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

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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.

Introduction

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

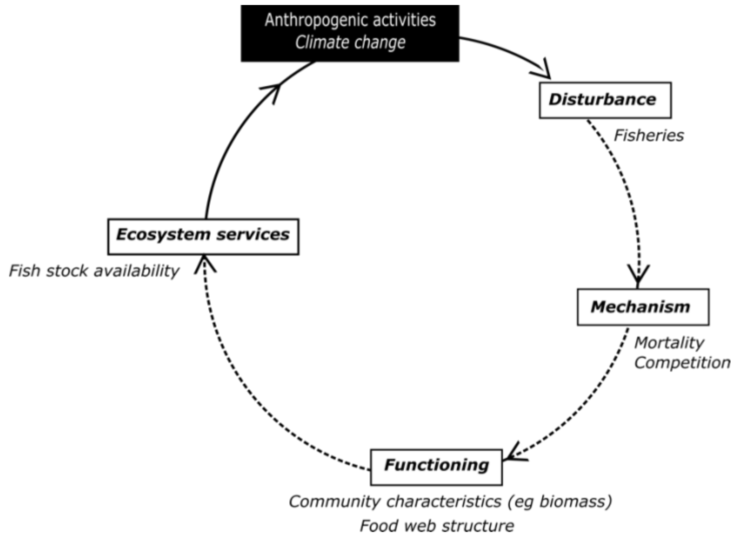

Figure 1. Cycle of ecosystem disturbance using the example of fisheries. Anthropogenic activities create disturbances that modify the underlying mechanisms of ecosystem functioning, thereby affecting ecosystem services that support anthropogenic activities.

Much research over the past few decades has focused on links between altered biodiversity (mainly species loss but also gains in the context of exotic species) and ecosystem functioning (e.g. Hooper *et al.* 2005; Cardinale *et al.* 2012; Harvey *et al.* 2013). Although most research in this field has concentrated on terrestrial systems, the number of manipulative experiments that assess the influence of benthic diversity on ecosystem functioning (BEF relationships) in marine systems has also recently increased rapidly (O'Connor & Crowe 2005; Cardinale 2011; Solan *et al.* 2012; Gamfeldt *et al.* 2014; Séguin *et al.* 2014). These relationships have received much attention as they underpin many ecosystem services (Isbell *et al.* 2011; Balvanera *et al.* 2014; Cardinale *et al.* 2012). It is now generally accepted that higher biodiversity may increase ecosystem function efficiency, e.g. in terms of nutrient cycling (Cardinale *et al.* 2012; Gamfeldt *et al.* 2014; Piot *et al.* 2014), and/or resilience (Oliver *et al.* 2015). Moreover, there is general agreement on the importance of focusing on species-specific traits rather than species richness *per se* to describe links between biodiversity and metrics of ecosystem functioning (e.g. decomposition rates, nutrient uptake) (Mouillot *et al.* 2011; Gagic *et* *al.* 2015; Strong *et al.* 2015; Cernansky 2017).

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

Unlike fish or shrimp farming, bivalve culture is considered to have low ecosystem impacts since animals are dependent on ambient supplies of plankton and organic particles for food (i.e. there is no addition of food to the natural environment). However, bivalve aquaculture accelerates nutrient dynamics due to bivalve excretion and mineralization of sedimented organic-rich bivalve biodeposits, with consequences at farm- and larger spatial scales (Richard *et al.* 2007a; Woods *et al.* 2012; Lacoste & Gaertner-Mazouni 2016). Increased biodeposition to the seafloor is recognized to change benthic community structure at both large and small spatial scales, depending on farm layout and environmental conditions (Hartstein & Rowden 2004; McKindsey *et al.* 2011). The subsequent impacts of those changes on benthic ecosystem functioning (e.g. nutrient cycling, trophic cascading) have only rarely been addressed in the context of aquaculture (but see Heilskov *et al.* 2006; Lacoste *et al.* 2019). Studies have shown that diversity of biofouling communities in the water column may influence ecosystem functioning since it is, in part, responsible for variations in nutrient fluxes at the culture structure – water column interface in different ecosystems (Mazouni *et al.* 2001; Richard *et* *al.* 2006; Jansen *et al.* 2011; Lacoste *et al.* 2014).

