

Influence of suspended and off-bottom mussel culture on the sea bottom and benthic habitats: a review¹

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Abstract:

Influence of this activity on the environment. We take a holistic approach to review off-bottom and suspended mussel culture effects on the benthic environment and benthic communities. Both longline and "bouchot" mussel culture add much physical structure (infrastructure and mussels) to the environment, altering hydrosedimentary processes by modifying currents and increasing sedimentation locally, and providing habitat for many benthic organisms. Biodeposition from mussels and these organisms increases benthic organic loading and linked biogeochemical processes to influence O₂, pH, redox potentials, dissolved sulphides, and other sediment parameters, benthic respiration and nutrient fluxes, and benthic infaunal communities. Mussel culture may also influence seagrasses and algae, although this has not been well-studied. Far-field effects on the benthos may occur through a number of mechanisms, including aggregation of epibenthic macrofauna in culture sites, alteration of plankton communities, and the enhancement of exotic and indigenous pest species owing to the addition of physical structure to the environment. Quantitative relationships between farming level and benthic influences are lacking, making predictions of effects difficult.

Résumé :

L'aquaculture est le secteur de l'industrie alimentaire dont la croissance est la plus rapide. Dans un contexte de développement durable, l'influence de cette activité sur l'environnement doit être quantifiée. Nous présentons une synthèse des travaux concernant les impacts de la mytiliculture au-dessus du substrat et en suspension sur les communautés benthiques et leur biotope. La mytiliculture (filières ou bouchots) introduit dans le milieu des structures physiques—structures d'élevage et moules—qui altèrent la dynamique hydrosédimentaire (modification des courants, augmentation locale des taux de sédimentation) et génèrent des habitats favorables à de nombreux organismes benthiques. Les biodépôts rejetés par les moules et les organismes associés accroissent l'eutrophisation et les processus biogéochimiques, modifiant la demande en O₂, le pH, les potentiels redox, les concentrations en sulfures dissous, les flux de CO₂ et de nutriments à l'interface eau-sédiment, ainsi que les assemblages endofauniques. La mytiliculture peut aussi modifier la dynamique des herbiers et des macroalgues, cependant ces effets restent peu documentés. À plus large échelle, les effets sur le benthos sont liés notamment aux concentrations des épibiontes macrobenthiques dans les concessions, aux changements locaux des communautés planctoniques et à la prolifération d'espèces invasives ou autres espèces nuisibles à cause de l'addition de structures physiques dans le milieu. Les relations quantitatives associant les caractéristiques des fermes mytilicoles et leurs impacts sur le compartiment benthique sont encore peu connues ce qui rend difficile toute prévision des conséquences potentielles sur l'environnement.

1. Introduction

Aquaculture is the fastest growing sector of the food industry, increasing at a rate of about 7% per year since the 1970s and accounting for 43% of the total annual fisheries production of 160 million tonnes in 2008. Projections suggest that this production will increase greatly in the future (FAO Fisheries and Aquaculture Department 2010). This increased production has raised concerns about the impacts of the activity on local environments (e.g., Black 2001) and there has been much work towards understanding the role of aquaculture in the ecosystem (e.g., Davenport et al. 2003; Holmer et al. 2008). Although concerns were initially largely directed at the influence of finfish cage culture on the environment, concerns have also been raised about the influence of farming bivalves. With respect to the aquaculture-environment interactions related to farmed bivalves, the greatest concerns relate to enhanced localized biodeposition (Mattsson and Lindén 1983), filtration of the water column (Troost et al. 2009), alteration of nutrient and oxygen exchanges (Richard et al. 2007*b*), the transfer of disease and hitchhiking species (McKindsey et al. 2007), and wider ecological effects, including the creation of novel habitat (Forrest et al. 2009).

Of the 20.5 million tonnes of molluscs produced worldwide annually, about 11.5 million tonnes is of bivalves from aquaculture production. This includes greater than 4 million tonnes each of both clams and oysters and about 1.5 million tonnes each of scallops and mussels (Figure 1). Notwithstanding this breakdown in production data, the majority of research on the interactions between farmed bivalves and the environment has concentrated on mussels and, to a lesser extent, oysters. This may reflect the fact that production of all groups of bivalves, with the exception of mussels, is at least an order of magnitude greater in Asian countries, where aquaculture has been a culturally accepted part of the coastal environment for centuries (Costa-Pierce et al. 2005), than in western ones, where the bulk of research on aquaculture-environment interactions has been done.

Recent reviews have examined the interactions between clam and oyster aquaculture and the environment (Dumbauld et al. 2009; Forrest et al. 2009), but there has been no recent review of the influence of mussel culture on the environment. The influence of mussel culture on plankton communities due to filtration and with respect to disease and hitchhiking species is likely quite similar to that of other types of bivalve culture. In contrast, given the differences in culture methods used for different types of bivalves (e.g., infaunal clams grown in sediments, oysters or mussels grown on the bottom, off-bottom tray culture of oysters, and suspended or off-bottom culture of mussels), it is likely that the influence of suspended or off-bottom mussel culture on the benthic environment differs somewhat from that of other types of bivalve culture.

Increasingly, regulators in western countries are relying on a variety of benthic indicators to evaluate the influence of aquaculture installations on the environment (Borja et al. 2009). Similarly, a variety of groups have promoted the use of benthic indicators as a means to ensure the sustainability of aquaculture operations by encouraging their operators to manage farms to maintain a certain benthic condition.

Given the above, in this review we present a synthesis of the scientific information available on the influence of suspended and off-bottom mussel aquaculture on the

benthic environment and “benthic” communities. We concentrate on direct and indirect effects resulting from the physical structure added to the environment for mussel culture and from enrichment due to biodeposition by farmed mussels and associated organisms. Other issues discussed include far-field effects and knowledge gaps that need to be addressed to understand better the influence of mussel culture on the benthic environment and benthic communities. We have restricted discussion to off-bottom and suspended mussel culture as we believe that other species and culture types have been well-enough addressed in recent reviews and because we believe that a more concise review will be more valuable to managers and regulators. When pertinent information is only available from the non-mussel aquaculture studies, this is included where appropriate.

2. Overview of mussel culture methods and physical structure

Mussel aquaculture around the world is practiced using two main approaches: bottom culture, accounting for approximately 15% of overall production, and suspended and off-bottom culture, accounting for about 85%. Although bottom culture is used in the US, it is mainly practiced in Europe, particularly in the Netherlands, Germany, Ireland and the UK. In short, the technique consists of transferring juvenile mussels from natural, high density beds, to sheltered beds where the stocking density is managed to improve productivity and market value (Spencer 2002). This review does not consider the method further.

Small mussels (spat) used for off-bottom and suspended farming are obtained from various sources, ranging from hatchery-raised individuals, to mussels caught from the natural environment from wild stock using collectors placed in the environment to this end, to harvesting spat from natural sources such as from rocky coasts or algae. Spat is then added to grow-out structures such as rope or mesh socking material for continuous or dropper lines or wooden *bouchots*. Spat are often maintained in place for some period using a natural material that will degrade over time, providing the mussels time to affix themselves to grow-out structures by their byssal threads. Depending on the location, mussels may also be sorted thereafter and resocked or otherwise manipulated (e.g., to remove fouling organisms) prior to the final harvest for market.

Suspended and off-bottom culture is done using three main approaches. In Spain, Scotland and South Africa, mussel culture is mainly done using rafts (Boyd and Heasman 1998; Okumus and Stirling 1998; Fuentes et al. 2000). This culture technique involves suspending mussels attached on ropes or in socks, typically 8-10 m in length, from moored rafts. The second method, the use of *bouchots*, was developed in and is currently restricted to France (Garen et al. 2004). This technique involves the uses of poles or stakes (*bouchots*) driven into the sea bottom in low intertidal zones in areas with macrotidal regimes, such as the English Channel. The third type of suspended culture is the longline system, which is used in a wide variety of environments, from the open sea to enclosed areas. It consists of a series of backlines, single or paired, anchored at both ends and floated in the water by buoys. In some cases, the position of the backline in the water column is controlled by the addition of a series of ropes (legs) attached at regular intervals along the length of the line with block anchors at the opposite ends that sit on the sea bottom. The number of legs is varied through the year and their length adjusted to maintain the growing bivalves at the appropriate level in the water column to maximize

growth and minimize impacts from fouling, ice, etc. Mussels are grown on lines or socks hung singly from backlines (dropper lines) or along continuous lines that are looped along under the backlines.

Considerable physical structure may be added in suspended and off-bottom mussel culture. In longline systems, this includes the backlines, legs and block anchors, buoys, and droppers or continuous lines used to grow mussels. For raft systems, there is the raft structure and the infrastructure that support the product being grown. As an example, consider the situation in Tracadie Bay, Prince Edward Island, eastern Canada. Assuming that mussel leases cover roughly half of the surface area of the bay, ca. 7 km² (Cranford et al. 2007), that mussel long lines are spaced at ca. 12.5 m intervals within the sites (Drapeau et al. 2006), and that half of this area is being farmed and using blocks at any one time (a conservative estimate), a back of the envelope calculation assuming a block spacing of 5 m suggests that there may be almost 60 thousand block anchors on the bottom of the bay at any one time. Assuming that the associated legs are ca. 2.5 m long, this suggests that there is ca. 150 km of rope used for legs in the bay. Given that there is at least 1 buoy for each anchor block (often more), there are also at least as many buoys as anchor blocks at each site. Unlike blocks and buoys, which are added and removed throughout the farming process, backlines are typically left in place. This suggests that there are also over 500 km of rope used as backlines in the bay. Assuming again that half of the leased area contains mussels at any time and that individual mussel dropper lines are spaced at ca. 40 cm intervals and each is ca. 1.8 m long (Drapeau et al. 2006), a similar calculation suggests that there are ca. 2250 km of socking material (and product) in the bay. Socking material varies among sites and with farming methods, with dropper socks typically being made of polypropylene mesh or rope and various types of materials being used for spat collection. Raft systems, although quite compressed in space, typically have much greater density of product and infrastructure and may thus also represent considerable physical structure in the water column. For the *bouchot* system, the physical structure is limited to the *bouchots*. In general (see Ottman and Sornin 1985), individual *bouchots* are ca. 4 to 6 m high and are sunk half way in the sediment. Individual *bouchots* are installed in single or twinned rows, each some 50 to 100 m long with individual *bouchots* spaced to give 110 to 130 *bouchots* per 100 m and, if twinned, rows of *bouchots* are separated by ca. 2 m. Rows are separated by 10 to 30 m and farms often cover 20 hectares or more in low intertidal hydrodynamically energetic areas. In addition to the inert physical structure used in all types of suspended and off-bottom mussel culture, there is also the product itself which acts as a surface for various physical and biological processes.

These structures modify current regimes which may influence various ecosystem processes. The structures are also colonized by a large suite of hard-bottom associated species that may otherwise not find suitable habitat in a given area (e.g., muddy bottoms or water column). These organisms form communities that are functionally similar to benthic communities and are thus considered in this review as part of the "benthic" community (see off-bottom macrofauna). These too have a variety of direct and cascading effects on the surrounding ecosystem.

3. Physical structure effects

3.1. Hydrosedimentary modification

Suspended mussel culture is known to influence and be influenced by hydrodynamic circulation at a wide range of spatial scales. Mussel culture systems present a porous barrier and are hierarchical, with individual bivalves and their associated fouling organisms nested within culture units (e.g., socks,), these being nested within culture gear (longlines or rafts), which are nested within farms, and so on (Plew et al. 2005; Stevens et al. 2008; Fréchette 2010). An understanding of processes operating at each scale, as well as the relations between these scales, is needed to predict how hydrodynamics influence the settlement and recruitment of organisms within culture systems and to understand cascading effects on the ecosystem.

At the farm level, a number of studies have shown that suspended mussel culture infrastructure may alter hydrodynamics and reduce flow rates in both raft (Pérez Camacho and Beiras 1995; Blanco et al. 1996; Boyd and Heasman 1998; Riethmüller et al. 2006a, 2006b; Herman 2007; Duarte et al. 2008; Petersen et al. 2008) and longline (Gibbs et al. 1991; Plew et al. 2005; Strohmeier et al. 2005; Strohmeier et al. 2008) systems. Further studies have shown that dropper line diameter (Plew et al. 2005) and dropper line and larger-scale spacing (i.e., long-line and raft) as well as farm size and configuration may influence current velocities (Boyd and Heasman 1998; Smith et al. 2006; Aure et al. 2007; Duarte et al. 2008; Stevens et al. 2008). At a bay scale, work on oyster longline systems by Makita and Saeki (2004) has shown that although culture structures increase retention time within farm sites, they do not reduce inflow and outflow volumes. Rather, they influence the relative exchange rates of different areas within an embayment, creating areas that are much better flushed than others. In contrast, Lo et al. (2008) suggest that flushing times for an entire bay in Taiwan were greatly altered by the presence of aquaculture structures (mostly suspended oyster culture but also some fish culture), such that flushing rates that were normally 3-7 days increased to 5-13 days when culture structures were present. Increased retention and reduced flow rates modify deposition regimes within farms and thus influence communities on the seafloor. It has also been suggested that shell deposits on the bottom due to fall-off may slow flow across the sediments, increasing sedimentation rates (de Jong 1994; Lloyd 2003). Anchor blocks may have similar effects, although their presence may also produce localized scouring and alter bottom sediments as has been shown for natural and artificial blocks (Cusson and Bourget 1997; Guichard et al. 2001).

Ottman and Sornin (1981) suggest a number of mechanisms by which *bouchots* may modify sediments within and surrounding culture sites, which have been long known to increase sedimentation and the proportion of fine sediments in culture sites (Marteil 1979). During ebb tide, currents are reduced by 25 to 50 % due to increased drag due to *bouchots* in culture sites (Sornin 1979, cited in Ottman and Sornin 1985) and Sornin (1981) suggests that currents may be reduced by a factor of 3 in *bouchot* sites. Reduced currents may increase sedimentation, although some sediment may be resuspended during the following flood tide. *Bouchots* may also dampen wave energy within sites by up to 50 %, further increasing sedimentation (Nikodic 1981). In fact, a recent study modeling wave action and sediment transport (Allard et al. 2008) assumed that the friction coefficient due to *bouchots* was ten times that due to open sandy areas. At a fine scale, Sornin (1981) suggests that scouring occurs around the base of *bouchots*, an

observation also made by Grant (2010). Turbulence due to *bouchots* also mixes otherwise stratified waters and currents are oriented in the direction of the bouchot rows. Furthermore, 30 cm diameter *bouchots* may grow to ca. 70 cm in diameter as mussels grow (Cayocca et al. 2008), further influencing the impact of the site on bottom sediments through physical processes alone. In a study of 3 *bouchot* farms and 3 reference sites, Grant (2010) found that *bouchots* sites were, on average, characterized by finer sediments than reference sites but that the former showed progressive size sorting toward *bouchots* such that sediments adjacent to them were coarser than those between them. This was also reflected by more pronounced sediment sorting and skewness in farm sites relative to that observed in reference sites.

3.2. Habitat modification/creation

3.2.1. off-bottom macrofauna effects

Bivalves growing in suspended culture create favourable habitats for other invertebrates by providing refuges from predation and adverse environmental conditions (Gutiérrez et al. 2003) and a direct source of food for other invertebrates. Indeed, fouling associated with suspended bivalve culture is a universal concern for the industry (Enright 1993; Dürr and Watson 2010). According to Heasman (1996), the main fouling taxa include macroalgae, barnacles, hydroids, tunicate ascidians, and mussel spat although other taxa, such as calcareous tube building polychaetes, may be locally important. Many studies have reported diverse assemblages of algae, invertebrates and fishes associated with suspended bivalve culture (e.g., Tenore and González 1976; Khalaman 2001a, 2001b; LeBlanc et al. 2003b; Murray et al. 2007). Macroalgae have been reported to grow associated with longline mussel culture in Nova Scotia (Lawrence et al. 2000), in Tasmania (Crawford et al. 2003), and Russia (Khalaman 2001a). At times, the biomass and diversity of the associated organisms may be considerable. For example, Lutz-Collins (2009a, 2009b) found ca. 30 species and up to ca. 600 individual polychaetes and ca. 800 tunicates 30 cm^{-1} of mussel socks in Prince Edward Island, eastern Canada, and Tenore and González (1976) reported over 100 species on mature mussel socks in Spanish raft mussel culture and up to 430 g dw of fouling organisms (mostly holothurians) m^{-1} mussel sock. Fouling by some species, especially exotic tunicates, may contribute even greater biomass to the suspended culture infrastructure. For example, Grant et al. (1998) report a mean biomass of ca. 1350 g of *Ciona intestinalis* m^{-1} mussel ropes from South Africa mussel rafts and McKindsey et al. (2009) and Ramsay et al. (2008) report mean biomasses of the same species of ca. and 360 g and generally $> 1000\text{ g m}^{-1}$, respectively, from experimental mussel lines in Prince Edward Island.

In addition to being implicated in the introduction of a great proportion of exotic species in coastal waters around the world (Carlton 1992; Ruiz and Carlton 2003), many studies have shown that suspended bivalve culture sites act as a focus for a large number of invasive species, including tunicate ascidians, algae, molluscs, etc. The great quantity of artificial and biological (i.e., bivalves) structure in suspended bivalve culture is relatively free from benthic predators and may act to perpetuate infestations once they are established (see review in McKindsey et al. 2007). Risk assessments by Crawford (2003) and Forrest et al. (2009) suggest that the potential for spreading pest species with aquaculture transfers constitutes the greatest environmental risk associated with bivalve farming.

