods. The exact methods used by growers usually depend on the species being cultured, the size of the operation, the amount of financial and staff resources available to the business, and local environmental conditions.

2.1.1. Intertidal on-bottom culture

Intertidal aquaculture has a long tradition in many countries and tends to focus primarily on bivalves (e.g. clams, scallops, and oysters) and other shellfish species (e.g. abalone). Due to their intertidal location,

cultured organisms are usually submerged and then exposed to the air with each tidal cycle. 'On-bottom culture' involves directly seeding sediments with juvenile shellfish (Fig. 2) which can be protected from predators by using nets, cages, or pipes (Dumbauld et al. 2009, McDonald et al. 2015, Hagan & Wilkerson 2018). Once the shellfish reach a marketable size, harvesting can take place manually (e.g. by hand or with hand tools like rakes and hacks) or mechanically (e.g. suction dredging, dragging, and sediment liquefaction; Ferriss et al. 2019).

2.1.2. Intertidal off-bottom culture

'Off-bottom culture' grows shellfish just above the sediment or higher up in the water column (reviewed by Lu 2015). For the purposes of this review, we distinguish between off-bottom methods located within the intertidal zone, which we categorize as 'intertidal off-bottom culture', and methods which deploy gear at greater depths, which we categorize as 'subtidal off-bottom culture'. Intertidal longlines are an example of intertidal off-bottom culture. These grow shellfish directly on horizontal lines suspended from posts anchored into the sediment, or within hanging bags or hanging baskets which can be equipped with floats to rotate shellfish during each tidal cycle (e.g. Bulmer et al. 2012). In contrast, rack-and-bag culture grows shellfish in bags, cages, or baskets which are secured on top of steel rails running horizontally above the sediment. Alternatively, stake culture grows shellfish directly attached to vertical posts or stakes anchored into the sediment (McKindsey et al. 2011). Lastly, tray culture grows shellfish in trays which rest directly on top of the sediment and may even be stacked on top of one another to conserve space.

2.1.3. Subtidal off-bottom culture

Subtidal off-bottom culture primarily consists of suspended gear (Fig. 3). However, all of the intertidal off-bottom gears described above can be deployed in deeper, subtidal waters. Suspended longline culture involves suspending lines horizontally in the water via a series of floatation buoys (Scarratt 2000, Clements & Comeau 2019). Shellfish are then hung vertically from the longlines inside bags, trays, nets, sleeves, or socks, or the shellfish may even be attached directly to vertical lines (e.g. scallop ear hanging) (reviewed by Grant et al. 2003). Alterna-

tively, 'suspended bag' or 'suspended cage' cultures grow shellfish inside mesh bags or cages floating at, or just below, the surface of the water (reviewed by Howarth et al. 2021). Many suspended systems can be sunk to deeper depths, or onto the seafloor, to help avoid damage from storms and sea ice. Other forms of suspended shellfish culture include raft culture, where shellfish are hung from floating rafts (Williamson et al. 2015).

2.2. Effects of shellfish aquaculture on water and sediment biochemistry

Shellfish aquaculture impacts water quality and sediment biogeochemistry in a variety of ways. Mussels, oysters, scallops, clams, and other bivalves feed by pumping in water and filtering out food particles comprised of bacteria, phyto- and zooplankton, detritus, and other organic matter (Newell 2004). After capture, particles are either sorted, digested, and released as faeces, or rejected and ejected as undigested 'pseudofaeces'. Both faeces and pseudofaeces sink toward the seafloor following their release and are collectively referred to as 'biodeposits' (Shumway et al. 1985, Beninger et al. 1999). As biodeposits transfer nutrients from the water column to the seabed, they can increase the nutrient and organic content of sediments underlying shellfish farms (Crawford et al. 2003, Dumbauld et al. 2009). This can lead to enhanced bacterial activity and, in extreme cases, oxygen depletion and an increase in sulphides (Nizzoli et al. 2006, Richard et al. 2007, Hargrave et al. 2008, Vinther & Holmer 2008). Conversely, by removing organic particles from the water column, high bivalve densities can reduce turbidity, increasing the amount of light reaching the seafloor (Newell & Koch 2004, Ferreira & Bricker 2019, Petersen et al. 2019). Bivalves also excrete nitrogenous wastes (mostly as NH_4^+) directly into the water column that can influence coastal nitrogen cycling (Pietros & Rice 2003, Cranford et al. 2007, Ferreira & Bricker 2019). All of these effects have the potential to interact with eelgrass, as reviewed in the sections below.