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

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

Impacts of bivalve aquaculture on the benthic ecosystem

Bivalve aquaculture affects the environment in different ways, with a variety of near- and far-field cascading effects. Studies on the interactions between culture systems and natural environments are important for analysing and managing the environmental effects of aquaculture and vice versa. Although the following section provides an update of previous reviews (Prins *et al.* 1998; Cranford *et al.* 2003; Newell 2004; Forrest *et al.* 2009, Dumbauld *et al.* 2009; McKindsey *et al.* 2011) it does not present an exhaustive review of the positive or negative impacts of aquaculture on the environment; rather we highlight the complexity of ecosystem responses and the difficulty of finding relevant indicators (see Valenti *et al.* 2018) given the variety and heterogeneity of studied systems. Table 1 synthesizes the main ecosystem properties that are evaluated in aquaculture-environment interactions studies.

Benthic loading impacts sediment characteristics and nutrient exchanges

Part of the material filtered by bivalves is excreted as feces or pseudo-feces, collectively known as biodeposits, in the water column. Biodeposits have a greater sinking velocity than their constituent particles thereby increasing sedimentation rates within suspended bivalve culture sites (Callier *et al.* 2006; Giles *et al.* 2006; Zúñiga *et al.* 2014). Biodeposit production and sedimentation rates vary among species, bivalve sizes and diets, and vary greatly over short time scales (days). Waste dispersal around shellfish farms has been modelled for few systems (Giles *et al.* 2009; Weise *et al.* 2009), and there is an acknowledged need to gather further information on biodeposit production and composition under natural conditions, and the redistribution and integration of biodeposits once they reach the seafloor. Improved predictions also requires a consideration of the communities that live associated with cultured bivalves (including the species living on the structure, on and among bivalve clumps) since they may significantly contribute to benthic organic loading (Lacoste & Gaertner-Mazouni 2015 and references therein). Notwithstanding the above, it is clear that suspended bivalves may greatly increase sedimentation rates under farms relative to that in reference areas. Zúñiga *et al.* (2014) found that sedimentation fluxes under mussel rafts in Spain (86–536 g m^{-2} d^{-1}) was 6-7 folds the rate observed at a reference site, although the highly hydrodynamic environment attenuates the organic carbon arriving at the seafloor. Giles and Pilditch (2006) showed that sedimentation under a mussel farm in New Zealand (240-540 g m^{-2} d^{-1}) was increased by 106 g m^{-2} d^{-1} compared to the reference site. In contrast, Comeau *et al.* (2014) did not observe differences in organic sedimentation rates under experimental mussel rafts compared to neighbouring reference sites in Canada.

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

Accumulation of biodeposits on the seafloor and OM processing may further modify oxygen and nutrient exchanges at the sediment-water interface. Many studies have shown that benthic oxygen consumption is increased under aquaculture structures relative to that outside of farms (Giles & Pilditch 2006; Nizzoli *et al.* 2006; Thouzeau *et al.* 2007) as are benthic ammonium and phosphate releases (Giles *et al.* 2006; Nizzoli *et al.* 2006; Richard *et al.* 2007b; Erler *et al.* 2017) due to the mineralization of accumulated OM. In deep areas or those with strong hydrodynamic conditions, biodeposit dispersion and degradation reduce the amount of organic material that arrives at the seafloor, attenuating expected impacts on benthic biogeochemistry and nutrient fluxes (Gallardi 2014; Lacoste & Gaertner-Mazouni 2016; Lacoste *et al.* 2018a).

