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Biodiversity–Ecosystem Functioning (BEF) approach to further understanding aquaculture–environment interactions with application to bivalve culture and benthic ecosystems

Lacoste Elise ^{1,2,*}, McKindsey Christopher W. ³, Archambault Philippe ⁴

¹ UMR 241 EIO Université de Polynésie française Tahiti ,Polynésie française

² MARBEC Univ Montpellier CNRS Ifremer IRD Sète, France

³ Maurice Lamontagne Institute Fisheries and Oceans Canada Mont-Joli ,Canada

⁴ Département de biologie Faculté des Sciences et de Génie Université Laval Québec ,Canada

* Corresponding author : Elise Lacoste, email address : eliz.lacoste@gmail.com

Abstract :

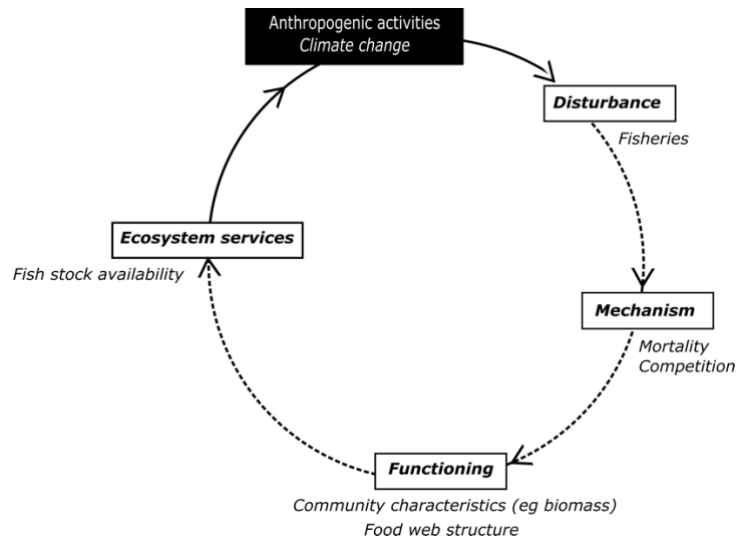
Coastal benthic ecosystems may be impacted by numerous human activities, including aquaculture, which continues to expand rapidly. Indeed, today aquaculture worldwide provides more biomass for human consumption than do wild fisheries. This rapid development raises questions about the interactions the practice has with the surrounding environment. In order to design strategies of sustainable ecosystem exploitation and marine spatial planning, a better understanding of coastal ecosystem functioning is needed so that tools to quantify impacts of human activities, including aquaculture, may be developed. To achieve this goal, some possible directions proposed are integrated studies leading to new concepts, model development based on these concepts and comparisons of various ecosystems on a global scale. This review draws on existing literature to (i) briefly summarize the major ecological interactions between off-bottom shellfish aquaculture and the environment, (ii) introduce research on the influence of benthic diversity on ecosystem functioning (BEF relationships) and (iii) propose a holistic approach to conduct aquaculture–environment studies using a BEF approach, highlighting the need for integrated studies that could offer insights and perspectives to guide future research efforts and improve the environmental management of aquaculture.

Keywords : aquaculture–environment interactions, benthic system, biodiversity, ecosystem functioning, shellfish.

34 **Introduction**

35 Increasing human activities, including the pervasive effects of climate change, have dramatically
36 increased the rate of ecosystem disturbances with impacts on their structure and functioning (Gosling
37 2013). In turn, changes in functional ecosystem performance alter the way many ecosystem services
38 are delivered and thus the benefits humanity derives from nature. This observation has motivated
39 numerous studies to evaluate the consequences of disturbance on biological communities and
40 ecosystem functioning. As an example, Fig. 1 illustrates the modifications that arise from fisheries
41 impacting mechanisms underlying ecosystem functioning and fish stock availability as an ecosystem
42 service. Due to the complex food web functioning and the multiple interactions between species (e.g.
43 trophic cascades), the removal of species targeted by fisheries may have both direct and indirect
44 effects, negative or not on several other species (Pauly *et al.* 1998; Andersen & Pedersen 2009).

45



46

47 Figure 1. Cycle of ecosystem disturbance using the example of fisheries. Anthropogenic activities
 48 create disturbances that modify the underlying mechanisms of ecosystem functioning, thereby
 49 affecting ecosystem services that support anthropogenic activities.

50

51 Much research over the past few decades has focused on links between altered biodiversity (mainly
 52 species loss but also gains in the context of exotic species) and ecosystem functioning (e.g. Hooper
 53 *et al.* 2005; Cardinale *et al.* 2012; Harvey *et al.* 2013). Although most research in this field has
 54 concentrated on terrestrial systems, the number of manipulative experiments that assess the influence
 55 of benthic diversity on ecosystem functioning (BEF relationships) in marine systems has also
 56 recently increased rapidly (O'Connor & Crowe 2005; Cardinale 2011; Solan *et al.* 2012; Gamfeldt
 57 *et al.* 2014; Séguin *et al.* 2014). These relationships have received much attention as they underpin
 58 many ecosystem services (Isbell *et al.* 2011; Balvanera *et al.* 2014; Cardinale *et al.* 2012). It is now
 59 generally accepted that higher biodiversity may increase ecosystem function efficiency, e.g. in terms
 60 of nutrient cycling (Cardinale *et al.* 2012; Gamfeldt *et al.* 2014; Piot *et al.* 2014), and/or resilience
 61 (Oliver *et al.* 2015). Moreover, there is general agreement on the importance of focusing on species-
 62 specific traits rather than species richness *per se* to describe links between biodiversity and metrics
 63 of ecosystem functioning (e.g. decomposition rates, nutrient uptake) (Mouillot *et al.* 2011; Gagic *et*

64 *al.* 2015; Strong *et al.* 2015; Cernansky 2017).