2.3. Effects of shellfish aquaculture on eelgrass

2.3.1. Positive interactions

Several authors have suggested that shellfish aquaculture may have positive effects on seagrass. This is because the filter-feeding activity of cultured



Fig. 2. Examples of intertidal shellfish aquaculture. (A) On-bottom clam farm seeded with spat (photo: by Pangea Shellfish Company). (B,C) On-bottom geoduck *Panopea generosa* farm and subsequent harvesting using a high-pressured water jet powered by a support vessel (photos: Jeff Cornwell). (D) Hanging-bag oyster farm (photo: Penn Cove Shellfish). (E) Rack-and-bag oyster farm (photo: Pangea Shellfish Company). (F) Tray culture oyster farm (photo: Pangea Shellfish Company)

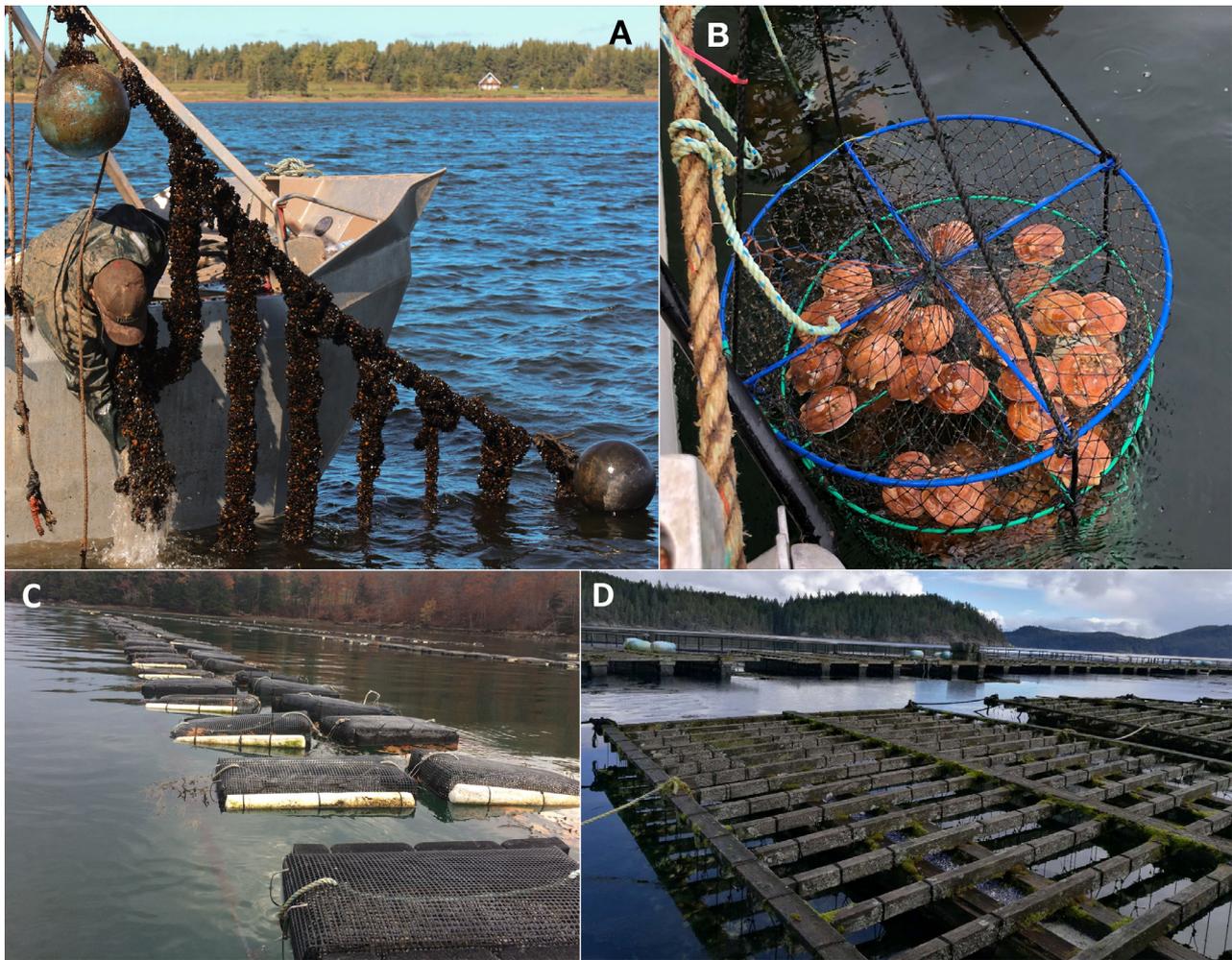


Fig. 3. Examples of sub-tidal off-bottom culture. (A) Suspended longline mussel farm (photo: Aaron Ramsay). (B) Suspended longline scallop farm (photo: Dana Morse). (C) Suspended oyster cage farm (photo: Oyster Gro). (D) Suspended raft oyster farm (photo: British Columbia Shellfish Growers Association)

bivalves can reduce turbidity, providing more light to seagrasses (Newell & Koch 2004, Ferreira & Bricker 2019, Petersen et al. 2019) and other submerged aquatic vegetation (Bulmer et al. 2012, Sandoval-Gil et al. 2016). In addition, their biodeposits can increase concentrations of nitrogen and phosphorus in sediments, which could provide more nutrients for seagrass growth (Peterson & Heck 2001a, Newell & Koch 2004, Dumbauld et al. 2009, Skinner et al. 2014, Qin et al. 2021).

