

2021-03-15

# Offshore longline mussel farms: a review of oceanographic and ecological interactions to inform future research needs, policy and management

Mascorda Cabre:, L

<http://hdl.handle.net/10026.1/16861>

---

10.1111/raq.12549

Reviews in Aquaculture

Wiley

---

*All content in PEARL is protected by copyright law. Author manuscripts are made available in accordance with publisher policies. Please cite only the published version using the details provided on the item record or document. In the absence of an open licence (e.g. Creative Commons), permissions for further reuse of content should be sought from the publisher or author.*

## 1 **Abstract**

2 With a growing human population and the need to protect our oceans from overfishing, there is a  
3 requirement for society to source alternative means of sustainable protein. Mussel aquaculture has  
4 rapidly expanded in many countries serving as an important supply of protein, but its development has  
5 been limited due to competition for coastal space and the associated environmental impacts of farming  
6 in inshore waters. Offshore aquaculture developments have the potential to overcome such issues. This  
7 review synthesises the current literature on the ecological and oceanographic interactions of longline  
8 offshore mussel farms with the aim to elucidate the main knowledge gaps in a context of management  
9 and conservation. Large offshore aquaculture installations interact with the hydrodynamics of the area  
10 causing water flow distortions and current attenuation, wake formation and distorting water column  
11 stratification which can have an effect on the supply of nutrient and seston as well as altering material  
12 dispersal, biodeposition and resuspension, having in turn, a knock on effect on the carrying capacity of  
13 the system, ultimately affecting the surrounding ecology and its ecosystem services. Offshore mussel  
14 farm studies report an increase biomass or numbers of benthic and pelagic organisms beneath and  
15 around mussel ropes relative to control sites using the structure for shelter, refuge and nursery.  
16 Improving our understanding of offshore aquaculture-environment interactions is crucial to identify the  
17 priorities needed for future research to inform policy and management practices as well as its role as  
18 part of the Blue Growth Agenda and as ‘other effective area-based conservation measures’ (OECMs).

19

20 Keywords: Aquaculture, Blue Growth, Ecology, MPAs, Mussel Farm, Oceanography.

21

## 22 **Introduction**

23 The 21st century is faced with the challenge of satisfying human demand for sustainable protein (Duarte  
24 *et al.* 2009; Strand *et al.* 2017). World fish consumption has increased from an average of 9.9 kg per  
25 capita in the 1960s to 20.3 kg per capita in 2016, with 151.2 million tonnes in total produced for human  
26 consumption (FAO 2018). Capture fisheries have not been able to keep up with this increase in demand  
27 (Galparsoro *et al.* 2020; Jackson *et al.* 2001; Pauly *et al.* 2002) as over 89% of global wild marine fish  
28 stocks are overexploited (FAO 2016), with production remaining relatively static since the 1980s. Such  
29 shortfall has been met by increasing marine farming of fin-fish, shellfish, and seaweed (Duarte *et al.*  
30 2009; Landmann *et al.* 2019; Strand *et al.* 2017).

31 Over the past 50 years, global aquaculture has grown and expanded dramatically, accounting for almost  
32 half of the world's fish food supply from marine sources and reaching 110.2 million tonnes in 2016  
33 worth an estimated value of USD 243.5 billion (FAO 2018). It is one of the fastest growing production  
34 industries on the planet with a current annual growth rate of 5.8% since 2001, with China being at the  
35 forefront holding 61.5% of the world's production (FAO 2018). Such growth has been related to the  
36 "Green Revolution" (greater grain yields since 1950s) being named a "Blue Revolution" (O'Donncha  
37 *et al.* 2016). This requires increasing use of public coastal space putting the industry's development into  
38 conflict with other users and societal demands such as tourism, nature protection, fisheries, energy  
39 production or transport (Callier *et al.* 2017; Galparsoro *et al.* 2020; Lacoste *et al.* 2018; Landmann *et*  
40 *al.* 2019; Lester *et al.* 2018; Stelzenmüller *et al.* 2013; Strand *et al.* 2017).

41 This paper aims to review the interactions that offshore longline mussel aquaculture farms have in  
42 relation to the offshore physical and ecological marine environment by explaining our current  
43 understanding of: (i) the effect of farms on background oceanography; (ii) the consequent ecological  
44 effects and response; (iii) the relevance in a context of management, policy and conservation and; (iv)  
45 the main knowledge gaps that need addressing in order to foster the development of a sustainable  
46 industry.

47

## 48 Bivalve aquaculture

49 The latest FAO State of the World Fisheries and Aquaculture 2018 report states that the global shellfish  
50 industry produced 17.1 million tonnes of molluscs (USD 29.2 billion) in 2016, representing 58.8% of  
51 the combined production of marine and coastal aquaculture. Mussels accounted for about 8% of  
52 shellfish production with around 15 million tonnes. China is the largest producer of aquaculture mussel  
53 (14.2 million tonnes) accounting for 83% of total production (FAO 2018).

54 As one of the most important non-fed species in aquaculture (no need to be provided with an external  
55 source of food as filter feeding organisms directly feed on the plankton in the surrounding environment)  
56 (FAO 2016; Lucas 2012; STECF 2018), molluscs are the most consumed aquaculture category after  
57 finfish (*Table 1*) (Ellis *et al.* 2007; FAO 2018; STECF 2018). With the appropriate environmental  
58 conditions, molluscs such as mussels and oysters that have a free-swimming larval stage will also self-  
59 seed providing a relatively cost effective harvestable crop if suitable habitat is provided (Stevens *et al.*  
60 2008). Naturally, mussels and oysters are ecosystem engineers that form large wild beds. These  
61 biogenic reefs provide important services through their effects on nutrient cycling, habitat structure,  
62 water filtration, biodiversity and food web dynamics. Due to their appeal as a food source, exploitation

63 of natural beds for commercial purposes (dredging) and farming is widespread (Landmann *et al.* 2019;  
64 Strand *et al.* 2017; Tyler-Walters 2008).

## 65 Types of mussel farming

66 Mussels can be produced by either ‘bottom’ or ‘off-bottom’ cultivation accounting for approximately  
67 15% and 85% of overall production respectively (Mckindsey *et al.* 2011). Bottom culture involves  
68 dredging mussels from natural subtidal or intertidal beds to move them to more sheltered areas where  
69 they can expand and grow. To help reduce the heavy predation by crabs and starfish attracted to bottom  
70 culture, the vast majority of cultivated mussels are grown ‘off-bottom’, suspended above the seabed  
71 (Spencer 2002).

72 There are three principle methods of off-bottom culture: raft, pole and longline (STECF 2018). In raft  
73 culture (Figure 1 a), seed is attached to ropes suspended from moored, floating rafts (Aypa 1990). Pole  
74 culture (Figure 1 b), or ‘bouchot’, involves growing mussels on wooden stakes driven into the ground  
75 in low intertidal zones (Gouilletquer 2020; Mckindsey *et al.* 2011). The most employed technique is the  
76 continuous longline design (Figure 1 c-d) as it supports a substantial crop with minimum infrastructure  
77 (STECF 2018; Stevens *et al.* 2008).

78 Although it is a rapidly evolving industry, longline farms are typically large developments of at least  
79 100 ha with more than 200 longlines. With an average length of 120-150m, each longline consists of  
80 two parallel “backbone” ropes supported by buoys at regular intervals keeping the structure afloat and  
81 moorings anchored to the seabed (Figure 1 c-d) (Plew 2005; Plew *et al.* 2005; Stevens *et al.* 2008).  
82 Mussels are attached to line droppers, evenly spaced ropes that continuously loop from the “backbone”  
83 and have lengths between 5-30 m depending on water depth and nutrient availability (Landmann *et al.*  
84 2019; Stevens *et al.* 2008). In areas with strong currents, waves and winds, longline farms have been  
85 submerged 5-10m using buoyancy controls or altering the mooring design (Figure 1 d) allowing mussels  
86 to grow faster and have higher meat/shell ratios, making them a preferred method and becoming the  
87 dominant technique used (Brenner *et al.* 2009; Buck 2007; Gagnon & Bergeron 2017; Kapetsky *et al.*  
88 2013; Stevens *et al.* 2008).

## 89 Impacts of inshore mussel farming

90 Overall, aquaculture systems have two main outputs of pollution: animal faeces and waste from added  
91 feed which accumulate under and around the structures as biodeposits (Giles *et al.* 2009; Hilborn *et al.*  
92 2018; Keeley *et al.* 2009; Rampazzo *et al.* 2013). Inshore mussel farms located in low energy  
93 environments with a mild hydrodynamic regime are considered to have localised effects (Callier *et al.*  
94 2006; Chamberlain *et al.* 2001; Giles *et al.* 2009; Hartstein & Stevens 2005). Non-fed aquaculture such

95 as bivalve farming does not report to have as many negative effects as finfish farming (Danovaro *et al.*  
96 2004; Fabi *et al.* 2009; Hilborn *et al.* 2018; Keeley *et al.* 2009; Rampazzo *et al.* 2013).

97 With a role in the provision of ecosystem goods and services, mussel farms can mitigate the  
98 consequences of nutrient loading and eutrophication (Ferreira *et al.* 2011; Gallardi 2014; Kumar &  
99 Cripps 2012; Matarazzo Suplicy 2018; Newell *et al.* 2019) having a positive contribution to the  
100 surrounding ecology due to their sediment stabilization capacity, biofiltration function and ability to  
101 uptake CO<sub>2</sub> (Matarazzo Suplicy 2018; Sheehan *et al.* 2019; Solandt *et al.* 2020). Research indicates that  
102 production of non-fed species can be a more sustainable source of protein crucial in providing food  
103 security with minimal environmental impact (FAO 2016; Hilborn *et al.* 2018; Matarazzo Suplicy 2018).  
104 This has been acknowledged worldwide by environmental groups and certification bodies, such as  
105 World Wildlife Foundation (WWF) and Aquaculture Stewardship Council (ASC), as being a highly  
106 sustainable form of seafood production (Matarazzo Suplicy 2018) and are recommended as a 'best  
107 choice' or 'super green option' by the Marine Conservation Society (Marine Conservation Society 2018).

108 Nonetheless, with the intensification of shellfish farming in sheltered inshore locations, the increased  
109 amounts of biodeposits in the form of faeces, pseudo-faeces and marine litter are accumulated beneath  
110 and around the farm, affecting the benthic community structure below (Callier *et al.* 2006; Chamberlain  
111 *et al.* 2001; Fabi *et al.* 2009; Hartstein & Stevens 2005; Keeley *et al.* 2009; Kumar & Cripps 2012;  
112 Mckindsey *et al.* 2011; Rampazzo *et al.* 2013). This is amplified by changes in water flow velocities as  
113 the farm obstructs any background currents present showing that, local hydrodynamic regimes have a  
114 major influence on a farm's magnitude and severity of effects, especially in low energy environments  
115 (Cranford *et al.* 2009; Grant & Bacher 2001; Matarazzo Suplicy 2018; Stevens & Petersen 2011;  
116 Strohmeier *et al.* 2005, 2008). The large amounts of organic loading can influence biogeochemical  
117 processes, altering sediment physicochemical parameters that have an effect on benthic respiration with  
118 wider ecological effects including the creation of novel habitat and ultimately the modification of  
119 benthic infaunal communities. As organic matter (OM) increases, natural soft-sediment communities  
120 dominated by large filter-feeders are replaced by smaller, opportunistic deposit-feeding organisms and  
121 altering pelagic assemblages (Callier *et al.* 2009; Chamberlain *et al.* 2001; Danovaro *et al.* 2004; Fabi  
122 *et al.* 2009; Grant *et al.* 2012; Hartstein & Stevens 2005; Keeley *et al.* 2009; Matarazzo Suplicy 2018;  
123 Newell 2004; Rampazzo *et al.* 2013). Raising concerns about the increasing range of aquaculture-  
124 environment interactions of intensive bivalve aquaculture (Gallardi 2014; Kumar & Cripps 2012;  
125 Landmann *et al.* 2019) have led the industry to acquire a certain negative reputation within the public  
126 view (Gentry *et al.* 2017).

127 Inshore mussel farms have been found to increase the structural complexity of the seabed underneath  
128 due to mussel fall-off from the ropes, creating habitats for other invertebrates by providing food and  
129 refuge from predation (Gutiérrez *et al.* 2003; Sheehan *et al.* 2019) and attracting scavengers and other

130 predators (D'Amours *et al.* 2008; Inglis & Gust 2003). Studies have reported diverse assemblages of  
131 fishes, invertebrates and algae as well as an increase in biodiversity and biomass (LeBlanc *et al.* 2003;  
132 Murray *et al.* 2007; Sheehan *et al.* 2019). Other effects include the aggregation of epibenthic  
133 macrofauna and the modification of plankton communities (Bendell 2014; Chamberlain *et al.* 2001;  
134 Gallardi 2014; Mckindsey *et al.* 2011).

135 Generally, mussel farms have varying effects on the marine benthic environment and associated benthic  
136 assemblages depending on the type of culture and the oceanography and hydrodynamic regime of the  
137 area (Chamberlain *et al.* 2001; Kumar & Cripps 2012; Mckindsey *et al.* 2011); while some report  
138 negative impacts (Chamberlain *et al.* 2001; Cranford *et al.* 2009; Hargrave *et al.* 2008; Kaspar *et al.*  
139 1985; Keeley 2013; Nizzoli *et al.* 2005, 2006; Stenton-Dozey *et al.* 1999 2001) others result in little or  
140 no ecological change relative to surrounding habitats (Crawford *et al.* 2003; D'Amours *et al.* 2008;  
141 Danovaro *et al.* 2004; Dimitriou *et al.* 2015; Inglis & Gust 2003; Lasiak *et al.* 2006; McKindsey *et al.*  
142 2012; Wilding & Nickell 2013; Ysebaert *et al.* 2009).

#### 143 A move from inshore to offshore mussel farming

144 As the inshore industry is reaching a saturation stage with its expansion becoming a potential space  
145 usage conflict, offshore shellfish developments are becoming increasingly attractive by extending the  
146 industry to high hydrodynamic areas, reducing spatial constraints, visual effects, increasing production  
147 capacity and potentially reducing the ecological effects experienced by inshore developments (Brenner  
148 *et al.* 2009; Buck *et al.* 2018; Fairbanks 2016; Gagnon & Bergeron 2017; Gallardi 2014; Gentry *et al.*  
149 2016 2017; Gibbs 2004; Kapetsky *et al.* 2013; Keeley *et al.* 2009; Lacoste *et al.* 2018; Landmann *et al.*  
150 2019; Muñiz *et al.* 2019; O'Donncha *et al.* 2016; Plew *et al.* 2005; Stevens *et al.* 2007, 2008). Compared  
151 to inshore environments which tend to be oligotrophic in nature, offshore environments have good water  
152 quality with continuous good oxygen conditions, lower nutrients and lower primary productivity  
153 reducing the risks of exposure to biotoxins such as toxic phytoplankton blooms (red tides), and low  
154 exposure to diseases, parasites or terrestrial sources of contamination such as pollutants and pesticides,  
155 common issues of inshore mussel farming (Brenner *et al.* 2009; Buck *et al.* 2005; Kapetsky *et al.* 2013;  
156 Lucas 2012; Stevens *et al.* 2007, 2008). Therefore, offshore mussel farms may not only increase  
157 production but have the potential to grow healthier and qualitatively better mussels than those grown  
158 inshore, compensating the investment (Brenner *et al.* 2009).