65 Estuarine and coastal ecosystems deliver a wide range of ecosystem services while facing multiple
66 natural and anthropogenic disturbances. An important example of such human disturbance in these
67 ecosystems is aquaculture. This industry may profoundly alter ecosystem functioning (e.g. primary
68 productivity), which in turn could constrain commercial species production (Ferriss *et al.* 2015; Price
69 *et al.* 2015). With the continued development of aquaculture over the past few decades comes
70 concerns about its environmental impacts and interactions with other activities in coastal areas (e.g.
71 tourism, fisheries) (Edwards 2015; Bricker *et al.* 2016). Knowledge of aquaculture-environment
72 interactions (AEI) is therefore essential for the sustainable development of the aquaculture industry
73 and efficient marine spatial planning (Dempster & Holmer 2009).

74 Unlike fish or shrimp farming, bivalve culture is considered to have low ecosystem impacts since
75 animals are dependent on ambient supplies of plankton and organic particles for food (i.e. there is
76 no addition of food to the natural environment). However, bivalve aquaculture accelerates nutrient
77 dynamics due to bivalve excretion and mineralization of sedimented organic-rich bivalve
78 biodeposits, with consequences at farm- and larger spatial scales (Richard *et al.* 2007a; Woods *et al.*
79 2012; Lacoste & Gaertner-Mazouni 2016). Increased biodeposition to the seafloor is recognized to
80 change benthic community structure at both large and small spatial scales, depending on farm layout
81 and environmental conditions (Hartstein & Rowden 2004; McKindsey *et al.* 2011). The subsequent
82 impacts of those changes on benthic ecosystem functioning (e.g. nutrient cycling, trophic cascading)
83 have only rarely been addressed in the context of aquaculture (but see Heilskov *et al.* 2006; Lacoste
84 *et al.* 2019). Studies have shown that diversity of biofouling communities in the water column may
85 influence ecosystem functioning since it is, in part, responsible for variations in nutrient fluxes at the
86 culture structure – water column interface in different ecosystems (Mazouni *et al.* 2001; Richard *et*

87 *al.* 2006; Jansen *et al.* 2011; Lacoste *et al.* 2014).

88 As pointed out by Snelgrove *et al.* (2014), the effective application of biodiversity–ecosystem
89 function (BEF) research to societal needs in the Anthropocene represents the next great challenge
90 for ecology. BEF studies may help understand how ecosystems work and respond to changes. In this
91 sense, aquaculture seems an ideal opportunity to apply BEF research to elucidate impacts of
92 anthropogenic disturbance on ecosystem diversity and functioning (and services). As such, organic
93 loading in the form of bivalve biodeposition could serve as a model system to describe links between
94 benthic community diversity and ecosystem functioning in terms of either nutrient or oxygen fluxes
95 at the sediment-water interface or trophic links.

96 In this review, we highlight aquaculture-related modifications (focusing on off-bottom bivalve
97 aquaculture) and suggest a holistic approach that includes studies done within a BEF framework to
98 link biodiversity changes to ecosystem functioning. As a previous review emphasized the role of
99 water column diversity (*i.e.* commercial species and biofouling communities) on ecosystem
100 functioning (Lacoste & Gaertner-Mazouni 2015), we here focus on the benthic compartment. We
101 wish to demonstrate that further empirical studies are needed to adopt a holistic vision – *i.e.* by
102 simultaneously considering environmental parameters, multi-level biodiversity descriptors
103 (including functional diversity), and ecosystem functioning indicators.

104

105 **Impacts of bivalve aquaculture on the benthic ecosystem**

106 Bivalve aquaculture affects the environment in different ways, with a variety of near- and far-field
107 cascading effects. Studies on the interactions between culture systems and natural environments are
108 important for analysing and managing the environmental effects of aquaculture and vice versa.
109 Although the following section provides an update of previous reviews (Prins *et al.* 1998; Cranford

110 *et al.* 2003; Newell 2004; Forrest *et al.* 2009, Dumbauld *et al.* 2009; McKindsey *et al.* 2011) it does
111 not present an exhaustive review of the positive or negative impacts of aquaculture on the
112 environment; rather we highlight the complexity of ecosystem responses and the difficulty of finding
113 relevant indicators (see Valenti *et al.* 2018) given the variety and heterogeneity of studied systems.
114 Table 1 synthesizes the main ecosystem properties that are evaluated in aquaculture-environment
115 interactions studies.