Although several field studies have reported seagrass to exhibit a positive response to naturally occurring bivalves (e.g. Reusch et al. 1994, Peterson & Heck 2001a,b), such positive interactions have only been observed within an aquaculture setting a handful of times (Tallis et al. 2009). For example, a study in Mexico found evidence that suspended oyster

farms increased water and sediment NH_4^+ concentrations, which correlated with an increase in eelgrass growth, shoot size, and photosynthesis (Sandoval-Gil et al. 2016). Similarly, the establishment of a suspended oyster farm in New Zealand correlated with an increase in seagrass (*Zostera muelleri*) cover beneath and adjacent to the farm (Bulmer et al. 2012). Interestingly, the authors of a study in Japan suggested that oyster farms may reduce eelgrass epiphyte loads by feeding on suspended diatoms that would otherwise settle upon eelgrass (Smith et al. 2018). Likewise, field observations of wild mussel beds in Florida, USA, reported reduced seagrass (*Thalassia testudinum*) epiphyte loads and increased sediment nutrient concentrations, which correlated with an increase in seagrass growth and leaf size (Peterson & Heck 2001a).

In summary, while there is some evidence that shellfish farming can benefit eelgrass, it is an area that would greatly benefit from further research. Such efforts should focus on assessing the influence of shellfish farming activity on turbidity, sediment nutrient concentrations, and epiphyte abundance, and how these measures correlate with eelgrass dynamics.