159 Following the need for a more precise definition suitable for the development of a common legal  
160 framework as required by the United Nations Convention on the Law of the Sea (UNCLOS), this paper  
161 defines 'offshore aquaculture' as:

162 'the establishment of aquaculture farms in exposed locations, in areas with a high energy  
163 environment and exposed to substantial oceanic conditions (large waves, storms and strong currents)  
164 located more than 1km from the nearest coast and requiring reasonable infrastructure'

165 This definition is therefore, encompassing other terms such as 'remote area', 'open water', 'open  
166 ocean', 'offshore' or 'off-coast', used in the literature to define the type of farm under review, but  
167 focusing on the physical and environmental conditions of the area (Buck *et al.* 2018; Froehlich *et al.*  
168 2017b; Kapetsky *et al.* 2013; Lovatelli *et al.* 2013; Plew *et al.* 2005; Ryan, 2004; Stevens *et al.* 2008;  
169 Troell *et al.* 2009).

170 As oppose to what is seen inshore, offshore mussel farms are situated in highly dynamic systems with  
171 high energy background currents and waves capable of dispersing biodeposits (Fabi *et al.* 2009; Kumar  
172 & Cripps 2012; Lacoste *et al.* 2018; Lin *et al.* 2016). Although the significant volumes of organic  
173 loading produced by mussel farms have the potential to be dissipated, offsetting the effects seen beneath  
174 inshore developments (Lacoste *et al.* 2018; Lin *et al.* 2016), the structure itself may have an effect on  
175 water flow (Plew *et al.* 2005, 2006; Tseung *et al.* 2016). The influence of small farms to an area with a  
176 high energy hydrodynamic regime is likely to be small compared to the natural variability and dynamics  
177 of an offshore marine environment. However, the effect of large developments like that of a typical  
178 offshore longline mussel farm may be substantial causing blockage to the flow and dissipating energy  
179 (Plew *et al.* 2005, 2006; Tseung *et al.* 2016). High hydrodynamic regimes can alter the rate at which  
180 biodeposits accumulate and/or dissipate extending the footprint of an offshore mussel farm over larger  
181 areas (Giles *et al.* 2009; Lacoste *et al.* 2018), indicating a strong relationship between the oceanography  
182 of a farm, organic enrichment in seabed sediments, and a subsequent modification of macro-invertebrate  
183 and pelagic composition (Figure 2) (Fabi *et al.* 2009; Lacoste *et al.* 2018; Lin *et al.* 2016; Rampazzo *et*  
184 *al.* 2013).

185 Despite the potential benefits of offshore farming, there is very limited offshore aquaculture presence  
186 due to economic costs, suitability of location in terms of hydrodynamic regime and ecological carrying  
187 capacity, the need for planning and large-scale infrastructure engineering designs (Buck *et al.* 2018;  
188 Galparsoro *et al.* 2020; Lacoste *et al.* 2018; Stevens *et al.* 2008), licensing intricacies and lack of clear  
189 policy and management, social perceptions and political obstacles (Fairbanks 2016; Galparsoro *et al.*  
190 2020; Kapetsky *et al.* 2013; Upton & Buck 2013). Additionally, the limited knowledge describing the  
191 influence of offshore developments available is causing difficulties for this industry to flourish.  
192 Particularly, quantitative and qualitative relationships between farming level and benthic influences are  
193 lacking, making predicting environmental farm effects challenging (Froehlich *et al.* 2017a; Mckindsey  
194 *et al.* 2011; Upton & Buck 2013).

195 In order for this industry to develop and become a sustainable source of protein, it is paramount that we  
196 understand its potential impacts to assess and quantify its benefits and be able to optimise its  
197 development and management. Expansion of the offshore aquaculture industry requires improved  
198 understanding of aquaculture-ecologic and oceanographic interactions (Callier *et al.* 2017; Fabi *et al.*  
199 2009; Galparsoro *et al.* 2020; Lacoste *et al.* 2018; Landmann *et al.* 2019; Lester *et al.* 2018; Lin *et al.*  
200 2016; Stelzenmüller *et al.* 2013; Strand *et al.* 2017; Tseung *et al.* 2016; Upton & Buck 2013), crucial  
201 to clarify what needs to be prioritised to inform consenting, useful impact assessments, efficient marine  
202 spatial planning (MSP) and inform policy makers within a context of ecosystem-based management.

203

## 204 **Methods**

205 Following an extensive amount of research and literature on the effects of inshore mussel farms, this  
206 review concentrates its literature review on a critical account of what has been published on offshore  
207 longline mussel farms. Specifically, the areas relevant to its influence on water flow and consequent  
208 ecological effects were identified as the main focus for a thorough literature review analysis through  
209 keyword searches in scientific journals, ‘grey’ literature and press publications.

210 A basic background information check was performed in order to establish the need for this review and  
211 to identify the most relevant literature available. Then a general literature search through Google  
212 Scholar and Web of Science were used to have an overview of the topic which included search terms  
213 such as ‘offshore shellfish’, ‘offshore aquaculture’, ‘remote aquaculture’, ‘open water aquaculture’,  
214 ‘open ocean aquaculture’, ‘off-coast aquaculture’ and any combination of those as well as searching for  
215 relevant literature reviews already published. This was followed by a more specific literature research  
216 which expanded on previous terms to include keywords such as ‘mussel’, ‘longline’, ‘long-line’,  
217 ‘*Mytilus*’, ‘*Perna*’, ‘oceanography’, ‘flow’, ‘hydrodynamic’, ‘current regime’, ‘management’,  
218 ‘conservation’, ‘ecology’, ‘plankton’, ‘MPA’ and any combination of those in Google Scholar, Web of  
219 Science, Elsevier and ScienceDirect on publications between 2000 and 2020.

220 A paper management system (Mendeley®) was used to store and classify the relevant literature which  
221 was filtered by date. Literature was then read and assessed on its relevance to this review. Where  
222 literature directly assessed the effect of offshore mussel aquaculture on benthic and pelagic ecosystems  
223 or oceanographic and ecological effects, the papers were identified as key references for each topic and  
224 used accordingly. When a Google search identified literature in English, French or Spanish, these were  
225 analysed however, literature was specifically searched in English only. Any other language not spoken  
226 by the authors was omitted from the analysis.

227 While there likely exists other publications that look at offshore aquaculture, such as ‘polyculture’ or  
228 ‘renewable energy’, these studies were not included since the focus of this review was to assess the  
229 specific knowledge in regards to offshore longline mussel farms alone.

230

## 231 **Results**

232 This section describes the results of a thorough literature review on the knowledge regarding the effects  
233 of offshore longline mussel farms to date.

### 234 **Influence of offshore farms on water flow**

235 Large offshore aquaculture installations impact local hydrodynamics by acting as physical obstacles to  
236 water flow. As a porous structure, water flow blockage is partial, differing from the effects that other  
237 well-studied solid structures (i.e islands or sea defences) have on the flow (O’Donncha *et al.* 2013; Plew  
238 *et al.* 2006) by creating velocity shears and mixing layers and producing small scale turbulence causing  
239 enhanced dispersion (Figure 3) (Matarazzo Suplicy 2018; O’Donncha *et al.* 2013, 2016; Plew 2013;  
240 Plew *et al.* 2005, 2006), For instance, reducing current velocities within the farm (drag-induced  
241 modifications) resulting in an effect on the velocity profile of the water column, generating increased  
242 vorticity and vertical circulations at the flanks with the acceleration of currents beneath it (Plew *et al.*  
243 2005, 2006; Shi *et al.* 2011; Tseung *et al.* 2016) which may have considerable impacts to the  
244 surrounding environment which could result in an increase seabed scour and biodeposit resuspension  
245 (Danovaro *et al.* 2004; Fabi *et al.* 2009; Plew 2013; Plew *et al.* 2005, 2006; Rampazzo *et al.* 2013;  
246 Tseung *et al.* 2016). Due to increased drag, it may also determine the formation of a wake downstream  
247 of the farm (Figure 2 and Figure 3) (Plew *et al.* 2005, 2006; Tseung *et al.* 2016).

248 Although environmental impacts of shellfish aquaculture focus on ecological aspects such as  
249 biodeposition, nutrient depletion and benthic impacts, extensive effects may be associated with wave  
250 attenuation, wake formation, current distortion and disruption of stratification (Boyd & Heasman 1998;  
251 Grant & Bacher 2001; Plew 2013; Plew *et al.* 2005, 2006; Stevens *et al.* 2008; Strohmeier *et al.* 2005)  
252 which will in turn inform the extent of a mussel farm’s ecological impacts and footprint. Perturbations  
253 in the current regime may have an effect on the supply of nutrient, seston, material dispersal and feeding  
254 behaviour, if not taken into account, this could result in an overestimate of the overall carrying capacity  
255 of the system and should not be neglected (Duarte *et al.* 2008; Lin *et al.* 2016; O’Donncha *et al.* 2013;  
256 Plew 2013). Such effects are closely related to the underlying hydrodynamics of the area. Particularly,  
257 its carrying capacity or performance will be influenced by a range of factors such as the overall  
258 dimensions, extent, shape and layout of the farm (orientation of the farm’s structures to prevailing

259 currents and waves and/or spacing between headlines), the density of both the farm and the mussels on  
260 the ropes (farm's canopy), the bathymetry, topography and geology of the area, the current and weather  
261 regime characteristics (background current speeds) as well as the ecology, physicochemical and  
262 biological parameters of the surrounding marine environment (Aure *et al.* 2007; Lin *et al.* 2016;  
263 Pechlivanidis *et al.* 2018; Stenton-Dozey 2013).

264 A collection of elements that form a porous obstacle to water flow can be described as canopies. For  
265 instance, terrestrial forests, wetland marshes and kelp beds are naturally occurring canopies which have  
266 been broadly studied showing to reduce water flow velocities within, generate velocity shears, mixing  
267 layers and producing small-scale turbulence which enhance dispersion (Hondolero & Edwards 2017;  
268 Jackson & Winant 1983; Plew *et al.* 2005, 2006; Rosman *et al.* 2013). Contrary to emergent canopies  
269 that extend upwards from the floor and when aquatic, are either fully or partly covering the entire water  
270 column, mussel farms are highly porous structures that extend downward from the water surface and  
271 present a gap between the canopy and the seabed or bottom boundary thus referred to as suspended  
272 canopies (Plew *et al.* 2006; Tseung *et al.* 2016). When a suspended canopy extends downwards few  
273 meters below the water surface this can also be referred to as submerged canopy such as those created  
274 by submerged longline mussel farms (Plew *et al.* 2006).

275 In order to understand water flow interactions of shellfish suspended canopies, the extensive relevant  
276 literature around emergent canopies is indebted, especially in terms of flow distortion and current  
277 attenuation, edge effects, patchiness, within canopy transport, wake formation and interaction with  
278 stratification. However, it must be noted that unlike natural canopies, shellfish structures are highly  
279 ordered and heterogeneous canopies in terms of organisation (longline spacing, depth, dropper  
280 diameter...) (Stevens & Petersen 2011).

## 281 Water flow modification

282 In coastal areas, emergent canopies rooted to the seafloor such as seagrass meadows, salt marshes,  
283 mangroves, and kelp forests provide shore protection by preventing erosion, increasing sedimentation  
284 and mitigating flooding by restraining waves and currents due to their wave attenuation capacity.  
285 Although the ecosystem services of such emergent canopies are relatively well studied, aquatic  
286 suspended canopies which have most of their biomass near the surface such as certain forests of kelp  
287 (*Macrocystis* sp), vegetated platforms that serve as breakwaters or longline mussel farms which may  
288 provide similar ecosystem services have been neglected (Alleway *et al.* 2019; Chen *et al.* 2019;  
289 Mckindsey *et al.* 2011; Plew *et al.* 2005, 2006).

290 During wave attenuation, energy is transferred from the wave field to turbulence as the waves propagate  
291 through a canopy. Although wave-driven flexible structures such as a longline mussel farms move and  
292 flex to accommodate this transfer of energy, such drag-induced water flow velocity modifications have

293 been detected within suspended aquaculture structures (Plew *et al.* 2005) where bottom friction and  
294 structure drag generated turbulence within the canopy has shown the potential to enhance mixing both  
295 horizontally and vertically (Figure 3) (Plew *et al.* 2006; Stevens *et al.* 2008). As longline mussel farms  
296 do not extend over the full water depth, flow diversion is expected to be both vertically and horizontally  
297 around the canopy being the latter the predominant direction as longline mussel farm' dimensions are  
298 two to three orders of magnitude greater horizontally than vertically (Plew *et al.* 2006). This is supported  
299 by hydrodynamic studies of offshore mussel farms showing that water flow velocities are reduced both  
300 near the bed (bottom boundary layer friction) and within the canopy, while the highest velocities are  
301 found around and beneath the farm, in the gap between the seabed and the bottom of the suspended  
302 canopy (Figure 3) (Plew 2013; Plew *et al.* 2006).

303 Limited field studies show that some of the water flow approaching the farm is diverted under and  
304 around inducing downwelling on the upstream side of the farm (Lin *et al.* 2016; Plew *et al.* 2005;  
305 Rampazzo *et al.* 2013). The spatial distribution of such flow changes is not simple as there are areas for  
306 instance, around the corners of a farm and beneath, where the disturbed flow accelerates (Stevens *et al.*  
307 2008). Currents within the suspended canopy have been found to be as little as 25% those of the outside  
308 water flow with water speed reductions reaching up to 90% in extreme cases (Hulot *et al.* 2018; Lin *et al.*  
309 *et al.* 2016; Plew 2013). A study of an inshore but highly hydrodynamic mussel farm in Cobscook Bay  
310 (USA), used hydrodynamic and material transport models to show how flow is diverted around the farm  
311 with velocities increasing outside the structure while flow attenuation is up to 50% at the centre  
312 (O'Donncha *et al.* 2016).

313 Studies have identified that a main factor key to water flow modification is the angle of inference  
314 between upstream longlines and water flow. If upstream longlines are aligned to the flow, only a fraction  
315 of water goes through which is substantially slowed down creating great velocity gradients (Delaux *et al.*  
316 *et al.* 2011) although, this could reduce seston supply as downstream ropes would be within the influence  
317 of upstream ones (Plew 2005). Alternatively, when perpendicular to the current, water flow  
318 modification is widely spread creating less vorticity (Delaux *et al.* 2011). Both small (0°C) (Delaux *et al.*  
319 *et al.* 2011) and large (90°C) angles have been found to cause greater drag and greater alterations to  
320 vertical flow (Delaux *et al.* 2011; Plew *et al.* 2006). This can be attenuated by lower space between  
321 ropes (Plew 2005) hence, drag is a function of farm orientation to the flow, density, spacing and  
322 ultimately, overall farm arrangement (Delaux *et al.* 2011; Plew 2005; Smaal *et al.* 2019; Stevens *et al.*  
323 2008). Taking into account the angle of the farm to the flow and water residence time (the time a particle  
324 spends in a given place, how long it takes to go through the system) within the canopy Plew *et al.* (2006)  
325 found that farms perform best when developed approximately 45°C to the flow while, Delaux *et al.*  
326 (2011) found that larger farms at 50-90°C angle to the current, water flow reduction was decreased.

327 Water flow velocity increases beneath the farm may both affect the location of biodeposit material on  
328 the seabed and increase seabed shear stress increasing the possibility of sediment and biodeposit  
329 resuspension influencing the depositional footprint of the farm (Giles *et al.* 2009; Plew 2013; Rampazzo  
330 *et al.* 2013). The increase of flow velocity beneath the farm strongly depends on the farm's density  
331 stratification and the gap between the bottom of the farm and the seabed. Numerical models suggest  
332 that highest beneath the farm velocities occur when longlines extend to about 80% of the water depth  
333 (Plew 2013, 2011). A study of New Zealand mussel longline farms has shown that beneath the farm  
334 velocities are off-set by around the farm horizontal water flow diversion producing an increase of seabed  
335 shear stress of up to 20% (Plew 2013, 2011).