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

Benthic community diversity

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

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

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

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

Table 1. Overview of the main impacts of suspended bivalve aquaculture on the benthic ecosystem described in aquaculture-environment interactions studies (not exhaustive). Studies are divided into those that concentrated on 1) only sediment biogeochemistry, 2) benthic communities (macrofauna and meiofauna and/or bacteria), 3) sediment-water 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	Canada	Hatcher *et al.* 1994 Callier *et al.* 2006 Hargrave *et al.* 2008a Cranford *et al.* 2009 Weise *et al.* 2009
			floating bags & table, oysters		Mallet *et al.* 2006
			raft, oysters		Comeau *et al.* 2014
			raft farm, mussels	Spain	Zúñiga *et al.* 2014
Macro-infaunal communities	-	Grain size, sediment OM content	longlines, mussels	Ireland	Chamberlain *et al.* 2001
			oysters & mussels	Australia	Crawford *et al.* 2003
			longlines, mussels	New Zealand	Hartstein and Rowden 2004
			longlines, mussels	Canada	Callier *et al.* 2008 McKindsey *et al.* 2009, 2012
			longlines, mussels	Italy	Fabi *et al.* 2009
			mussels	New Zealand	Wong and O'Shea 2011

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

Ecosystem-wide effects

While benthic conditions are the most thoroughly studied impacts related to marine aquaculture, other risk factors remain less clear. For example, impacts (e.g. vulnerability to disease, genetic, trophic transfers) on populations of mobile macro-organisms, such as crustaceans, have been rarely quantified (see Callier *et al.* 2017 for a review). However, the addition of aquaculture-related physical structure in the environment creates refuges from predation and adverse environmental conditions (Gutierrez *et al.* 2003) and fall-off of cultivated and associated organisms may serve as food sources for wild populations (Miron *et al.* 2002; D'Amours *et al.* 2008) and attract mobile organisms to farms. Several studies have shown that many fishes may be attracted to farm sites as they feed on bivalve-associated organisms (Carbines 1993; Brooks 2000; Gerlotto *et al.* 2001; Cartier & Carpenter 2013) and, in turn, be a food source for other predators (Brehmer *et al.* 2003). In general, a higher density and diversity of wild fish is observed at farms relative to reference areas, suggesting that aquaculture facilities act as fish aggregating devices (Barret *et al.* 2018). The extent to which these animals are attracted to the structure itself (e.g. as a refuge from predators) or to the prey associated with the structure is unclear (Würsig & Gailey 2002) and is likely species-specific. For example, Drouin *et al.* (2015) showed that lobster *Homarus americanus* is more attracted by the shelter created by mussel farming anchors whereas winter flounder *Pseudopleuronectes americanus* seems to benefit from a trophic effect induced by the farm.

Conversely, aquaculture may also repulse some organisms by displacing their habitat or due to disturbances created by husbandry activities. For example, Becker *et al.* (2011) suggested that three decades of shellfish aquaculture have displaced breeding and pupping harbour seals. Kelly *et al.* (1996) also showed that some birds avoid areas used for shellfish aquaculture, resulting in a net decrease of overall shorebird use of open tidal flats that have been used for aquaculture.

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

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

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

The main influences of bivalve culture on the sea floor were highlighted in the previous section. Most studies on aquaculture-environment interactions to date have assessed a single or limited number of potential effects (e.g. modification of macrofaunal diversity and sulfides) whereby links between disturbances and functioning are only addressed superficially (Table 1). Although some studies have measured benthic diversity and benthic fluxes simultaneously, few have explored the functional role of species in nutrient dynamics. We here propose a more holistic approach for studying aquaculture-environment interactions based on the BEF framework. The main concepts of this approach are represented in Fig. 2.