A number of studies have shown suspended bivalve culture sites to increase the abundance of a variety of fish and vagile macroinvertebrates. Although this may be because the physical structure of suspended bivalve culture sites attracts fish and other large taxa – that the structures act as “fish aggregation devices” (Rountree 1989; Nelson 2003), it seems more likely that this is a cascading effect from the presence of the diverse assemblages associated with suspended bivalve culture sites.

Organisms growing on or otherwise associated with bivalves grown in suspension culture may also provide habitat for or otherwise attract other organisms, including algae, invertebrates, fish, and more mobile macroinvertebrates. For example, a number of studies have shown that various species of toxic phytoplankton may grow associated with algae growing on farmed mussels in eastern Canada (e.g., Lawrence et al. 2000; Levasseur et al. 2003). Recently, Robichaud (2008) observed that a greater abundance of invertebrates is associated with mussel socks fouled with *Styela clava* than socks that are not fouled by this structure-providing species in Prince Edward Island. Similarly, in Russia, Khalaman (2001*b*) showed that macroinvertebrate communities associated with farmed mussels with large abundances of the ascidian *Styela rustica* had a greater average species richness than did macroinvertebrate communities associated with farmed mussels with fewer *S. rustica*.

The organisms associated with suspended mussel culture may provide benefits for fishes. For example, Brooks (2000) suggests that the epifauna associated with mussel rafts in Washington may support greater than 11 times the biomass of prey for commercial fish species than does the underlying benthos. Carbines (1993) found a positive correlation between algal cover and the number of young spotties (*Notolabrus celidotus*) on mussel lines and noted that fish were also associated with encrusting invertebrates and algae on mooring ropes in New Zealand mussel farms. The study also used a manipulative experiment to show the functional relationship between algal cover and fish abundance. More recent studies done on mussel farms in New Zealand found a variety of demersal fish species associated with mussel lines; although some pelagic species were also present, they did not make regular use of the farms (Morrisey et al. 2006). In Washington, Brooks (2000) suggests that mussel rafts attract schools of shiner perch (*Cymatogaster aggregata*) that feed on the mussel line-associated community. Brehmer et al. (2003) examined the distribution of fish and fish schools in a French Mediterranean longline mussel growing area and found a greater number of fish schools within mussel culture sites than outside of the sites. However, fish schools within the mussel sites were smaller than those found outside. Gerlotto et al. (2001) report that the abundance of fish, particularly *Sparus auratus*, increased following the introduction of suspended mussel culture in the same area and attribute this to increased prey availability at the farm site as benthivorous fish were observed feeding on mussels in the mussel site. In all of these studies, it is unknown whether the effect of fish aggregation is due to the fish being attracted by the added vertical structure, the farmed product, or the associated organisms.

3.2.2. epibenthic macrofauna effects

The addition of physical structure (anchor blocks) to the benthic environment will directly alter benthic communities under blocks and some benthic species (mobile and sessile) associated with the provision of hard substrate. Although there is limited information on the importance of physical structure associated with suspended bivalve aquaculture on

the seafloor, there is considerable information on the importance of artificial structures used as reefs to enhance specific areas for fisheries species (Jensen et al. 2000; Seaman 2000; Brickhill et al. 2005) and much can be extrapolated from the relevant artificial reef literature.

Anchor blocks used for suspended mussel aquaculture may directly affect a variety of organisms. The most direct effect is the crushing/smothering of benthic organisms under blocks. However, other types of communities may develop under the blocks, as has been shown in natural boulder fields (Cruz Motta et al. 2003). Increased abundance of epibenthic macrofauna in mussel culture sites (see Table 1 for overview) may be due to either the provision of structure (anchor blocks), to food or other types of organisms from fall-off from culture structures, or modification of benthic conditions. Although in most cases the provision of food may be the likely mechanism (see further), a manipulative study showed that the abundance of lobsters at one site in eastern Canada was due to the presence of anchor blocks and not to mussel fall-off (C. McKindsey, unpublished data).

Bottom structures also provide considerable surface area for sessile and other hard-substrate associated organisms (plant and animal) that are not normally found on soft sediment bottoms, which are often encountered in coastal areas where bivalve aquaculture is practiced. Thus, diverse fouling communities may develop on these structures (Carbines 1993; personal observations). In general, hard-bottom communities are generally more diverse, have a greater biomass (Ricciardi and Bourget 1999) and are more productive (Cusson and Bourget 2005; Cowles et al. 2009) than soft-bottom ones. Given this and the greater surface area of blocks added for aquaculture relative to the area of seafloor occupied by the blocks, it is likely that they will, overall, increase local diversity and productivity.

Fall-off of mussels and associated organisms from culture structures creates benthic structure. In some cases, fall-off may be considerable and dramatically alter benthic communities from soft-bottom ones to hard-bottom mussel reef-type communities. For example, Leonard (2004) showed that an average of 130 g m⁻² of mussels (not including broken or empty shells in traps) fell daily to the bottom under mussel lines in eastern Canada. In New Zealand, Kaspar et al. (1985) reported the build-up of live mussels and shell material under a mussel farm and Inglis and Gust (2003) found that living mussels and mussel shells covered 55% of the bottom within farm sites, but were absent from non-farm sites, thus substantially increasing the physical structure within farm sites. Also in New Zealand, de Jong (1994) reports that clumps of mussels up to 20-30 cm thick covered 38 % of the seafloor beneath mussel lines, reaching a density of 250 m⁻², and were the most noticeable visual impact of mussel farms. Although not quantified, Iglesias (1981) and Freire and González-Gurriarán (1995) also noted an abundance of mussels, shell and shell fragments below mussel rafts in the Ría de Arosa, Spain.

The physical structure provided by the mussels and associated organisms that fall from suspended bivalve operations provides a habitat for species normally associated with hard-bottom communities, thus often increasing local benthic diversity and related parameters. A number of studies on this are summarized in Table 1. As for block anchors used in culture operations (see above) the physical structure from fall-off may indirectly increase local benthic diversity and productivity. For example, Kaspar et al. (1985) found that mussel culture fall off-related structure allowed for the development of a community with tunicates, calcareous polychaetes, and sponges – species normally

associated with hard-bottom reefs. More recently, tunicates have been observed to form dense populations directly under fouled longlines in Prince Edward Island (A. Ramsay, personal communications). Kaspar et al. (1985) also discuss the importance of how such a changed habitat is important for providing food to a variety of pelagic and epibenthic predators and a number of studies have shown evidence to support this. For example, Iglesias (1981) typically found a greater number, biomass, and diversity of fishes in mussel raft sites than in control sites and attributed this to increased habitat heterogeneity due to drop-off. Chesney and Iglesias (1979) found the same trend for fish community richness, diversity and biomass, although there were temporal variations in these trends in both studies.

Bivalves and their associated fauna that drop from suspended culture operations also enhance the amount of food available to benthic predators and scavengers. Many studies have reported increased numbers and/or biomass of benthic predators within mussel farm sites, relative to control sites, that likely prey on bivalves or other organisms from suspended culture (see summary in Table 1). These include starfish (Saranchova and Kulakovskii 1982), crabs (Miron et al. 2002), and benthivorous fishes (Gerlotto et al. 2001). D'Amours et al. (2008) reported increased abundances of a number of fish and macroinvertebrate species within 4 suspended mussel farms in Prince Edward Island. Although some of these species, such as lobster, were likely more abundant because of the added physical structure on the bottom, others were probably more abundant because of mussel and associated species falling from the mussel lines. Clynick et al. (2008) evaluated the abundance of several fish and macroinvertebrate species at 2 suspended mussel farms in the Magdalen Islands, eastern Canada, and found variable results; some species were more abundant in farms at some times whereas others were not. Romero et al. (1982) studied the spatial distribution of crabs relative to the location of mussel culture sites in the Ría de Arosa, Spain, over 4 seasons and found that the abundance and biomass of the 3 dominant crab species (accounting for 99% of the total crab abundance and biomass) in farm sites was, on average, greater than twice that observed in control sites. A subsequent study done in the same area showed that the diet of one of these crabs switches from mostly algae in a control site to mostly mussels in a mussel culture site (Freire et al. 1990). Similarly, Freire and González-Gurriarán (1995) studied the ecology of a second crab species and found that it too increased the proportion of mussels in its diet within mussel farms. This effect is not limited to crabs. Olaso Toca (1979, 1982) studied the distribution of echinoderms in the same ría and observed 10 times the biomass of echinoderms (mostly starfish and sea cucumbers) within mussel sites relative to control locations, the starfish feeding on the mussels that had fallen from the rafts overhead and the sea cucumbers feeding on settling particulate matter. The abundance of sea urchins is also greater under these mussel rafts than in areas distant from them but this is likely due to their falling from the culture structures (Olaso Toca 1979, 1982). Inglis and Gust (2003) report that mussels on the bottom serve to aggregate the predatory starfish *Coscinasterias muricata* under mussel lines in Pelorus Sound, New Zealand, where they feed on fallen mussels. They suggest that this food source likely increases the starfish's reproductive output by enhancing growth and gonad maturation rates. Using modeling, they further suggested that this aggregating behaviour could also enhance fertilization success, which is a function of the distance between reproductive adults in broadcast spawners such as *C. muricata*.

4. Biodeposition and benthic enrichment

Mussels feed by filtering water. Part of what is filtered is excreted as faeces following digestion and a further fraction may be rejected as pseudofaeces following sorting and selection by the mussel and prior to being ingested. Production of pseudofaeces is typically a function of the quantity and quality of food available with a greater fraction of pseudofaeces being produced when seston quantity is high and/or seston quality is low. Collectively faeces and pseudofaeces are known as biodeposits. Biodeposits have a greater sinking velocity than their constituent particles and generally increase the flux of organic matter to the sea bottom near mussel farms (Dame 1996; Newell 2004). The degree to which biodeposits accumulate in the vicinity of a farm is a function of four factors: the rate of biodeposit production, initial dispersal (i.e., the transport of biodeposits in the water column due to hydrodynamic processes until their first contact with the seabed), the redistribution of biodeposits on the sediment surface via creep, saltation and/or resuspension (i.e., erosion), and the rate of biodeposit decay (Giles 2009).

Biodeposit production and settlement rates vary among species, mussel size, and diet and are quite variable over short time scales (days) (see review in Weise et al. 2009). Smaller mussels produce a proportionally (relative to mussel biomass) greater quantity of biodeposits than do larger mussels. In contrast, biodeposits produced by smaller mussels are smaller and have a lower settlement rate and are thus more likely to be advected further afield by prevailing currents, resulting in reduced localized biodeposition. Sinking velocity ranged within 0.2-4.5 cm s⁻¹ for *Perna canaliculus* measuring 2.7-11.4 cm (Giles and Pilditch 2004). De Jong (1994) reported that *P. canaliculus* faecal pellets sank at a rate of 1.2 ± 0.1 cm s⁻¹ although the size of the mussels studied was not given and Hartstein and Stevens (2005) reported that faecal pellets from 6 cm individuals of the same species settled at 3.0 ± 0.4 cm s⁻¹. Callier et al. 2006 measured faecal pellet sinking velocities ranging from 0.27 to 1.81 cm s⁻¹, for *Mytilus edulis* ranging in shell length from 3 to 7 cm. Miller et al. (2002) found sinking velocities for *Atrina zelandica* faecal pellets ranged from 1.1 to 3.0 cm s⁻¹ (18.5 – 26 cm individuals). Variations in sinking velocity are also due in part to variations in faecal composition. Both Giles (2006) and Chamberlain (2002) report that sinking velocity is greatly influenced by the relative concentration of silt in mussel diets, with sinking rates of faeces from mussels fed a diet supplemented with silt being up to 4 times greater than those fed a diet of pure phytoplankton.

Recent advances have used this information, together with hydrodynamic modeling, to predict footprints of benthic loading around mussel farms (see reviews in Giles 2009; Weise et al. 2009). In short, the degree to which biodeposits are dispersed initially and redistributed subsequently is positively correlated with local current regimes (e.g., Hartstein and Stevens 2005; Giles 2009). These works have highlighted knowledge gaps with respect to the information available on biodeposit production. First, many studies that have evaluated biodeposit production have done so under laboratory conditions (e.g. Tenore and Dunstan 1973; Chamberlain 2002). The degree to which such estimates reflect what occurs in the field is unknown. Studies that have evaluated biodeposit production under field conditions (e.g., Kautsky and Evans 1987; Cranford and Hill 1999; Callier et al. 2006; Weise et al. 2009) have used methods (e.g., the use of cages in sediment traps) that may also influence food delivery and thus biodeposit production. In all cases, biodeposit production was measured for a single or low

numbers of mussels and not by complete mussel socks. It is likely that mussels in a mussel sock function differently from the sum of a series of individual mussels as the interactions between mussels and the environment are scale-dependent (Smith et al. 2006; Stevens et al. 2008; Fréchette 2010). Although recent work (McKindsey et al. 2009) has addressed these issues by measuring biodeposit production by small mussel socks suspended over large sediment traps, only a single size class of mussels was evaluated in one site at one time of the year. Such work should be extended to establish how well extrapolations from single mussels reflect the reality of mussels on socks within farms in the field.

Notwithstanding the above, it is clear that biodeposit production by mussels in suspension may be considerable. For example, Dahlbäck and Gunnarsson (1981) found that sedimentation rates under a longline mussel farm in Sweden were $3 \text{ g C m}^{-2} \text{ d}^{-1}$ – about 3 times that observed in a reference area. Hatcher et al (1994) showed that mean annual sedimentation in an eastern Canada longline mussel farm was ca. $88.7 \text{ g m}^{-2} \text{ d}^{-1}$ – more than $50 \text{ g m}^{-2} \text{ d}^{-1}$ greater than that of a control area. Hartstein and Stevens (2005) showed sedimentation rates within a northern South Island, New Zealand, mussel site were $133 \text{ g m}^{-2} \text{ d}^{-1}$ (compared with $24 \text{ g m}^{-2} \text{ d}^{-1}$ at a control site). Tenore et al (1982), observed sedimentation rates of from ca. 0.2 up to ca. $2.4 \text{ g C m}^{-2} \text{ d}^{-1}$ in a mussel raft area in Spain, and Grenz (1989, cited in Grenz et al. 1990) suggested that mussels grown in suspension in the Thau Lagoon, southern France, may produce $<345 \text{ kg m}^{-2} \text{ yr}^{-1}$ ash-free dry weight of biodeposits.

Although there is considerable information on the organic matter content of material sedimenting in mussel culture sites (e.g., Kautsky and Evans 1987; Weise et al. 2009) and from mussels in experimental field situations (e.g., Jaramillo et al. 1992; Callier et al. 2006), there is much less information available concerning the organic matter content of the faeces and pseudofaeces themselves, especially from field studies or mussels fed a natural diet. As pointed out by Iglesias et al. (1998), data on biodeposition and sedimented material provide quite different information. The quality of organic and other matter in biodeposits will influence the rate at which it breaks down as more labile components may be released to the environment rapidly (Fabiano et al. 1994; Giles and Pilditch 2006; Carlsson et al. 2010).

A further knowledge gap is the degree to which biodeposits are redistributed in the environment following initial deposition to the seafloor. Although resuspension may be negligible in areas with weak currents (Weise et al. 2009), it may be of greater importance in areas with stronger currents (Giles 2009) and remains one of the main sources of uncertainty in biodeposition / impact models (Grant et al. 2005). Recent work has started to address this gap (Giles and Pilditch 2004; Giles 2009; Walker and Grant 2009).

Although knowledge of the biodeposition from the farmed organisms may be useful for predicting organic loading from mussel aquaculture, numerous authors (e.g., Stenton-Dozey et al. 2001; Giles et al. 2006; McKindsey et al. 2009) have also pointed out that the organisms associated with farmed mussels may also contribute substantially to the deposition of organic matter to the sea bottom.

Increased organic loading to the bottom from biodeposition by mussels and associated organisms and of the organisms themselves influences the biogeochemical properties of benthic sediments, including modifying benthic respiration and nutrient fluxes at the

sediment surface-water interface, as well as the communities that live associated with them. These issues are discussed, in turn, below, although it must be kept in mind that these variables are all tightly linked.

4.1. Sediment biogeochemistry

Biodeposits can be rich in carbon and nitrogen (Kautsky and Evans 1987) and be of great nutritional value (C:N ratios between 4.8 and 8.5; Kautsky and Evans 1987; Loo and Rosenberg 1989; Ahn 1993; Miller et al. 2002). The quality of biodeposits depends on the diet (Miller et al. 2002), which may vary widely in space and time (Bayne et al. 1993). Biodeposits contain predominantly broken down material and are already colonised by large populations of microorganisms when they are egested (Fabiano et al. 1994). Their decomposition may increase nutrient release rates from bottom sediments in culture sites relative to that in reference areas (Newell et al. 2002). Several studies have shown that increased biodeposition from mussel aquaculture may alter benthic sediment geochemistry (Dahlbäck and Gunnarsson 1981; Mattsson and Lindén 1983). The decomposition of mussel biodeposits is a complicated process with some labile components being degraded quickly (hours to days) while refractive components may be very stable. Although measurement of mussel biodeposit decay rates is essential to understand and quantify their contribution to the benthic regeneration of nutrients, little has been published on biodeposit quality and their decay rates (Grenz et al. 1990; but see Fabiano et al. 1994; Giles and Pilditch 2006; Carlsson et al. 2010).