336 Another implication of flow modification by longline mussel farms is the influence of depth and near  
337 seabed water flow. Although there's an overall lack of information about velocity changes with depth  
338 in large suspended canopies, increased velocities on the seabed of a mussel farm have been measured  
339 (Plew 2005). When developed in deeper water, it is more likely that a greater water diversion under the  
340 canopy occurs (Plew *et al.* 2006) however, in shallower waters for instance where the gap between the  
341 canopy and seabed is around 0.1 and 0.3 of the water depth, the underflow appears to be restricted.  
342 Although a smaller gap increases below farm water velocity, this in turn increases velocities within the  
343 farm and bed friction which restricts such underflow (depth-average velocity) reducing vertical  
344 transport. This effect is greater as the gap decreases (Plew 2011; Plew *et al.* 2006). This is further  
345 demonstrated by numerical models where the size of the gap beneath the farm shows to modify bed  
346 shear stress up to a 66% increase (assuming no water diversion around the farm) which could increase  
347 sediment transport and resuspension (Plew 2011). In an actual farm, water flow is diverted horizontally  
348 as well as vertically resulting in a reduction of depth-average velocity which has been estimated to be  
349 of about 40% (Plew 2011). It has been suggested that increasing canopy density lowers velocities within  
350 the canopy relative to higher below the canopy velocities, generating greater bed friction and total drag  
351 (Plew 2011) while increasing canopy thickness may alter longline drag due to its proximity to the seabed  
352 (Plew 2005).

### 353 Wake formation

354 A region of flow recirculation behind an object, a wake, can be formed downstream of a mussel farm  
355 (Tseung *et al.* 2016; Plew *et al.* 2005, 2006). The wake consists of two main zones, a steady wake with  
356 approximately constant velocity and a velocity recovery zone where velocity increases again (Tseung  
357 *et al.* 2016) (Figure 2 and Figure 3). As upstream longlines divert the water flow producing lower  
358 velocities within the farm and acceleration around and/or beneath it (Gibbs *et al.* 1991; Plew *et al.*  
359 2006), numerical and experimental studies indicate the possible balanced of such flow alterations by  
360 the formation of a steady slow velocity wake downstream, where longlines have lower drag, with a  
361 subsequent velocity recovery zone (Tseung *et al.* 2016).

362 Through a study of an offshore mussel farm in New Zealand, Plew *et al.* (2006)  
363 suggested that lower dissipation rates downstream of the farm could be due to a  
364 low-velocity wake formation while orientation of longlines to the water flow  
365 have an important influence on the farm's net drag and wake formation (Delaux  
366 *et al.* 2011; Plew *et al.* 2005). Numerical models suggest that flow distortions  
367 can reach considerable distances (from 0.6 to 4 times the canopy length) from  
368 the structure (Tseung *et al.* 2016), observing different degrees of water flow  
369 acceleration away from the installations depending on background  
370 hydrodynamics and farm structure. Stratification distortion and particle  
371 residence time

372 The effects of offshore longline aquaculture farms on material transport and residence times are  
373 important in terms of carrying capacity and the extent of a farm's footprint (Plew 2013; Stevens *et al.*  
374 2008). The pulse residence time (PRT) is the time needed to flush a given fraction (95%) of a  
375 conservative tracer or dye from a water body after being introduced to a given location. PRT can be  
376 seen as a self-purification capacity measure of a farm thanks to both tidal exchange rates with the outer  
377 sea and turbulent dispersion. Even in an inshore development under high current velocities, flushing  
378 times can be increased as high as 10 to 20% within its footprint (O'Donncha *et al.* 2016), reducing food  
379 renewal flows and accumulating biodeposits within the structure by altering sedimentation rates (Lin *et al.*  
380 2016; O'Donncha *et al.* 2016; Stevens *et al.* 2007, 2008) which can then be transported further afield  
381 by beneath farm accelerating currents. Therefore, changes in current speeds, even when localised, can  
382 impact material transport altering the farm's footprint.

383 Differences in water density due to temperature and salinity cause stratification (layering of water  
384 bodies) which can reduce PRT, limiting both nutrient and biodeposit flux in and from the canopy.  
385 Longline mussel farms may influence these by blocking or diverting water layers, generating internal  
386 waves or enhancing vertical mixing through within farm turbulence (Plew 2013). Changes in the depth  
387 and layout of isopycnals have already been observed in the field due to offshore mussel farm structures  
388 interacting with stratification (Plew 2013; Plew *et al.* 2005, 2006). Experimental studies have shown  
389 that stratified water moving through a porous structure can produce internal waves which can be  
390 propagated away from the structure (Plew 2013) and that density stratification can inhibit vertical  
391 diversion favouring horizontal diversion instead (Plew *et al.* 2006) or even restrict the development of  
392 the shear layer and further reduce vertical diversion and transport (Plew 2011). However, the influence  
393 of stratification depends on a wide range of factors such as background hydrodynamics or tides as well  
394 as the surface and density of the farm. This can also have an effect on the formation and extend of a  
395 wake (Plew 2013). Such interactions are poorly understood and its magnitude and spatial scales are key  
396 to determine any ecological consequences hence more research is needed (Plew 2013; Stevens *et al.*  
397 2008).

## 398 Ecological interactions with offshore farms

399 The influence of offshore large structures on the surrounding environment and the current regimes of  
400 the area can influence various ecosystem processes which can result in a range of direct and cascading  
401 effects on the surrounding ecosystem (Figure 2). For instance, by adding physical structure to the  
402 environment both through the introduction of hard infrastructure, which contributes to ocean sprawl  
403 (Heery *et al.* 2017) and the organisms themselves, which in turn can modify hydro-sedimentary  
404 processes as they modify currents, increase local sedimentation and biodeposits (Kumar & Cripps  
405 2012; Landmann *et al.* 2019) or create new habitats for benthic assemblages (Mckindsey *et al.* 2011;  
406 Sheehan *et al.* 2019).

## 407 Benthic ecology and habitat modification

### 408 *Biodeposition and benthic enrichment*

409 As filter feeders, mussels pump water in and trap suspended material. Undigested and unwanted  
410 material is mixed with mucus and expelled as faeces and pseudofaeces, respectively (Chamberlain  
411 2002; Mckindsey *et al.* 2011; Spencer 2002). The magnitude of these depend on the quality and quantity  
412 of food available with a greater fraction of pseudofaeces being produced when seston quantity is high  
413 and/or seston quality is low (Mckindsey *et al.* 2011). It is estimated that mussels assimilate 80% of  
414 ingested food (Chamberlain 2002).

415 Mussel farm biodeposition material varies greatly in size as it also includes mussel shell (Hartstein &  
416 Stevens 2005). Biodeposits sink at greater velocities than their constituent particles, increasing the flux  
417 of OM reaching the seafloor directly beneath the farm (Mckindsey *et al.* 2011; Newell 2004). Biodeposit  
418 accumulation depends on four main factors: (i) production rate, (ii) initial dispersal (hydrodynamic  
419 transport), (iii) redistribution once on the sediment surface (creep, saltation, resuspension, erosion), and  
420 (iv) rate of decay (Giles *et al.* 2009, 2006; Mckindsey *et al.* 2011). In addition, rates vary among species,  
421 size and diet. Although smaller mussels produce a proportionally greater biodeposit quantity than larger  
422 ones, faeces are smaller having lower settlement rates due to their low density thus, being advected  
423 further afield by prevailing currents (Chamberlain 2002; Hartstein & Stevens 2005; Mckindsey *et al.*  
424 2011). As mussel settle on the ropes during summer, small mussels dominate farm densities during  
425 highly hydrodynamic winter months producing higher amounts of low density biodeposits that although  
426 smaller in size, may be advected further afield.

427 Along with an increase in organic content and finer sediment, some authors have found reduced oxygen  
428 conditions beneath mussel farms. Other authors have drawn attention to the organisms associated with  
429 mussel farms and their contribution to the deposition of OM to the seafloor (Giles *et al.* 2006). Studies  
430 on highly hydrodynamic offshore mussel farms have found that the sediment beneath had no

431 significantly greater OM content, carbon/nitrogen ratios or particle size than reference sites. Although  
432 an increase of biodeposits underneath the structure has been observed in certain developments, studies  
433 have found that physical and chemical changes reduce to natural levels approximately 30 to 300 m from  
434 the farm site, depending on the hydrodynamics of the area and the extent of the farm (Hartstein &  
435 Rowden 2004; Hartstein & Stevens 2005; Lacoste *et al.* 2018). Once on the seabed, biodeposits can  
436 either remain immobile due to lack of significant water movement on the sediment-water interface  
437 (Hartstein & Stevens 2005; Lin *et al.* 2016) or, given the right amount of energy, especially during  
438 storm seasons, biodeposits can be resuspended back into the ecosystem (Giles *et al.* 2009; Lin *et al.*  
439 2016).

440 The reduction of tidal current horizontal velocity coupled with induced downwelling within offshore  
441 mussel farms can accelerate biodeposition, including both plankton and filter-feeding produced detritus  
442 (containing chlorophyll- $\alpha$ ), significantly affecting net biological processes (Giles *et al.* 2009; Lin *et al.*  
443 2016). However, the different conditions of each farm site will produce different results and further  
444 studies as well as long term monitoring programmes are needed to support this (Fabi *et al.* 2009).

#### 445 *Infaunal community changes/modifications*

446 Benthic infauna not only rework sediments increasing oxygen penetration into the benthos but also  
447 enhance remineralisation of OM and through various bioturbation techniques, influence nutrient  
448 exchange rates between sediments and the water column (Callier *et al.* 2009). The magnitude of a farm's  
449 impact on benthic infauna communities is influenced by the farm (size, stocking density, age of  
450 development) and the site characteristics (hydrodynamic regime, bathymetry) (Hartstein & Rowden  
451 2004; Hartstein & Stevens 2005; Lacoste *et al.* 2018). As communities may take 10 to 15 years to reach  
452 a new equilibrium following a disturbance (Mckindsey *et al.* 2011), if an offshore mussel farm is  
453 developed within heavily fished grounds, its impacts may be shadowed by the underlying effects of  
454 dredges and towed fishing gears.

455 Studies on offshore farms to date show either a reduction in infaunal densities (Hartstein & Rowden  
456 2004), no effect on the meiofaunal abundance, taxa richness or community structure (Danovaro *et al.*  
457 2004) or a combination of both (Lacoste *et al.* 2018). Overall, offshore mussel culture effects on benthic  
458 infaunal communities are usually limited in magnitude unless extreme conditions are given (poor  
459 flushing rates or exceeding densities) and fluctuations have been seen to be linked with natural seasonal  
460 and inter-annual rather than because of the mussel farm itself (Fabi *et al.* 2009; Lacoste *et al.* 2018).  
461 Impacts of offshore farms will then be tightly dependant on not only the hydrodynamics of the area but  
462 seasonal changes if any, and the type of habitat where the development is found. Ultimately, time,  
463 biodeposition loading and hydrodynamics will determine the degree of infaunal community  
464 modification (Callier *et al.* 2008; Chamberlain *et al.* 2001; Lacoste *et al.* 2018; Ysebaert *et al.* 2009).

465

*Mobile macrofauna interactions*

466 Mobile benthic fauna, including fish and crustaceans, can be affected by mussel aquaculture operations.  
467 The main mechanisms are: (i) the addition of physical structure (anchor blocks or mussel fall-off), (ii)  
468 the provision of food from mussel fall-off or from other types of organisms growing on the longlines  
469 and farm infrastructure (Callier *et al.* 2017; Keeley 2013; Mckindsey *et al.* 2011) and, (iii) the exclusion  
470 of other fishing activities (mobile and static gear) within the farm.

471 In a large development, mussel fall-off may be considerable, dramatically altering benthic habitats  
472 towards more heterogeneous hard-bottom biogenic reef-type communities. Mussels and shells have  
473 been found to cover 55% of the seafloor beneath offshore farms, substantially increasing the physical  
474 structure underneath. As mussels and associated epifauna fall from the aquaculture structures, build up  
475 and represent an attractive food source for benthic predators and scavengers (Figure 6 and Figure 7)  
476 (Callier *et al.* 2017; Inglis & Gust 2003; Mckindsey *et al.* 2011). Offshore farm studies report increased  
477 numbers and/or greater biomass of macrofauna such as crabs, lobsters and sea stars within farm sites,  
478 relative to control sites pointing to an increase in predatory organisms beneath the mussel ropes (Lacoste  
479 *et al.* 2018).

480 Although the knowledge of additional seafloor physical structure associated with offshore  
481 aquaculture is very limited, there is considerable literature on the importance of artificial  
482 structures (specially offshore windfarms), enhancing mobile macrofauna communities,  
483 operating as reefs (Callier *et al.* 2017; Heery *et al.* 2017; Inger *et al.* 2009). Much can be  
484 extrapolated from the relevant artificial reef (AR) literature where other types of communities  
485 may develop under and around the blocks supporting farms (Callier *et al.* 2017; Mckindsey *et al.*  
486 *et al.* 2011). Hard-bottom associated species that may otherwise not be there due to a lack of  
487 suitable habitat (e.g, offshore muddy bottoms or deep waters) or as a consequence of years of  
488 dredging and towing for commercial fisheries, can now colonise these structures and the  
489 surrounding ecosystem forming communities that are functionally similar to hard-bottom  
490 habitats (Figure 2) (Callier *et al.* 2017; Inglis & Gust 2003; Lacoste *et al.* 2018; Mckindsey *et al.*  
491 *et al.* 2011). As hard-bottom communities often are more diverse and have greater biomass and  
492 higher productivity than soft-bottom ones, this can have a knock on effect on the complexity  
493 of the habitat and even increase local diversity and productivity (Mckindsey *et al.*  
494 2011).Pelagic Ecology

495 Compared to benthic habitats, there is very little research on the effects of mussel farming on pelagic  
496 ecosystems with no studies on the effects of offshore mussel farms therefore, the following section aims  
497 to extrapolate what is known from other mussel farms in order to understand the importance of this  
498 issue and the need for research on the topic.

499 Although most research focuses on mussel farm effects on the water column chemistry and plankton  
500 communities (Cranford *et al.* 2008; Froján *et al.* 2018; La Rosa *et al.* 2002; Trotter *et al.* 2008), recent

501 attention has been given to farms attracting pelagic fish and vagile macroinvertebrates as well as  
502 interacting with planktonic communities (Figure 4 and Figure 5). Additionally, organisms growing  
503 among mussel longlines and other farm structures such as algae and invertebrate organisms (epifauna)  
504 may also attract such organisms (Callier *et al.* 2017; Mckindsey *et al.* 2011).

505 Shellfish farms have been identified to affect nearby fishery resources through three possible  
506 interactions: (i) attraction or displacement of adults, (ii) recruitment reductions through the direct  
507 consumption of eggs and larvae and, (iii) food web effects. Farms can have a wide range of direct and  
508 indirect effects on the organisms at both individual and population level, this in turn have implications  
509 for the management of fisheries and their ecosystems (Gibbs 2004).

#### 510 *Offshore mussel farms as fish aggregation devices (FADs)*

511 Offshore longline mussel farms not only add structure to the seabed in the form of anchor blocks and  
512 mussel fall-off, but add physical structure to the water column (buoys, ropes, etc.) where otherwise  
513 would be absent (Figure 2 and Figure 4-6) (Callier *et al.* 2017; Cornelisen 2013). Floating structures  
514 occurring in the open ocean are known to attract pelagic fish, widely recognised to act as FADs  
515 (Kingsford 1993; Matarazzo Suplicy 2018; Nelson 2003). As many studies have found that wild fish  
516 are attracted to aquaculture developments (Callier *et al.* 2017; Cornelisen 2013), farms are being  
517 thought to be acting as FADs due to the physical structure (Carpenter *et al.* 2009; Clavelle *et al.* 2018;  
518 Keeley *et al.* 2009) and its overall cascading effect.