116

117 ***Benthic loading impacts sediment characteristics and nutrient exchanges***

118 Part of the material filtered by bivalves is excreted as feces or pseudo-feces, collectively known as
119 biodeposits, in the water column. Biodeposits have a greater sinking velocity than their constituent
120 particles thereby increasing sedimentation rates within suspended bivalve culture sites (Callier *et al.*
121 2006; Giles *et al.* 2006; Zúñiga *et al.* 2014). Biodeposit production and sedimentation rates vary
122 among species, bivalve sizes and diets, and vary greatly over short time scales (days). Waste
123 dispersal around shellfish farms has been modelled for few systems (Giles *et al.* 2009; Weise *et al.*
124 2009), and there is an acknowledged need to gather further information on biodeposit production
125 and composition under natural conditions, and the redistribution and integration of biodeposits once
126 they reach the seafloor. Improved predictions also requires a consideration of the communities that
127 live associated with cultured bivalves (including the species living on the structure, on and among
128 bivalve clumps) since they may significantly contribute to benthic organic loading (Lacoste &
129 Gaertner-Mazouni 2015 and references therein). Notwithstanding the above, it is clear that
130 suspended bivalves may greatly increase sedimentation rates under farms relative to that in reference
131 areas. Zúñiga *et al.* (2014) found that sedimentation fluxes under mussel rafts in Spain (86–536 g
132 m⁻² d⁻¹) was 6-7 folds the rate observed at a reference site, although the highly hydrodynamic

133 environment attenuates the organic carbon arriving at the seafloor. Giles and Pilditch (2006) showed
134 that sedimentation under a mussel farm in New Zealand (240-540 g m⁻² d⁻¹) was increased by 106 g
135 m⁻² d⁻¹ compared to the reference site. In contrast, Comeau *et al.* (2014) did not observe differences
136 in organic sedimentation rates under experimental mussel rafts compared to neighbouring reference
137 sites in Canada.

138 Given high variability of biodeposition patterns, subsequent impacts of organic loading on sediment
139 characteristics range from low (Danovaro *et al.* 2004; Mallet *et al.* 2006; Holmer *et al.* 2015), to
140 slight (McKindsey *et al.* 2012; Dimitriou *et al.* 2015) to severe (Stenton-Dozey *et al.* 2001; Hargrave
141 *et al.* 2008a; Cranford *et al.* 2009). The main changes described by several authors in association
142 with biodeposit loading in shellfish areas are increased sediment organic material content (%OM) or
143 total free sulphides (TFS) or decreased redox potential (RedOx) (Hargrave *et al.* 2008a; Cranford *et al.*
144 *et al.* 2009; Comeau *et al.* 2014). However, several studies have shown that TFS and RedOx are often
145 not sensitive enough to detect the effect of mussel aquaculture on benthic sediments (Callier *et al.*
146 2007; Comeau *et al.* 2014; Lacoste *et al.* 2019). The authors concluded that sedimented organic
147 material may be rapidly processed by infauna communities or be resuspended, preventing negative
148 effects of shellfish biodeposition on benthic sediments. The capacity of the benthic system to
149 mineralize biodeposition in the short term is a key process that defines sediment %OM increases.

150 Accumulation of biodeposits on the seafloor and OM processing may further modify oxygen and
151 nutrient exchanges at the sediment-water interface. Many studies have shown that benthic oxygen
152 consumption is increased under aquaculture structures relative to that outside of farms (Giles &
153 Pilditch 2006; Nizzoli *et al.* 2006; Thouzeau *et al.* 2007) as are benthic ammonium and phosphate
154 releases (Giles *et al.* 2006; Nizzoli *et al.* 2006; Richard *et al.* 2007b; Erler *et al.* 2017) due to the
155 mineralization of accumulated OM. In deep areas or those with strong hydrodynamic conditions,

156 biodeposit dispersion and degradation reduce the amount of organic material that arrives at the
157 seafloor, attenuating expected impacts on benthic biogeochemistry and nutrient fluxes (Gallardi
158 2014; Lacoste & Gaertner-Mazouni 2016; Lacoste *et al.* 2018a).

159
160 One of the current challenges for environmental impact assessment of aquaculture is the
161 quantification of links between organic loading from biodeposition and biogeochemical and benthic
162 community conditions to inform predictive models. To our knowledge, only Weise *et al.* (2009) have
163 described a relationship between predicted biodeposition to the seafloor (using shellfish DEPOMOD
164 model) and benthic communities. This study observed decreased values for infaunal trophic index
165 scores (ITI, Word 1979) – an index of the tolerance of the benthic communities to organic enrichment
166 – with increasing predicted biodeposit fluxes. Given the complexity of interactions occurring in
167 sediments and the plethora of production systems, further empirical studies are needed to quantify
168 these relationships.

169
170 ***Benthic community diversity***

171 Typically, the accumulation and decomposition of biodeposits from cultured bivalves affects benthic
172 communities according to the Pearson and Rosenberg (1978) model of organic enrichment, with a
173 progressive appearance of opportunistic species (e.g. *Capitella* spp.) directly under and in the
174 vicinity of aquaculture facilities. Many studies over the past 30 years have reported results on this
175 topic for different cultivated species and ecosystems (see reviews of Newell 2004; Forrest *et al.*
176 2009; McKindsey *et al.* 2011) but without showing consistent effects. Some authors have reported a
177 lower diversity of infaunal species (Chamberlain *et al.* 2001; Stenton-Dozey *et al.* 2001; Hartstein
178 & Rowden 2004) and a dominance of opportunistic species beneath mussel farms (Mirto *et al.* 2000;

179 Chamberlain *et al.* 2001; Hartstein & Rowden 2004; Callier *et al.* 2007), whereas others have
180 detected minor (Brizzi *et al.* 1995; Mirto *et al.* 2000; Grant *et al.* 2012) or no negative effects on
181 macrofaunal community structure (Crawford *et al.* 2003; Danovaro *et al.* 2004; Miron *et al.* 2005;
182 Mallet *et al.* 2006). In some cases, shellfish aquaculture also promotes benthic macrofauna biomass
183 and diversity (Grant *et al.* 1995; Callier *et al.* 2007; D'Amours *et al.* 2008; Theodorou *et al.* 2015).
184 To date, most studies have focused on macrofauna (i.e. the fraction > 500µm or > 1mm, depending
185 on the study). To complete the description of community changes in the context of aquaculture, there
186 is also a need to identify benthic compartments other than macrofauna, such as meiofauna and
187 bacteria. Few studies have described responses of these communities to organic loading due to
188 bivalve biodeposition (Mirto *et al.* 2000; Danovaro *et al.* 2003; Mahmoudi *et al.* 2008; Pollet *et al.*
189 2015; Lacoste *et al.* 2019) although these compartments may respond quickly to disturbance
190 (Zeppilli *et al.* 2015 and references therein) and play a fundamental role in biogeochemical cycles
191 (Schratzberger & Ingels 2017).