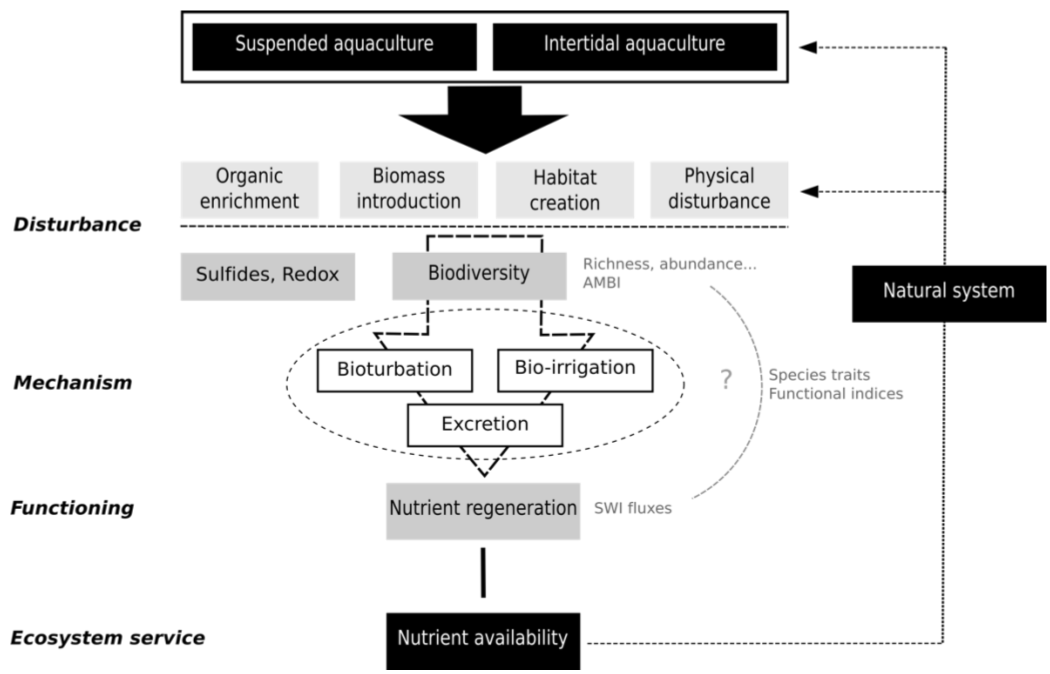

Figure 2. BEF approach to the bivalve aquaculture-environment interactions for benthic systems with a focus on nutrient availability as an example of ecosystem service. The main idea is to explore the mechanisms at the origin of ecosystem functioning to better predict the impacts of disturbances due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

Status of knowledge and limitations in marine systems

Following initial studies on terrestrial ecosystem functioning (Gamfeldt *et al.* 2014), the number of manipulative experiments to assess BEF relationships in marine systems has rapidly increased (Cardinale 2011; Solan *et al.* 2012). Several studies focusing specifically on sediment processes have shed light on the major role of benthic organisms on organic transfers in coastal ecosystems (Cloern 1982; Chauvaud *et al.* 2000; Grall & Chauvaud 2002). Sediment communities drive many critical ecosystem functions, in particular nitrogen recycling, which is usually the driver of eutrophication processes. In shallow environments, inorganic nitrogen regeneration in sediments can provide between 20% and 100% of the annual requirement for primary production (Welsh 2003) and thus understanding the mechanisms that drive this cycling is a key to understanding coastal productivity. Laboratory and field studies have shown the significant effect of macrofauna on ecosystem processes through sediment particle reworking (bioturbation), solute transfers in sediments (bio-irrigation), and impacts on microbial processes, each of which alter the flow of energy and matter (Solan *et al.* 2004; O'Connor & Crowe 2005; Ieno *et al.* 2006; Waldbusser & Marinelli 2006). A large body of scientific work has clearly shown how burrowers import O_2 into their burrows and enhance microbial aerobic activity via intermittent ventilation (Kristensen 1988, 2000; Glud 2008). Nevertheless, many of these studies are laboratory experiments using a single macrofaunal species (but see Kristensen *et al.* 2014; Belley & Snelgrove 2016; Politi *et al.* 2019). Such simple communities do not consider ecological interactions present among organisms such as predation, competition or facilitation which may greatly influence processes, including nutrient regeneration. Thus, although the roles of macrofauna (via bioturbation and bio-irrigation) may be well-identified, more integrated approaches require further knowledge, in particular concerning the roles of other biological compartments, such as meiofauna and bacteria. In particular, there is a recent and growing interest to study the role of meiofauna, since it has been shown that these organisms may modulate the biological interactions within sediments (Bonaglia *et al.* 2014; Lacoste *et al.* 2018b) and play a significant role in benthic ecosystem processes and services (Schratzberger & Ingels 2017). Until now, the paucity of information on this group likely reflects the labour-intensive nature of obtaining such data, which is particularly demanding both in terms of field work and species identification. New tools (e.g.