519 Longline mussel farms offer a three-dimensional habitat for other organisms such as macroalgae,  
520 bryozoans or tunicates by providing substrate, food source and refuge from predation and adverse  
521 environmental conditions (Clavelle *et al.* 2018; Gutiérrez *et al.* 2003). Consequently, providing a direct  
522 food source for other predators, making farms attractive to higher food-web organisms such as pelagic  
523 fishes and other vagile organisms (Callier *et al.* 2017; Mckindsey *et al.* 2011).

524 Offshore farm observations in France and New Zealand report how the introduction of mussels to the  
525 area was followed by an increase in dominant fish species densities, some of which with commercial  
526 value. Pelagic species were found to be more common in the vicinity of the farm than in open water.  
527 Some were feeding on the mussels due to an increase in prey availability and others, including juveniles,  
528 were swimming through the longlines concluding that schools of fish could be attracted to the structure  
529 for shelter, refuge and nursery (Brehmer *et al.* 2003; Gerlotto *et al.* 2001; Keeley *et al.* 2009; Mckindsey  
530 *et al.* 2011).

531 Observations of birds and mammals interacting with suspended mussel farm structures show a positive  
532 or neutral effect on such species (Clement 2013; Keeley *et al.* 2009; Roycroft *et al.* 2007). Although  
533 studies on the interactions of seabirds and marine mammals with inshore mussel longlines found no

534 significant difference in overall species richness and diversity between mussel farm and control sites,  
535 significantly higher numbers of seabirds heavily used mussel buoys as perching platforms for preening  
536 (Clement 2013; Roycroft *et al.* 2007). Some authors have stressed the potential for issues suggesting  
537 that interactions with marine mammals should not be overlooked as there is considerable uncertainty in  
538 the long-term and ecosystem-wide consequences, especially with the expansion of the industry in terms  
539 of scale and into the offshore environment. However, interactions are thought to be low risk as threats  
540 mainly arise from loose ropes or the site overlapping with migratory routes which can be easily  
541 echolocated (Callier *et al.* 2017; Gentry *et al.* 2016; Keeley *et al.* 2009; Matarazzo Suplicy 2018).

#### 542 *Modifications of the mesoplankton community*

543 Longline mussel aquaculture places the bivalves in direct contact with the pelagic food web (Grant *et al.*  
544 *et al.* 2008; Maar *et al.* 2008; Mckindsey *et al.* 2011). Due to their extensive filtration activity and grazing  
545 (Spencer 2002), large numbers of bivalve filter feeders like *Mytilus sp.* lead to ecosystem changes as  
546 they remove large quantities of phytoplankton and nutrients from the water column enhancing a ‘top-  
547 down’ control of planktonic communities within aquaculture areas (Grant & Pastres 2019; Hulot *et al.*  
548 2018; Lehane & Davenport 2002, 2006; Petersen 2004; Prins *et al.* 1997). Shape and composition of  
549 particles play a role in the shaping of the mesoplankton community. During the filtration process,  
550 mussels tend to select larger cells as available. Coupled with an increased fertilisation through faeces  
551 and pseudo-faeces, primary production is stimulated, shifting the system towards a dominance of  
552 smaller planktonic species within the water column of the aquaculture development (Hulot *et al.* 2018;  
553 Strohmeier *et al.* 2012). Within inshore farms, a significant depletion of larger species (zooplankton) is  
554 induced (Grant *et al.* 2008; Maar *et al.* 2008; Mckindsey *et al.* 2011) and food resources available to  
555 other organisms are shifted, altering the overall ecological carrying capacity of the area (Jiang & Gibbs  
556 2005; Sequeira *et al.* 2008).

557 As the farm interacts with water currents reducing flows, the residence time of planktonic organisms  
558 increases, increasing their exposure to consumption, which can reduce both the biomass and production  
559 of plankton, described to be one of the main drivers of planktonic variability (Ferreira *et al.* 2007; Hulot  
560 *et al.* 2018). In a bay where the drag of an offshore mussel farm raft amplified water residence times,  
561 an increase in seston depletion was seen (Newell & Richardson 2014). A phytoplankton study spatially  
562 monitoring chlorophyll- $\alpha$  (chl- $\alpha$ ) concentrations in an offshore longline mussel farm in China reported  
563 a drastic decrease of up to 80% in surface chl- $\alpha$  concentration (Lin *et al.* 2016). Such a dramatic  
564 depletion can be further exacerbated by tides and stratification, becoming more serious during neap  
565 tides, especially during periods of low phytoplankton biomass (i.e. winter and summer) (Lin *et al.*  
566 2016). Additionally, a relatively high value of chl- $\alpha$  in the water below the submerged longline  
567 aquaculture coupled with salinity and temperature measurements showed an evident downward trend  
568 of water flow (Lin *et al.* 2016). This is further supported by a study performed in Italy observing how

569 total phosphorus content reached highest concentrations underneath a farm (Rampazzo *et al.* 2013)  
570 illustrating the impact that hydrodynamic effects of the farm may have (Figure 2).

## 571 Management, policy and offshore aquaculture conservation

572 Although the move of the industry offshore may ease some of the inshore space usage conflicts, the  
573 development of large offshore farms may occupy historically fished areas causing particular distress  
574 among certain parts of the fishing community (Fairbanks 2016; Keeley *et al.* 2009; Upton & Buck  
575 2013). This can be in turn offset by an increase use of the area by recreational and other commercial  
576 fishers benefiting from the farm's FAD effect, especially during harvest due to fouling organisms from  
577 mussels and mussel lines (Clavelle *et al.* 2018; Keeley *et al.* 2009). The exclusion of fishing activities  
578 (mobile and static gear) from farmed grounds may not only provide the potential to enhance both  
579 commercial and non-commercial species producing a spill over effect but also present the prospect for  
580 benthic habitats to be restored to previous state (Clavelle *et al.* 2018; Halpern *et al.* 2009; Sheehan *et al.*  
581 *et al.* 2019). In terms of conservation, this has been seen to be serving as a *de facto* marine protected areas  
582 (MPAs) (Clavelle *et al.* 2018; Halpern *et al.* 2009; Sheehan *et al.* 2019).

583 As marine biodiversity continues to decline and with it the ecosystem services we so depend on, it is  
584 paramount to reconcile nature conservation and the sustainable development of the oceans (European  
585 Commission 2019; Le Gouvello *et al.* 2017; Sala *et al.* 2018). If we want to at least try to meet  
586 international marine conservation targets such as the Convention on Biological Diversity's (CBD) Aichi  
587 Target 11 (marine biodiversity protection) and Target 6 (sustainable fisheries) by 2030, and the  
588 Sustainable Development Goals (SDGs) 2 (food security and zero hunger) and SDG 14 (conservation  
589 and sustainable development) within the UN's 2030 Agenda (Convention on Biological Diversity 2010:  
590 2020; Duarte *et al.* 2020; Le Gouvello *et al.* 2017; Sala *et al.* 2018; United Nations 2015), the Blue  
591 Economy and in particular aquaculture as the fastest growing food industry in the world, must move  
592 forward together (Blanchard *et al.* 2017; Ferreira *et al.* 2009; Froehlich *et al.* 2017a; Matarazzo Suplicy  
593 2018).

594 In order to meet international targets, the global number of MPAs has grown exponentially over the  
595 past decade, a vast amount of which allow extraction of resources being designated as "partially  
596 protected areas" (PPAs) (Horta e Costa *et al.* 2016; Sala *et al.* 2018; Singh *et al.* 2018; Zupan *et al.*  
597 2018). Some literature reports that while no-take MPAs are the most effective tool to restore and  
598 conserve biodiversity, the greatest number of PPAs have no different protection than non-MPAs  
599 (Claudet *et al.* 2020; Edgar *et al.* 2014; Galparsoro *et al.* 2020; Rees *et al.* 2020; Sala *et al.* 2018).  
600 Nevertheless, other authors report that highly and moderately regulated PPAs are effective compared  
601 to unprotected areas. When placed adjacent to fully protected MPAs, highly regulated PPAs can  
602 enhance their ecological benefits and in turn, increase their ecosystem service outcomes (Zupan *et al.*

603 2018). It could be argued that compared to some PPAs, offshore mussel farms provide more biodiversity  
604 protection than non-managed MPAs. For instance, offshore mussel farming might be preferable to other  
605 destructive extractive activities (Le Gouvello *et al.* 2017) such as trawl fishing already happening in  
606 multi-use MPAs (Sala *et al.* 2018). In particular, for MPA-communities it not only provides food  
607 security and economic resilience but it presents as a sustainable alternative to overfishing (Le Gouvello  
608 *et al.* 2017; Sala *et al.* 2018).

609 Following the six IUCN's categories of MPAs, the most used Categories V and IV (multi-purpose)  
610 already allow certain aquaculture activities (Day *et al.* 2012) while all but Category I, may allow some  
611 type of aquaculture (Le Gouvello *et al.* 2017). As the world is far from achieving the UN's marine  
612 conservation targets of protecting 10% of the oceans by 2020 (now updated to 30% in 'highly protected'  
613 areas by 2030) (Convention on Biological Diversity 2020), we must grasp every chance we have to  
614 truly protect and restore biodiversity at all levels as long as management and regulations are in place,  
615 well implemented and enforced (Sala *et al.* 2018). The CBD's zero-draft report (Convention on  
616 Biological Diversity 2020) highlights that as part of the new 2030 and 2050 Goals, we must meet  
617 people's food security and livelihood needs through a sustainable use of the oceans by conserving and  
618 enhancing biodiversity in managed ecosystems. Misinterpretation of IUCN's guidelines is common  
619 (Horta e Costa *et al.* 2016) thus, for a well-developed joint aquaculture conservation venture, designated  
620 areas need clear conservation objectives along with detailed information on resource extraction,  
621 management plans and implementation and enforcement (European Commission 2019; Sala *et al.*  
622 2018).

623 New guidance from IUCN to support achieve CBD Aichi Target 11 has described 'other effective area-  
624 based conservation measures' (OECMs) as an important tool alongside MPA designation (Convention  
625 on Biological Diversity 2018). Although creation and governance might be different to well-managed  
626 MPAs, the underlying principles and ultimate goals of OECMs should result in the same outcomes  
627 providing yet another opportunity for aquaculture conservation cooperation delivering socio-economic  
628 as well as ecological benefits (Rees *et al.* 2020; Sala *et al.* 2018). To achieve the UN's SDGs, the  
629 remaining 70% (if 30% of the oceans are protected by 2030) of our seas should be managed sustainably  
630 (Rees *et al.* 2020). If we ought to conserve biodiversity and protect ecosystem services, we must go  
631 beyond the use of MPAs or PPAs. OECMs within a wider range of natural resource management  
632 interventions are needed to contribute to the development of wider governance conservation  
633 frameworks (FAO 2018; Rees *et al.* 2020). In addition to no-take-zones, we need every area that protects  
634 biodiversity at any level (FAO 2018; Sala *et al.* 2018) to meet the right environmental, social and  
635 economic sustainability goals

636 A clear opportunity to enhance offshore aquaculture and conservation (FAO 2018; Galparsoro *et al.*  
637 2020; Rees *et al.* 2020) is the implementation of an ecosystem-based approach for aquaculture (EAA)

638 proposed (FAO 2018; Soto *et al.* 2008) to be at the forefront of Blue Growth goals in conservation  
639 aquaculture for the planning, development and management of the industry (European Commission  
640 2019; FAO 2018; Froehlich *et al.* 2017a; Klinger *et al.* 2018) providing fundamental area-based  
641 frameworks (FAO 2018; Galparsoro *et al.* 2020). This must be developed in a context of connectivity  
642 and co-location through tools like MSP which integrate management of land, water and other resources  
643 enabling a sustainable growth of the industry minimizing conflict, integrating clear social, economic  
644 and environmental objectives (FAO 2018; Galparsoro *et al.* 2020; Rees *et al.* 2020). However, in the  
645 case of offshore aquaculture, EAA efforts are hindered by lack of research, knowledge and guidelines  
646 which must be supported with effective governance (Le Gouvello *et al.* 2017; Weitzman 2019).  
647 Economic benefits may be more likely to materialise if planned and performed appropriately (European  
648 Commission 2019).

649

## 650 **Discussion**

651 Even though offshore mussel farming has the potential to be a great sustainable source of protein, it still  
652 remains well below its production potential. It has been argued that the main reasons are due to negative  
653 public perception affecting the market, long and difficult licencing procedures, lack of clear policy and  
654 management, space constrains and environmental and economic factors (European Commission 2019;  
655 Fairbanks 2016; Galparsoro *et al.* 2020; Kapetsky *et al.* 2013; Matarazzo Suplicy 2018). Improvement  
656 of governance with the establishment of adequate legislative frameworks, simplified administrative  
657 procedures along the promotion of the industry as a sustainable practice are paramount to minimise  
658 conflicts and environmental impacts for the sustainable development of the industry offshore (European  
659 Commission 2019; Galparsoro *et al.* 2020; Matarazzo Suplicy 2018).

660 Understanding the interactions of offshore longline mussel farms with the hydrodynamic regime of the  
661 area can help determine the extent of ecological effects. The available literature shows that a vast  
662 amount of knowledge and research gaps concerning offshore aquaculture-environment interactions  
663 exist, which are needed to inform management and legislation as well as to understand and assess  
664 ecological benefits and consequences.

665 As few studies include pre-development data relying on the comparison between farm sites and  
666 reference locations, the authors highlight the need to include baseline studies as well as long-term  
667 monitoring of marine systems to fully understand natural, temporal and spatial variations that may  
668 otherwise disguise underlying anthropogenic disturbances (Callier *et al.* 2017; Mckindsey *et al.* 2011;  
669 Underwood 1990; Upton & Buck 2013).

670 The identified below priorities should be focused on offshore longline mussel farms in order to help the  
671 industry develop and be part of a sustainable ‘Blue Revolution’ as part of the ‘Blue Growth Agenda’  
672 with objectives such as the development of smart green aquaculture and biodiversity conservation as  
673 part of an EAA (European Commission 2019; FAO 2018; Froehlich *et al.* 2017a; Hambrey & Evans  
674 2016; Klinger *et al.* 2018; Smaal *et al.* 2019; Soto *et al.* 2008; Upton & Buck 2013).

#### 675 Influence of the farm on water flow

676 To date, studies have focused on either ecological or oceanographic effects of mussel farms with the  
677 majority concentrating on describing the latter through numerical modelling though lacking the link  
678 between the two (Plew *et al.* 2005). In light of preliminary evidence, models suggest that hydrodynamic  
679 regimes play a crucial role in understanding offshore aquaculture-environment interactions, providing  
680 an important insight into the behaviour of background oceanographic currents when in contact with a  
681 porous structure like that of an offshore farm (Chen *et al.* 2019; Gagnon & Bergeron 2017; Newell &  
682 Richardson 2014; O’Donncha *et al.* 2013, 2016; Plew 2011; Plew *et al.* 2005; Stevens & Petersen 2011).  
683 This is crucial as any change in the background currents due to the establishment of a farm happens  
684 before any other interaction and will determine nutrient and organic loading transport and therefore, the  
685 extent of any other impacts, especially the dispersion of biodeposits which in turn will determine the  
686 overall knock-on ecological effects (Lin *et al.* 2016; Stevens & Petersen 2011).