Organic matter is decomposed by microbes following a sequence of oxidative reductions (Figure 2). The distribution of these reactions with sediment depth depends on the supply of oxidants and labile organic matter, the diffusion of solutes and sediment reworking by fauna or physical disturbances (Valiela 1995). In coastal muddy sediments, aerobic mineralization usually occurs within depths of 0.1-1cm, while Nitrate, Mn, and Fe metabolism occurs between 1-10 cm. Sulfate reduction mainly occurs at a sediment depth of 10-100 cm, while methanogenesis occurs at greater depths (Aller and Aller 1998) (Figure 2). The deposition of organically rich biodeposits under mussel farms may increase oxygen demand locally. When the decay of biodeposits consumes oxygen at a rate greater than that of renewal by water exchange, this can create anoxic conditions and induce sulfate reduction to occur near the surface. Dissolved sulphides (HS^- , H_2S , S^{2-}) thus produced may be transformed into metal sulphides such as iron monosulphides (FeS), greigite (Fe_3S_4) and ultimately pyrite (FeS_2), a very insoluble compound (Figure 3). Free sulphides, especially undissociated hydrogen sulphides (H_2S), are highly toxic and may enter the cells by passive diffusion. The H_2S and organic sulphides, primarily dimethyl sulphide, are the source of the “rotten-egg” odor of anoxic marine sediments (Valiela 1995).

Sediment redox potential ($E_{\text{h}_{\text{NHE}}}$) and sulphide levels have been successfully used to detect organic loading under fish cages (Hargrave et al. 1997; Anderson et al. 2005). Numerous studies have shown increased %OM and/or total free sulphide (S) and/or decreased redox potentials of bottom sediments within or close to farm boundaries. For example, Dahlbäck and Gunnarsson (1981) showed increased sedimentation and sulfate reduction under mussel lines relative to a reference area in Sweden. Tenore et al. (1982) showed that sulfate reduction was 63% greater at mussel culture sites compared with control sites in Spain. Hargrave et al. (2008) studied spatial variations between mussel lease and non-lease locations at 58 stations on geochemical parameters in

Prince Edward Island embayment. They found that average %OM and S concentration were significantly higher and $E_{h_{NHE}}$ significantly lower in mussel lease sites than in non-lease sites. They also demonstrated the importance of considering site variations due to physical and bathymetric factors. Higher levels of % OM, S and lower redox potentials and finer-grained sediments were generally observed in deeper parts of the bay (< 4 m) as compared with sediments at intermediate depths (2-4 m). The authors suggest that this pattern was due to resuspension of biodeposits from more shallow sites and their subsequent deposition in deeper areas of the bay. This study showed that broad spatial scale (bay-wide), geochemical parameters were highly correlated with grain size and that lease- scale, organic enrichment effects could be detected by differences in S and $E_{h_{NHE}}$.

However, several studies have also shown that these parameters are often not sensitive enough to detect the effect of mussel aquaculture on benthic sediments (e.g., Anderson et al. 2005; Miron et al. 2005; Callier et al. 2007). For instance, da Costa and Nalesso (2006) measured sediment %OM at sites within the farm and at 50 m, 200 m and ca. 1000 m (reference). Sediment %OM ranged from 4.9% to 9% during the year but did not differ among distances. The authors concluded that the mussel farm had no negative impacts on the benthic environment, and that the relatively high organic matter content was due to the presence of a nearby mangrove forest and riverine organic input. In depositional environments, detritus from other sources, such as plankton, seagrass or biodeposits from species associated with the cultured species may obscure the influence of mussel biodeposition (Stenton-Dozey et al. 2001). Moreover, some infaunal species are very efficient at mitigating organic loading (Valdemarsen et al. 2010) and rapid mineralization of mussel biodeposits may lead to a decoupling of sedimentation and sediment chemical characteristics (Giles et al. 2006).

Decreased infaunal biodiversity and the disappearance of large species due to increased biodeposition rates (see section on infauna, below) may further increase organic enrichment effects by reducing sediment reworking. Benthic infauna rework sediments, enhancing oxygen penetration into benthic sediments and the mineralization of organic matter (Aller and Aller 1998; Michaud et al. 2010). The various sediment bioturbation activities (e.g. feeding, burrowing, etc.) also influence nutrient exchange rates between sediments and the water column (Rosenberg 2001; Michaud et al. 2006) and have been shown to be important in modifying oxygen consumption, CO₂ release, and sulfate reduction in sediments impacted by a fish farms in Denmark (Heilskov and Holmer 2001). Heilskov et al. (2006) examined the influence of different types of infaunal assemblages in sediments from under Danish and Cypriot fish farms supplemented with fish farm waste on these same parameters and ammonium, nitrate, and phosphate fluxes. They found that these parameters were correlated with bio-irrigation in sediments such that loss of large bio-irrigating species led to reduced mineralization of enriched sediments. This review found no evaluation of this effect for mussel or other types of bivalve culture.

4.2. Biogeochemical fluxes

Nutrient regeneration in shallow waters is mainly controlled by benthic remineralization regulating the production (fluxes) and standing stocks (concentrations) of nutrients in the water (Kaspar et al. 1985; e.g., Baudinet et al. 1990; Mazouni et al. 1996). Biodeposition from farmed bivalves typically increases oxygen consumption and nutrient fluxes at the

water-sediment (benthic) interface (Baudinet et al. 1990; Hatcher et al. 1994; Christensen et al. 2003; Richard et al. 2007a; Richard et al. 2007b). In addition, as farmed bivalves grow, organic matter accumulates within the culture structure matrix, and the abundance and biomass of the associated organisms increase (Taylor et al. 1997; Mazouni et al. 2001; Richard et al. 2006), leading to substantial oxygen consumption and nutrient fluxes at the interface between culture structures (i.e., cultured and fouling organism) and the water column (i.e., the pelagic interface; see Leblanc et al. 2003a; Mazouni 2004; Nizzoli et al. 2006; Richard et al. 2006, 2007a, 2007b). Aquaculture structures contain a high biomass of hard-substratum and infaunal macrofauna whereas the seafloor within culture areas is typically dominated by soft sediment infaunal communities. These differences may lead to different biogeochemical processes occurring in each location and differences in the relative fluxes of nutrients and oxygen (Mazouni et al. 2001; Richard et al. 2006).

Although many studies have shown that benthic oxygen consumption is increased under aquaculture structures relative to that outside of farms (Mazouni et al. 1996; Christensen et al. 2003; Giles and Pilditch 2006; Giles et al. 2006; Carlsson et al. 2009; Alonso-Pérez et al. 2010), this is not always observed (Grant et al. 1995; Stenton-Dozey et al. 2001; Richard et al. 2007a, 2007b). In contrast, oxygen uptake has consistently been shown to be increased by bivalve culture structures (Mazouni et al. 1998, 2001; LeBlanc et al. 2002; Mazouni 2004; Nizzoli et al. 2006; Richard et al. 2006, 2007b). Moreover, some studies have suggested that fouling organisms and accumulated biodeposits growing on and accumulated within culture structures, respectively, may further increase oxygen uptake and nutrient fluxes (Mazouni et al. 2001; Nizzoli et al. 2006; Richard et al. 2007b).

Benthic ammonium (Giles et al. 2006; Nizzoli et al. 2006), phosphate (Carlsson et al. 2009) and silicate fluxes are typically greater within mussel culture sites than in control zones (Baudinet et al. 1990; Hatcher et al. 1994; Richard et al. 2007a, 2007b; Alonso-Pérez et al. 2010). At times, fluxes of these nutrients from culture structures are greater than those measured in controls (Richard et al. 2006, 2007b). Increased ammonium and phosphate releases measured at the benthic interface in culture zones likely result, in part, from the degradation of mussel biodeposits which are rich in nitrogen and phosphorus (Kautsky and Evans 1987).

Increased silicate fluxes from benthic and pelagic interfaces likely result from the dissolution of diatom tests in mussel biodeposits (Balzer et al. 1983). Mussel biodeposits include large diatom cells and chain forms (pseudofaeces) and frustules of small diatom cells and chains forms (faeces) (Navarro and Thompson 1997). Diatomaceous tests are made of biogenic silica (Balzer et al. 1983). Many studies have also shown that fluxes of silicate may vary over seasonal and annual cycles (Hatcher et al. 1994; Nizzoli et al. 2006; Richard et al. 2007a, 2007b; Carlsson et al. 2009).

Richard et al. (2006) showed that the mean contribution of the non-mussel part of two-year-old mussel lines accounted for 83% and 95% of the nitrate and nitrite releases, respectively, from culture structures. This is likely due to both the metabolism of the associated fauna and the degradation/mineralization of biodeposits trapped between bivalve shells. Biodeposits are a good source of nitrogen (Sornin et al. 1983; Boucher and Boucher-Rodoni 1988; Grenz et al. 1990) and may contribute to $\text{NO}_2\text{-NO}_3$ releases after nitrification (Henricksen and Kemp 1988; Gilbert et al. 1997; Christensen et al. 2003). A net release of nitrate from the benthic interface under mussel farms is often

observed, although there may be great daily (Alonso-Pérez et al. 2010) and seasonal (Giles et al. 2006; Richard et al. 2007a, 2007b) variability. However, a few studies have not observed nitrate fluxes to be enhanced by mussel farming (Baudinet et al. 1990; Nizzoli et al. 2006; Carlsson et al. 2009).

Many factors may explain differences among studies, including variation in hydrodynamic regimes. For example, Alonso-Pérez et al. (2010) did not observe differences in dissolved inorganic nutrients and suspended particulate matter quality and quantity between a mussel raft site and other study sites. They suggested that differences between their study and others (e.g., Hatcher et al. 1994; Stenton-Dozey et al. 2001; Giles and Pilditch 2006) may be due to their study site, the Ría de Vigo, Spain, being an area with strong upwelling and short water residence times whereas the other studies were done in semi-enclosed shallow areas with weak currents. Although this may be true with respect to comparisons with the study of Souchu et al. (2001), which took water samples from a boat next to culture structures, it is not a fair comparison with the other studies (Nizzoli et al. 2006; Richard et al. 2007a), which measured fluxes in mesocosms chambers and samples were taken by SCUBA divers from culture structures. Small-scale effects (i.e., relating to the surface of culture structures) may have been obscured by natural variability and active hydrodynamics in the Alonso-Pérez et al. (2010) study.

The atomic Si:N:P ratio of 16:16:1 was first published by Redfield (1934) and formalized by Redfield et al. (1963). This “Redfield” ratio was based on direct analysis of these elements in zooplankton and phytoplankton collected by towing nets at numerous sites in the upper ocean. As Falkowski and Davis (2004) point out, Redfield’s concept is an elegant empirical observation that has no simple reductionist explanation. They further point out that it is a powerful organizing principle that illustrates how biological processes can alter the distribution of elements in the oceans and may be used to help guide us to understand natural biogeochemical patterns and how humans (in the present case, in the context of bivalve aquaculture) influence them (Falkowski and Davis 2004). Furthermore, Loladze and Elser (2011) recently suggested that their results reinforce Redfield’s original argument and support the validity of subsequent biogeochemical models that rely on an inherent significance of N:P = 16 for plankton. Numerous studies (e.g., Hatcher et al. 1994; Richard et al. 2007a, 2007b) have suggested that modification of natural nutrient fluxes by mussel aquaculture activities may alter these ratios at both the benthic and pelagic interfaces. Richard et al. (2006) observed greater N/P ratios at pelagic interfaces than in control areas, suggesting that mussel lines could reduce the probability of nitrogen deficiency in adjacent waters. In contrast, Alonso-Pérez et al. (2010) did not observe this change in N/P ratios in the pelagic environment (but see comments above on this study).

Similarly, Si:P ratios < 16 may indicate that silicates are limiting. However, this may also result from greater phosphate fluxes rather than altered nitrogen and silicate fluxes at mussel farms sites (Richard et al. 2007a). Phosphate release may be enhanced by the dissolution of ferric oxides and hydroxides under reduced conditions (Mazouni et al. 1996). By increasing N and Si releases, biodeposit remineralization may increase Si:N and N:P ratios, reducing potential nitrogen and silica limitation in overlying waters of oligotrophic ecosystems (Richard et al. 2007a, 2007b). Giles et al. (2006) showed that dissolved inorganic nitrogen release under a mussel farm accounted for up 94% of the primary production requirements for the Firth of Thames, New Zealand, highlighting the importance of such culture-related fluxes.

Together, these studies show that mussel culture may modify nutrient fluxes and thus nutrient dynamics – at least in the vicinity of farms. In short, pelagic surfaces have the greatest effect on nitrate and nitrite whereas benthic interfaces associated with mussel farming have the greatest effect on silicate turnover. Whether the impact of modified nutrient ratios is a significant factor influencing primary producers will depend on, among many factors, the culture site itself and the quantity of mussels grown, but may lead to cascading effects that are much greater than simple shifts in nutrient levels (Hatcher et al. 1994).

4.3. Infauna

The influence of biodeposition from mussel aquaculture on infaunal communities is well studied and, for the most part, follows the Pearson and Rosenberg (1978) model of organic enrichment. As the level of organic input increases, typical soft sediment communities dominated by large filter-feeders are replaced by smaller, more deposit-feeding organisms, starting with small polychaetes (e.g., *Capitella* spp.), shifting to nematodes, and finally ending up with anoxic conditions and mats of the bacteria *Beggiatoa* spp. Biomass and species richness may increase with limited organic loading whereas abundance may increase with moderate loading as smaller, opportunistic, species come to dominate. At great loading rates, all standard measures of benthic condition are reduced as bottom sediments become hypoxic or even anoxic.

One of the first studies to evaluate the influence of suspended mussel culture on infaunal communities was by Mattsson and Lindén (1983) who showed how a longline mussel farm in Sweden changed the structure of the underlying benthic fauna by decreasing the abundance of sensitive species, increasing the abundance of opportunistic species, and generally decreasing abundance, biomass, species richness and diversity. Results from subsequent studies have been variable. Some studies have not detected effects related to mussel culture on infaunal communities (Crawford et al. 2003), whereas others have shown that mussel farms may modify microbial (Mirto et al. 2000), meiofaunal (Mirto et al. 2000) and/or infaunal communities (Hartstein and Rowden 2004). It is also clear that effects may be very local. For example, Callier et al. (2008) observed that communities in a sample station directly below mussel lines were characterized by a lower abundance of organisms than those from stations 3 to 300 m distant, that species richness increased along the transect studied, and that infaunal biomass was greater at intermediate distances from the farm, indicating that opportunistic polychaetes likely benefited from an enriched benthic environment due to organic loading from the longline culture site. A summary of these and further studies on the influence of mussel culture on infaunal communities is given in Table 1.

Differences in the magnitude of a farm's influence on benthic infaunal communities likely depend on both farm- (e.g., farm size, stocking density, and age of operation) and site-specific (e.g., bathymetry and hydrodynamic regime) characteristics (Black 2001; Hartstein and Rowden 2004; Hartstein and Stevens 2005). All else being equal, communities underlying farms in more hydrodynamically active areas are less impacted by biodeposition-related effects than are farms in areas with weaker currents as biodeposits are more widely dispersed in the former. Logically, the degree of modification of infaunal communities is a function of the rate of biodeposit loading in a given site. This is seen from studies conducted along transects from culture sites (e.g., Chamberlain et al. 2001; Callier et al. 2008; Ysebaert et al. 2009). However, very few

studies have measured loading rates and responses by infaunal communities simultaneously and thus the relation between the two is largely unknown (Callier et al. 2009). Similarly, although many studies suggest that the benthic effects of mussel farms are limited to confined areas, a review of Table 1 suggests that the information is simply not available to provide rigorous support for this conclusion. Very few studies have compared communities at a variety of spatial scales and those that do often fail to detect a steady community structure outside of farm areas to allow them to claim that the communities at the maximum distances evaluated along transects represent 'background' conditions.

Similarly, few studies compare reference data for any metrics from before the establishment of mussel farms, relying only on post-impact assessments among farm and reference locations (but see Callier et al. 2007). De Paz et al. (2008) have shown that marine benthic systems must be studied over long periods to understand the natural temporal and spatial variations that may otherwise mask system responses to anthropogenic disturbances. Benthic communities from numerous sites were sampled in the bay of Mont Saint-Michel in 2002, one year prior to a large spatial restructuring of oyster and mussel farms there (Olivier et al., unpublished data). Five years later, Houliez (2007) resampled several sites where *bouchots* had either been removed or established, but did not detect significant changes in macrozoobenthic communities. Sites where *bouchots* had been removed and newly established *bouchot* sites remained characterized by muddy fine sediments and more mobile clean fine sands, respectively, and similarly by benthic communities normally associated with those habitats although infaunal assemblages in new *bouchot* sites were relatively more homogeneous than they had been previously. Thus although the influence of culture sites may be evident over short time scales in some locations, they are not in others, such as high energy sites where communities may take 10 to 15 years to reach a new equilibrium following a disturbance (Retière 1979; Dauvin 1987, 1998), showing that long-term studies are necessary in some locations.

The only study to examine the influence of *bouchots* on infaunal communities in long-established culture sites was that of Grant (2010). She observed both small-scale (m- or within-farm) and meso-scale (km) effects of this type of farming. All sites were dominated by polychaetes and bivalves, but the abundance of the dominant bivalve species and total abundance were greater directly adjacent to *bouchots* than at positions between the rows of *bouchots*. Taxonomic richness was reduced in samples taken adjacent to *bouchots* relative to samples from between rows of *bouchots*, whereas the pattern for variation in taxonomic distinctness was inversed. Overall (see Table 1), none of these measures differed between farm sites and reference sites. In contrast, multivariate analyses showed clear differences in infaunal community structure between farm and reference sites with almost no overlap in community structure from the two habitat types and there was a clear trend for diversity and evenness to be reduced in the farm sites. These trends seem to be a function of sediment type (coarseness) rather than organic enrichment as this latter factor did not differ between farm and reference sites whereas sediment composition did.