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

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

While the functional approach is becoming a major concept in ecology and ecosystem management, there are several gaps that cause uncertainty in ecological interpretations and limit comparisons across studies. A main challenge is the limited availability of biological and ecological traits for marine species, although some databases of traits are now available (Faulwetter *et al.* 2014). Although there are multiple methods to measure functional diversity (Villéger *et al.* 2008; Laliberté & Legendre 2010; Mouchet *et al.* 2010), to date, there is no standard accepted methodology to select the most appropriate traits to compute the different indices (Marchini *et al.* 2008). Thus, until a unified framework is adopted, the choice of the number of functional traits is partly based on subjective rationale (Hortal *et al.* 2015; de Bello *et al.* 2017).

BEF approach to study aquaculture-environment interactions

Wild sessile populations, particularly infauna, are commonly used as indicators of farm environmental performance as these organisms integrate effects on benthic sediments. Changes in community structure brought about by bivalve farming activities may also be expected to affect sediment oxygen and nitrogen dynamics. To date, field experiments have tested the responses of macro-faunal communities whereas others have measured effects on ecosystem functions including nutrient fluxes; few studies have examined the two and assessed the feedback of macrofauna on fluxes in response to organic enrichment in bivalve aquaculture (Table 1). Lacoste *et al.* (2019) showed that benthic responses (measured as SWI nutrient fluxes) may not be linearly related to organic enrichment (mussel biodeposits), likely due to varying responses of infaunal organisms with different functional roles. Some species that benefit from intermediate organic enrichment may have a positive effect on nutrient release to the water column whereas, at higher levels of enrichment, large bio-irrigating species (*Cistenides gouldii*) may be lost with a net negative effect on mineralization. Similar results have been observed around fish farms where mineralization rates were highly correlated with the presence of the large and active irrigating climax species *Hediste diversicolor* and *Limecola balthica* (Heilskov *et al.* 2006). It is not straightforward to infer immediate effects of organic enrichment on nutrient regeneration and cascading effects on whole ecosystem nutrient dynamics because of the idiosyncratic role of species and the importance of sediment characteristics. Nonetheless, the exercise seems important given the myriad uses of coastal areas and the potential impacts that aquaculture may have on the functioning these ecosystems. Empirical studies are needed to advance theoretical and methodological knowledge to further understand these relationships. Thus, dose-response studies are an interesting approach to evaluate thresholds at which changes in community diversity may alter ecosystem functioning. The contrasting benthic conditions created by aquaculture along gradients may also represent an excellent opportunity to empirically evaluate the effects of diversity modifications on benthic fluxes under field conditions. Although some studies have addressed this point with experimental (Callier *et al.* 2009; Robert *et al.* 2013; Lacoste *et al.* 2019) and natural (Dimitriadis & Koutsoubas 2011) gradients of organic enrichment for bivalve and fish farm systems, further investigations are required that simultaneously consider changes of benthic functional diversity and consequences for ecosystem functioning.