687 Although recent theoretical, experimental, observational and numerical modelling studies have focused  
688 on the wave attenuation effect of canopies, full understanding of the alterations to the mean wave-driven  
689 currents and water flow are still limited, especially its links to particulate matter and water exchange  
690 rates through the canopy margins and water column (Chen *et al.* 2019) as well as its effects to  
691 resuspension of biodeposits due to increase velocities beneath the farm (Fabi *et al.* 2009; Plew 2013;  
692 Rampazzo *et al.* 2013). Ultimately, water flow modification and diversion depend on different factors  
693 such as bathymetry, density stratification, bottom friction, canopy density, proportion of water depth  
694 occupied as well as proximity to other developments and to the coast (Plew 2011).

695 Due to the high complexity of interactions between prevailing currents and biodeposits, representing  
696 spatio-temporal interactions at a farm scale are difficult to predict and explain based on numerical  
697 models or laboratory based studies alone. Therefore, it is important to reflect the reality of such with  
698 more *in situ* studies. In particular, further detailed field studies undertaking extensive investigations of  
699 mean wave-driven currents and water flow modification measurements are needed to better understand  
700 alterations to the current and turbulence structure, validate models through critical observations to  
701 resolve existing gaps on how offshore farms generate current and stratification distortions, wave  
702 attenuation and wake formation. This will ultimately help decipher offshore aquaculture-environment  
703 interactions to understand biodeposition and resuspension, nutrient depletion and how such

704 hydrodynamic regimes and pathways influence the local ecology (Lin *et al.* 2016; Plew *et al.* 2005;  
705 Stevens & Petersen 2011) and overall ecosystem services capacity of the farm helping estimate  
706 consequent ecological impacts (Chen *et al.* 2019; Plew 2013; Stevens *et al.* 2008) and the farm's  
707 footprint (Tseung *et al.* 2016, Plew *et al.* 2005, 2006) in order to provide factual and effective MSP  
708 (FAO 2018; Klinger *et al.* 2018; Landmann *et al.* 2019; Mckindsey *et al.* 2011; Plew 2013).

709 Although currents are key agents for the industry, the questions of whether water flow will be diverted  
710 horizontally or vertically around the canopy and what effect stratification has on this still remain not  
711 fully understood (Plew *et al.* 2006). A range of indexes have been developed in order to calculate  
712 dispersal rates and times (Callier *et al.* 2009; Cranford *et al.* 2009; Hartstein & Stevens 2005; Lovatelli  
713 *et al.* 2013; McKindsey *et al.* 2006; Stevens *et al.* 2008) however these are far from being able to portrait  
714 a real image due to the complexity of an offshore longline mussel farm system.

715 In general, the spatial and temporal variability in currents induced by offshore longline structures  
716 requires more research at the small to medium (metres to hundreds of metres) scales (Plew 2013).  
717 Detailed field studies, in particular more research is required, but not limited to:

- 718 - the magnitude and extent of overall water flow modification
- 719 - the magnitude and extent of a wake formation
- 720 - the magnitude and spatial scales of changes to water column processes such as stratification  
721 of density, temperature or nutrients, which influence vertical density variations affecting  
722 water flows and carrying capacity around the structures
- 723 - whether the structures induce significant vertical mixing
- 724 - whether different longline stocking densities or designs and orientation to the water flow  
725 significantly alter wave and current attenuation
- 726 - if refraction (changes in the direction of wave propagation) or reflection of waves occurs
- 727 - the extent and importance of fouling which can change the drag of shellfish structures through  
728 smothering and decreasing drag
- 729 - interaction between the seabed (bottom boundary layer) and the bottom of the farm  
730 (biodeposition and resuspension)
- 731 - hydrodynamic and physicochemical model validation
- 732 - how the above can be best utilised to engineer the most efficient farm design and outlay

### 733 Ecological interactions

734 There is insufficient information to widely support the statements that ecological effects of offshore  
735 mussel farms (i) are limited to restricted areas, (ii) have no significant impacts on benthic and pelagic  
736 habitats and species or (iii) biodeposit effects are minimal due to dispersal by high hydrodynamic flows.  
737 It is clear that long-term monitoring of marine benthic and pelagic systems is needed in order to fully

738 understand natural temporal and spatial variations that may disguise anthropogenic disturbances (Fabi  
739 *et al.* 2009; Lacoste *et al.* 2018; Mckindsey *et al.* 2011).

740 Although biodeposit production data and hydrodynamic modelling have been coupled to investigate  
741 and predict the benthic loading footprint of mussel farms (Giles *et al.* 2009; Weise *et al.* 2009), there  
742 are still important gaps in knowledge in respect to net biological process and biodeposition (Giles *et al.*  
743 2009; Hartstein & Rowden 2004; Hartstein & Stevens 2005; Lacoste *et al.* 2018; Lin *et al.* 2016).  
744 Studies support the strong relationship between the hydrodynamic regime of a farm site, OM  
745 enrichment in seabed sediments by biodeposits, and a subsequent modification of infauna and  
746 macrofauna (Hartstein & Stevens 2005; Lacoste *et al.* 2018; Lin *et al.* 2016).

747 While there is a lack of studies on the impacts of offshore developments, it is clear that the shifting  
748 baseline from a soft-bottom to a hard-bottom like habitat and the consequent increase in food  
749 availability can attract the attention of mobile macrofauna and even shift diets of organisms (Callier *et al.*  
750 *et al.* 2007; Lacoste *et al.* 2018; Mckindsey *et al.* 2011). This coupled with the exclusion of mobile fishing  
751 gear within the farm providing safe ground for species to colonise the restored habitat opens a window  
752 to the need of further investigation in order to understand if an offshore mussel farm could potentially  
753 develop macrofaunal communities (Callier *et al.* 2017; Inglis & Gust 2003; Mckindsey *et al.* 2011)  
754 where otherwise would be bare ground with the implications that this can have to commercial species.

755 It is still uncertain the mechanisms behind the FAD effect of mussel farms. This review recommends  
756 further studies to clarify if it is due to the fish being attracted by the added physical structure or enhanced  
757 by it, the shift to a more complex hard substrate, the farmed product itself, the associated organisms,  
758 the refuge given by the mussel matrix or a combination of these (Callier *et al.* 2017; Keeley *et al.* 2009;  
759 Mckindsey *et al.* 2011). The different mechanisms by which species are attracted (or repelled) and the  
760 subsequent direct and indirect effects at the individual and population levels are also unknown but  
761 important to study (Callier *et al.* 2017; Clavelle *et al.* 2018) in terms of interactions with nearby  
762 fisheries, recreational fishing, MPAs and in a management perspective. Ultimately, the significance of  
763 the argument relies on the uncertainty of whether the FAD effect is attracting fish communities  
764 aggregating from elsewhere or it is enhancing the population and whether it is in turn favouring  
765 particular species altering the existing fish assemblages and the community overall (Keeley *et al.* 2009).  
766 Nonetheless, it is yet unknown whether this increase may have positive or negative effects on the wider  
767 population (Keeley *et al.* 2009).

768 Some studies have investigated the potential modification of the mesoplankton community by mussel  
769 farms (Hulot *et al.* 2018; Lehane & Davenport 2002) as well as chl- $\alpha$  concentration alterations in  
770 offshore developments (Lin *et al.* 2016). As levels of sestonic depletion by mussel farms are highly  
771 variable throughout the literature, specially due to seasonal variations (Hulot *et al.* 2018; Strohmeier *et*

772 *al.* 2008) it is clear that not all planktonic populations would benefit from the hydrodynamic effects of  
773 an offshore mussel farm and any alterations in residence time in the same way. When studying the  
774 effects of an offshore mussel farm on the planktonic community, it is important to account for the  
775 different mechanisms involved in this complex process, from an enhancement of plankton residence  
776 time, to alterations due to seasonal stratifications.

777 Most studies have mainly been done under laboratory conditions with no field validations and in most  
778 cases, low numbers of mussels have been used. This is far from representative of a large offshore mussel  
779 farm and it is unlikely that results can be extrapolated due to the variety of factors at stake. Although  
780 recent studies have made significant progress on understanding such complexity, efforts must continue  
781 to focus on, but not limited to, research to understand:

- 782 - biodeposit quantity, quality and its decay rates (OM content of faeces and pseudofaeces)
- 783 - biodeposition dispersal
- 784 - redistribution and resuspension of biodeposits in the environment following initial deposition  
785 to the seafloor. This is thought to be crucial in areas with strong currents
- 786 - changes in sediment physicochemical parameters after biodeposition
- 787 - whether different longline stocking densities or designs and orientation to the water flow have  
788 an impact on the above ecological effects
- 789 - whether different bathymetry and underlying environmental characteristics of the area such as  
790 depth, habitat types or climate have an impact on the above ecological effects
- 791 - investigating the role of the epibiont community
- 792 - studying functional change of planktonic communities due to mussel predation and residence  
793 time alteration

## 794 Management, policy and conservation

795 It may seem strange to most to have conservation and aquaculture in the same sentence, let alone  
796 complementing each other as for many, aquaculture is mainly an undesirable industry following coastal  
797 aquaculture's long resume of environmental impacts (Fairbanks 2016; Froehlich *et al.* 2017a; Le  
798 Gouvello *et al.* 2017). While true, the industry has dramatically changed in the last 20 years (Froehlich  
799 *et al.* 2017a), but public perception on the industry's reputation has yet to catch up. Changes in practices  
800 and improved technology have shifted the role that aquaculture can have in conservation (Froehlich *et al.*  
801 *et al.* 2017a; Le Gouvello *et al.* 2017), biogenic reef habitat (shellfish reef) restoration (Alleway *et al.*  
802 2019; Froehlich *et al.* 2017a; Le Gouvello *et al.* 2017; Zu Ermgassen *et al.* 2020) and as a crucial  
803 sustainable source of protein (FAO 2016; Hilborn *et al.* 2018; Matarazzo Suplicy 2018).

804 Rope-grown mussel cultivation has been shown to be compatible with MPA objectives, with growing  
805 evidence and guidelines on how the blue economy sector can contribute to conservation through the  
806 creation of *de facto* refuges, this industry has the potential to add the economic benefits of conservation  
807 to its list of ecosystem service benefits. With the prospective to recover damaged habitats, boost  
808 ecosystem services and benefit biodiversity if effectively managed, offshore mussel farms may have  
809 the ability to become part of a wider marine conservation strategy as OECMs (Convention on Biological  
810 Diversity 2018; Rees *et al.* 2020). However, more empirical evidence is needed to support this and  
811 move away from the perception that aquaculture is excluding other activities often seen as costs to other  
812 blue economic sectors (Froehlich *et al.* 2017a; Haines *et al.* 2018). Thus the need to clearly understand  
813 the objectives of MPAs and aquaculture to establish positive and negative synergies (Froehlich *et al.*  
814 2017a; Le Gouvello *et al.* 2017) having at its core an integrated ecosystem-based approach (Rees *et al.*  
815 2020; Sala *et al.* 2018).

816 Although some argue that sustainable fisheries and conservation should not be merged, they are  
817 complementary (Sala *et al.* 2018) requiring an integrated ecosystem-based approach to management  
818 (Solandt *et al.* 2020) where offshore aquaculture can be a part of the solution. Offshore mussel farming  
819 has the potential to enhance fisheries by achieving sustainable resource extraction within a healthy  
820 ocean (Clavelle *et al.* 2018; FAO 2018; Froehlich *et al.* 2017a; Le Gouvello *et al.* 2017; Sheehan *et al.*  
821 2019) throughout a mosaic of interconnected ecological ‘corridors’ (Solandt *et al.* 2020). Though, we  
822 must keep in mind that there’s a distinction between biodiversity focused areas and areas important for  
823 the ecosystem services they provide which do not always share the same objectives (Rees *et al.* 2020).

824 The implementation of conservation regulations and ecological effectiveness are mutualistic hence the  
825 need to invest in management, control and enforcement as a priority (Duarte *et al.* 2020; Edgar *et al.*  
826 2014; Solandt *et al.* 2020; Zupan *et al.* 2018). Research has demonstrated that age and size of any marine  
827 conservation designation and the number and type of extraction activities allowed is correlated to its  
828 success (Edgar *et al.* 2014; Zupan *et al.* 2018). To ensure the sustainable management of offshore  
829 aquaculture, an understanding of environment-activity interactions is required (Callier *et al.* 2017;  
830 Galparsoro *et al.* 2020; Kapetsky *et al.* 2013; Lacoste *et al.* 2018; Landmann *et al.* 2019; Lester *et al.*  
831 2018; Stelzenmüller *et al.* 2013; Strand *et al.* 2017) thus, the need to provide rigorous advice on the  
832 feasibility of co-locating offshore aquaculture with other blue economy developments in a context of  
833 marine conservation (Sheehan *et al.* 2019).

834 Managers, scientists, users and conservationists have a role to play on the success of MPAs in a context  
835 of increasing expansion of societal demands into the ocean therefore, biodiversity conservation must  
836 embrace sustainable economic activities (Le Gouvello *et al.* 2017). In particular, it is paramount to  
837 improve our understanding on:

- 838 - offshore aquaculture-environment interactions and overall footprint
- 839 - rigorous advice on MSP and co-location of offshore aquaculture with other blue economy
- 840 developments and MPA designation
- 841 - cooperation of offshore aquaculture and MPAs conservation objectives, resource extraction and
- 842 management plans

843

## 844 **Conclusions**

845 The growing demand for aquatic protein suggests that aquaculture will continue to grow with bivalve  
846 farming playing a crucial role as an efficient and ecologically viable option. The increasing interest to  
847 move large-scale developments into the offshore environment has made this an innovative and attractive  
848 research field that requires creative solutions to address the challenges of such a dynamic environment.

849 This review has shown that offshore longline mussel aquaculture can have a myriad of influences from  
850 water currents to benthic and pelagic communities. After a thorough examination on (i) the effect of  
851 farms on background oceanography and (ii) the consequent ecological effects and response, it can be  
852 said that farm-scale changes in currents are almost certain with interactions at local, bay-wide and  
853 regional scales. Impacts of large offshore farms on the local hydrodynamic regime are highly likely and  
854 preliminary evidence indicates that the orientation and spacing of structures has an important effect and  
855 can induce spatial variations in currents. Thus, farm size (farm structures and layout) and farm location  
856 informs the intensity of the aquaculture-environment interactions which may decrease with distance  
857 from the farm.

858 While physical interactions have direct consequences such as the attenuation of wave energy, the  
859 formation of a wake and the effect on stratification, this review described the importance of physical  
860 effects on ecological processes such as an increase in material and plankton residence times which can  
861 increase biodeposition and seston depletion, modify the benthic habitat and promote the farm as a FAD.  
862 It is clear that the relationship between the physical and ecological systems lacks understanding.  
863 Although physical effects on currents will persist for the duration that the structures and crop are in  
864 place, return to ambient conditions on removal will be nearly immediate. On the contrary, ecological  
865 consequences of modified currents may not be seen instantaneously but appreciated gradually and  
866 persist for longer.

867 Although the (iv) main knowledge gaps highlighted a range of research priorities, the authors consider  
868 that priority and importance should not only be driven by lack of knowledge or scientific interest but  
869 also socio-ecological and management needs. Mussel farming offers a variety of ecosystem services  
870 each of which has some intrinsic value. A mussel farm's 'positive' or 'negative' influence on the system

871 depends on what has been used to weigh the different factors which can be moved either side of the  
872 balance following fickle societal values. Thus, the idea of promoting a threshold of acceptable change  
873 should be evaluated at a site by site basis. With the compel to move towards ecosystem-based  
874 management, it might be appropriate to consider trade-offs between not only what can be perceived as  
875 environmental ‘negative’ or ‘positive’ impacts but where and how research efforts are targeted  
876 depending on their absolute suitability.