2.3.2. Neutral and negative interactions

Although shellfish aquaculture may benefit eelgrass, most studies report neutral or negative effects. Everett et al. (1995) assessed aquatic vegetation cover within a series of experimental oyster stake and rack-and-bag oyster culture plots in Oregon, USA. They concluded that after 18 mo of farming activity, stake culture significantly reduced eelgrass cover by up to 75%, while rack-and-bag culture caused the near disappearance of eelgrass under farm infrastructure. The exact drivers underlying these negative interactions were not fully determined, but the authors suggested they may have been due to physical disturbance caused by the initial placement of the gear and/or increased sedimentation (5–10 cm buildup of fine sediments was observed within aquaculture plots). Wisehart et al. (2007) also reported lower densities of eelgrass in intertidal longline oyster plots in Washington State, USA, compared with nearby reference areas. Interestingly, they observed significantly lower eelgrass seed densities and seed production within hand-harvested, intertidal longline plots compared to on-bottom culture sites that were mechanically harvested, and therefore subject to greater degrees of physical disturbance. This paradoxical trend is discussed in further detail at the end of this section. In contrast, model simulations and analyses of existing field data by Dumbauld & McCoy (2015) concluded that oyster aquaculture had little impact on eelgrass cover in a bay in Washington State, and might even enhance eelgrass presence when considered at the wider estuarine landscape scale. Similarly, Ward et al. (2003) analysed >130 ha of satellite imagery taken over a 13 yr period in Baja California, Mexico, and concluded that rack-and-bag oyster culture had no detectable long-term effects on eelgrass coverage.

Several studies in eastern Canada have reported negative interactions between subtidal off-bottom shellfish farms and eelgrass, but these negative effects were highly localized. For example, Skinner et al. (2013) surveyed 15 suspended oyster bag farms

in New Brunswick and found that eelgrass biomass (both above- and belowground) was between 5 and 79% lower within shellfish aquaculture farm leases compared to reference areas located 300 m away. These negative effects were largely limited to a 25 m radius from lease boundaries and quickly diminished with increasing distance. They also observed that eelgrass displayed a 38% reduction in photosynthetic efficiency and capacity within farm boundaries, suggesting that shading from aquaculture infrastructure could have been a major factor underlying these negative trends. A subsequent field manipulation study supported this notion, as experimental shading reduced eelgrass shoot density, above- and belowground biomass, canopy height, leaf size, and photosynthetic capacity (Skinner et al. 2014). These negative responses were detected within 67 d after exposure to 26% subsurface irradiance (i.e. less light) and exhibited no substantial recovery 253 d after shading treatments were removed.

Increased spacing of aquaculture gear is frequently reported to reduce the impact of shellfish aquaculture on eelgrass (e.g. Everett et al. 1995, Crawford et al. 2003, Wisehart et al. 2007, Skinner et al. 2014). For example, Rumrill & Poulton (2004) established a series of experimental intertidal oyster longlines in California, USA, with varying distance between gears. Overall, eelgrass cover and density were significantly lower within narrower gear plots (~0.46 and ~0.76 m apart) compared to wider gear plots (~1.5 and ~3 m apart). These experimental oyster plots also caused substantial sedimentation, particularly around the intertidal stakes which supported the longlines.

A recent and thorough meta-analysis by Ferriss et al. (2019) examined 125 studies worldwide and compared shellfish aquaculture and eelgrass interactions between gear types and harvest methods. Generally, shellfish aquaculture had negative effects on eelgrass density and biomass. However, the extent of these impacts was highly variable and depended on the production and harvest methods being used, as well as the geographic region. For instance, their analysis determined that longline culture (no distinction was made between intertidal and sub-tidal gears) negatively impacted eelgrass density, whereas suspended bag methods had a neutral effect. The authors suggested that suspended bag systems may have had less impact on eelgrass than other gear types as they can potentially cause less shading. For example, a study in South Australia observed that suspended bag aquaculture caused 68% less shading than other off-bottom methods (Madigan et al. 2000). This could explain why dense beds of seagrass

(mostly *Heterozostera tasmanica*) have been observed growing directly under suspended oyster bags and baskets in Tasmania (Crawford et al. 2003). Furthermore, in New Brunswick, Canada, oyster growers using suspended bags are required to leave slack in their lines to allow gear to move with the tides (Transport Canada 2007, Skinner et al. 2013). Not only does this reduce physical strain on the gear, but it also prevents any areas of the seabed from becoming permanently shaded, reducing the impacts on eelgrass (reviewed by Howarth et al. 2021).