192 Analysis of community changes associated with aquaculture facilities includes univariate analysis
193 of diversity indices (e.g. richness, abundance, Shannon) as well as multivariate analyses to describe
194 community taxonomic composition (e.g. ordination techniques). Other alternative biotic indicators
195 may also be used (e.g. *AZTI's Marine Biotic Index* (AMBI, Borja *et al.* 2000) or ITI) but the results
196 are very context-dependent and appear to not be useful in all cases. Few studies have evaluated
197 benthic invertebrate functional diversity in the context of fish (Dimitriadis & Koutsoubas 2011) or
198 shellfish (Lacoste *et al.* 2019) aquaculture. However, it is increasingly recognized that integrating
199 functional information (on the basis of species trait values) deepens understanding of community
200 functioning (Diaz & Cabido 2001).

201

202 To date, the range of aquaculture impacts reported in the literature is largely based on ecological
 203 indices for macro-infauna (Miron *et al.* 2005; Borja *et al.* 2009). The species diversity approach to
 204 describing aquaculture impacts is thus incomplete as it ignores some compartments and the
 205 functional consequences of species assemblage modifications on ecosystem processes. We suggest
 206 that a more holistic understanding of the effect of bivalve culture on ecosystem processes would be
 207 gained by using a multi-indicator approach, including functional ones, based on several taxonomic
 208 levels (from bacteria to macrofauna).

209

210 Table 1. Overview of the main impacts of suspended bivalve aquaculture on the benthic ecosystem described in
 211 aquaculture-environment interactions studies (not exhaustive). Studies are divided into those that concentrated on 1)
 212 only sediment biogeochemistry, 2) benthic communities (macrofauna and meiofauna and/or bacteria), 3) sediment-water
 213 interface (SWI) fluxes and 4) both benthic communities and SWI fluxes.

Benthic diversity	Ecosystem functioning	Sediment biogeochemistry	Culture type	Sites	References
-	-	Sedimentation, sediment OM content, sulfides, redox potential	longlines, mussels floating bags & table, oysters raft, oysters raft farm, mussels	Canada Spain	Hatcher <i>et al.</i> 1994 Callier <i>et al.</i> 2006 Hargrave <i>et al.</i> 2008a Cranford <i>et al.</i> 2009 Weise <i>et al.</i> 2009 Mallet <i>et al.</i> 2006 Comeau <i>et al.</i> 2014 Zúñiga <i>et al.</i> 2014
Macro-infaunal communities	-	Grain size, sediment OM content	longlines, mussels oysters & mussels longlines, mussels longlines, mussels mussels	Ireland Australia New Zealand Canada Italy New Zealand	Chamberlain <i>et al.</i> 2001 Crawford <i>et al.</i> 2003 Hartstein and Rowden 2004 Callier <i>et al.</i> 2008 McKindsey <i>et al.</i> 2009, 2012 Fabi <i>et al.</i> 2009 Wong and O'Shea 2011

			<i>bouchot</i> mussels	France	Grant <i>et al.</i> 2012
			raft, mussels	Scotland	Wilding and Nickell 2013
			longlines, mussels	Greece	Dimitriou <i>et al.</i> 2015
			offshore longlines, mussels	Canada	Lacoste <i>et al.</i> 2018a
Meiofauna and/or Bacteria	-	Sedimentation, grain size, redox potential	longlines, mussels	Italy	Mirto <i>et al.</i> 2000 Danovaro <i>et al.</i> 2004
			control experiment, mussels	Canada	Pollet <i>et al.</i> 2015
-	SWI fluxes	Grain size, sediment OM content	table, oysters	France	Mazouni <i>et al.</i> 1996 Mazouni 2004
			mussels	New Zealand	Giles and Pilditch 2006 Giles <i>et al.</i> 2006
			ropes, mussels	Italy	Nizzoli <i>et al.</i> 2005, 2006, 2011
			Longlines, mussels	Canada	Richard <i>et al.</i> 2007a,b
			Rafts, mussels	Spain	Alonso-Perez <i>et al.</i> 2010
			longlines, pearl-oysters	French Polynesia	Gaertner-Mazouni <i>et al.</i> 2012
			oysters	Australia	Erler <i>et al.</i> 2017
Macro-infaunal communities	SWI fluxes	Grain size, sediment OM content, sulphides, redox potential	raft, mussels	South Africa	Stenton-Dozey <i>et al.</i> 2001
			longlines, mussels	New zealand	Christensen <i>et al.</i> 2003
			mesocosms, mussels	Canada	Callier <i>et al.</i> 2009
			mesocosms, mussels		Robert <i>et al.</i> 2013
			mesocosms, mussels		Lacoste <i>et al.</i> 2019