877 In the context of promoting sustainable practices through (iii) management, policy and conservation, it  
878 is important to have a coexistence of marine resource exploitation and smart environmental  
879 management hence, the idea of co-use of marine waters by aquaculture and other sectors and co-  
880 management in terms of environmental conservation has lately become more tangible with new  
881 legislation. Coupling offshore mussel farms with marine conservation with the idea of using them as *de*  
882 *facto* MPAs, particularly as OECMs, may have a decisive role to play in complementing stricter  
883 conservation measures. Although combining offshore longline mussel farms with conservation or as an  
884 integrative approach (EAA) with large scale developments poses a challenge, it is paramount that we  
885 continue this research to better describe the oceanographic and ecological interactions to understand  
886 how they can be minimised as future policy will depend on it.

887 To avoid repetition of the so called ‘race to fish’ with a ‘rush to farm offshore’, more information is  
888 crucial to underpin policies, strategic decisions and inform management measures needed to make sure  
889 that the offshore aquaculture expansion does not arise an array of impacts but rather an increased  
890 sustainable harvest. Offshore mussel aquaculture has the potential to be one of the most environmentally  
891 sustainable industries but it will need governance support to be able to deliver the right conservation  
892 measures through the right regulations. Ultimately, it has the capacity to play a crucial role in the future  
893 of our oceans and livelihoods.

## 894 **Acknowledgements**

895 The authors would like to thank Offshore Shellfish Ltd. for funding this work and providing knowledge  
896 and insights into offshore aquaculture practices. The authors are grateful to the editor and four  
897 anonymous reviewers for their valuable comments that improved this review.

898

## 899 **References**

- 900 Alleway HK, Gillies CL, Bishop MJ, Gentry RR, Theuerkauf SJ, Jones R (2019) The ecosystem  
901 services of marine aquaculture: valuing benefits to people and nature. *BioScience* **69**: 59–68.
- 902 Aure J, Strohmeier T, Strand Ø (2007) Modelling current speed and carrying capacity in long-line blue  
903 mussel (*Mytilus edulis*) farms. *Aquaculture Research* **38**: 304–312.

- 904 Aypa SM (1990) Chapter 4. Mussel Culture. *Food and Agriculture Organization of the United Nations*  
905 (FAO) Retrieved from <http://www.fao.org/3/ab737e/AB737E04.htm>
- 906 Bendell LI (2014) Community composition of the intertidal in relation to the shellfish aquaculture  
907 industry in coastal British Columbia, Canada. *Aquaculture* **433**: 384–394.
- 908 Blanchard JL, Watson RA, Fulton EA, Cottrell RS, Nash KL, Bryndum-Buchholz A *et al.* (2017)  
909 Linked sustainability challenges and trade-offs among fisheries, aquaculture and agriculture.  
910 *Nature Ecology and Evolution* **1**: 1240–1249.
- 911 Boyd AJ, Heasman KG (1998) Shellfish mariculture in the Benguela system: water flow patterns within  
912 a mussel farm in Saldanha Bay, South Africa. *Journal of Shellfish Research* **17**: 25–32.
- 913 Brehmer P, Gerlotto F, Guillard J, Sanguinède F, Guénnegan Y, Buestel D (2003) New applications of  
914 hydroacoustic methods for monitoring shallow water aquatic ecosystems: the case of mussel  
915 culture grounds. *Aquatic Living Resources* **16**: 333–338.
- 916 Brenner M, Ramdohr S, Effkemann S, Stede M (2009) Key parameters for the consumption suitability  
917 of offshore cultivated blue mussels (*Mytilus edulis* L.) in the German Bight. *European Food*  
918 *Research and Technology* **230**: 255–267.
- 919 Buck BH (2007) Experimental trials on the feasibility of offshore seed production of the mussel *Mytilus*  
920 *edulis* in the German Bight: installation, technical requirements and environmental conditions.  
921 *Helgoland Marine Research* **61**: 87–101.
- 922 Buck BH, Thielges DW, Walter U, Nehls G, Rosenthal H (2005) Inshore-offshore comparison of  
923 parasite infestation in *Mytilus edulis*: implications for open ocean aquaculture. *Journal of Applied*  
924 *Ichthyology* **21**: 107–113.
- 925 Buck BH, Troell MF, Angel DL, Chopin T, Krause G, Grote B (2018) State of the art and challenges  
926 for offshore integrated multi-trophic aquaculture (IMTA). *Frontiers in Marine Science*, **5**: 1–21.
- 927 Callier MD, Byron CJ, Bengtson DA, Cranford PJ, Cross SF, Focken U *et al.* (2017) Attraction and  
928 repulsion of mobile wild organisms to finfish and shellfish aquaculture: a review. *Reviews in*  
929 *Aquaculture* **0**: 1–26.
- 930 Callier MD, McKindsey CW, Desrosiers G (2007) Multi-scale spatial variations in benthic sediment  
931 geochemistry and macrofaunal communities under a suspended mussel culture. *Marine Ecology*  
932 *Progress Series* **348**: 103–115.
- 933 Callier MD, McKindsey CW, Desrosiers G (2008) Evaluation of indicators used to detect mussel farm  
934 influence on the benthos: two case studies in the Magdalen Islands, Eastern Canada. *Aquaculture*  
935 **278**: 77–88.
- 936 Callier MD, Richard M, McKindsey CW, Archambault P, Desrosiers G (2009) Responses of benthic  
937 macrofauna and biogeochemical fluxes to various levels of mussel biodeposition: an *in situ*  
938 “benthocosm” experiment. *Marine Pollution Bulletin* **58**: 1544–1553.
- 939 Callier MD, Weise AM, McKindsey CW, Desrosiers G (2006) Sedimentation rates in a suspended  
940 mussel farm (Great-Entry Lagoon, Canada): biodeposit production and dispersion. *Marine*  
941 *Ecology Progress Series* **322**: 129–141.
- 942 Carpenter SR, Mooney HA, Agard J, Capistrano D, DeFries RS, Díaz S *et al.* (2009) Science for  
943 managing ecosystem services: Beyond the Millennium Ecosystem Assessment Stephen. *PNAS*  
944 **106**: 1305–1312.

- 945 Chamberlain J (2002) Modelling the environmental impacts of suspended mussel (*Mytilus edulis* L.)  
 946 farming. Napier University. Retrieved from  
 947 <https://ethos.bl.uk/OrderDetails.do?uin=uk.bl.ethos.251351>
- 948 Chamberlain J, Fernandes TF, Read P, Nickell TD, Davies IM (2001) Impacts of biodeposits from  
 949 suspended mussel (*Mytilus edulis* L.) culture on the surrounding surficial sediments. *ICES Journal*  
 950 *of Marine Science* **58**: 411–416.
- 951 Chen H, Liu X, Zou Q-P (2019) Wave-driven flow induced by suspended and submerged canopies.  
 952 *Advances in Water Resources* **123**: 160–172.
- 953 Claudet J, Loiseau C, Sostres M, Zupan M, Claudet J, Loiseau C *et al.* (2020) Underprotected Marine  
 954 Protected Areas in a global biodiversity hotspot. *One Earth* **2**: 380–384.
- 955 Clavelle T, Lester SE, Gentry R, Froehlich HE (2018) Interactions and management for the future of  
 956 marine aquaculture and capture fisheries. *Wiley* **20**: 368–388.
- 957 Clement D (2013) Effects on Marine Mammals. In P. Sagar (Ed.), *Literature review of ecological effects*  
 958 *of aquaculture* 4.1-4.19. Ministry for Primary Industries, Cawthron Institute & National Institute  
 959 for Water and Atmospheric Research Ltd.
- 960 Convention on Biological Diversity (2010) Aichi Biodiversity Targets. Strategic Plan 2011-2020.  
 961 Retrieved from <https://www.cbd.int/sp/targets/>
- 962 Convention on Biological Diversity (2018) Protected areas and other effective area-based conservation  
 963 measures (Decision 14/8). Retrieved from [https://www.cbd.int/doc/decisions/cop-14/cop-14-dec-](https://www.cbd.int/doc/decisions/cop-14/cop-14-dec-08-en.pdf)  
 964 [08-en.pdf](https://www.cbd.int/doc/decisions/cop-14/cop-14-dec-08-en.pdf)
- 965 Convention on Biological Diversity (2020) Zero Draft Of The Post-2020 Global Biodiversity  
 966 Framework. Retrieved from  
 967 <https://www.cbd.int/doc/c/efb0/1f84/a892b98d2982a829962b6371/wg2020-02-03-en.pdf>
- 968 Cornelisen C (2013) Effects on wild fish. In R. Ford (Ed.), *Literature review of ecological effects of*  
 969 *aquaculture* 5.1-5.14. Ministry for Primary Industries, Cawthron Institute & National Institute for  
 970 Water and Atmospheric Research Ltd.
- 971 Cranford PJ, Hargrave BT, Doucette LI (2009) Benthic organic enrichment from suspended mussel  
 972 (*Mytilus edulis*) culture in Prince Edward Island, Canada. *Aquaculture* **292**: 189–196.
- 973 Cranford PJ, Li W, Strand Ø, Strohmeier T (2008) Phytoplankton depletion by mussel aquaculture:  
 974 high resolution mapping, ecosystem modeling and potential indicators of ecological carrying  
 975 capacity. *International Council for the Exploration of the Seas (ICES)*.
- 976 Crawford CM, Macleod CKA, Mitchell IM (2003) Effects of shellfish farming on the benthic  
 977 environment. *Aquaculture* **224**: 117–140.
- 978 D'Amours O, Archambault P, McKindsey CW, Johnson LE (2008) Local enhancement of epibenthic  
 979 macrofauna by aquaculture activities. *Marine Ecology Progress Series* **371**: 73–84.
- 980 Danovaro R, Gambi C, Luna GM, Mirto S (2004) Sustainable impact of mussel farming in the Adriatic  
 981 Sea (Mediterranean Sea): evidence from biochemical, microbial and meiofaunal indicators.  
 982 *Marine Pollution Bulletin* **49**: 325–333.
- 983 Day J, Dudley N, Hockings M, Holmes G, Laffoley D, Stolton S *et al.* (2012) Guidelines for applying  
 984 the IUCN protected area management categories to Marine Protected Areas. *Gland, Switzerland:*

- 985 *IUCN*.
- 986 Delaux S, Stevens CL, Popinet S (2011) High-resolution computational fluid dynamics modelling of  
987 suspended shellfish structures. *Environmental Fluid Mechanics* **11**: 405–425.
- 988 Dimitriou PD, Karakassis I, Pitta P, Tsagaraki TM, Apostolaki ET, Magiopoulos I *et al.* (2015) Mussel  
989 farming in Maliakos Gulf and quality indicators of the marine environment: good benthic below  
990 poor pelagic ecological status. *Marine Pollution Bulletin* **101**: 784–793.
- 991 Duarte CM, Agusti S, Barbier E, Britten GL, Castilla JC, Gattuso JP *et al.* (2020) Rebuilding marine  
992 life. *Nature* **580**: 39–51.
- 993 Duarte CM, Holmer M, Olsen Y, Soto D, Marbà N, Guiu J *et al.* (2009) Will the oceans help feed  
994 humanity? *BioScience* **59**: 967–976.
- 995 Duarte P, Labarta U, Fernández-Reiriz MJ (2008) Modelling local food depletion effects in mussel rafts  
996 of Galician Rias. *Aquaculture* **274**: 300–312.
- 997 Edgar GJ, Stuart-Smith RD, Willis TJ, Kininmonth S, Baker SC, Banks S *et al.* (2014) Global  
998 conservation outcomes depend on marine protected areas with five key features. *Nature* **506**: 216–  
999 220.
- 1000 Ellis T, Gardiner R, Gubbins M, Reese A, Smith D *et al.* (2007) The EU Blue Economy Report 2019.  
1001 *European Commission (2019)*. (Vol. 35) SEAFISH. Retrieved from  
1002 <ftp://ftp.fao.org/docrep/fao/011/i0250e/i0250e.pdf>
- 1003 European Commission (2019) The EU Blue Economy Report 2019. Retrieved from  
1004 [https://op.europa.eu/en/publication-detail/-/publication/676bbd4a-7dd9-11e9-9f05-  
1005 01aa75ed71a1/language-en/](https://op.europa.eu/en/publication-detail/-/publication/676bbd4a-7dd9-11e9-9f05-01aa75ed71a1/language-en/)
- 1006 Fabi G, Manoukian S, Spagnolo A (2009) Impact of an open-sea suspended mussel culture on  
1007 macrobenthic community (Western Adriatic Sea). *Aquaculture* **289**: 54–63.
- 1008 Fairbanks L (2016) Moving mussels offshore? Perceptions of offshore aquaculture policy and  
1009 expansion in New England. *Ocean and Coastal Management* **130**: 1–12.
- 1010 FAO (2016) The State of World Fisheries and Aquaculture 2016 - Contributing to food security and  
1011 nutrition for all. *Food and Agriculture Organization of the United Nations*. Retrieved from  
1012 <http://www.fao.org/3/a-i5555e.pdf>
- 1013 FAO (2018) The State of World Fisheries and Aquaculture 2018 - Meeting the sustainable development  
1014 goals. *Food and Agriculture Organization of the United Nations*. Retrieved from  
1015 <ftp://ftp.fao.org/docrep/fao/011/i0250e/i0250e.pdf>
- 1016 Ferreira JG, Hawkins AJS, Bricker SB (2007) Management of productivity, environmental effects and  
1017 profitability of shellfish aquaculture - the Farm Aquaculture Resource Management (FARM)  
1018 model. *Aquaculture* **264**: 160–174.
- 1019 Ferreira JG, Hawkins AJS, Bricker SB (2011) The role of shellfish farms in provision of ecosystem  
1020 goods and services. In SE Shumway (Ed.), *Shellfish aquaculture and the environment*, pp. 3–31.  
1021 John Wiley & Sons, Inc.
- 1022 Ferreira JG, Sequeira A, Hawkins AJS, Newton A, Nickell TD, Pastres R *et al.* (2009) Analysis of  
1023 coastal and offshore aquaculture: application of the FARM model to multiple systems and  
1024 shellfish species. *Aquaculture* **292**: 129–138.