The meta-analysis by Ferriss et al. (2019) also revealed that, while on-bottom aquaculture generally reduced the density and biomass of eelgrass, it was often associated with an increase in growth and reproduction. This paradoxical trend might be due to reductions in eelgrass density leading to reduced competition for light and space among any remaining eelgrass, potentially enhancing their growth and reproduction (Olesen & Sand-Jensen 1994). In addition, sexual and asexual reproduction in seagrasses is often reported to increase in response to disturbance and is thought to be a mechanism to help encourage recovery processes (reviewed by Cabaço & Santos 2012). Lastly, the meta-analysis indicated that mechanical harvesting methods had the largest initial impact on eelgrass and required the longest time for recovery. Conversely, hand harvesting methods had less impact on eelgrass, presumably because they can be more spatially targeted, resulting in less disruption to eelgrass roots and rhizomes, leading to faster recovery times (Cabaço et al. 2005, Wootton & Keough 2016).

2.3.3. Summary and directions for future research

As reviewed above, there are many ways shellfish aquaculture can interact with eelgrass. There is potential for an interplay of positive factors (e.g. reduced turbidity and provision of nutrients) and negative factors (e.g. shading and increased sedimentation). There is also potential for paradoxical trends such as reductions in eelgrass cover and density yet higher rates of reproduction and growth. Some studies suggest that any negative effects shellfish aquaculture may have on eelgrass tend to be confined to areas under and immediately surrounding shellfish farms, rapidly diminishing with increasing distance. There is also some evidence to suggest that greater distances between gear, and using suspended bags and hand harvesting, may have less impact on eelgrass than other methods. This information could

help regulators establish operational and siting guidelines that minimize the potential for negative interactions between shellfish aquaculture and eelgrass. However, at present, there is not enough evidence to confidently inform such an approach. Therefore, these areas of research would greatly benefit from larger field comparisons and modelling studies to further investigate eelgrass dynamics, health, and survival with proximity to shellfish farms, and which make comparisons between different gears, gear spacings, stocking densities and durations, and harvest methods. As impacts are likely to vary across regions, these studies should be conducted throughout the natural range of eelgrass with particular attention paid to eelgrass in areas subject to ongoing, broadscale environmental stressors (e.g. in water bodies subject to eutrophication and/or ocean warming). Such information could help regulators predict the extent to which different gears, gear spacings, and harvest methods may impact eelgrass, as well as the area of impact extending beyond farm boundaries.

3. FINFISH AQUACULTURE AND EELGRASS INTERACTIONS

3.1. Gear and methods

There is substantially less variation in gear design associated with marine finfish aquaculture than with shellfish aquaculture. This is because most finfish farms grow fish within 'open net-pens' (Fig. 4). These typically extend downward into the water column for at least several metres and are usually anchored to the seabed via a network of ropes, anchors, and moorings. The fish can be hand-fed, although most large facilities deliver feed pellets to the pens using automated feed barges, surface pipes, and blowers. Large, remote operations may also have on-site accommodation for staff, storage buildings, and oxygen aeration equipment. To accommodate this array of infrastructure, modern finfish farms are usually sited in greater depths (e.g. >10 m) than shellfish farms.

3.2. Effects of finfish aquaculture on water and sediment biochemistry

As open net-pens are designed to maximize water exchange, any resulting waste products are released into the surrounding water (Lawson 1995). Most of



Fig. 4. Examples of large, modern finfish farms. (A) Feed barge delivering feed to circular open net-pens via a series of pipes and blowers (photo: Cooke Aquaculture). (B) Farm with square net-pens using a similar feed system; however, there are also oxygen aeration units, and storage and accommodation facilities (photo: Grieg Seafoods)