214

215

216 *Ecosystem-wide effects*

217 While benthic conditions are the most thoroughly studied impacts related to marine aquaculture,
218 other risk factors remain less clear. For example, impacts (e.g. vulnerability to disease, genetic,
219 trophic transfers) on populations of mobile macro-organisms, such as crustaceans, have been rarely
220 quantified (see Callier *et al.* 2017 for a review). However, the addition of aquaculture-related
221 physical structure in the environment creates refuges from predation and adverse environmental
222 conditions (Gutierrez *et al.* 2003) and fall-off of cultivated and associated organisms may serve as
223 food sources for wild populations (Miron *et al.* 2002; D'Amours *et al.* 2008) and attract mobile
224 organisms to farms. Several studies have shown that many fishes may be attracted to farm sites as
225 they feed on bivalve-associated organisms (Carbines 1993; Brooks 2000; Gerlotto *et al.* 2001;
226 Cartier & Carpenter 2013) and, in turn, be a food source for other predators (Brehmer *et al.* 2003).
227 In general, a higher density and diversity of wild fish is observed at farms relative to reference areas,
228 suggesting that aquaculture facilities act as fish aggregating devices (Barret *et al.* 2018). The extent
229 to which these animals are attracted to the structure itself (e.g. as a refuge from predators) or to the
230 prey associated with the structure is unclear (Würsig & Gailey 2002) and is likely species-specific.
231 For example, Drouin *et al.* (2015) showed that lobster *Homarus americanus* is more attracted by the
232 shelter created by mussel farming anchors whereas winter flounder *Pseudopleuronectes americanus*
233 seems to benefit from a trophic effect induced by the farm.
234 Conversely, aquaculture may also repulse some organisms by displacing their habitat or due to
235 disturbances created by husbandry activities. For example, Becker *et al.* (2011) suggested that three
236 decades of shellfish aquaculture have displaced breeding and pupping harbour seals. Kelly *et al.*
237 (1996) also showed that some birds avoid areas used for shellfish aquaculture, resulting in a net
238 decrease of overall shorebird use of open tidal flats that have been used for aquaculture.

239 Recently, a few studies have explored the direct trophic interactions between bivalve aquaculture
240 and wild populations. Using stable isotope analysis, Huang *et al.* (2018) showed that scallop faeces
241 may serve as new food source for benthic organisms, including meiofauna, further improving the
242 quality of lower level consumers as a food item in the benthic food web. Such results are important
243 and should be further explored since cascading effects to higher trophic levels could have a crucial
244 importance for ecosystem functioning, including on commercial species. A recent study (Sardenne
245 *et al.* 2019) showed that fallen farmed mussels contributed almost half of the diet of large lobsters
246 whereas small lobsters fed mostly on farm-associated crabs. In Norway, work has shown that wastes
247 from salmon farms may be transferred and picked up by organisms over significant distances (500
248 m to > 1 km), although the impacts of this on animals that assimilate such wastes may have
249 ecosystem-level consequences (White *et al.* 2017; Woodcock *et al.* 2018). Thus, impacts may
250 include both ecological effects and effects on the fisheries due to altered productivity, distribution,
251 or catchability of target species.

252 This field of research remains largely unexplored and should be addressed to place aquaculture-
253 related effects in context with other activities (e.g. fisheries) in areas where they may overlap.

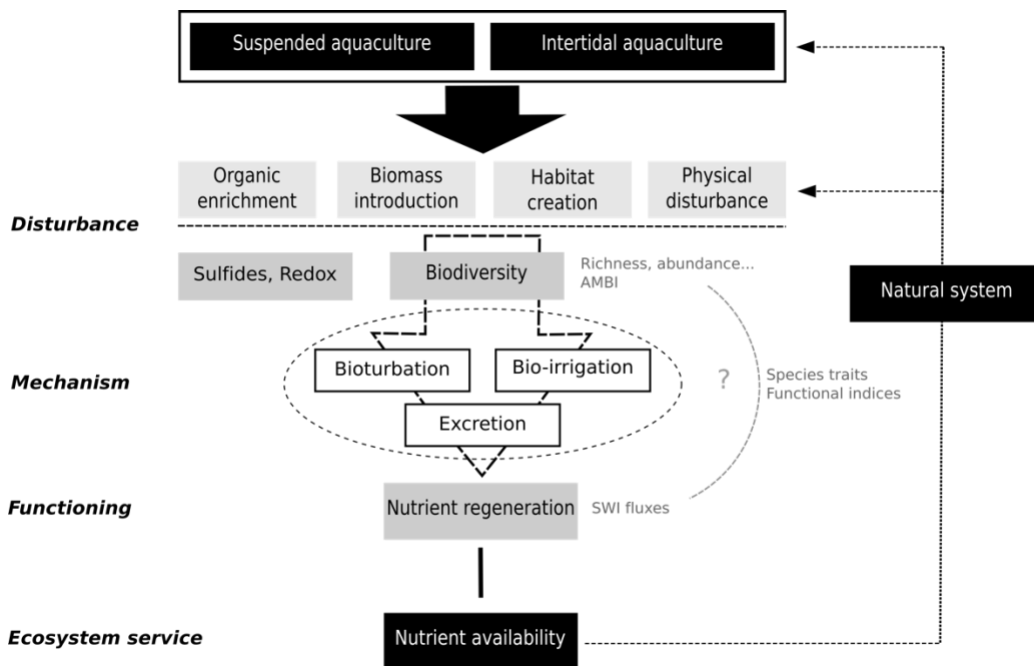
254

255 **Predicting the impacts of bivalve aquaculture on the benthic system using the biodiversity** 256 **ecosystem functioning (BEF) framework**