- 1025 Froehlich HE, Gentry RR, Halpern BS (2017) Conservation aquaculture: shifting the narrative and  
1026 paradigm of aquaculture's role in resource management. *Biological Conservation* **215**: 162–168.
- 1027 Froehlich HE, Smith A, Gentry RR, Halpern BS (2017) Offshore Aquaculture: I know it when I see it.  
1028 *Frontiers in Marine Science* **4**: 154.
- 1029 Froján M, Castro CG, Zúñiga D, Arbones B, Alonso-Pérez F, Figueiras FG (2018) Mussel farming  
1030 impact on pelagic production and respiration rates in a coastal upwelling embayment (Ría de Vigo,  
1031 NW Spain). *Estuarine, Coastal and Shelf Science* **204**: 130–139.
- 1032 Gagnon M, Bergeron P (2017) Observations of the loading and motion of a submerged mussel longline  
1033 at an open ocean site. *Aquacultural Engineering* **78**: 114–129.
- 1034 Gallardi D (2014) Effects of bivalve aquaculture on the environment and their possible mitigation: a  
1035 review. *Fisheries and Aquaculture Journal* **5**: 8.
- 1036 Galparsoro I, Murillas A, Pinarbasi K, Sequeira AMM, Stelzenmüller V, Borja Á *et al.* (2020) Global  
1037 stakeholder vision for ecosystem-based marine aquaculture expansion from coastal to offshore  
1038 areas. *Reviews in Aquaculture* **12**: 2061–2079.
- 1039 Gentry RR, Froehlich HE, Grimm D, Kareiva P, Parke M, Rust M *et al.* (2017) Mapping the global  
1040 potential for marine aquaculture. *Nature Ecology & Evolution* **1**: 1317–1324.
- 1041 Gentry RR, Lester SE, Kappel CV, White C, Bell TW, Stevens J *et al.* (2016) Offshore aquaculture:  
1042 spatial planning principles for sustainable development. *Ecology and Evolution* **7**: 733–743.
- 1043 Gerlotto F, Brehmer P, Buestel D, Sanguinede F (2001) A method for acoustic monitoring of a mussel  
1044 longline ground using vertical echosounder and multibeam sonar. In *ICES Annual Science  
1045 Conference Oslo, 26-29 september 2001*, p. 14. International Council for the Exploration of the  
1046 Sea.
- 1047 Gibbs MM, James MR, Pickmere SE, Woods PH, Shakespeare BS, Hickman RW *et al.* (1991)  
1048 Hydrodynamic and water column properties at six stations associated with mussel farming in  
1049 Pelorus sound, 1984–85. *New Zealand Journal of Marine and Freshwater Research* **25**: 239–254.
- 1050 Gibbs MT (2004) Interactions between bivalve shellfish farms and fishery resources. *Aquaculture* **240**:  
1051 267–296.
- 1052 Giles H, Broekhuizen N, Bryan KR, Pilditch CA (2009) Modelling the dispersal of biodeposits from  
1053 mussel farms: the importance of simulating biodeposit erosion and decay. *Aquaculture* **291**: 168–  
1054 178.
- 1055 Giles H, Pilditch CA, Bell DG (2006) Sedimentation from mussel (*Perna canaliculus*) culture in the  
1056 Firth of Thames, New Zealand: impacts on sediment oxygen and nutrient fluxes. *Aquaculture* **261**:  
1057 125–140.
- 1058 Gouletquer P (2020) Cultured Aquatic Species Information Programme. *Mytilus edulis*. *Food and  
1059 Agriculture Organization of the United Nations (FAO)*. Retrieved from  
1060 [http://www.fao.org/fishery/culturedspecies/Mytilus\\_edulis/en](http://www.fao.org/fishery/culturedspecies/Mytilus_edulis/en)
- 1061 Grant C, Archambault P, Olivier F, McKindsey CW (2012) Influence of “bouchot” mussel culture on  
1062 the benthic environment in a dynamic intertidal system. *Aquaculture Environment Interactions* **2**:  
1063 117–131.
- 1064 Grant J, Bacher C (2001) A numerical model of flow modification induced by suspended aquaculture

- 1065 in a Chinese bay. *Canadian Journal of Fisheries and Aquatic Sciences* **58**: 1003–1011.
- 1066 Grant J, Bacher C, Cranford PJ, Guyondet T, Carreau M (2008) A spatially explicit ecosystem model  
1067 of seston depletion in dense mussel culture. *Journal of Marine Systems* **73**: 155–168.
- 1068 Grant J, Pastres R (2019) Ecosystem models of bivalve aquaculture: implications for supporting Goods  
1069 and Services. In A. Smaal, JG Ferreira, J Grant, JK Petersen & Ø. Strand (Eds.), *Goods and*  
1070 *Services of marine bivalves*, pp. 507–526. Springer Open.
- 1071 Gutiérrez JL, Jones CG, Strayer DL, Iribarne OO (2003) Mollusks as ecosystem engineers: the role of  
1072 shell production in aquatic habitats. *Oikos* **101**: 79–90.
- 1073 Haines R, Hattam C, Pantzar M, Russi D (2018) Study on the Economic Benefits of MPAs and SPMs.  
1074 *European Commission*.
- 1075 Halpern BS, Lester SE, Kellner JB (2009) Spillover from marine reserves and the replenishment of  
1076 fished stocks. *Environmental Conservation* **36**: 268–276.
- 1077 Hambrey J, Evans S (2016) Aquaculture in England, Wales and Northern Ireland: an analysis of the  
1078 economic contribution and value of the major sub-sectors and the most important farmed species.  
1079 *SEAFISH*.
- 1080 Hargrave BT, Doucette LI, Cranford PJ, Law BA, Milligan TG (2008) Influence of mussel aquaculture  
1081 on sediment organic enrichment in a nutrient-rich coastal embayment. *Marine Ecology Progress*  
1082 *Series* **365**: 137–149.
- 1083 Hartstein ND, Rowden AA (2004) Effect of biodeposits from mussel culture on macroinvertebrate  
1084 assemblages at sites of different hydrodynamic regime. *Marine Environmental Research* **57**: 339–  
1085 357.
- 1086 Hartstein ND, Stevens CL (2005) Deposition beneath long-line mussel farms. *Aquacultural*  
1087 *Engineering* **33**: 192–213.
- 1088 Heery EC, Bishop MJ, Critchley LP, Bugnot AB, Airoidi L, Mayer-Pinto M *et al.* (2017) Identifying  
1089 the consequences of ocean sprawl for sedimentary habitats. *Journal of Experimental Marine*  
1090 *Biology and Ecology* **492**: 31–48.
- 1091 Hilborn R, Banobi J, Hall SJ, Pucylowski T, Walsworth TE (2018) The environmental cost of animal  
1092 source foods. *Frontiers in Ecology and the Environment* **16**: 329–335.
- 1093 Hondolero D, Edwards MS (2017) Changes in ecosystem engineers: the effects of kelp forest type on  
1094 currents and benthic assemblages in Kachemak Bay, Alaska. *Marine Biology* **164**:81.
- 1095 Horta e Costa B, Claudet J, Franco G, Erzini K, Caro A, Gonçalves, EJ (2016) A regulation-based  
1096 classification system for Marine Protected Areas (MPAs). *Marine Policy* **72**: 192–198.
- 1097 Hulot V, Saulnier D, Lafabrie C, Gaertner-Mazouni N (2018) Shellfish culture: a complex driver of  
1098 planktonic communities. *Reviews in Aquaculture* **12**: 33–46.
- 1099 Inger R, Attrill MJ, Bearhop S, Broderick AC, Grecian JW, Hodgson DJ *et al.* (2009) Marine renewable  
1100 energy: potential benefits to biodiversity? An urgent call for research. *Journal of Applied Ecology*  
1101 **46**: 1145–1153.
- 1102 Inglis GJ, Gust N (2003) Potential indirect effects of shellfish culture on the reproductive success of  
1103 benthic predators. *Journal of Applied Ecology* **40**: 1077–1089.

- 1104 Jackson GA, Winant CD (1983) Effect of a kelp forest on coastal currents. *Continental Shelf Research*  
1105 **2**: 75–80.
- 1106 Jackson JBC, Kirby MX, Berger WH, Bjorndal KA, Botsford LW, Bourque BJ *et al.* (2001) Historical  
1107 overfishing and the recent collapse of coastal ecosystems. *Science* **293**: 629–637.
- 1108 Jiang W, Gibbs MT (2005) Predicting the carrying capacity of bivalve shellfish culture using a steady,  
1109 linear food web model. *Aquaculture* **244**: 171–185.
- 1110 Kapetsky JM, Aguilar-Manjarrez J, Jenness J (2013) A global assessment of offshore mariculture  
1111 potential from a spatial perspective. *FAO Fisheries and Aquaculture Technical Paper No. 549*.  
1112 FAO, Rome.
- 1113 Kaspar HF, Gillespie PA, Boyer IC, McKenzie AI (1985) Effects of mussel aquaculture on the nitrogen  
1114 cycle and benthic communities in Kenepuru Sound, Marlborough Sounds, New Zealand. *Marine*  
1115 *Biology* **85**: 127–136.
- 1116 Keeley N (2013) Benthic Effects. In D. Morrissey (Ed.), *Literature review of ecological effects of*  
1117 *aquaculture*, pp. 3.1-3.33. Ministry for Primary Industries, Cawthron Institute & National Institute  
1118 for Water and Atmospheric Research Ltd.
- 1119 Keeley N, Forrest B, Hopkins G, Gillespie P, Knight B, Webb S *et al.* (2009) Sustainable aquaculture  
1120 in New Zealand: review of the ecological effects of farming shellfish and other non-fish species.  
1121 *Ministry of Fisheries. Cawthron Report No. 1476, pp 150 plus appendices.*
- 1122 Kingsford MJ (1993) Biotic and abiotic structure in the pelagic environment: importance to small fishes.  
1123 *Bulletin of Marine Science* **53**: 393–415.
- 1124 Klinger DH, Maria A, Davíðsdóttir B, Winter A, Watson JR (2018) The mechanics of blue growth:  
1125 management of oceanic natural resource use with multiple, interacting sectors. *Marine Policy* **87**:  
1126 356–362.
- 1127 Kumar M, Cripps S (2012) Chapter 4: Environmental Aspects. In J. S. Lucas & P. C. Southgate (Eds.),  
1128 *Aquaculture: farming aquatic animals and plants*, pp. 84–106. John Wiley & Sons, Ltd.
- 1129 La Rosa T, Mirto S, Favalaro, E, Savona B, Sarà G, Danovaro R *et al.* (2002) Impact on the water  
1130 column biogeochemistry of a Mediterranean mussel and fish farm. *Water Research* **36**: 713–721.
- 1131 Lacoste É, Drouin A, Weise AM, Archambault P, McKindsey CW (2018) Low benthic impact of an  
1132 offshore mussel farm in Îles-de-la-Madeleine, eastern Canada. *Aquaculture Environment*  
1133 *Interactions* **10**: 473–485.
- 1134 Landmann J, Ongsiek T, Goseberg N, Heasman K, Buck B, Paffenholz J-A *et al.* (2019) Physical  
1135 modelling of blue mussel dropper lines for the development of surrogates and hydrodynamic  
1136 coefficients. *Journal of Marine Science and Engineering* **7**: 65.
- 1137 Lasiak TA, Underwood AJ, Hoskin M (2006) An experimental assessment of the potential impacts of  
1138 longline mussel farming on the infauna in an open coastal embayment. *Aquatic Conservation:*  
1139 *Marine and Freshwater Ecosystems* **16**: 289–300.
- 1140 Le Gouvello R, Hochart LE, Laffoley D, Simard F, Andrade C, Angel D *et al.* (2017) Aquaculture and  
1141 marine protected areas: potential opportunities and synergies. *Aquatic Conservation: Marine and*  
1142 *Freshwater Ecosystems* **27**: 138–150.
- 1143 LeBlanc A, Landry T, Miron G (2003) Identification of fouling organisms covering mussel lines and

- 1144 impact of a common defouling method on the abundance of foulers in Tracadie Bay, Prince  
1145 Edward Island. *Canadian Technical Report of Fisheries and Aquatic Sciences* **2477**: 18.
- 1146 Lehane C, Davenport J (2002) Ingestion of mesozooplankton by three species of bivalve; *Mytilus edulis*,  
1147 *Cerastoderma edule* and *Aequipecten opercularis*. *Journal of the Marine Biological Association*  
1148 *of the United Kingdom* **82**: 615–619.
- 1149 Lehane C, Davenport J (2006) A 15-month study of zooplankton ingestion by farmed mussels (*Mytilus*  
1150 *edulis*) in Bantry Bay, Southwest Ireland. *Estuarine, Coastal and Shelf Science* **67**: 645–652.
- 1151 Lester SE, Stevens JM, Gentry RR, Kappel CV, Bell TW, Costello CJ *et al.* (2018) Marine spatial  
1152 planning makes room for offshore aquaculture in crowded coastal waters. *Nature Communications*  
1153 **9**: 945.
- 1154 Lin J, Li C, Zhang S (2016) Hydrodynamic effect of a large offshore mussel suspended aquaculture  
1155 farm. *Aquaculture* **451**: 147–155.
- 1156 Lovatelli A, Manjarrez J, Soto D (2013) Expanding mariculture farther offshore. Technical,  
1157 environmental, spatial and governance challenges. *FAO Technical Workshop, 22-25 March 2010*.
- 1158 Lucas JS (2012) Chapter 23 Bivalve Molluscs. In JS Lucas & PC Southgate (Eds.), *Aquaculture:*  
1159 *farming aquatic animals and plants*, pp. 541–566. John Wiley & Sons, Ltd.
- 1160 Maar M, Nielsen TG, Petersen JK (2008) Depletion of plankton in a raft culture of *Mytilus*  
1161 *galloprovincialis* in Ría de Vigo, NW Spain. *Aquatic Biology* **4**: 127–141.
- 1162 Marine Conservation Society (2018) Good fish guide: mussel, *Mytilus edulis* (Farmed). Retrieved  
1163 March 12, 2019, from <https://mcsuk.org/goodfishguide/fish/498>
- 1164 Matarazzo Suplicy F (2018) A review of the multiple benefits of mussel farming. *Reviews in*  
1165 *Aquaculture* **12**: 204–223.
- 1166 McKindsey CW, Archambault P, Callier MD, Frédéric O (2011) Influence of suspended and off-bottom  
1167 mussel culture on the sea bottom and benthic habitats: a review. *Canadian Journal of Zoology* **89**:  
1168 622–646.
- 1169 McKindsey CW, Archambault P, Simard N (2012) Spatial variation of benthic infaunal communities  
1170 in baie de Gaspé (eastern Canada) - Influence of mussel aquaculture. *Aquaculture* **356**: 48–54.
- 1171 McKindsey CW, Thetmeyer H, Landry T, Silvert W (2006) Review of recent carrying capacity models  
1172 for bivalve culture and recommendations for research and management. *Aquaculture* **261**: 451–  
1173 462.
- 1174 Muñoz O, Revilla M, Rodríguez JG, Laza-Martínez A, Fontán A (2019) Annual cycle of phytoplankton  
1175 community through the water column: study applied to the implementation of bivalve offshore  
1176 aquaculture in the southeastern Bay of Biscay. *Oceanologia* **61**: 114–130.
- 1177 Murray LG, Newell CR, Seed R (2007) Changes in the biodiversity of mussel assemblages induced by  
1178 two methods of cultivation. *Journal of Shellfish Research* **26**: 153–162.
- 1179 Nelson PA (2003) Marine fish assemblages associated with fish aggregating devices (FADs): effects of  
1180 fish removal, FAD size, fouling communities, and prior recruits. *Fishery Bulletin* **101**: 835–850.
- 1181 Newell CR, Brady DC, Richardson J (2019) Farm-scale production models. In . Smaal, JG Ferreira, J  
1182 Grant, JK Petersen & Ø Strand (Eds.), *Goods and services of marine bivalves*, pp. 485–506.