the carbon released by fish farms occurs as 'particulate wastes' which derive from faeces and uneaten feed (Islam 2005, Wang et al. 2012, Reid et al. 2013). These particulate wastes quickly settle onto the seafloor and rarely disperse more than a few hundred metres (Brager et al. 2015, Price et al. 2015, Bannister et al. 2016, Filgueira et al. 2017). Consequently, these wastes can accumulate under net-pens, resulting in a nutrient-enriched layer of organic matter overlying the sediment. This organic enrichment can increase bacterial decomposition and may lead to oxygen depletion and a build-up of sulphides (Holmer et al. 2007, Pusceddu et al. 2007, Hargrave 2010, Price et al. 2015, Hamoutene et al. 2018). However, the quantity of particulate wastes produced by finfish aquaculture has been significantly reduced over the last 3 decades due to the development of more efficient feeds and feeding systems (Islam 2005, Sørensen 2012, Sprague et al. 2016).

In contrast, 'dissolved wastes' are excreted by fish directly into the water column and represent most

of the nitrogen released from finfish farms (á Norði et al. 2011, Wang et al. 2012). Up to 90% of all the nitrogen excreted by marine finfish is ammonia (NH_3), which is rapidly converted to NH_4^+ due to the pH of seawater (reviewed by Leung et al. 1999). Correspondingly, several studies have reported elevated NH_4^+ concentrations near fish farms (Navarro et al. 2008, Sanderson et al. 2008, Jansen et al. 2018). However, a comprehensive review by Price et al. (2015) concluded that most studies have found no direct evidence of fish farms increasing dissolved nitrogen concentrations of surrounding waters. This is partly because dissolved nitrogenous wastes can quickly be diluted and dispersed by tides and currents, rapidly assimilated by marine organisms (e.g. bacteria, phytoplankton, macroalgae, and seagrass), and lost to the atmosphere through volatilization (Dalsgaard & Krause-Jensen 2006, Dailer et al. 2010). In addition, the release of nitrogen from fish farms can exhibit strong daily pulses and seasonal fluctuations (Karakassis et al. 2001). Thus, any

increase in dissolved nitrogen is likely to be small, localized, and short-lived (reviewed by Howarth et al. 2019).

3.3. Effects of finfish aquaculture on seagrass

3.3.1. Evidence from temperate ecosystems: *Zostera marina*

To date, only one field study has investigated the effects of finfish aquaculture on eelgrass in a temperate setting, and the results were inconclusive. This was conducted by Cullain et al. (2018) at a finfish farm in Port Mouton Bay, Nova Scotia, in eastern Canada. The finfish farm had been in operation for 20 yr prior to the study and was a relatively small operation, with annual production levels estimated at 760 t. Species farmed alternated between rainbow trout *Oncorhynchus mykiss* and Atlantic salmon *Salmo salar*. Although the finfish farm was situated at a depth of 12 m, the authors surveyed eelgrass patches in depths of 1.7–2.9 m at distances of 300 m, 700 m, and 3 km from the fish farm. These eelgrass patches were then compared to several reference areas in Nova Scotia. No eelgrass data were available prior to the creation of the finfish farm.

Their results indicated that eelgrass cover was statistically lower in Port Mouton Bay than in the reference areas, and that eelgrass cover exhibited a general declining trend with increasing proximity to the fish farm. Shoot density, and above- and below-ground biomass also exhibited similar trends but were not statistically significant. Likewise, there was no difference in canopy height or tissue nitrogen content between eelgrass patches near the farm compared to reference areas. All other variables exhibited inconsistent trends. For example, epiphyte cover was substantially higher in eelgrass patches located 700 m away from the farm but was almost non-existent 300 m and 3 km away. A modelling study also suggested a link may exist between anecdotal reports of eelgrass deterioration within the bay and nitrogen effluents emanating from the finfish farm (McIver et al. 2018). However, a subsequent modelling study concluded that dissolved nitrogen concentrations within the bay during active years of the finfish farm were well below the nitrogen toxicity threshold for eelgrass (Filgueira et al. 2021). Overall, a single field study is insufficient to reach any definitive conclusions on finfish aquaculture and eelgrass interactions in temperate ecosystems. Therefore, further investigation is clearly warranted.