257 The main influences of bivalve culture on the sea floor were highlighted in the previous section.
258 Most studies on aquaculture-environment interactions to date have assessed a single or limited
259 number of potential effects (e.g. modification of macrofaunal diversity and sulfides) whereby links
260 between disturbances and functioning are only addressed superficially (Table 1). Although some
261 studies have measured benthic diversity and benthic fluxes simultaneously, few have explored the

262 functional role of species in nutrient dynamics. We here propose a more holistic approach for
 263 studying aquaculture-environment interactions based on the BEF framework. The main concepts of
 264 this approach are represented in Fig. 2.

265



266

267 Figure 2. BEF approach to the bivalve aquaculture-environment interactions for benthic systems
 268 with a focus on nutrient availability as an example of ecosystem service. The main idea is to explore
 269 the mechanisms at the origin of ecosystem functioning to better predict the impacts of disturbances
 270 due to aquaculture.

271

272 **Status of knowledge and limitations in marine systems**

273 Following initial studies on terrestrial ecosystem functioning (Gamfeldt *et al.* 2014), the number of
 274 manipulative experiments to assess BEF relationships in marine systems has rapidly increased
 275 (Cardinale 2011; Solan *et al.* 2012). Several studies focusing specifically on sediment processes have
 276 shed light on the major role of benthic organisms on organic transfers in coastal ecosystems (Cloern
 277 1982; Chauvaud *et al.* 2000; Grall & Chauvaud 2002). Sediment communities drive many critical

278 ecosystem functions, in particular nitrogen recycling, which is usually the driver of eutrophication
279 processes. In shallow environments, inorganic nitrogen regeneration in sediments can provide
280 between 20% and 100% of the annual requirement for primary production (Welsh 2003) and thus
281 understanding the mechanisms that drive this cycling is a key to understanding coastal productivity.
282 Laboratory and field studies have shown the significant effect of macrofauna on ecosystem processes
283 through sediment particle reworking (bioturbation), solute transfers in sediments (bio-irrigation),
284 and impacts on microbial processes, each of which alter the flow of energy and matter (Solan *et al.*
285 2004; O'Connor & Crowe 2005; Ieno *et al.* 2006; Waldbusser & Marinelli 2006). A large body of
286 scientific work has clearly shown how burrowers import O₂ into their burrows and enhance microbial
287 aerobic activity via intermittent ventilation (Kristensen 1988, 2000; Glud 2008). Nevertheless, many
288 of these studies are laboratory experiments using a single macrofaunal species (but see Kristensen *et al.*
289 *et al.* 2014; Belley & Snelgrove 2016; Politi *et al.* 2019). Such simple communities do not consider
290 ecological interactions present among organisms such as predation, competition or facilitation which
291 may greatly influence processes, including nutrient regeneration. Thus, although the roles of
292 macrofauna (via bioturbation and bio-irrigation) may be well-identified, more integrated approaches
293 require further knowledge, in particular concerning the roles of other biological compartments, such
294 as meiofauna and bacteria. In particular, there is a recent and growing interest to study the role of
295 meiofauna, since it has been shown that these organisms may modulate the biological interactions
296 within sediments (Bonaglia *et al.* 2014; Lacoste *et al.* 2018b) and play a significant role in benthic
297 ecosystem processes and services (Schratzberger & Ingels 2017). Until now, the paucity of
298 information on this group likely reflects the labour-intensive nature of obtaining such data, which is
299 particularly demanding both in terms of field work and species identification. New tools (e.g.

300 metabarcoding) could provide the opportunity to progress in this sense as has been shown by recent
301 studies (Boufahja *et al.* 2015; Carugati *et al.* 2015).

302 The effect of a species' behaviour on biogeochemical processes is now widely based on functional
303 groups, which, for benthic species, may be defined according to bioturbation mode, depth of
304 burrowing, or feeding guild (Solan *et al.* 2004; Piot *et al.* 2014; Wrede *et al.* 2017). Given the
305 importance of species identity, it is now accepted that species diversity alone does not guarantee the
306 stability of ecosystems or their resistance to disturbances (Mouillot *et al.* 2013; Gagic *et al.* 2015;
307 Jacquet *et al.* 2016) since the loss of a given species may also lead to the loss of a specific function
308 and thus alter ecosystem biological and chemical processes. As an example, Dubois *et al.* (2007)
309 observed changes in trophic pathways between two benthic communities without apparent changes
310 of the overall taxonomic diversity. Those changes were attributed to the replacement of filter-feeders
311 usually associated with the tube worms *Lanice conchilega*, in oyster farming areas. Conversely,
312 apparent changes of taxonomic diversity may be buffered by functional redundancies in communities
313 (Walker 1992; Snelgrove 1998) such that functional impacts on benthic assemblages are not always
314 matched by their structural counterparts (Bolam 2012). Thus, the removal of a highly functionally-
315 redundant species from a community may not result in a substantial reduction of community
316 functions, although this could be context dependent especially in case of ecosystem disturbance
317 (Hiddink *et al.* 2009). This potential decoupling between taxonomic diversity and ecosystem
318 functioning indicates that a functional based approach of diversity should be preferred to investigate
319 the effect of human disturbance at the ecosystem-functioning level (Mouillot *et al.* 2006, 2013).