It is difficult to infer generality of effects from a series of individual studies that examine a single or a limited number of farms in isolation using a variety of methods. To address this, Keeley et al (2009) recently reviewed environmental effects studies done for permitting purposes for 54 farm sites in the Marlborough Sounds, New Zealand, that cover a large range of environmental and husbandry conditions using the same

methods. Briefly, infaunal abundance was typically increased under mussel sites relative to areas immediately adjacent to (≥ 50 m distant) and in reference locations whereas species richness was slightly increased or decreased due to enrichment from biodeposition. Moreover, community structure remained very similar between farmed and unfarmed areas except for general increased abundance of polychaetes under farm sites, suggesting low-level positive effects of enrichment on this group of organisms and not a major disruption of functional integrity. A comparison of the results from this meta-analysis with the results of studies outlined in Table 1 shows broad agreement with these findings, suggesting that, overall, the impacts of suspended mussel culture on benthic infaunal communities are typically limited in magnitude except under extreme conditions (poor flushing or exceedingly great stocking densities).

5. Seagrass and algae

There are a number of mechanisms by which off-bottom and suspended mussel culture may influence the abundance of benthic plants and algae:- via increased sediment stability and loading and altered sediment biogeochemistry, by increased shading from overlying culture structures, by modified nutrient levels or altered turbidity, and by impacts from physical disturbance during harvesting and other husbandry activities. There are few examples of such effects reported from the literature and the causative mechanisms are rarely clear. Although the focus of a study by Barranguet (1997) was not on benthic macrophytes, it was found that incident light under a Mediterranean mussel farm site was reduced relative to a control site and that organic matter and other linked parameters also differed between sites. Any of these factors might have impacted macrophytes. In the Chausey Archipelago in France, it appears that the reduced currents and increased sediment stability in bouchot sites located in high dynamic areas (Grant 2010) allow eelgrass to establish between bouchots, a process that is not observed to the same extent outside culture sites (Godet et al. 2008; F. Olivier, personal observations).

Other than this work in mussel sites, the only other studies on the interactions between suspended or off-bottom bivalve culture and macrophytes appear to be those associated with the influence of oyster aquaculture. Although Crawford et al (2003) observed healthy seagrass beds and the accumulation of algae as a result of their falloff from the culture structures under a longline oyster culture site in Australia, other studies have found oyster culture to impact various seagrass health metrics (e.g., Carlton et al. 1991; Pregnall 1993; Everett et al. 1995; Rumrill and Poulton 2004; Wisehart et al. 2007; Tallis et al. 2009; Vaudrey et al. 2009). However, the culture methods examined in these studies are not directly comparable with those used for mussel culture and so are not considered further here.

In general, intensive grazing by cultured bivalves is expected to reduce turbidity, increasing light penetration to the bottom and thus extending the depth to which benthic macrophytes and microphytobenthos can grow (Newell 2004; Newell and Koch 2004). However, De Casabianca et al. (1997) compared contemporary and historical data on macrophyte communities in the Thau Lagoon, France, which they claim have shifted from a dominance by *Zostera* to communities composed of opportunistic algae (*Ulva* and *Gracilaria* spp.) over the past century, and suggested that this succession was caused by elevated levels of nitrogen and increased turbidity resulting from eutrophication by

extensive off-bottom culture of oysters and mussels. In contrast, Deslous-Paoli et al. (1998) also reviewed studies on macrophyte distributions from the same lagoon (with no reference to De Casabianca et al. 1997) and concluded that *Zostera* spp. has extended its distribution from shallow regions to areas up to 5 m depth in some areas of the lagoon. These latter authors attribute this increased distribution to reduced turbidity in culture regions as a result of bivalve filter feeding. On a near-field scale, macrophytes could be found between culture trestles but were completely absent underneath, indicating either a shading effect of these structures (Deslous-Paoli et al. 1998) or effects due to biodeposition.

6. Far-field benthic effects

A number of far-field benthic effects may arise from processes occurring within mussel culture sites. One major effect may be due to the proliferation of species associated with mussel culture sites. For example, Inglis and Gust (2003) suggest that aggregated seastars under mussel culture sites may greatly increase fertilization success to a point that outbreaks of the animals may occur with consequent impacts on benthic communities. D'Amours et al. (2008) suggest that that mussel culture sites attract benthic organisms, especially predators, from the surrounding areas. It is unclear what impact reduced abundances of predators in the surrounding environment will have on benthic communities.

Jellyfish have a benthic stage (the polyp) that requires a hard substrate for attachment, and which produces ephyrae that metamorphose into the swimming medusae. Richardson et al. (2009) suggested that a large addition of appropriate artificial hard substrate in the water column, such as that created by the physical structure and shading provided by aquaculture structures (Hoover and Purcell 2009), may in turn lead to the proliferation of extra medusae. This appears to have occurred in Taiwan, where the jellyfish *Aurelia aurita* often irrupted in blooms when the embayment was filled with oyster aquaculture rafts, but which disappeared from the system when the culture structures were removed (Lo et al. 2008). Of several possibilities examined by Lo et al. (2008), the direct provision of physical structure and shading by aquaculture structures that enhanced the abundance of polyps best accounted for the observed changes in jellyfish abundance. Enhanced jellyfish production to the point that blooms develop may have a large number of cascading effects on the rest of the ecosystem (Richardson et al. 2009), ranging from effects on algal communities through microzooplankton up to important fisheries species. As pointed out earlier, mussel culture areas may serve as a focus for exotic species. These species may then be able to propagatae into the greater environment with consequent impacts on surrounding benthic communities (see review in McKindsey et al. 2007).

Mussels feed on a wide variety of food types measuring from 3 to 6000 μm (Kreeger and Newell 1996; Davenport et al. 2000; Wong et al. 2003; Lehane and Davenport 2006) and suspended and off-bottom mussel aquaculture places the bivalves in direct contact with the pelagic food web (Maar et al. 2008). Studies have shown that grazing by farmed mussels and their associated epifauna may impact the structure of plankton communities at farm sites and at larger spatial scales (Prins et al. 1998; e.g., Petersen 2004), reducing zooplankton standing stocks or altering community size structure. However, little research has examined the *in situ* effect of suspended mussel farming on

zooplankton communities. Lehane and Davenport (2006) examined the stomach contents of farmed *Mytilus edulis* and found that ingested zooplankton was composed of calanoid and harpacticoid copepods, crustacean nauplii, barnacle cyprids, bivalve larvae, amphipods, and ostracods. Maar et al. (2008) examined the depletion of zooplankton within *Mytilus galloprovincialis* raft culture in Spain and noted that meroplankton, including barnacle nauplii and gastropod and polychaete larvae, were significantly depleted at raft center, edge and downstream positions relative to upstream ones. The authors showed that the ingestion of zooplankton, especially copepodites and gastropod larvae, contributed the most (86%) to the total planktonic carbon ingested by farmed mussels and associated fauna under high current conditions (although some of these larvae may have recruited to culture structures, as was suggested to occur for hydroids and barnacles).

Although many species of plankton may elicit escape responses to inhalant currents caused by mussels, escape success differs greatly among species. For example, Cowden (1984) offered meroplankton of 6 species of echinoderms, polychaetes, and a barnacle to *Mytilus edulis* and found that survival was ca. 50% for two species of sea urchins and below 20% for the other species. Green et al. (2003) evaluated the escape response of 3 species of copepods to the flow field created by *M. edulis* and found that escapement success differed greatly among species, larval stages, and position relative to flow created by the mussels. Similar responses were also observed under simulated predator flow fields (Titelman and Kjørboe 2003). Gendron et al. (2003) evaluated the ability of *M. edulis* to ingest stage I lobster (*Homarus americanus*) in a lab study and found that although mussels may inhale larvae when placed in close proximity, they more often would either ignore them or close their mantle and, of the stage I lobster that were inhaled, most escaped thereafter.

Given that many types of meroplankton may be consumed by mussels and that Lehane and Davenport (2002) have shown that mussels in suspension consume a greater quantity of meroplankton than those on the bottom, mussel culture may thus reduce the number of individuals able to recruit to the natural environment (Gibbs 2004). Reduced recruitment may consequently influence benthic communities, as has been shown to occur in a number of studies not related to aquaculture (Ólafsson et al. 1994; Navarrete et al. 2005). This review found no study that has evaluated how depletion of meroplankton by bivalve culture may impact benthic communities (but see Gibbs 2004).

Mussel culture may also change the planktonic food resources available to other species and this should be considered when determining the ecological carrying capacity of an area (Jiang and Gibbs 2005; Sequeira et al. 2008). Similarly, as sedimentation rates to the benthos are a function of the plankton communities in an area (e.g., Wassmann 1998), sedimentation rates outside of farm areas may be reduced. Reduced sedimentation may influence benthic communities and enhance differences between benthic communities within and outside of culture sites.

7. Perspectives

This review has shown that suspended and off-bottom mussel culture has myriad influences on the benthic environment and benthic communities. The question remains: which ones are important and which ones are not? As Dumbauld (2009) suggests, the

question reduces to: “What are we / or should we be managing for?”. If management is to be ecosystem-based, then it may be appropriate to consider tradeoffs between components as “negative” impacts on some components (e.g., eelgrass or benthic infauna) may be offset by “positive” impacts on others (e.g., epibenthic macrofauna or reduction of eutrophication due to filtration by the farmed bivalves).

Coastal systems in which the bulk of mussel farming occurs offer a variety of ecosystem services, each of which has some intrinsic value. Whether or not, on balance, mussel farming has a positive or negative influence on these systems is clearly dependent on the values that are used to weigh the different components. The degree to which each is valued is a moving target that follows fickle societal values and the idea of setting some type of ecological carrying capacity or limit of acceptable change (Shelby and Heberlein 1984; Zeldis et al. 2006; Guyondet et al. 2010) is clearly a function of the social carrying capacity of an area for bivalve culture (McKindsey et al. 2006; Dempster and Sanchez-Jerez 2008).

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References

- Ahn, I.Y. 1993. Enhanced particle flux through the biodeposition by the Antarctic suspension-feeding bivalve *Laternula elliptica* in Marian Cove, King George Island. *J. Exp. Mar. Biol. Ecol.* 171: 75-90.
- Allard, J., Bertin, X., Chaumillon, E., and Pouget, F. 2008. Sand spit rhythmic development: A potential record of wave climate variations? Arçay Spit, western coast of France. *Mar. Geol.* 253: 107-131.
- Aller, R.C., and Aller, J.Y. 1998. The effect of biogenic irrigation intensity and solute exchange on diagenetic reaction rates in marine sediments. *J. Mar. Res.* 56: 905-936.
- Alonso-Pérez, F., Ysebaert, T., and Castro, C.G. 2010. Effects of suspended mussel culture on benthic-pelagic coupling in a coastal upwelling system (Ría de Vigo, NW Iberian Peninsula). *J. Exp. Mar. Biol. Ecol.* 382: 96-107.
- Anderson, M.R., Tlusty, M.F., and Pepper, V.A. 2005. Organic enrichment at cold water aquaculture sites - the case of coastal Newfoundland. *In Environmental Effects of Marine Finfish Aquaculture. Edited by B. Hargrave.* Springer, Berlin. pp. 99-113.
- Aure, J., Strohmeier, T., and Strand, Ø. 2007. Modelling current speed and carrying capacity in long-line blue mussel (*Mytilus edulis*) farms. *Aquacult. Res.* 38: 304-312.

- Balzer, W., Grasshoff, K., Dieckmann, P., Haardt, H., and Petersohn, U. 1983. Redox-turnover at the sediment–water interface studied in a large bell jar system. *Oceanol. Acta*, 6: 337-344.
- Barranguet, C. 1997. The role of microphotobenthic primary production in a Mediterranean mussel culture area. *Estuar. Coast. Shelf Sci.* 44: 753-765.
- Baudinet, D., Alliot, E., Berland, B., Grenz, C., Plante-Cuny, M., Plante, R., and Salen-Picard, C. 1990. Incidence of mussel culture on biogeochemical fluxes at the sediment-water interface. *Hydrobiologia*, 207: 187-196.
- Bayne, B.L., Iglesias, J.I.P., Hawkins, A.J.S., Navarro, E., Heral, M., and Deslous-Paoli, J.M. 1993. Feeding behaviour of the mussel, *Mytilus edulis*: responses to variations in quantity and organic content of the seston. *J. Mar. Biol. Assoc. U.K.* 73: 813-829.
- Black, K.D.E. 2001. Environmental impacts of aquaculture. CRC Press, Boca Raton.
- Blanco, J., Zapata, M., and Moroño, Á. 1996. Some aspects of the water flow through mussel rafts. *Sci. Mar.* 60: 275-282.
- Borja, Á., Rodríguez, J.G., Black, K., Bodoy, A., Emblow, C., Fernandes, T.F., Forte, J., Karakassis, I., Muxika, I., Nickell, T.D., Papageorgiou, N., Pranovi, F., Sevastou, K., Tomasetti, P., and Angel, D. 2009. Assessing the suitability of a range of benthic indices in the evaluation of environmental impact of fin and shellfish aquaculture located in sites across Europe. *Aquaculture*, 293: 231-240.
- Boucher, G., and Boucher-Rodoni, R. 1988. In situ measurement of respiratory metabolism and nitrogen fluxes at the interface of oyster beds. *Mar. Ecol. Prog. Ser.* 44: 229-238.
- Boyd, A.J., and Heasman, K.G. 1998. Shellfish mariculture in the Benguela system: Water flow patterns within a mussel farm in Saldanha Bay, South Africa. *J. Shellfish. Res.* 17: 25-32.
- Brehmer, P., Gerlotto, F., Guillard, J., and Sanguinède, F. 2003. New applications of hydroacoustic methods for monitoring shallow water aquatic ecosystems: the case of mussel culture grounds. *Aquat. Living Resour./Ressour. Vivantes Aquat.* 16: 333-338.
- Brickhill, M.J., Lee, S.Y., and Connolly, R.M. 2005. Fishes associated with artificial reefs: attributing changes to attraction or production using novel approaches. *J. Fish. Biol.* 67: 53-71.
- Brooks, K.M. 2000. Literature review and model evaluation describing the environmental effects and carrying capacity associated with the intensive culture of mussels (*Mytilus edulis galloprovincialis*), 128 p. Taylor Resources.
- Callier, M.D., McKindsey, C.W., and Desrosiers, G. 2007. Multi-scale spatial variations in benthic sediment geochemistry and macrofaunal communities under a suspended mussel culture. *Mar. Ecol. Prog. Ser.* 348: 103-115.
- Callier, M.D., McKindsey, C.W., and Desrosiers, G. 2008. Evaluation of indicators used to detect mussel farm influence on the benthos: two case studies in the Magdalen Islands, Eastern Canada. *Aquaculture*, 278: 77-88.
- Callier, M.D., Richard, M., McKindsey, C.W., Archambault, P., and Desrosiers, G. 2009. Responses of benthic macrofauna and biogeochemical fluxes to various levels of mussel biodeposition: an in situ "benthocosm" experiment. *Mar. Pollut. Bull.* 58: 1544–1553.
- Callier, M.D., Weise, A.M., McKindsey, C.W., and Desrosiers, G. 2006. Sedimentation rates in a suspended mussel farm (Great-Entry Lagoon, Canada): biodeposit production and dispersion. *Mar. Ecol. Prog. Ser.* 322: 129-141.

- Carbines, G.D. 1993. The ecology and early life history of *Notolabrus celidotus* (Pisces: Labridae) around mussel farms in the Marlborough Sounds. MSc thesis, University of Canterbury, Christchurch.
- Carlsson, M.S., Glud, R.N., and Petersen, J.K. 2010. Degradation of mussel (*Mytilus edulis*) fecal pellets released from hanging long-lines upon sinking and after settling at the sediment. *Can. J. Fish. Aquat. Sci.* 67: 1376-1387.
- Carlsson, M.S., Holmer, M., and Petersen, J.K. 2009. Seasonal and spatial variations of benthic impacts of mussel longline farming in a eutrophic Danish fjord, Limfjorden. *J. Shellfish. Res.* 28: 791-801.
- Carlton, J.T. 1992. Dispersal of living organisms into aquatic ecosystems as mediated by aquaculture and fisheries activities. *In* Dispersal of living organisms into aquatic ecosystems. *Edited by* A. Rosenfield and R. Mann. Maryland Sea Grant, College Park. pp. 13-46.
- Carlton, J.T., Ruiz, G.M., and Everett, R.A. 1991. The structure of benthic estuarine communities associated with dense suspended populations of the introduced Japanese oyster *Crassostrea gigas*: Years 1 and 2. Final Report to South Slough National Estuarine Reserve. SOS Technical Report 1-91, iv + 79 p. South Slough National Estuarine Research Reserve.
- Cayocca, F., Bassoullet, P., Le Hir, P., Jestin, H., and Cann, P. 2008. Sedimentary processes in a shellfish farming environment, Mont Saint Michel Bay, France. *Proc. Mar. Sci.* 9: 431-446.
- Chamberlain, J. 2002. Modelling the environmental impacts of suspended mussel (*Mytilus edulis* L.) farming. PhD dissertation, Napier University, Edinburgh.
- Chamberlain, J., Fernandes, T.F., Read, P., Nickell, T.D., and Davies, I.M. 2001. Impacts of biodeposits from suspended mussel (*Mytilus edulis* L.) culture on the surrounding surficial sediments. *ICES J. Mar. Sci.* 58: 411-416.
- Chesney, E.J., Jr., and Iglesias, J. 1979. Seasonal distribution, abundance and diversity of demersal fishes in the inner Ria de Arosa, northwest Spain. *Estuar. Coast. Mar. Sci.* 8: 227-239.
- Christensen, P.B., Glud, R.N., Dalsgaard, T., and Gillespie, P. 2003. Impacts of longline mussel farming on oxygen and nitrogen dynamics and biological communities of coastal sediments. *Aquaculture*, 218: 567-588.
- Clynick, B.G., Archambault, P., and McKindsey, C.W. 2008. Distribution and productivity of fish and macroinvertebrates in aquaculture sites in the Magdalen islands (Québec, Canada) *Aquaculture*, 283: 203-210.
- Costa-Pierce, B.A., Desbonnet, A., Edwards, P., and Baker, D. 2005. *Urban Aquaculture*. CABI Publishing, Cambridge.
- Cowden, C., Young, C.M., and Chia, F.S. 1984. Differential predation on marine invertebrate larvae by two benthic predators. *Mar. Ecol. Prog. Ser.* 14: 145-149.
- Cowles, A., Hewitt, J.E., and Taylor, R.B. 2009. Density, biomass and productivity of small mobile invertebrates in a wide range of coastal habitats. *Mar. Ecol. Prog. Ser.* 384: 175-185.
- Cranford, P.J., and Hill, P.S. 1999. Seasonal variation in food utilization by the suspension-feeding bivalve molluscs *Mytilus edulis* and *Placopecten magellanicus*. *Mar. Ecol. Prog. Ser.* 190: 223-239.
- Cranford, P.J., Strain, P.M., Dowd, M., Hargrave, B.T., Grant, J., and Archambault, M.C. 2007. Influence of mussel aquaculture on nitrogen dynamics in a nutrient enriched coastal embayment. *Mar. Ecol. Prog. Ser.* 347: 61-78.
- Crawford, C. 2003. Qualitative risk assessment of the effects of shellfish farming on the environment in Tasmania, Australia *Ocean Coast. Manage.* 46: 47-58.