3.3.2. Evidence from the Mediterranean Sea: *Posidonia oceanica* and *Cymodocea nodosa*

Nearly all investigations into the effects of open net-pen finfish aquaculture on seagrass have been conducted in the Mediterranean Sea. All of these studies have examined the response of 2 species (*P. oceanica* and, to a lesser extent, *C. nodosa*) to finfish farms stocked with gilthead seabream *Sparus aurata* and European seabass *Dicentrarchus labrax*. In general, these Mediterranean studies reported decreases in seagrass cover with increasing proximity to finfish farms for distances up to 300 m, and the gradual regression of seagrass directly under cages followed by their disappearance (Table 2). These trends have been linked to increases in water and sediment nutrient concentrations, sulphide accumulation, sedimentation/burial, epiphyte loads, and increased grazing pressure from sea urchins and other herbivores (also see reviews by Holmer et al. 2003, 2008, Cullain et al. 2018).

Although this comprehensive body of research indicates that Mediterranean finfish farms can have clear negative impacts on seagrass, environmental conditions are likely very different in the Mediterranean compared to North America and the rest of Europe. Mediterranean waters are generally low in nutrients (oligotrophic) and have very low turbidity. In addition, many of the studies listed in Table 2 investigated finfish farms in highly sheltered areas, in shallow depths (<20 m), and situated directly above seagrass beds. In addition, *P. oceanica* has a depth limit of around 40 m (Mayot et al. 2006, Zubak et al. 2020), which is much deeper than the 12 m maximum depth frequently reported for eelgrass (see references within Table 1). Consequently, (1) there may be less potential for finfish aquaculture to overlap and interact with eelgrass in temperate regions; and (2) it is unknown how much relevance Mediterranean studies have for finfish aquaculture in temperate regions due to the differences in environmental conditions and seagrass species present. In recent years, more stringent regulations have been introduced by several Mediterranean governments, meaning Mediterranean finfish farms are now situated at an average depth of 28 m at a distance of 870 m from shore (Papageorgiou et al. 2021).

3.3.3. Summary and directions for future research

Based on the extensive body of literature from the Mediterranean, and the single field study in Canada,

Table 2. Overview of published responses of *Posidonia oceanica* and *Cymodocea nodosa* meadows to open net-pen finfish aquaculture in the Mediterranean Sea

Category Parameter	Response	References
Seagrass tissues/physiology		
Carbohydrate content	Decrease	Delgado et al. (1997), Ruiz et al. (2001), Holmer et al. (2008), Pérez et al. (2008)
Nitrogen content	Increase	Pérez et al. (2008), Apostolaki et al. (2009b, 2012)
Phosphorus content	Increase	Apostolaki et al. (2007, 2009a,b), Holmer et al. (2008), Pérez et al. (2008)
Sulphide content	Increase	Frederiksen et al. (2007)
Growth-promoting metabolites	Decrease	de Kock et al. (2020)
Stress-related metabolites	Increase	de Kock et al. (2020)
Photosynthesis	Decrease	Delgado et al. (1997), Cancemi et al. (2003), Apostolaki et al. (2010)
Meadow structure		
Above- and belowground biomass	Decrease	Delgado et al. (1999), Apostolaki et al. (2009a)
Percentage cover	Decrease	Delgado et al. (1997), Ruiz et al. (2001), Holmer et al. (2008)
Shoot density	Decrease	Delgado et al. (1999), Pergent et al. (1999), Ruiz et al. (2001), Díaz-Almela et al. (2008), Holmer et al. (2008), Apostolaki et al. (2009a), Rountos et al. (2012)
Shoot mortality	Increase	Díaz-Almela et al. (2008), Holmer et al. (2008)
Morphology		
Leaf growth	Decrease	Ruiz et al. (2001), Apostolaki et al. (2009a)
Leaf / shoot size and area	Decrease	Delgado et al. (1999), Dimech et al. (2002), Holmer et al. (2008), Apostolaki et al. (2009a), Rountos et al. (2012)
Rhizome growth	Decrease	Delgado et al. (1999), Marbà et al. (2006b), Holmer et al. (2008), Apostolaki et al. (2009a), de Kock et al. (2020)
Associated community		
Epiphyte load	Increase	Delgado et al. (1997, 1999), Pergent et al. (1999), Cancemi et al. (2003), Balata et al. (2010), Rountos et al. (2012)
Grazing pressure	Increase	Delgado et al. (1997, 1999), Ruiz et al. (2001), Holmer et al. (2008), Ruiz Fernandez et al. (2009), Apostolaki et al. (2011b)
Sediment biochemistry		
Sulphides	Increase	Frederiksen et al. (2007), Holmer & Frederiksen (2007), Holmer et al. (2008)
Organic content	Increase	Dimech et al. (2002), Cancemi et al. (2003), Apostolaki et al. (2011a)
Nitrogen	Increase	Cancemi et al. (2003), Apostolaki et al. (2011a)
Oxygen	Decrease	Apostolaki et al. (2010)
Phosphorus	Increase	Cancemi et al. (2003), Holmer et al. (2008), Apostolaki et al. (2011a)
Water biochemistry/hydrography		
Nitrogen	Increase	Kocak & Aydin-Onen (2014)
Sedimentation/burial	Increase	Holmer et al. (2007, 2008), Díaz-Almela et al. (2008), Apostolaki et al. (2011a)