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

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

BEF approach to maintain ecosystem functioning and services

The idea behind using BEF approach in AEI studies relies on the development of predictive tools to assess the impacts of aquaculture on whole ecosystem functioning in areas where bivalve farming is extensively practiced. This is in line with the ecosystem approach to aquaculture (EAA) (Soto *et al.* 2008; Aguilar-Manjarrez *et al.* 2010) which states that development and management of this industry should take account of the full range of ecosystem functions and services and should not threaten their sustained delivery to society. Today, standard monitoring of shellfish culture sites is not required in most jurisdictions (e.g. in Europe and Canada), and thus the level of impact and science recommendations are currently only informative. Moreover, “classic” indicators used to evaluate aquaculture impacts (e.g. sulphide levels, species richness) provide information on how benthic sediments are affected, but do not set limits as to what is “acceptable” or “unacceptable” regarding a reference ecosystem state. Moving towards predicting aquaculture impacts in relation to whole ecosystem functioning and service delivery would thus seem of interest for both society and decision makers. Hargrave *et al.* (2008b) proposed a "nomogram" to classify benthic enrichment zones based on different biogeochemical variables. Zones were defined to range from oxic to anoxic with different indicators values and corresponding effects on macrobenthic infaunal biodiversity. Such a unified model would be useful to identify benthic habitat quality as defined for example in the EU Water Framework Directive (EC, 2000). However, whether these empirical relationships are applicable in many ecosystems requires further study since sediment composition (e.g. grain size, silt or sand), for example, greatly influences biogeochemical processes (Martinez-Garcia *et al.* 2015). Recently, Brigolin *et al.* (2017) proposed a biogeochemical model to quantify benthic recycling of organic matter under contrasted forcing linked to mussel farms (i.e. POC deposition fluxes). To our knowledge, this is the only study to have estimated the direct effect of mussel biodeposition on biogeochemical processes in sediments. The model suggested that greater mineralization of organic matter with increased oxygen consumption would occur below mussel farms relative to reference sites. Coupled with dose-response experiments, such a modeling approach could contribute to developing a deeper understanding of the global impact of aquaculture on ecosystem functioning and to, for example, attempt to quantify eutrophication in coastal waters.

Whereas eutrophication is one of the greatest global threats to the marine environment, the place of aquaculture in the eutrophication process remains unpredictable and debated (Bergström 2014). On the one hand, some studies conclude that filter feeding bivalves can contribute to the net removal of nitrogen from coastal environments through the incorporation into animal tissue and enhanced denitrification in underlying sediments (Edebo *et al.* 2000; Carlsson *et al.* 2012; Smyth *et al.* 2013). These effects have led several authors to suggest that shellfish aquaculture could mitigate eutrophication in coastal waters (Cerco & Noel 2007; Bricker *et al.* 2014; Rose *et al.* 2014). However, enhanced denitrification under aquaculture sites does not always occur (Kellog *et al.* 2014) and other researchers have expressed concern that this approach could have negligible positive effects or even negative effects (Newell 2004; Pomeroy *et al.* 2006; Fulford *et al.* 2010; Carmichael *et al.* 2012). There is also strong evidence to suggest that bivalve cultivation may have a positive effect on the nutrient pools in the water column due to the constant excretion of inorganic nutrients by the cultivated organisms and nutrient export (instead of denitrification) from the underlying sediments (Christensen *et al.* 2003; Nizzoli *et al.* 2006, 2011; Murphy *et al.* 2016; Erler *et al.* 2017). Overall, there remains ambiguity surrounding the magnitude and direction of N losses in bivalve aquaculture systems due to uncertainty about the different nitrate reduction pathways including denitrification, anammox and dissimilatory nitrate reduction to ammonium.

Future research directions

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

Through our literature review, we identified several gaps that represent many research opportunities to improve our knowledge of fundamental drivers of sediment processes impacted by a local source of disturbance, such as organic enrichment from biodeposition, in a framework where we consider the impacts of aquaculture on ecosystem functioning and services:

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

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