- Crawford, C., Macleod, C.K.A., and Mitchell, I.M. 2003. Effects of shellfish farming on the benthic environment. *Aquaculture*, 224: 117-140.
- Cruz Motta, J.J., Underwood, A.J., Chapman, M.G., and Rossi, F. 2003. Benthic assemblages in sediments associated with intertidal boulder-fields. *J. Exp. Mar. Biol. Ecol.* 285-286: 383-401.
- Cusson, M., and Bourget, E. 1997. Influence of topographic heterogeneity and spatial scales on the structure of the neighbouring intertidal endobenthic macrofaunal community. *Mar. Ecol. Prog. Ser.* 150: 181-193.
- Cusson, M., and Bourget, E. 2005. Global patterns of macroinvertebrate production in marine benthic habitats. *Mar. Ecol. Prog. Ser.* 297: 1-14.
- D'Amours, O., Archambault, P., McKindsey, C.W., and Johnson, L.E. 2008. Local enhancement of epibenthic macrofauna by aquaculture activities. *Mar. Ecol. Prog. Ser.* 371: 73-84.
- da Costa, K.G., and Nalesso, R.C. 2006. Effects of mussel farming on macrobenthic community structure in Southeastern Brazil. *Aquaculture*, 258: 655-663.
- Dahlbäck, B., and Gunnarsson, L.Å.H. 1981. Sedimentation and sulfate reduction under a mussel culture. *Mar. Biol.* 63: 269-275.
- Dame, R.F. 1996. Ecology of marine bivalves: an ecosystem approach. CRC Press, Boca Raton.
- Danovaro, R., Gambi, C., and Mirto, S. 2004. Sustainable impact of mussel farming in the Adriatic Sea (Mediterranean Sea): evidence from biochemical, microbial and meiofaunal indicators. *Mar. Pollut. Bull.* 49: 325-333.
- Dauvin, J.C. 1987. Evolution à long terme (1977-1986) des populations d'Amphipodes des sables fins de la Pierre Noire (Baie de Morlaix, Manche Occidentale) après la catastrophe de l'Amoco Cadiz. *Mar. Environ. Res.* 21: 247-273.
- Dauvin, J.C. 1998. The fine sand *Abra alba* community of the Bay of Morlaix twenty years after the Amoco Cadiz oil spill. *Mar. Pollut. Bull.* 36 669-676.
- Davenport, J., Black, K., Burnell, G., Cross, T., Culloty, S., Ekarante, S., Furness, B., Mulcahy, M., and Thetmeyer, H. 2003. *Aquaculture: the ecological issues*. Blackwell Publishing, Oxford.
- Davenport, J., Smith, R.J.J.W., and Packer, M. 2000. Mussels *Mytilus edulis*: significant consumers and destroyers of mesozooplankton. *Mar. Ecol. Prog. Ser.* 198: 131-137.
- De Casabianca, T., Laugier, T., and Collart, D. 1997. Impact of shellfish farming eutrophication on benthic macrophyte communities in the Thau lagoon, France. *Aquacult. Int.* 5: 301-314.
- de Jong, R.J. 1994. The effects of mussel farming on the benthic environment. MSc thesis, School of Biological Sciences, University of Auckland, Auckland.
- de Paz, L., Neto, J.M., Marques, J.C., and Laborda, A.J. 2008. Response of intertidal macrobenthic communities to long term human induced changes in the Eo estuary (Asturias, Spain): Implications for environmental management. *Mar. Environ. Res.* 66: 288-299.
- de Wit, R., Stal, L.J., Lomstein, B.A., Herbert, R.A., van Gernerden, H., Viaroli, P., Cecherelli, V.U., Rodriguez-Valera, F., Bartoli, M., Giordani, G., Azzoni, R., Schaub, B., Welsh, D.T., Donnelly, A., Cifuentes, A., Anton, J., Finster, K., Nielsen, L.B., Pedersen, A.G.U., Neubauer, A.T., Colangelo, M.A., and Heijs, S.K. 2001. ROBUST: The ROle of BUffering capacities in STabilising coastal lagoon ecosystems. *Cont. Shelf Res.* 21: 2021-2041.
- Dempster, T., and Sanchez-Jerez, P. 2008. Aquaculture and coastal space management in Europe: An ecological perspective. *In Aquaculture in the ecosystem. Edited by*

- M. Holmer, K. Black, C.M. Duarte, N. Marbà and I. Karakassis. Springer-Link. pp. 87-116.
- Deslous-Paoli, J.M., Souchu, P., Mazouni, N., Juge, C., and Dagault, F. 1998. Relations milieu-ressources: impact de la conchyliculture sur un environnement launaire mediterraneen (Thau). *Oceanol. Acta*, 21: 831-843.
- Drapeau, A., Comeau, L.A., Landry, T., Stryhn, H., and Davidson, J. 2006. Association between longline design and mussel productivity in Prince Edward Island, Canada. *Aquaculture*, 261: 879-889.
- Duarte, P., Labarta, U., and Fernández-Reiriz, M.J. 2008. Modelling local food depletion effects in mussel rafts of Galician rias. *Aquaculture*, 274: 300-312.
- Dumbauld, B.R., Ruesink, J.L., and Rumrill, S.S. 2009. The ecological role of bivalve shellfish aquaculture in the estuarine environment: a review with application to oyster and clam culture in West Coast (USA) estuaries. *Aquaculture*, 290: 196–223.
- Dürr, S., and Watson, D.I. 2010. Biofouling and antifouling in aquaculture. *In Biofouling. Edited by S. Dürr and J.C. Thomason. Wiley-Blackwell, Oxford. pp. 267-287.*
- Enright, C. 1993. Control of fouling in bivalve aquaculture. *World Aquacult.* 24: 44-46.
- Everett, R.A., Ruiz, G.M., and Carlton, J.T. 1995. Effect of oyster mariculture on submerged aquatic vegetation: an experimental test in a Pacific Northwest estuary. *Mar. Ecol. Prog. Ser.* 125: 205-217.
- Fabi, G., Manoukian, S., and Spagnolo, A. 2009. Impact of an open-sea suspended mussel culture on macrobenthic community (Western Adriatic Sea). *Aquaculture*, 289: 54-63.
- Fabiano, M., Danovaro, R., Olivari, E., and Mistic, C. 1994. Decomposition of faecal matter and somatic tissue of *Mytilus galloprovincialis*: changes in organic matter composition and microbial succession. *Mar. Biol.* 119: 375-384.
- Falkowski, P.G., and Davis, C.S. 2004. Natural proportions. *Nature* 431: 131.
- FAO Fisheries and Aquaculture Department. 2010. Global datasets, FishStat Plus - Universal software for fishery statistical time series. Available from <http://www.fao.org/fishery/statistics/software/fishstat/en> [accessed March 22, 2010].
- Forrest, B.M., Keeley, N.B., Hopkins, G.A., Webb, S.C., and Clement, D.M. 2009. Bivalve aquaculture in estuaries: Review and synthesis of oyster cultivation effects. *Aquaculture*, 298: 1-15.
- Fréchette, M. 2010. Hierarchical structure of bivalve culture systems and optimal stocking density. *Aquacult. Int.* 18: 99–114.
- Freire, J., Fernández, L., and González-Gurriarán, E. 1990. Influence of mussel raft culture on the diet of *Liocarcinus arcuatus* (Leach) (Brachyura: Portunidae) in the Ría de Arousa (Galicia, NW Spain). *J. Shellfish. Res.* 9: 45-57.
- Freire, J., and González-Gurriarán, E. 1995. Feeding ecology of the velvet swimming crab *Necora puber* in mussel raft areas of the Ría de Arousa (Galicia, NW Spain). *Mar. Ecol. Prog. Ser.* 119: 139-154.
- Fuentes, J., Gregorio, V., Giraldez, R., and Molares, J. 2000. Within-raft variability of the growth rate of mussels, *Mytilus galloprovincialis*, cultivated in the Ria de Arousa (NW Spain). *Aquaculture*, 189: 39-52.
- Garen, P., Robert, S., and Bougrier, S. 2004. Comparison of growth of mussel, *Mytilus edulis*, on longline, pole and bottom culture sites in the Pertuis Breton, France. *Aquaculture*, 232: 511-524.
- Gendron, L., Weise, A.M., Fréchette, M., Ouellet, P., McKindsey, C.W., and Girard, L. 2003. Evaluation of the potential of cultured mussels (*Mytilus edulis*) to ingest

- stage I lobster (*Homarus americanus*) larvae. Can. Tech. Rep. Fish. Aquat. Sci. 274, vii + 20 p.
- Gerlotto, F., Brehmer, P., Buestel, D., and Sanguinède, F. 2001. A method of acoustic monitoring of mussel longline ground using vertical echosounder and multibeam sonar ICES CM 2001/R:01, 14 p.
- Gibbs, M.M., James, M.R., Pickmere, S.E., Woods, P.H., Shakespeare, B.S., Hickman, R.W., and Illingworth, J. 1991. Hydrodynamics and water column properties at six stations associated with mussel farming in Pelorus Sound, 1984-1985. N. Z. J. Mar. Freshw. Res. 25: 239-254.
- Gibbs, M.T. 2004. Interactions between bivalve shellfish farms and fishery resources. Aquaculture, 240: 267-296.
- Gilbert, F., Souchu, P., Bianchi, M., and Bonin, P. 1997. Influence of shellfish farming activities on nitrification, nitrate reduction to ammonium and denitrification at the water-sediment interface of the Thau lagoon, France. Mar. Ecol. Prog. Ser. 151: 143-153.
- Giles, H. 2006. Dispersal and remineralisation of biodeposits: ecosystem impacts of mussel aquaculture. PhD dissertation, University of Waikato, Hamilton.
- Giles, H. 2009. Modelling the dispersal of biodeposits from mussel farms: The importance of simulating biodeposit erosion and decay. Aquaculture, 291: 168-178.
- Giles, H., and Pilditch, C.A. 2004. Effects of diet on sinking rates and erosion thresholds of mussel *Perna canaliculus* biodeposits. Mar. Ecol. Prog. Ser. 282: 205-219.
- Giles, H., and Pilditch, C.A. 2006. Effects of mussel (*Perna canaliculus*) biodeposit decomposition on benthic respiration and nutrient fluxes. Mar. Biol. 150: 251-261.
- Giles, H., Pilditch, C.A., and Bell, D.G. 2006. Sedimentation from mussel (*Perna canaliculus*) culture in the Firth of Thames, New Zealand: Impacts on sediment oxygen and nutrient fluxes. Aquaculture, 261: 125-140.
- Godet, L., Fournier, J., van Katwijk, M., Olivier, F., Le Mao, P., and Retière, C. 2008. Before and after wasting disease in common eelgrass *Zostera marina* along the French Atlantic coasts: a general overview and first accurate mapping. Dis. Aquat. Org. 79: 249-255.
- González-Gurriarán, E. 1986. Seasonal changes of benthic megafauna in the Ría de Muros e Noia (Galicia, Northwest Spain). II. Decapod crustaceans (Brachyura). Mar. Biol. 92: 201-210.
- Grant, C. 2010. Rôle des installations mytilicoles dans la structuration spatiale des communautés benthiques ; cas des assemblages de sédiments grossiers de l'est de l'archipel Chausey (France). MSc thesis, Université de Québec à Rimouski, Rimouski.
- Grant, J., Cranford, P., Hargrave, B., Carreau, M., Schofield, B., Armsworthy, S., Burdett-Coutts, V., and Ibarra, D. 2005. A model of aquaculture biodeposition for multiple estuaries and field validation at blue mussel (*Mytilus edulis*) culture sites in eastern Canada. Can. J. Fish. Aquat. Sci. 62: 1271-1285.
- Grant, J., Hatcher, A., Scott, D.B., Pocklington, P., Schafer, C.T., and Winters, G.V. 1995. A multidisciplinary approach to evaluating impacts of shellfish aquaculture on benthic communities. Estuaries, 18: 124-144.
- Grant, J., Stenton-Dozey, J.M.E., Monteiro, P., Pitcher, G., and Heasman, K. 1998. Shellfish culture in the Benguela System: a carbon budget of Saldanha Bay for raft culture of *Mytilus galloprovincialis*. J. Shellfish. Res. 17: 41-49.
- Green, S., Visser, A.W., Titelman, J., and Kiørboe, T. 2003. Escape responses of copepod nauplii in the flow field of the blue mussel, *Mytilus edulis*. Mar. Biol. 142: 727-733.

- Grenz, C., Hermin, M.-N., Baudinet, D., and Daumas, R. 1990. *In situ* biochemical and bacterial variation of sediments enriched with mussel biodeposits. *Hydrobiologia*, 207: 153-160.
- Guichard, F., Bourget, E., and Robert, J.L. 2001. Scaling the influence of topographic heterogeneity on intertidal benthic communities: Alternate trajectories mediated by hydrodynamics and shading. *Mar. Ecol. Prog. Ser.* 217: 27-41.
- Gutiérrez, J.L., Jones, C.G., Strayer, D.L., and Iribarne, O.O. 2003. Mollusks as ecosystem engineers: the role of shell production in aquatic habitats. *Oikos*, 101: 79-90.
- Guyondet, T., Roy, S., Koutitonsky, V.G., Grant, J., and Tita, G. 2010. Integrating multiple spatial scales in the carrying capacity assessment of a coastal ecosystem for bivalve aquaculture. *J. Sea Res.* 64: 341-359.
- Hargrave, B.T., Doucette, L.I., Cranford, P.J., Law, B.A., and Milligan, T.G. 2008. Influence of mussel aquaculture on sediment organic enrichment in a nutrient-rich coastal embayment. *Mar. Ecol. Prog. Ser.* 365: 137-149.
- Hargrave, B.T., Phillips, G.A., Doucette, L.I., White, M.J., Milligan, T.G., Wildish, D.J., and Cranston, R.E. 1997. Assessing benthic impacts of organic enrichment from marine aquaculture. *Water Air Soil Pollut.* 99: 641-650.
- Hartstein, N.D., and Rowden, A.A. 2004. Effect of biodeposits from mussel culture on macroinvertebrate assemblages at sites of different hydrodynamic regime. *Mar. Environ. Res.* 57: 339-357.
- Hartstein, N.D., and Stevens, C.L. 2005. Deposition beneath long-line mussel farms. *Aquacultural Engineering* 33: 192-213.
- Hatcher, A., Grant, J., and Schofield, B. 1994. Effects of suspended mussel culture (*Mytilus* spp.) on sedimentation, benthic respiration and sediment nutrient dynamics in a coastal bay. *Mar. Ecol. Prog. Ser.* 115: 219-235.
- Heasman, K.G. 1996. The influence of oceanographic conditions and culture methods on the dynamics of mussel farming in Saldanha Bay, South Africa. MSc thesis, Rhodes University, Grahamstown.
- Heilskov, A.C., Alperin, M., and Holmer, M. 2006. Benthic fauna bio-irrigation effects on nutrient regeneration in fish farm sediments. *J. Exp. Mar. Biol. Ecol.* 339: 204-225.
- Heilskov, A.C., and Holmer, M. 2001. Effects of benthic fauna on organic matter mineralization in fish-farm sediments: importance of size and abundance. *ICES J. Mar. Sci.* 58: 427-434.
- Henriksen, K., and Kemp, W.M. 1988. Nitrification in estuarine and coastal marine sediments. *In* Nitrogen cycling in coastal marine environments. *Edited by* T.H. Blackburn and J. Sorensen. J. Wiley & Sons, Chichester.
- Herman, P.M.J. 2007. Managing Benthic Ecosystems in Relation to Physical Forcing and Environmental Constraints (MaBenE): Final Report EVK3-CT-2002-00071, 107 p. Netherlands Institute of Ecology (NIOO-KNAW).
- Holmer, M., Black, K., Duarte, C.M., Marbà, N., and Karakassis, I. 2008. Aquaculture in the ecosystem. Springer.
- Holmer, M., Wildish, D.J., and Hargrave, B. 2005. Organic enrichment from marine finfish aquaculture and effects on sediment biogeochemical processes. *In* The handbook of environmental chemistry, Vol 5M. Water pollution. *Edited by* B.T. Hargrave. Springer-Verlag, Berlin. pp. 181-206.
- Hoover, R.A., and Purcell, J.E. 2009. Substrate preferences of scyphozoan *Aurelia labiata* polyps among common dock-building materials. *Hydrobiologia*, 616: 259-267.