- 1183 Springer Open.
- 1184 Newell CR, Richardson J (2014) The effects of ambient and aquaculture structure hydrodynamics on  
1185 the food supply and demand of mussel rafts. *Journal of Shellfish Research* **33**: 257–272.
- 1186 Newell RIE (2004) Ecosystem influences of natural and cultivated populations of suspension-feeding  
1187 bivalve molluscs: a review. *Journal of Shellfish Research* **23**: 51–61.
- 1188 Nizzoli D, Welsh DT, Bartoli M, Viaroli P (2005) Impacts of mussel (*Mytilus galloprovincialis*)  
1189 farming on oxygen consumption and nutrient recycling in a eutrophic coastal lagoon.  
1190 *Hydrobiologia* **550**: 183–198.
- 1191 Nizzoli D, Welsh DT, Fano, EA, Viaroli P (2006) Impact of clam and mussel farming on benthic  
1192 metabolism and nitrogen cycling, with emphasis on nitrate reduction pathways. *Marine Ecology*  
1193 *Progress Series* **315**: 151–165.
- 1194 O’Donncha F, Hartnett M, Nash S (2013) Physical and numerical investigation of the hydrodynamic  
1195 implications of aquaculture farms. *Aquacultural Engineering* **52**: 14–26.
- 1196 O’Donncha F, James SC, Ragnoli, E (2016) Modelling study of the effects of suspended aquaculture  
1197 installations on tidal stream generation in Cobscook Bay. *Renewable Energy* **102**: 65–76.
- 1198 Pauly D, Christensen V, Guénette S, Pitcher TJ, Sumaila UR, Walters CJ *et al.* (2002) Towards  
1199 sustainability in world fisheries. *Nature* **418**: 689–695.
- 1200 Pechlivanidis G, Keramaris, E, Savvidis Y (2018) Turbulent simulation of the flow around different  
1201 positions of mussel shocks. *Proceedings* **2**: 574.
- 1202 Petersen J (2004) Methods for measurement of bivalve clearance rate-hope for common understanding.  
1203 *Marine Ecology Progress Series* **276**: 309–310.
- 1204 Plew DR (2005) PhD Thesis The hydrodynamic effects of long-line mussel farms.
- 1205 Plew DR (2013) Hydrodynamic effects. In B Knight (Ed.), *Literature review of ecological effects of*  
1206 *aquaculture*, pp. 11.1-11.23. Ministry for Primary Industries, Cawthron Institute & National  
1207 Institute for Water and Atmospheric Research Ltd.
- 1208 Plew DR (2011) Depth-averaged drag coefficient for modeling flow through suspended canopies.  
1209 *Journal of Hydraulic Engineering* **137**: 234–247.
- 1210 Plew DR, Spigel RH, Stevens CL, Nokes RI, Davidson MJ (2006) Stratified flow interactions with a  
1211 suspended canopy. *Environmental Fluid Mechanics* **6**: 519–539.
- 1212 Plew DR, Stevens CL, Spigel RH, Hartstein ND (2005) Hydrodynamic implications of large offshore  
1213 mussel farms. *IEEE Journal of Oceanic Engineering* **30**: 95–108.
- 1214 Prins TC, Smaal AC, Dame RF (1997) A review of the feedbacks between bivalve grazing and  
1215 ecosystem processes. *Aquatic Ecology* **31**: 349–359.
- 1216 Rampazzo F, Berto D, Giani M, Brigolin D, Covelli S, Cacciatore F *et al.* (2013) Impact of mussel  
1217 farming on sedimentary geochemical properties of a Northern Adriatic area influenced by  
1218 freshwater inflows. *Estuarine, Coastal and Shelf Science* **129**: 49–58.
- 1219 Rees SE, Sheehan, EV, Stewart BD, Clark R, Appleby T, Attrill MJ *et al.* (2020) Emerging themes to  
1220 support ambitious UK marine biodiversity conservation. *Marine Policy* **117**: 103864.

- 1221 Rosman JH, Denny MW, Zeller RB, Monismith SG, Koseff JR (2013) Interaction of waves and currents  
1222 with kelp forests (*Macrocystis pyrifera*): Insights from a dynamically scaled laboratory model.  
1223 *Association for the Sciences of Limnology and Oceanography* **58**: 790–802.
- 1224 Roycroft D, Kelly TC, Lewis LJ (2007) Behavioural interactions of seabirds with suspended mussel  
1225 longlines. *Aquaculture International* **15**: 25–36.
- 1226 Ryan J (2004) Farming the Deep Blue. *Bord Iascaigh Mhara - The Irish Sea Fisheries Board and Irish*  
1227 *Marine Institute*. Retrieved from  
1228 <http://www.bim.ie/media/bim/content/downloads/Farming,the,Deep,Blue.pdf>
- 1229 Sala, E, Lubchenco J, Grorud-Colvert K, Novelli C, Roberts C, Sumaila UR (2018) Assessing real  
1230 progress towards effective ocean protection. *Marine Policy* **91**: 11–13.
- 1231 Sequeira A, Ferreira JG, Hawkins AJS, Nobre A, Lourenço P (2008) Trade-offs between shellfish  
1232 aquaculture and benthic biodiversity: a modelling approach for sustainable management.  
1233 *Aquaculture* **274**: 313–328.
- 1234 Sheehan, EV, Bridger D, Mascorda Cabre L, Cartwright A, Cox D, Rees S *et al.* (2019) Bivalves boost  
1235 biodiversity. *Food, Science and Technology*, pp 18–21.
- 1236 Shi J, Wei H, Zhao L, Yuan Y, Fang J, Zhang J (2011) A physical-biological coupled aquaculture model  
1237 for a suspended aquaculture area of China. *Aquaculture* **318**: 412–424.
- 1238 Singh GG, Cisneros-Montemayor AM, Swartz W, Cheung W, Guy JA, Kenny TA *et al.* (2018) A rapid  
1239 assessment of co-benefits and trade-offs among Sustainable Development Goals. *Marine Policy*  
1240 **93**: 223–231.
- 1241 Smaal AC, Ferreira JG, Grant J, Petersen JK, Strand, Ø (2019) Goods and Services of marine bivalves.  
1242 Springer Open.
- 1243 Solandt JL, Mullier T, Elliott S, Sheehan, EV (2020) Managing marine protected areas in Europe:  
1244 moving from ‘feature-based’ to ‘whole-site’ management of sites. In J. Humphreys & R. Clark  
1245 (Eds.), *Marine Protected Areas: Science, Policy and Management*, pp. 157–181.
- 1246 Soto D, Aguilar-Manjarrez J, Brugère C, Angel D, Bailey C, Black K *et al.* (2008) Applying an  
1247 ecosystem-based approach to aquaculture: principles, scales and some management measures. In  
1248 D. Soto J Aguilar-Manjarrez, & N. Hishamunda (Eds.), *Building an ecosystem approach to*  
1249 *aquaculture. FAO/Universitat de les Illes Balears Expert Workshop. 7–11 May 2007, Palma de*  
1250 *Mallorca, Spain. FAO Fisheries and Aquaculture Proceedings. No. 14.*, pp. 15–35.
- 1251 Spencer BE (2002) Molluscan shellfish farming. *Fishing News Books, a division of Blackwell*  
1252 *Publishing*.
- 1253 STECF (2018) Scientific, Technical and Economic Committee for Fisheries - Economic report of the  
1254 EU aquaculture sector (STECF-18-19). *Publications Office of the European Union, Luxembourg,*  
1255 *2018, ISBN 978-92-79-79402-5.* Retrieved from [https://op.europa.eu/en/publication-detail/-](https://op.europa.eu/en/publication-detail/-/publication/7f9c98f0-0fe4-11e9-81b4-01aa75ed71a1)  
1256 [/publication/7f9c98f0-0fe4-11e9-81b4-01aa75ed71a1](https://op.europa.eu/en/publication-detail/-/publication/7f9c98f0-0fe4-11e9-81b4-01aa75ed71a1)
- 1257 Stelzenmüller V, Schulze T, Gimpel A, Bartelings H, Bello, E, Bergh O *et al.* (2013) Guidance on a  
1258 better integration of aquaculture, fisheries, and other activities in the coastal zone: from tools to  
1259 practical examples. *COEXIST project*.
- 1260 Stenton-Dozey J (2013) Pelagic effects. In W. Paul Gillespie, Cawthron Institute, Nelson Philip Heath,  
1261 NIWA (Ed.), *Literature review of ecological effects of aquaculture*, pp. 0–21. Ministry for Primary

- 1262 Industries, Cawthron Institute & National Institute for Water and Atmospheric Research Ltd.
- 1263 Stenton-Dozey JME, Jackson LF, Busby AJ (1999) Impact of mussel culture on macrobenthic  
1264 community structure. *Marine Pollution Bulletin* **39**: 357–366.
- 1265 Stenton-Dozey J, Probyn T, Busby A (2001) Impact of mussel (*Mytilus galloprovincialis*) raft-culture  
1266 on benthic macrofauna, *in situ* oxygen uptake, and nutrient fluxes in Saldanha Bay, South Africa.  
1267 *Canadian Journal of Fisheries and Aquatic Sciences* **58**: 1–11.
- 1268 Stevens CL, Petersen JK (2011) Turbulent, stratified flow through a suspended shellfish canopy:  
1269 implications for mussel farm design. *Aquaculture Environment Interactions* **2**: 87–104.
- 1270 Stevens CL, Plew DR, Smith MJ, Fredriksson DW (2007) Hydrodynamic forcing of long-line mussel  
1271 farms: observations. *Journal of Waterway, Port, Coastal, and Ocean Engineering* **133**: 192–199.
- 1272 Stevens C, Plew D, Hartstein N, Fredriksson D (2008) The physics of open-water shellfish aquaculture.  
1273 *Aquacultural Engineering* **38**: 145–160.
- 1274 Strand, Ø, Bergh, Ø, Pastres R, Icely J, Galparsoro I, Éva K *et al.* (2017) Ecosystem approach to making  
1275 space for aquaculture. EU Horizon 2020 project grant no. 633476. *Aquaspace*.
- 1276 Strohmeier T, Aure J, Duinker A, Castberg T, Svardal A, Strand Ø (2005) Flow reduction, seston  
1277 depletion, meat content and distribution of diarrhetic shellfish toxins in a long-line Blue mussel  
1278 (*Mytilus edulis*) farm. *Journal of Shellfish Research* **24**: 15–23.
- 1279 Strohmeier T, Duinker A, Strand Ø, Aure J (2008) Temporal and spatial variation in food availability  
1280 and meat ratio in a longline mussel farm (*Mytilus edulis*). *Aquaculture* **276**: 83–90.
- 1281 Strohmeier T, Strand Ø, Alunno-Bruscia M, Duinker A, Cranford PJ (2012) Variability in particle  
1282 retention efficiency by the mussel *Mytilus edulis*. *Journal of Experimental Marine Biology and*  
1283 *Ecology* **412**: 96–102.
- 1284 Troell M, Joyce A, Chopin T, Neori A, Buschmann AH, Fang JG (2009) Ecological engineering in  
1285 aquaculture - potential for integrated multi-trophic aquaculture (IMTA) in marine offshore  
1286 systems. *Aquaculture* **297**: 1–9.
- 1287 Trottet A, Roy S, Tamigneaux E, Lovejoy C, Tremblay R (2008) Influence of suspended mussel farming  
1288 on planktonic communities in Grande-Entrée Lagoon, Magdalen Islands (Québec, Canada).  
1289 *Aquaculture* **276**: 91–102.
- 1290 Tseung HL, Kikkert GA, Plew DR (2016) Hydrodynamics of suspended canopies with limited length  
1291 and width. *Environmental Fluid Mechanics* **16**: 145–166.
- 1292 Tyler-Walters H (2008) *Mytilus edulis* common mussel. Retrieved January 29: 2019, from  
1293 <https://www.marlin.ac.uk/species/detail/1421>
- 1294 Underwood AJ (1990) Experiments in ecology and management: their logics, functions and  
1295 interpretations. *Australian Journal of Ecology* **15**: 365–389.
- 1296 United Nations (2015) Transforming our world: the 2030 Agenda for sustainable development. *UN*  
1297 *Sustainable Development Goals*. Retrieved from  
1298 <https://sustainabledevelopment.un.org/post2015/transformingourworld/publication>
- 1299 Upton HF, Buck EH (2013) Open ocean aquaculture. *Fisheries, Aquaculture and Marine Mammals:*  
1300 *Interrelationship, Background and Issues*, 65–94.

- 1301 Weise AM, Cromey CJ, Callier MD, Archambault P, Chamberlain J, McKindsey CW (2009) Shellfish-  
1302 DEPOMOD: modelling the biodeposition from suspended shellfish aquaculture and assessing  
1303 benthic effects. *Aquaculture* **288**: 239–253.
- 1304 Weitzman J (2019) Applying the ecosystem services concept to aquaculture: a review of approaches,  
1305 definitions, and uses. *Ecosystem Services* **35**: 194–206.
- 1306 Wilding TA, Nickell TD (2013) Changes in benthos associated with mussel (*Mytilus edulis* L.) farms  
1307 on the west-coast of Scotland. *PLoS ONE* **8**.
- 1308 Ysebaert T, Hart M, Herman PMJ (2009) Impacts of bottom and suspended cultures of mussels *Mytilus*  
1309 *sp.* on the surrounding sedimentary environment and macrobenthic biodiversity. *Helgoland*  
1310 *Marine Research* **63**: 59–74.
- 1311 Zu Ermgassen PSE, Thurstan RH, Corrales J, Alleway H, Carranza A, Dankers N *et al.* (2020) The  
1312 benefits of bivalve reef restoration: a global synthesis of underrepresented species. *Aquatic*  
1313 *Conservation: Marine and Freshwater Ecosystems* **30**: 2050–2065.
- 1314 Zupan M, Fragkopoulou E, Claudet J, Erzini K, Horta e Costa B, Gonçalves EJ (2018) Marine partially  
1315 protected areas: drivers of ecological effectiveness. *Frontiers in Ecology and the Environment* **16**:  
1316 1–7.
- 1317

1318 **Tables**

1319

**Table 1** Farmed organisms harvested from global aquaculture for human consumption in 2016.

Category	Number of species	Production (tonnes)	Value (USD 1000)
Finfish	369	54,091,148	138,537,549
Molluscs	109	17,139,140	29,201,729
Crustaceans	64	7,862,016	57,078,984
Others†	16	938,558	6,766,010
Total	558	80,030,862	231,584,272

SOURCE: Modified from FAO (2018b). † Frogs, reptiles and aquatic invertebrates.

## 1320 **Figure Legends**

1321 **Figure 1** Types of mussel farm design: a) raft (Aypa, 1990), b) pole or ‘bouchot’(Gouletquer 2020),  
1322 c) longline and, d) submerged longline (Stevens *et al.* 2008).

1323 **Figure 2** Main potential ecological and oceanographic effects of a longline mussel farm. The figure  
1324 represents one many designs that could be attributed to offshore longline mussel farm’s constantly  
1325 evolving outlines (Graphic Mascorda Cabre 2020)

1326 **Figure 3** Elevation (top) and plan views (bottom) of an offshore longline mussel farm indicating various  
1327 potential hydrodynamic processes: (a) water flow and current attenuation, (b) downwelling, (c) corner  
1328 acceleration, (d) accelerating undercurrent mixing layer, (e) upwelling, (f) recirculating zone, vortex or  
1329 wake formation downstream of the farm, (g) turbulence within mussel longlines and (h) waves. The  
1330 figure exemplifies one of many designs that could be attributed to offshore longline mussel farm’s  
1331 constantly evolving outlines (Graphic Mascorda Cabre 2020, adapted from Plew *et al.* 2005).

1332 **Figure 4** Schools of fish have been captured in an offshore longline mussel farm in Lyme Bay, South  
1333 West UK. Picture has been taken from the recording of a Non-baited Midwater Video (NMW) rig placed  
1334 at 6m depth. Longline ropes are full of mussels and biofouling (Mascorda Cabre 2020).

1335 **Figure 5** School of mullets have been captured in an offshore longline mussel farm in Lyme Bay, South  
1336 West UK. Picture has been taken from the recording of a Non-baited Midwater Video (NMW) rig placed  
1337 at 6m depth. Longline ropes are full of mussels and biofouling (Mascorda Cabre 2019).

1338 **Figure 6** ROV Videoray footage showing how the seabed underneath an offshore longline mussel farm  
1339 (Lyme Bay, UK) is being utilised by commercially valuable crustaceans and fish (Mascorda Cabre  
1340 2020).

1341 **Figure 7** ROV Videoray footage showing how the seabed underneath an offshore longline mussel farm  
1342 (Lyme Bay, UK) is being utilised by echinoderms and commercially valuable molluscs and gastropods  
1343 such as scallops and whelks (Mascorda Cabre 2019).