it appears that finfish farms can have a diverse range of effects on seagrass. However, like shellfish aquaculture, where these effects occur, they quickly diminish with increasing distance from fish farms and may be negligible at around 300 m from farm boundaries. At present, the vast majority of studies on the interactions between finfish aquaculture and seagrass have been conducted in the Mediterranean Sea. These studies examined the response of different species of seagrass (not eelgrass) in very different environmental conditions from finfish farms in temperate regions. We therefore suggest that additional

research is needed to investigate the effects of finfish aquaculture on eelgrass in temperate ecosystems.

One possible explanation as to why finfish aquaculture and eelgrass interactions are so understudied in temperate ecosystems is that they may rarely coincide with one another. Eelgrass is typically most common within the intertidal zone down to depths of around 7 m (Table 1), which is too shallow to accommodate large, modern finfish farms and their associated infrastructure. For example, Norway is the world's largest producer of farmed salmon (Iversen et al. 2020), but the majority of farms are situated in

deep fjords (sometimes reaching hundreds of metres in depth), characterised by steep, vertical granite walls that are likely uninhabitable by eelgrass (BarentsWatch 2020).

Ideally, future studies would monitor eelgrass beds prior to the establishment of finfish farms and, where impacts occur, investigate recovery processes during fallow years. To help determine the drivers underlying responses in eelgrass, these studies should investigate eelgrass dynamics, health, and survival in relation to their proximity to finfish farms, and assess their relationship with light availability, sedimentation rates, organic enrichment, and sediment and water biochemistry. Investigating multiple field sites would enable comparisons between depths, exposure (i.e. speed and direction of waves, currents, and wind) and stocking densities. Such studies would be invaluable for informing aquaculture management, and in developing operational and siting guidelines that help minimize the potential for eelgrass impacts.

4. CONCLUSIONS

Due to a multitude of interacting factors, eelgrass is declining throughout much of its range. Shellfish and finfish aquaculture have the potential to exacerbate several of these contributing factors, including shading, sedimentation, and eutrophication. As eelgrass can have clear and positive influences on coastal ecosystems, and because it is protected by a wide range of national and international policies, regulators must consider the potential impacts aquaculture may have on eelgrass and implement management practices that minimize them. While the interactions between shellfish aquaculture and eelgrass have been well studied across the globe, the interactions between finfish aquaculture and eelgrass have been subjected to very little investigation. Nonetheless, in both cases, more field and modelling studies are needed to better assess eelgrass survival, growth, and recovery processes in response to different production and harvesting methods, gear spacings, stocking densities, and culture durations. This information could help regulators establish unambiguous operational and siting guidelines that minimize the potential for negative interactions between shellfish aquaculture and eelgrass.

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