- Houliez, E. 2007. Impact de la restructuration conchylicole sur la structure des peuplements endofauniques intertidaux de la baie du mont Saint-Michel. MSc thesis, Université du Littoral Côte d'Opale, Calais.
- Iglesias, J. 1981. Spatial and temporal changes in the demersal fish community of the Ria de Arosa (NW Spain). *Mar. Biol.* 65: 199-208.
- Iglesias, J.I.P., Urrutia, M.B., Navarro, E., and Ibarrola, I. 1998. Measuring feeding and absorption in suspension-feeding bivalves: an appraisal of the biodeposition method. *J. Exp. Mar. Biol. Ecol.* 219: 71-86.
- Inglis, G.J., and Gust, N. 2003. Potential indirect effects of shellfish culture on the reproductive success of benthic predators. *J. Appl. Ecol.* 40: 1077-1089.
- Jaramillo, E., Bertran, C., and A., B. 1992. Mussel biodeposition in an estuary of southern Chile. *Mar. Ecol. Prog. Ser.* 82: 85-94.
- Jensen, A.C., Collins, K.J., and Lockwood, A.P.M. 2000. Artificial reefs in European seas. Kluwer, Dordrecht.
- Jiang, W.M., and Gibbs, M.T. 2005. Predicting the carrying capacity of bivalve shellfish culture using a steady, linear food web model. *Aquaculture*, 244: 171-185.
- Kaspar, H.F., Gillespie, P., Boyer, L.F., and Mackenzie, A.L. 1985. Effects of mussel aquaculture on the nitrogen cycle of benthic communities in Kenepuru Sound, Marlborough Sound, New Zealand. *Mar. Biol.* 85: 127-136.
- Kautsky, N., and Evans, S. 1987. Role of biodeposition by *Mytilus edulis* in the circulation of matter and nutrients in a Baltic coastal ecosystem. *Mar. Ecol. Prog. Ser.* 38: 201-212.
- Keeley, N., Forrest, B., Hopkins, G., Gillespie, P., Knight, B., Webb, S., Clement, D., and Gardner, J. 2009. Review of the ecological effects of farming shellfish and other non-fish species in New Zealand Cawthron Report No. 1476, 174 + xiv p. Cawthron Institute.
- Khalaman, V.V. 2001a. Fouling communities of mussel aquaculture installations in the White Sea. *Rus. J. Mar. Biol* 27: 227-237.
- Khalaman, V.V. 2001b. Succession of fouling communities on an artificial substrate of a mussel culture in the White Sea. *Rus. J. Mar. Biol* 27: 345-352.
- Kreeger, D.A., and Newell, R.I.E. 1996. Ingestion and assimilation of carbon from cellulolytic bacteria and heterotrophic flagellates by the mussels *Geukensia demissa* and *Mytilus edulis* (Bivalvia, Mollusca). *Aquat Microb Ecol* 11:205-214. *Aquat. Microb. Ecol.* 11: 205-214.
- Lawrence, J.E., Grant, J., Quilliam, M.A., Bauder, A.G., and Cembella, A.D. 2000. Colonization and growth of the toxic dinoflagellate *Prorocentrum lima* and associated fouling macroalgae on mussels in suspended culture. *Mar. Ecol. Prog. Ser.* 201: 147-154.
- LeBlanc, A.R., Landry, T., and Miron, G. 2002. Fouling organisms in a mussel cultivation bay: their effect on nutrient uptake and release. *Can. Tech. Rep. Fish. Aquat. Sci.* 2431, vii + 16 p.
- Leblanc, A.R., Landry, T., and Miron, G. 2003a. Fouling organisms of the blue mussel *Mytilus edulis*: their effect on nutrient uptake and release. *J. Shellfish. Res.* 22: 633-638.
- LeBlanc, A.R., Landry, T., and Miron, G. 2003b. Identification of fouling organisms covering mussel lines and impact of a common defouling method on the abundance of foulers in Tracadie Bay, Prince Edward Island. *Can. Tech. Rep. Fish. Aquat. Sci.* 2477, vii + 18 p.
- Lehane, C., and Davenport, J. 2002. Ingestion of mesozooplankton by three species of bivalve; *Mytilus edulis*, *Cerastoderma edule* and *Aequipecten opercularis*. *J. Mar. Biol. Assoc. U.K* 82: 615-619.

- Lehane, C., and Davenport, J. 2006. A 15-month study of zooplankton ingestion by farmed mussels (*Mytilus edulis*) in Bantry Bay, Southwest Ireland. *Estuar. Coast. Shelf Sci.* 67: 645-652.
- Leonard, M. 2004. Evaluation et caractérisation de la chute de moules dans la lagune de Havre-aux-Maisons aux Iles-de-la-Madeleine, Québec. BSc thesis, ENITA Clermont-Ferrand.
- Levasseur, M., Couture, J.-Y., Weise, A., Michaud, S., Elbrächter, M., Sauvé, G., and Bonneau, E. 2003. Pelagic and epiphytic summer distributions of *Prorocentrum lima* and *P. mexicanum* at two mussel farms in the Gulf of St. Lawrence, Canada. *Aquat. Microb. Ecol.* 30: 283-293.
- Lloyd, B.D. 2003. Potential effects of mussel farming on New Zealand's marine mammals and seabirds: a discussion paper, 1-35 pp. Department of Conservation, Te Papa Atawhai, Wellington.
- Lo, W.T., Purcell, J.E., Hung, J.J., Su, H.M., and Hsu, P.K. 2008. Enhancement of jellyfish (*Aurelia aurita*) populations by extensive aquaculture rafts in a coastal lagoon in Taiwan. *ICES J. Mar. Sci.* 65: 453-461.
- Loladze, I., and Elser, J.J. 2011. The origins of the Redfield nitrogen-to-phosphorus ratio are in a homeostatic protein-to-rRNA ratio. *Ecol. Lett.*
- Loo, L.O., and Rosenberg, R. 1989. Bivalve suspension-feeding dynamics and benthic-pelagic coupling in an eutrophicated marine bay. *J. Exp. Mar. Biol. Ecol.* 130: 253-276.
- Lutz-Collins, V., Quijón, P.A., and Davidson, J. 2009a. Blue mussel fouling communities: polychaete composition in relation to mussel stocking density and seasonality of mussel deployment and sampling. *Aquacult. Res.* 40: 1789-1792.
- Lutz-Collins, V., Ramsay, A., Quijón, P.A., and Davidson, J. 2009b. Invasive tunicates fouling mussel lines: evidence of their impact on native tunicates and other epifaunal invertebrates. *Aquatic Invasions*, 4: 213-220.
- Maar, M., Nielsen, T.G., and Petersen, J.K. 2008. Depletion of plankton in a raft culture of *Mytilus galloprovincialis* in Ría de Vigo, NW Spain. II. Zooplankton. *Aquat. Biol.* 4: 127-141.
- Makita, S., and Saeki, H. 2004. Influence of aquaculture facilities on water flow at semi-closed water areas. *Ocean '04 - MTS/IEEE Techno-Ocean '04: Bridges across the Oceans - Conference Proceedings*, pp. 169-175.
- Marteil, L. 1979. La conchyliculture française, 3^e Partie: L'ostreiculture et la mytiliculture. *Revue des Travaux de l'Institut des Pêches Maritimes*, 43: 10-130.
- Mattsson, J., and Lindén, O. 1983. Benthic macrofauna succession under mussels, *Mytilus edulis* L. (Bivalvia), cultured on hanging long-lines. *Sarsia* 68: 97-102.
- Mazouni, N. 2004. Influence of suspended oyster cultures on nitrogen regeneration in a coastal lagoon (Thau, France) *Mar. Ecol. Prog. Ser.* 276: 103-113.
- Mazouni, N., Gaertner, J.C., and Deslous-Paoli, J.M. 1998. Influence of oyster culture on water column characteristics in a coastal lagoon (Thau, France). *Hydrobiologia*, 373/374: 149-156.
- Mazouni, N., Gaertner, J.C., and Deslous-Paoli, J.M. 2001. Composition of biofouling communities on suspended oyster cultures: an in situ study of their interactions with the water column. *Mar. Ecol. Prog. Ser.* 214: 93-102.
- Mazouni, N., Gaertner, J.C., Deslous-Paoli, J.M., Landrein, S., and Geringer d'Oedenberg, M. 1996. Nutrient and oxygen exchanges at the water-sediment interface in a shellfish farming lagoon (Thau, France). *J. Exp. Mar. Biol. Ecol.* 205: 91-113.

- McKindsey, C.W., Landry, T., O'Beirn, F.X., and Davies, I.M. 2007. Bivalve aquaculture and exotic species: a review of ecological considerations and management issues. *J. Shellfish. Res.* 26: 281-294.
- McKindsey, C.W., Lecuona, M., Huot, M., and Weise, A.M. 2009. Biodeposit production and benthic loading by farmed mussels and associated tunicate epifauna in Prince Edward Island. *Aquaculture*, 295: 44-51.
- McKindsey, C.W., Thetmeyer, H., Landry, T., and Silvert, W. 2006. Review of recent carrying capacity models for bivalve culture and recommendations for research and management. *Aquaculture*, 261: 451-462.
- Michaud, E., Aller, R.C., and Stora, G. 2010. Sedimentary organic matter distributions, burrowing activity, and biogeochemical cycling: Natural patterns and experimental artifacts. *Estuar. Coast. Shelf Sci.* 90: 21-34.
- Michaud, E., Desrosiers, G., Mermillod-Blondin, F., Sundby, B., and Stora, G. 2006. The functional group approach to bioturbation: II. The effects of the *Macoma balthica* community on fluxes of nutrients and dissolved organic carbon across the sediment-water interface. *J. Exp. Mar. Biol. Ecol.* 337: 178-189.
- Miller, D.C., Norkko, A., and Pilditch, C.A. 2002. Influence of diet on dispersal of horse mussel *Atrina zelandica* biodeposits. *Mar. Ecol. Prog. Ser.* 242: 153-167.
- Miron, G., Landry, T., Archambault, P., and Frenette, B. 2005. Effects of mussel culture husbandry practices on various benthic characteristics. *Aquaculture*, 250: 138-154.
- Miron, G., Landry, T., and MacNair, N. 2002. Predation potential by various epibenthic organisms on commercial bivalves species in Prince Edward Island: preliminary results. *Can. Tech. Rep. Fish. Aquat. Sci.* 2392, ix + 33 p.
- Mirto, S., La Rosa, T., Danovaro, R., and Mazzola, A. 2000. Microbial and Meiofaunal response to intensive mussel-farm biodeposition in coastal sediments of the Western Mediterranean. *Mar. Pollut. Bull.* 40: 244-252.
- Morrisey, D.J., Cole, R.G., Davey, N.K., Handley, A.L., Bradley, A., Brown, S.N., and Madaraz, A.L. 2006. Abundance and diversity of fish on mussel farms in New Zealand. *Aquaculture*, 252: 277-288.
- Murray, L.G., Newell, C.R., and Seed, R. 2007. Changes in the biodiversity of mussel assemblages induced by two methods of cultivation. *J. Shellfish. Res.* 26: 153-162.
- Navarrete, S.A., Wieters, E.A., Broitman, B., and Castilla, J.C. 2005. Scales of benthic–pelagic coupling and the intensity of species interactions: From recruitment limitation to top-down control. *Proc. Nat. Acad. Sci. U. S. A.* 102: 18046-18051.
- Navarro, J.M., and Thompson, R.J. 1997. Biodeposition by the horse mussel *Modiolus modiolus* (Dillwyn) during the Spring diatom bloom. *J. Exp. Mar. Biol. Ecol.* 209: 1-13.
- Nelson, P.A. 2003. Marine fish assemblages associated with fish aggregating devices (FADs): effects of fish removal, FAD size, fouling communities, and prior recruits. *Fish. Bull.* 101: 835-850.
- Netto, S.A., and Valgas, I. 2010. The response of nematode assemblages to intensive mussel farming in coastal sediments (Southern Brazil). *Environ. Monit. Assess.* 162: 81-93.
- Newell, R.I.E. 2004. Ecosystem influences of natural and cultivated populations of suspension-feeding bivalve molluscs: a review. *J. Shellfish. Res.* 23: 51-61.
- Newell, R.I.E., Cornwell, J.C., and Owens, M.S. 2002. Influence of simulated bivalve biodeposition and microphytobenthos on sediment nitrogen dynamics: A laboratory study. *Limnol. Oceanogr.* 47: 1367-1379.

- Newell, R.I.E., and Koch, E.W. 2004. Modeling seagrass density and distribution in response to changes in turbidity stemming from bivalve filtration and seagrass sediment stabilization. *Estuaries*, 27: 793-806.
- Nikodic, J. 1981. Dynamique sedimentaire dans la partie occidentale de la baie du Mont Saint-Michel. Influence des installations ostricoles. PhD dissertation, Université de Nantes, Nantes.
- Nizzoli, D., Welsh, D.T., Fano, E.A., and Viaroli, P. 2006. Impact of clam and mussel farming on benthic metabolism and nitrogen cycling, with emphasis on nitrate reduction pathways. *Mar. Ecol. Prog. Ser.* 315: 151-165.
- Okumus, I., and Stirling, H.P. 1998. Seasonal variations in the meat weight, condition index and biochemical composition of mussels (*Mytilus edulis* L.) in suspended culture in two Scottish sea lochs. *Aquaculture*, 159: 249-261.
- Ólafsson, E.B., Peterson, C.H., and Ambrose, W.G., Jr. 1994. Does recruitment limitation structure populations and communities of macro-invertebrates in marine soft sediments: the relative significance of pre- and post settlement processes. *Oceanogr. Mar. Biol. Ann. Rev.* 32: 65-109.
- Olaso Toca, I. 1979. Biología de los equinodermos de la Ría de Arosa. *Bol. Inst. Espa. Oceano.* 5: 81-127.
- Olaso Toca, I. 1982. Ecología de los equinodermos de la Ría de Arosa. *Bol. Inst. Espa. Oceano.* 7: 4-29.
- Ottman, F., and Sornin, J.M. 1985. Observations on sediment accumulation as a result of mollusk culture systems in France. *In Proceedings of the International Symposium on Utilization of Coastal Ecosystems: Planning, Pollution and Productivity*, 21-27 Nov 1982, Rio Grande, Brazil. *Edited by* L.N. Chao and W.W. Kirby-Smith. pp. 329-337.
- Pearson, T.H., and Rosenberg, R. 1978. Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. *Oceanogr. Mar. Biol. Ann. Rev.* 16: 229-311.
- Pérez Camacho, A., and Beiras, U.L. 1995. Growth of mussels (*Mytilus edulis galloprovincialis*) on cultivation rafts: influence of seed source, cultivation site and phytoplankton availability. *Aquaculture*, 138: 349-362.
- Petersen, J.K. 2004. Grazing on pelagic primary producers - the role of benthic suspension feeders in estuaries. *In Estuarine Nutrient Cycling: the Influence of Primary Producers. Edited by* S.L. Nielsen, G.T. Banta and M.F. Pedersen. Kluwer, Dordrecht. pp. 129-152.
- Petersen, J.K., Nielsen, T.G., van Duren, L., and Maar, M. 2008. Depletion of plankton in a raft culture of *Mytilus galloprovincialis* in Ría de Vigo, NW Spain. I. Phytoplankton. *Aquat. Biol.* 4: 113-125.
- Plew, D.R., Stevens, C.L., Spigel, R.H., and Hartstein, N.D. 2005. Hydrodynamic implications of large offshore mussel farms. *IEEE J. Ocean. Eng.* 30: 95-108.
- Pregnall, M.M. 1993. Regrowth and recovery of eelgrass (*Zostera marina*) and recovery of benthic community structure in areas disturbed by commercial oyster culture in the South Slough National Estuarine Research Reserve, Oregon. MSc thesis, Bard College, Annandale-On-Hudson.
- Prins, T.C., Smaal, A.C., and Dame, R.F. 1998. A review of the feedbacks between bivalve grazing and ecosystem processes. *Aquat. Ecol.* 31: 349-359.
- Ramsay, A., Davidson, J., Landry, T., and Stryhn, H. 2008. The effect of mussel seed density on tunicate settlement and growth for the cultured mussel, *Mytilus edulis*. *Aquaculture*, 275: 194-200.