320 While the functional approach is becoming a major concept in ecology and ecosystem management,
321 there are several gaps that cause uncertainty in ecological interpretations and limit comparisons
322 across studies. A main challenge is the limited availability of biological and ecological traits for

323 marine species, although some databases of traits are now available (Faulwetter *et al.* 2014).
324 Although there are multiple methods to measure functional diversity (Villéger *et al.* 2008; Laliberté
325 & Legendre 2010; Mouchet *et al.* 2010), to date, there is no standard accepted methodology to select
326 the most appropriate traits to compute the different indices (Marchini *et al.* 2008). Thus, until a
327 unified framework is adopted, the choice of the number of functional traits is partly based on
328 subjective rationale (Hortal *et al.* 2015; de Bello *et al.* 2017).

329

330 ***BEF approach to study aquaculture-environment interactions***

331 Wild sessile populations, particularly infauna, are commonly used as indicators of farm
332 environmental performance as these organisms integrate effects on benthic sediments. Changes in
333 community structure brought about by bivalve farming activities may also be expected to affect
334 sediment oxygen and nitrogen dynamics. To date, field experiments have tested the responses of
335 macro-faunal communities whereas others have measured effects on ecosystem functions including
336 nutrient fluxes; few studies have examined the two and assessed the feedback of macrofauna on
337 fluxes in response to organic enrichment in bivalve aquaculture (Table 1). Lacoste *et al.* (2019)
338 showed that benthic responses (measured as SWI nutrient fluxes) may not be linearly related to
339 organic enrichment (mussel biodeposits), likely due to varying responses of infaunal organisms with
340 different functional roles. Some species that benefit from intermediate organic enrichment may have
341 a positive effect on nutrient release to the water column whereas, at higher levels of enrichment,
342 large bio-irrigating species (*Cistenides gouldii*) may be lost with a net negative effect on
343 mineralization. Similar results have been observed around fish farms where mineralization rates were
344 highly correlated with the presence of the large and active irrigating climax species *Hediste*
345 *diversicolor* and *Limecola balthica* (Heilskov *et al.* 2006). It is not straightforward to infer immediate

346 effects of organic enrichment on nutrient regeneration and cascading effects on whole ecosystem
347 nutrient dynamics because of the idiosyncratic role of species and the importance of sediment
348 characteristics. Nonetheless, the exercise seems important given the myriad uses of coastal areas and
349 the potential impacts that aquaculture may have on the functioning these ecosystems. Empirical
350 studies are needed to advance theoretical and methodological knowledge to further understand these
351 relationships. Thus, dose-response studies are an interesting approach to evaluate thresholds at which
352 changes in community diversity may alter ecosystem functioning. The contrasting benthic conditions
353 created by aquaculture along gradients may also represent an excellent opportunity to empirically
354 evaluate the effects of diversity modifications on benthic fluxes under field conditions. Although
355 some studies have addressed this point with experimental (Callier *et al.* 2009; Robert *et al.* 2013;
356 Lacoste *et al.* 2019) and natural (Dimitriadis & Koutsoubas 2011) gradients of organic enrichment
357 for bivalve and fish farm systems, further investigations are required that simultaneously consider
358 changes of benthic functional diversity and consequences for ecosystem functioning.

359 Knowledge of species' functional roles may further serve to improve sediment quality of organically
360 enriched sediments in the context of mitigating negative aquaculture effects (Slater & Carton 2009;
361 2010; Bergström *et al.* 2015, 2018). In a series of field and laboratory experiment, Bergström *et al.*
362 (2015) demonstrated the contribution of the gallery-building polychaete *Hediste diversicolor* to the
363 degradation of organic material beneath mussel farms. They estimated that polychaetes activity
364 stimulated the degradation of up to 80% of organic material reaching the bottom every day. The role
365 of the polychaete may be direct through the consumption of faecal pellets at the sediment surface or
366 indirect through the stimulation of bacterial processes in deeper sediment layers. Further worm
367 species have been identified that could help mitigate aquaculture wastes while producing additional
368 farmed marine biomass in integrated multitrophic aquaculture (IMTA) (Pombo *et al.* 2018).

369

370 The identification of potential candidates to mitigate wastes from aquaculture requires a deep
371 knowledge of species ecology and behaviour within sediments and on the relationships with
372 ecosystem processes that a BEF approach could inform. Aquaculture research offers a tremendous
373 opportunity to contrast environments with the same species being cultivated around the world and
374 thus improve our understanding of aquaculture – diversity – ecosystem functioning relationships. In
375 line with Strong *et al.* (2015), who proposed a practical monitoring application of BEF relationships
376 for the marine realm, we believe that there would be a benefit to provide surrogate indicators of
377 aquaculture impacts on ecosystem functionality based on a BEF approach.