- Redfield, A.C. 1934. On the proportions of organic derivatives in sea water and their relation to the composition of plankton. *In* James Johnstone Memorial Volume. *Edited by* R.J. Daniel. University Press of Liverpool, Liverpool. pp. 176-192.
- Redfield, A.C., Ketchum, P.H., and Richards, F.A. 1963. The influence of organisms on the composition of seawater. *In* *In the Sea*, Vol. 2. *Edited by* M.N. Hill. Wiley Interscience, New York. pp. 25-77.
- Retière, C. 1979. Contribution à la connaissance des peuplements benthiques du golfe normano-breton. PhD dissertation, Université de Rennes, Rennes.
- Ricciardi, A., and Bourget, E. 1999. Global patterns of macroinvertebrate biomass in marine intertidal communities. *Marine Ecology Progress Series* 185: 21-35.
- Richard, M., Archambault, P., Thouzeau, G., and Desrosiers, G. 2006. Influence of suspended mussel lines on the biogeochemical fluxes in adjacent water in the Îles-de-la-Madeleine (Quebec, Canada). *Can. J. Fish. Aquat. Sci.* 63: 1198-1213.
- Richard, M., Archambault, P., Thouzeau, G., and Desrosiers, G. 2007a. Summer influence of 1 and 2 yr old mussel cultures on benthic fluxes in Grande-Entrée lagoon, Îles-de-la-Madeleine (Québec, Canada). *Mar. Ecol. Prog. Ser.* 338: 131–143.
- Richard, M., Archambault, P., Thouzeau, G., McKindsey, C.W., and Desrosiers, G. 2007b. Influence of suspended scallop cages and mussel lines on pelagic and benthic biogeochemical fluxes in Havre-aux-Maisons Lagoon, Îles-de-la-Madeleine (Quebec, Canada). *Can. J. Fish. Aquat. Sci.* 64: 1491-1505.
- Richardson, A.J., Bakun, A., Hays, G.C., and Gibbons, M.J. 2009. The jellyfish joyride: causes, consequences and management responses to a more gelatinous future. *Trends Ecol. Evol.* 24: 312-322.
- Riethmüller, R., Jäger, N., Häse, C., Fernandes, L., and Neves, R. 2006a. Flow patterns around and within a raft mussel farm in the Ria de Vigo, Spain Report No. D3.2b, 31 p. GKSS, Hamburg.
- Riethmüller, R., Jäger, N., Häse, C., and Herman, P.M.J. 2006b. The patterns of suspended particulate matter within a raft mussel farm in the Ria de Vigo, Spain Report No. D2.2c, 26 p. GKSS, Hamburg.
- Robichaud, L.M. 2008. Influence de la mytiliculture et de l'ascidie envahissante *styela clava* sur les communautés de macroinvertébrés benthiques à l'Île-du-Prince-Édouard. MSc thesis, Université de Québec à Rimouski, Rimouski.
- Romero, P., González-Gurriarán, E., and Penas, E. 1982. Influence of mussel rafts on spatial and seasonal abundance of crabs in the Ría de Arousa, North-West Spain. *Mar. Biol.* 72: 201-210.
- Rosenberg, R. 2001. Marine benthic faunal successional stages and related sedimentary activity. *Sci. Mar.* 65: 107-119.
- Rountree, R.A. 1989. Association of fishes with fish aggregation devices: Effects of structure size on fish abundance. *Bull. Mar. Sci.* 44: 960-972.
- Ruiz, G.M., and Carlton, J.T. 2003. Invasive species: vectors and management strategies. Island Press, Washington.
- Rumrill, S.S., and Poulton, V.K. 2004. Ecological role and potential impacts of molluscan shellfish culture in the estuarine environment of Humboldt Bay, CA - Annual Report, 44 p. Oregon Department of State Lands, South Slough National Estuarine Research Reserve, Estuarine and Coastal Science Laboratory, Charleston.
- Saranchova, O.L., and Kulakovskii, É.E. 1982. Effect of environmental salinity on different developmental stages of sea stars *Asterias rubens* and mussels *Mytilus edulis*. *Sov. J. Mar. Biol.* 8: 32-36.

- Seaman, W.J., Jr. 2000. Artificial reef evaluation: with application to natural marine habitats. CRC Press, Boca Raton.
- Sequeira, A., Ferreira, J.G., Hawkins, A.J.S., Nobre, A., Lourenço, P., Zhang, X.L., Yan, X., and Nickell, T. 2008. Trade-offs between shellfish aquaculture and benthic biodiversity: A modelling approach for sustainable management. *Aquaculture*, 274: 313-328.
- Shelby, B., and Heberlein, T.A. 1984. A conceptual framework for carrying capacity determination. *Leisure Sciences: An Interdisciplinary Journal*, 6: 433 - 451.
- Smith, A., Nikora, V., Ross, A., and Wake, G. 2006. A lattice Boltzmann-based model of plankton–flow interaction around a mussel cluster. *Ecol. Model.* 192: 645-657.
- Sornin, J.-M., Feuillet, M., Héral, M., and Deslous-Paoli, J.-M. 1983. Effet des biodépôts de l'huître *Crassostrea gigas* sur l'accumulation de matière organique dans les parcs du bassin de Marennes-Oléron. *J. Moll. Stud.* 12: 185-197.
- Sornin, J.M. 1981. Processus sédimentaires et biodeposition liés à différents modes de conchyliculture. PhD dissertation, Université de Nantes, Nantes.
- Souchu, P., Vaquer, A., Collos, Y., Landrein, S., Deslous-Paoli, J.M., and Bertrand Bibent, B. 2001. Influence of shellfish farming activities on the biogeochemical composition of the water column in Thau lagoon. *Mar. Ecol. Prog. Ser.* 218: 141-152.
- Spencer, B.E. 2002. *Molluscan Shellfish Farming*. Blackwell Publishing, Malden.
- Stenton-Dozey, J., Probyn, T., and Busby, A. 2001. Impact of mussel (*Mytilus galloprovincialis*) raft-culture on benthic macrofauna, in situ oxygen uptake, and nutrient fluxes in Saldanha Bay, South Africa. *Can. J. Fish. Aquat. Sci.* 58: 1021-1031.
- Stenton-Dozey, J.M.E., Jackson, L.F., and Busby, A.J. 1999. Impact of mussel culture on macrobenthic community structure in Saldanha Bay, South Africa. *Mar. Pollut. Bull.* 39: 357-366.
- Stevens, C., Plew, D., Hartstein, N., and Fredriksson, D. 2008. The physics of open-water shellfish aquaculture. *Aquacult. Eng.* 38: 145-160.
- Strohmeier, T., Aure, J., Duinker, A., Castberg, T., Svardal, A., and Strand, O. 2005. Flow reduction, seston depletion, meat content and distribution of diarrhetic shellfish toxins in a long-line blue mussel farm. *J. Shellfish. Res.* 24: 15-24.
- Strohmeier, T., Duinker, A., Strand, O., and Aure, J. 2008. Temporal and spatial variation in food availability and meat ratio in a longline mussel farm (*Mytilus edulis*). *Aquaculture*, 276: 83-90.
- Tallis, H.M., Ruesink, J.L., Dumbauld, B., Hacker, S., and Wisehart, L.M. 2009. Oysters and aquaculture practices affect eelgrass density and productivity in a Pacific Northwest estuary. *J. Shellfish. Res.* 28: 251-261.
- Taylor, J.J., Southgate, P.C., and Rose, R.A. 1997. Fouling animals and their effect on the growth of silver-lip oysters, *Pinctada maxima* (Jameson) in suspended culture. *Aquaculture*, 153: 31-40.
- Tenore, K.R., Boyer, L.F., Cal, R.M., Corral, J., Garcia-Fernandez, C., Gonzalez, N., Gonzalez-Gurriaran, E., Hanson, R.B., Iglesias, J., Krom, M., Lopez-Jamar, E., McClain, J., Pamatmat, M.M., Perez, A., Rhoads, D.C., de Santiago, G., Tietjen, J., Westrich, J., and Windom, H.L. 1982. Coastal upwelling in the Rias Bajas, NW Spain: Contrasting the benthic regimes of the Rias de Arosa and de Muros. *J. Mar. Res.* 40: 701-772.
- Tenore, K.R., and Dunstan, W.M. 1973. Comparison of feeding and biodeposition of three bivalves at different food levels. *Mar. Biol.* 21: 190-195.
- Tenore, K.R., and González, N. 1976. Food chain patterns in the Ria de Arosa, Spain: an area of intense mussel aquaculture. *In Proceedings of the 10th European*

- Symposium on Marine Biology, Ostend, Belgium, September 17-23, 1975. Vol 2: Population dynamics of marine organisms in relation with nutrient cycling in shallow waters. *Edited by* G. Persoone and E. Jaspers. Universa Press, Wetteren. pp. 601-619.
- Titelman, J., and Kiørboe, T. 2003. Predator avoidance by nauplii. *Mar. Ecol. Prog. Ser.* 247: 137-149.
- Troost, K., Gelderman, E., Kamermans, P., Smaal, A.C., and Wolff, W.J. 2009. Effects of an increasing filter feeder stock on larval abundance in the Oosterschelde estuary (SW Netherlands). *J. Sea Res.* 61: 153-164.
- Valdemarsen, T., Kristensen, E., and Holmer, M. 2010. Sulfur, carbon, and nitrogen cycling in faunated marine sediments impacted by repeated organic enrichment. *Mar. Ecol. Prog. Ser.* 400: 37-53.
- Valiela, I. 1995. *Marine Ecological Processes*. Springer, New York.
- Vaudrey, J.M.P., Getchis, T., Shaw, K., Markow, J., Britton, R., and Kremer, J.N. 2009. Effects of oyster depuration gear on eelgrass (*Zostera marina* L.) in a low density aquaculture site in Long Island sound. *J. Shellfish. Res.* 28: 243-250.
- Walker, T.R., and Grant, J. 2009. Quantifying erosion rates and stability of bottom sediments at mussel aquaculture sites in Prince Edward Island, Canada. *J. Mar. Syst.* 75: 46-55.
- Wassmann, P. 1998. Retention versus export food chains: processes controlling sinking loss from marine pelagic systems. *Hydrobiologia*, 363: 29-57.
- Weise, A.M., Cromey, C.J., Callier, M.D., Archambault, P., Chamberlain, J., and McKindsey, C.W. 2009. Shellfish-DEPOMOD: Modelling the biodeposition from suspended shellfish aquaculture and assessing benthic effects. *Aquaculture*, 288: 239-253.
- Wisehart, L.M., Dumbauld, B.R., Ruesink, J.L., and Hacker, S.D. 2007. Importance of eelgrass early life history stages in response to oyster aquaculture disturbance. *Mar. Ecol. Prog. Ser.* 344: 71-80.
- Wong, W.H., Levinton, J.S., Twining, B.S., Fisher, N.S., Kelaher, B.P., and Alt, A.K. 2003. Assimilation of carbon from a rotifer by the mussels *Mytilus edulis* and *Perna viridis*: a potential food-web link. *Mar. Ecol. Prog. Ser.* 253: 175-182.
- Ysebaert, T., Hart, M., and Herman, P.M.J. 2009. Impacts of bottom and suspended cultures of mussels *Mytilus* spp. on the surrounding sedimentary environment and macrobenthic biodiversity. *Helgol. Mar. Res.* 63: 59-74.
- Zeldis, J., Felsing, M., and Wilson, J. 2006. Limits of acceptable change: a framework for managing marine farming. *Water & Atmosphere*, 14: 16-17.

Tables

Table 1. Overview of studies on the influence of mussel farms on benthic communities; only studies with some type of control location are included. Univariate diversity indices evaluated include: S - total number of species, N - total abundance, B - total biomass, H' - Shannon-Wiener diversity, d - Margalef's species richness, J' - Pielou's evenness, Hill's numbers N_1 and N_2 , ES_{100} - estimated number of genera, ITD – Index of trophic diversity, MI – Maturity index, $\Delta+$ - average taxonomic distinctness, and $\Lambda+$ - variation in taxonomic distinctness. Biotic indices evaluated include: I/D - indicator or dominant species, T - evaluation of trophic or taxonomic groups, and various derived indices (as indicated in table); Multivariate community structure analysis includes cluster analysis and various ordination techniques. Protocol indicates general sampling design, temporal replication, and sieve size used to retain infauna. Where multiple sites were studied, site names are listed as in the original references. Studies are divided into those that concentrated on infauna and those that concentrated on epibenthic macrofauna (crabs, starfish, fish, etc).

Reference and sites	Diversity	Biotic	Multivariate community structure	Protocol	Observations at farm site(s) relative to control station(s) or along transect(s)
<u>Benthic infauna studies</u>					
Callier et al. (2008), Canada - 2 longline farms	N, B, S, H', d, J'	$T, AMBI$	MDS-ANOSIM	Transect: 7 stations (0, 3, 6, 9, 15, 30, and 300 or 500 m); 1 date; 500 μ m	<p><u>Site HAM</u></p> <ul style="list-style-type: none"> • N, S, H', d lower; J' greater at 0 and 300 m • B greater at intermediate distances (due to 1 polychaete spp.) • AMBI suggests control site least degraded • Difference in benthic community structure <p><u>Site GE</u></p> <ul style="list-style-type: none"> • Dominance by deposit feeders (carnivores elsewhere) • No variation among stations for any other index
Chamberlain (2002), Chamberlain et al. (2001), Ireland, 2 longline farms, 1 raft site	N, S, H', d, J'	$I/D, ITI$	Cluster analysis, MDS-ANOSIM	<p>Longline sites: Transect : 3-4 stations site⁻¹ (0, 10, 20, and 40 m and 0, 10, and 30 m); 1 date; 500 μm</p> <p>Raft (site S): Transect : 4 stations and one further (control) station (0, 10, 20, 40 m and control at 50 m in different direction); 1 date; 500 μm</p>	<p><u>Site 1/A</u></p> <ul style="list-style-type: none"> • No variation among stations for diversity indices • Dominance of polychaetes • ITI not different among stations • No variation in multivariate structure <p><u>Site 2/B</u></p> <ul style="list-style-type: none"> • N greater but S, H', d, and J' lower • Dominance by deposit-feeders and opportunistic polychaetes • ITI reduced under farm and greatest at most distant • Clear differences in multivariate structure

						<u>Site S</u>
Christensen et al. (2003), New Zealand, longline farm	<i>N, S</i>	I/D	MDS	3 stations: below lines, between lines and 250 m from lines, 1 sampling date, 500 µm	<ul style="list-style-type: none"> No variation among stations for diversity indices Dominance of several opportunistic polychaetes Loss of a bivalve species, ITI not different among stations No difference in community structure <i>S</i> decreased Bioirrigating species decreased Opportunistic polychaetes species increased 	
Crawford et al. (2003), Australia, 2 longline farms with oysters and mussels	<i>N, S, H'</i>	<i>T</i>	Cluster analysis, ANOSIM	3 transects with 8 or 9 stations (middle 5 in farms), 1 date; 1 mm; and 2 video transects in farm, 1 upstream and 1 downstream.	<ul style="list-style-type: none"> <i>N, S, H'</i> did not vary within farms along transects Little variance observed with video transects Community structure varied little within farms along transects and, when it did, not in a way that suggested farm-related effects 	
da Costa and Nalesso (2006), Brazil, longline farm	<i>N, S, J', H'</i>		MDS-ANOSIM	Distance classes: 4 stations (0, 50, 200, 500 m); bi-monthly sampling (6 dates)	<ul style="list-style-type: none"> <i>N</i> lower and <i>H'</i> greater Differences in community structure Large temporal variation in all indices 	
Danovaro et al. (2004), Italy (meiofauna), longline farm	<i>N, S</i>	<i>T</i>		3 stations within farm and 3 locations 600 m distant (around farm), 4 dates (seasons), 37 µm	<ul style="list-style-type: none"> Variations between sampling period > between sites Temporal, but no farm-specific variation in <i>N, S</i> Community structure (taxonomic groups) not different 	
Fabi et al.(2009) Italy, longline farm	<i>N, S, H', d, J'</i>	<i>T</i>	Cluster analysis, MDS-ANOSIM	2 stations within and 2 stations upstream of farm, and transect downstream (0, 30, 60, 120, and 300 m), 4 dates (seasons), 500 µm	<ul style="list-style-type: none"> Temporal variation in all measures No variation between stations within and upstream of site or along gradient for diversity indices Deposit feeders more prevalent in farms and filter feeders outside of farms No multivariate effects relative to stations within farm 	
Grant (2010), France, 3 <i>bouchot</i> farms	<i>N, S, H', J', Δ+, A+</i>	I/D, AMBI	MDS-PERMANOVA	Stations at 4 distances (0, 1, 5, 12.5 m) upstream and downstream of <i>bouchots</i> in 3 farms (same design in 3 reference areas), 1 date, 2 mm	<ul style="list-style-type: none"> All sites dominated by polychaetes and bivalves Dominant bivalve species more abundant at 0 m in farm sites Other species more or less abundant in farm sites <i>N</i> greater adjacent to <i>bouchots</i> but not generally in <i>bouchot</i> sites <i>S</i> lower adjacent to <i>bouchots</i> but not generally in <i>bouchot</i> sites Trend for <i>H'</i> and <i>J'</i> to be lower in <i>bouchot</i> sites <i>Δ+</i> did not differ between <i>bouchot</i> and reference sites <i>A+</i> greater adjacent to <i>bouchots</i> but not generally in <i>bouchot</i> sites Trend for AMBI values to be greater in mussel sites and this was reflected by distribution of organisms in ecological groups 	
Grant et al. (1995), Canada, longline farm	<i>N, S, B, H'</i>	I/D	ABC plot analysis, Cluster analysis	1 farm station and 1 control station, 30 m distant, 9 dates (4 seasons), 500 µm	<ul style="list-style-type: none"> Temporal variation for all measures <i>N</i> lower, <i>H'</i> higher Similar species composition Greater abundance of predatory and scavenging species Clear differences in multivariate community structure 	

Hartstein and Rowden (2004), New Zealand, 3 longline farms		<i>T</i>	MDS-ANOSIM	4 stations in each farm and in each of 4 paired control sites, 4 dates (seasons), 1 mm	<p><u>Farms CC and EB (weak current regime)</u></p> <ul style="list-style-type: none"> • Variation between sites > variation between periods • Dominance of opportunistic polychaetes • Clear differences in multivariate community structure <p><u>Farm BP (strong current regime)</u></p> <ul style="list-style-type: none"> • No difference in community structure
Kaspar et al. (1985), New Zealand, longline farm	Diversity, <i>B</i>		Descriptive	1 farm site and 1 control site, 1 km distant, 2 dates, 1.68 mm (total dry weights)	<ul style="list-style-type: none"> • <i>B</i> did not differ between sites • Diversity lower (not qualified) – only polychaetes present • Dominance of polychaetes • Hard substrate-associated species on bottom
(Mattsson and Lindén 1983), Sweden, longline farm	<i>N, B, S, H'</i>	<i>T</i>	Cluster analysis	1 transect, 5 stations (2 under mussel lines, each separated by 10 m), twice yearly for 9 dates, including post-establishment period, harvesting and reseeded periods, and second site with 3 stations (1 under) for 3 dates and reference sites for 1 and 3 dates, 500 µm	<ul style="list-style-type: none"> • Initially no difference among stations • Loss of some species (brittle stars and others later on) • Dominance by opportunistic polychaetes • <i>N, B, H'</i> decreased • <i>H'</i> and <i>S</i> increased following harvesting
Miron et al. (2005), Canada, longline farm area	<i>N, S, H', J',</i> dominance		MDS, BIOENV	Sampled throughout bay with farms to evaluate links between husbandry and benthic conditions, 1 date, 1 mm	<ul style="list-style-type: none"> • No relationships between diversity measures and husbandry practices • Weak correlations with husbandry characteristics and multivariate community structure
Mirto et al. (2000), Italy, longline farm (meiofauna)	<i>N, S</i>	<i>T</i>		1 farm station and 1 control station, 800 m distant, 12 dates (1 year), 37 µm	<ul style="list-style-type: none"> • <i>N</i> decreased, especially for kinorhynch, ostracods, and turbellarians. • Altered community structure
Netto and Valgas (2010), Brazil, longline farm areas (nematodes)	<i>N, N₁, N₂,</i> <i>ES₁₀₀</i>	ITD, MI	MDS-ANOSIM, PCA	3 farm areas in bay, 3 paired control areas (300 m distant), each with 3 stations, 4 dates (1 year), 63 µm	<ul style="list-style-type: none"> • <i>N</i> did not differ; all other indices decreased • Proportion of selective deposit feeders greater and epigrowth feeders lesser • Temporal variation in multivariate community structure only observed in control sites; altered community structure
Robichaud (2008), Canada, 8 longline farms	<i>N, B, S,</i> productivity		MDS-DISTLM	8 farm areas with reference stations in the same bays (> 300 m distant), 1 date, 500 µm	<ul style="list-style-type: none"> • All locations dominated by polychaetes • <i>N</i> reduced • <i>S</i> did not differ • <i>B</i> and productivity tended to be lower (not significantly different) • Community structure differed but not in a consistent manner
Stenton-Dozey et al. (1999), South-Africa, 1 + 9 raft farm areas	<i>N, B, S, H', d,</i> <i>J'</i>	<i>T</i>	ABC plot analysis, cluster analysis	Transects in 3 directions from farm area with stations under and at 250 m intervals to 750 m on 1 date; annual samples under 9 rafts for 3	<ul style="list-style-type: none"> • <i>d</i> lower • <i>H'</i> lower for 1 transect • <i>J'</i> invariable • All indices increased after raft removal (recovery) • Deposit-feeder dominated at all sites

			years; 500 μm		<ul style="list-style-type: none"> • Carnivores were second dominant at mussel farm, while suspension feeders were dominant at reference sites • Loss of scavengers following removal of rafts • “disturbed” communities under > 50% of rafts (ABC plots) • biomass typically reduced (5 of 6 possible contrasts by date) • dominance by depositores, detritivores and carnivores, elsewhere suspension feeders (2 sites) or detritivores and suspension feeders
Stenton-Dozey et al. (2001), South Africa, raft farm	<i>B</i>	<i>T</i>	1 farm and 3 reference sites, c.a., 500 m to 1.5 km distant, 2 dates (winter and summer), sieve size not stated		
Tenore and González (1976), Spain, raft farms	<i>S, H'</i>		1 farm and 1 reference site, locations not stated, 297 μm		<ul style="list-style-type: none"> • <i>H'</i> decreased • Other variables could not be evaluated given the data available
Ysebaert et al. (2009), Spain, raft farm	<i>N, B, S, H', J'</i>	<i>T</i>	MDS-ANOSIM 5 transects with stations every 100 m (6 transect ⁻¹), 3 transects between rafts with outer stations outside of farm areas, 2 transects outside of farm area; 1 date; 1 mm.		<ul style="list-style-type: none"> • <i>N</i> and <i>S</i> did not vary • <i>B, H'</i> and <i>J'</i> lower • Mostly dominated by surface and subsurface deposit feeders; suspension feeders and carnivores less dominant • Community structure differed from references
<u>Epibenthic megafauna studies</u>					
Clynick et al. (2008), Canada, 2 longline farms	<i>N, S</i>		MDS-ANOSIM Stations in farm (between lines of 1 and 2 yr old mussels), seagrass, and sand habitats; 3 dates (spring, summer, fall), beam trawls and crab traps.		<ul style="list-style-type: none"> • Community structure typically (11 of 12 site \times date contrasts) did not differ between mussel sites and sand but always from seagrass • No patterns for macroinvertebrates (crabs, lobster)
Chesney and Iglesias (1979), Spain, raft farms (demersal fish)	<i>N, S, H', J', d</i>		Cluster analysis Station in raft area and one in reference area, ca. 1 km distant; sampled 4 seasons, 5 sample days season ⁻¹ ; trawls		<ul style="list-style-type: none"> • Seasonal variation • Diversity measures tended to be greater in raft area • One goby species more abundant, another one less abundant • Other species variable • Community structure did not differ between raft and reference areas
D'Amours et al. (2008), Canada, 4 longline farms	<i>N, S, J'</i>		MDS-PERMANOVA 5 distance classes (0, 50, 100, 500, 2000 m), 3 dates (spring, summer, fall), scuba transects		<ul style="list-style-type: none"> • <i>N</i> typically greater • <i>S</i> and <i>J'</i> temporally and spatially variable with no consistent trends • Community structure typically different with dominance of predators (seastars, crabs, gastropods)
González-Gurriarán (1986), Spain, raft areas (decapods)	<i>N, S, H', J', d</i>		Cluster analysis, correspondence analysis Station in 1 raft area, 3 mid-ria areas, and 3 beach areas, ca. 3 km between areas; sampled 4 seasons; trawls		<ul style="list-style-type: none"> • Large seasonal variation • <i>N</i>, overall, greater • <i>S</i> and <i>H'</i> variable trends • Substratum type, presence of rafts, salinity and depth influenced decapod community structure
Iglesias (1981),	<i>N, S, H'</i>		Cluster analysis, 1 raft, mid-ria and beach		<ul style="list-style-type: none"> • Some seasonal variation

Spain, raft areas (demersal fish)		PCA	station in each of 3 sections of ria, ca. 3- km between stations within sections; sampled 4 seasons; trawls	<ul style="list-style-type: none"> • N greatest • S, H' variable • Clear separation of community structure for 3 habitat types
Inglis and Gust (2003), New Zealand, 4 longline farms (seastar and other species)	N		Farms and paired control areas, stations in each area, scuba transects and baited traps	<ul style="list-style-type: none"> • Seastars (<i>Coscinasterias muricata</i>) more abundant • Scavenging hermit crabs, decorator crabs, and whelks less abundant than in control sites and/or sites not harvested recently • Other macrofaunal species without spatial trends
Kaspar et al. (1985), New Zealand, longline farm	Diversity		1 farm site and 1 reference site, 1 km distant, 4 dates, scuba diving, baited traps	<ul style="list-style-type: none"> • Greater diversity (not quantified) - associated with mussel fall-off (tunicates, seastars, fish) - than control site
Olaso Toca (1979; 1982), Spain, raft farms (echinoderms)	N , B		Raft, mid-ria and beach stations in each of 3 sections of one ria and 2 sections of another, various distances (km-scale) between stations within sections; sampled various times; trawls	<ul style="list-style-type: none"> • N, B greater for seastars, sea cucumbers, and sea urchins
Romero et al. (1982), Spain, raft farms (crabs)	N , S , H' , J'	Cluster analysis, PCA	Station in raft area and one in reference area, ca. 1 km distant; sampled 4 seasons, and 1 raft, mid-ria and beach station in each of 3 sections of ria, ca. 3- km between stations within sections, trawls	<ul style="list-style-type: none"> • N greatest and usually greatest for individual species • S, H', and J' greatest on most dates • Separation of communities based on structure due in part to detritus from mussels rafts

Table 2. Overview of studies on the influence of mussel farms on sediment biogeochemical indices. Indices considered include percentage Carbon, percentage organic matter, redox potentials, and sulphide levels. Where appropriate, data are provided for reference (Ref), boundary (Bdry), and farm (Farm) locations; the distance of reference locations is also indicated as Ref (m).

Study/site	Ref (m)	C (%)			OM (%)			Redox (Eh) (0-2cm)			Sulphide (uM) (0-2cm)		
		Ref	Bdry	Farm	Ref	Bdry	Farm	Ref	Bdry	Farm	Ref	Bdry	Farm
Crawford et al. (2003) PE	100	0.7	1.0	1.8				380	340	310	10	100	210
Crawford et al. (2003) SH	50	3.5	4.2	4.1				380	380	400	110	100	80
Crawford et al. (2003) EA	100	1.2	1.0	2.0				115	110	80	30	20	40
Chamberlain et al. (2001) site 1	60	2.9±0.2	2.7±0.2	-	-	-	-	200	420	-	-	-	-
Chamberlain et al.(2001) site 2	40	2.0±0.2	3.4±0.6	-	-	-	-	180	-90	-	-	-	-
Christensen et al. (2003) BB	250				7.1	12.1							
Hargrave et al. (2008) TB	100-1000				7.2±4.3	9.7±4.34		76±60		-51±78	753±272		1794±771
Callier et al. (2007) Site 1+ under	500-1000				3.2±0.1	6.4±2		-116±27		-113±23	2404±691		2145±271
Hartstein and Rowden (2004) CC	<200				5.4±0.9	10.6±2.3							
Hartstein and Rowden (2004) EB	<200				6.6±0.6	12.3±2.3							
Hartstein and Rowden (2004) BP	<200				2.9±0.8	3.2±0.7							

1. Figures

Figure 1. Global aquaculture production of bivalves (data from FAO, 2010), 1950-2008.

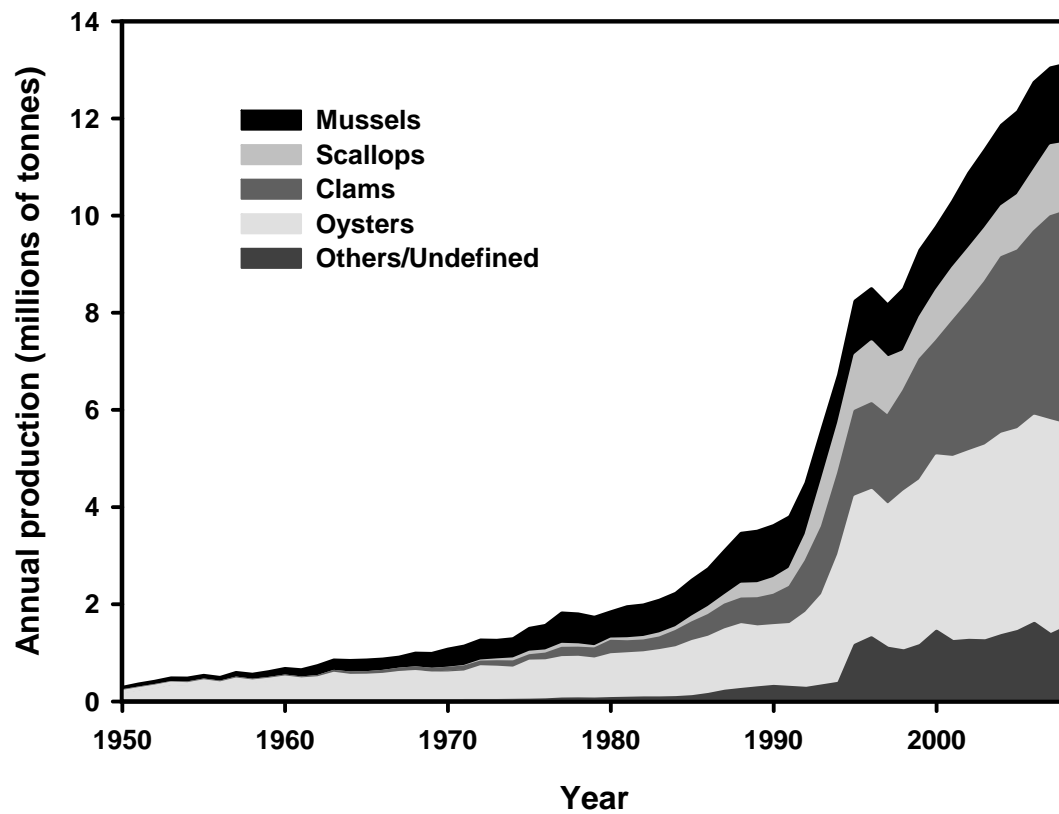


Figure 2. Vertical distribution of metabolic processes in coastal marine sediments.

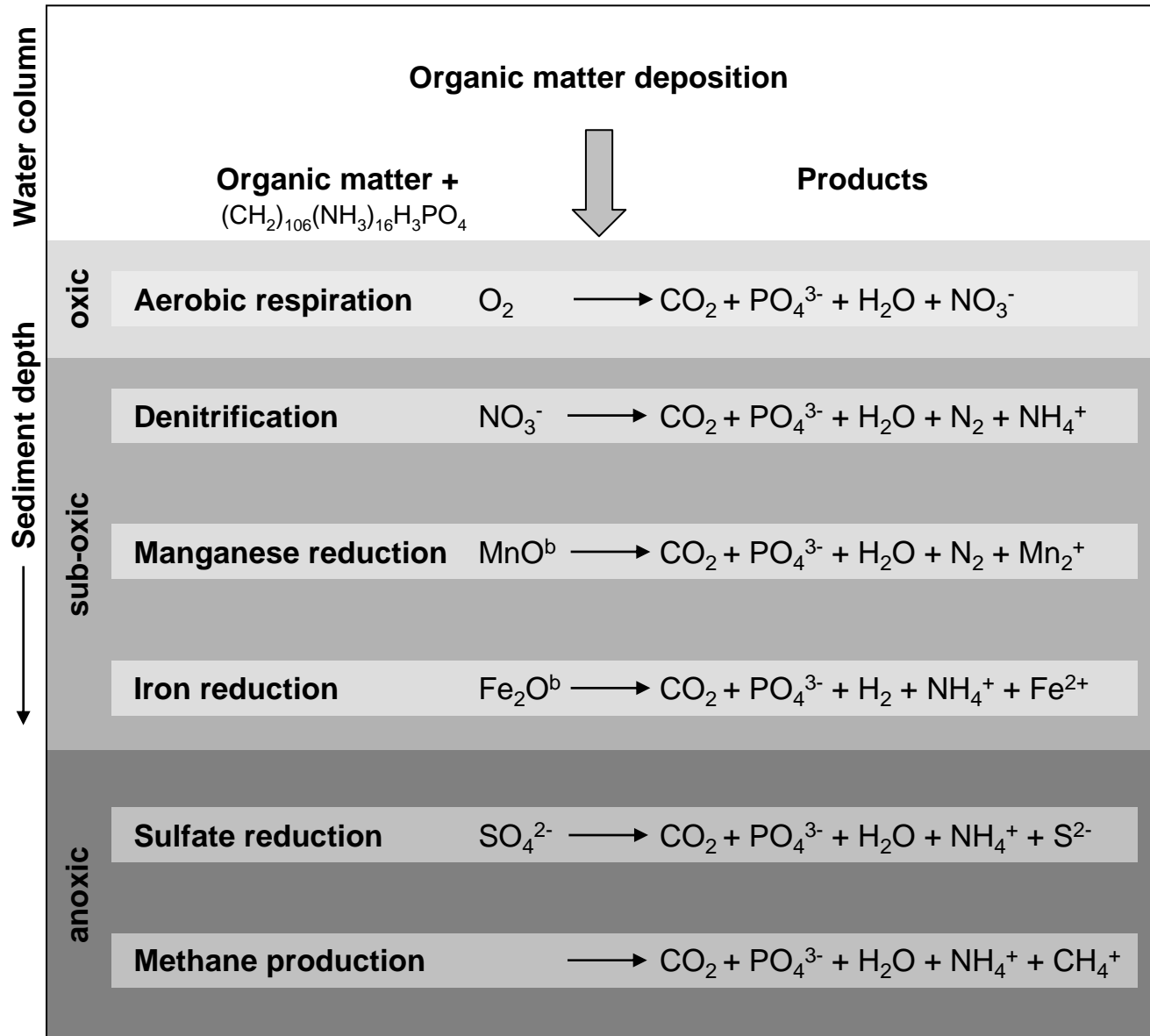


Figure 3. Sulfur cycling in oxidised and reduced sediments in marine systems (after de Wit et al. 2001; Holmer et al. 2005).