378

379 ***BEF approach to maintain ecosystem functioning and services***

380 The idea behind using BEF approach in AEI studies relies on the development of predictive tools to
381 assess the impacts of aquaculture on whole ecosystem functioning in areas where bivalve farming is
382 extensively practiced. This is in line with the ecosystem approach to aquaculture (EAA) (Soto *et al.*
383 2008; Aguilar-Manjarrez *et al.* 2010) which states that development and management of this industry
384 should take account of the full range of ecosystem functions and services and should not threaten
385 their sustained delivery to society. Today, standard monitoring of shellfish culture sites is not
386 required in most jurisdictions (e.g. in Europe and Canada), and thus the level of impact and science
387 recommendations are currently only informative. Moreover, “classic” indicators used to evaluate
388 aquaculture impacts (e.g. sulphide levels, species richness) provide information on how benthic
389 sediments are affected, but do not set limits as to what is “acceptable” or “unacceptable” regarding
390 a reference ecosystem state. Moving towards predicting aquaculture impacts in relation to whole
391 ecosystem functioning and service delivery would thus seem of interest for both society and decision

392 makers. Hargrave *et al.* (2008b) proposed a “nomogram” to classify benthic enrichment zones based
393 on different biogeochemical variables. Zones were defined to range from oxic to anoxic with
394 different indicators values and corresponding effects on macrobenthic infaunal biodiversity. Such a
395 unified model would be useful to identify benthic habitat quality as defined for example in the EU
396 Water Framework Directive (EC, 2000). However, whether these empirical relationships are
397 applicable in many ecosystems requires further study since sediment composition (e.g. grain size,
398 silt or sand), for example, greatly influences biogeochemical processes (Martinez-Garcia *et al.*
399 2015). Recently, Brigolin *et al.* (2017) proposed a biogeochemical model to quantify benthic
400 recycling of organic matter under contrasted forcing linked to mussel farms (i.e. POC deposition
401 fluxes). To our knowledge, this is the only study to have estimated the direct effect of mussel
402 biodeposition on biogeochemical processes in sediments. The model suggested that greater
403 mineralization of organic matter with increased oxygen consumption would occur below mussel
404 farms relative to reference sites. Coupled with dose-response experiments, such a modeling approach
405 could contribute to developing a deeper understanding of the global impact of aquaculture on
406 ecosystem functioning and to, for example, attempt to quantify eutrophication in coastal waters.

407 Whereas eutrophication is one of the greatest global threats to the marine environment, the place of
408 aquaculture in the eutrophication process remains unpredictable and debated (Bergström 2014). On
409 the one hand, some studies conclude that filter feeding bivalves can contribute to the net removal of
410 nitrogen from coastal environments through the incorporation into animal tissue and enhanced
411 denitrification in underlying sediments (Edebo *et al.* 2000; Carlsson *et al.* 2012; Smyth *et al.* 2013).
412 These effects have led several authors to suggest that shellfish aquaculture could mitigate
413 eutrophication in coastal waters (Cercó & Noel 2007; Bricker *et al.* 2014; Rose *et al.* 2014).
414 However, enhanced denitrification under aquaculture sites does not always occur (Kellogg *et al.* 2014)

415 and other researchers have expressed concern that this approach could have negligible positive
416 effects or even negative effects (Newell 2004; Pomeroy *et al.* 2006; Fulford *et al.* 2010; Carmichael
417 *et al.* 2012). There is also strong evidence to suggest that bivalve cultivation may have a positive
418 effect on the nutrient pools in the water column due to the constant excretion of inorganic nutrients
419 by the cultivated organisms and nutrient export (instead of denitrification) from the underlying
420 sediments (Christensen *et al.* 2003; Nizzoli *et al.* 2006, 2011; Murphy *et al.* 2016; Erler *et al.* 2017).
421 Overall, there remains ambiguity surrounding the magnitude and direction of N losses in bivalve
422 aquaculture systems due to uncertainty about the different nitrate reduction pathways including
423 denitrification, anammox and dissimilatory nitrate reduction to ammonium.

424

425 **Future research directions**

426 In this review, we wanted to highlight the possibility that a BEF approach may increase our
427 understanding of aquaculture-environment interactions, with an ultimate goal to provide advice for
428 a sustainable development of the industry in accordance with other multiple uses of marine areas,
429 including the conservation of wild species and habitat. The recently developed functional approach
430 represents a great opportunity to deepen our knowledge of the links between modifications of benthic
431 diversity under bivalve farms and the implications for ecosystem processes, as measured through
432 nutrient fluxes or food webs, and more largely on ecosystem service delivery. Such knowledge will
433 serve for future management and policy that consider the adequacy of marine use and service
434 delivery with ecosystem integrity preservation.

435 Through our literature review, we identified several gaps that represent many research opportunities
436 to improve our knowledge of fundamental drivers of sediment processes impacted by a local source

437 of disturbance, such as organic enrichment from biodeposition, in a framework where we consider
438 the impacts of aquaculture on ecosystem functioning and services:

- 439 - Investigating the role of further taxonomic groups (i.e. bacteria and meiofauna) in
440 aquaculture-environment interactions studies whose influence on sediment processes may be
441 of great importance;
- 442 - Simultaneously considering sediment characteristics, biodiversity and ecosystem function
443 indicators to model the influence of biodeposition on the whole ecosystem and improve our
444 understanding of BEF relationships;
- 445 - Developing tools to predict the impact of aquaculture on nutrient budgets as a surrogate of
446 eutrophication level;
- 447 - Developing models linking bivalve biodeposition to benthic biogeochemical processes to
448 prevent excessive organic loading leading to eutrophication;
- 449 - Investigating the effect of aquaculture on the trophic food web as a surrogate of ecosystem
450 functioning;
- 451 - Resolve the influence of aquaculture on the environment across a wide spectrum of
452 aquaculture practices (e.g. intertidal, coastal, offshore), habitats and environmental
453 conditions (e.g. eutrophic, oligotrophic);
- 454 - Identifying potential benthic invertebrates that could act as mitigation tools in sediment
455 impacted by bivalve farms using the BEF framework.

456
457

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