A REVIEW OF THE IMPACTS AND FUTURE DEVELOPMENT OF SUSPENDED-MUSSEL AQUACULTURE

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Abstract

1. Feeding an expanding human population is the most important socio-ecological problem facing today's society. Increasing demand, particularly for protein, is resulting in substantial increases in the price of food.

2. New sources of marine protein cannot be delivered by wild capture fisheries as these are at or beyond sustainable limits, or by increasing intensive aquaculture as this is dependent on marine and/or land based supplies of protein and oil

3. The cultivation of bivalves, such as mussels, is one solution to the global demand for high quality protein and this industry, based on seven species in a diverse range of habitats and farming operations, currently delivers >1.5 million tonnes annually.

4. Mussels are 'ecosystem engineers' and their culture can have major implications for supporting ecosystem through the accumulation of mussel biodeposits and feeding induced changes in planktonic assemblage.

5. Impacts are generally associated with areas of limited dispersion (benthic) and water exchange (pelagic) but are characteristically highly variable in nature and extent.

6. Mussel culture is currently primarily limited by toxic algae, the supply of juveniles, invasive species interactions and, most importantly, the lack of space in the coastal margin.

7. Major expansion of the industry is likely to occur in eutrophified restricted exchange environments, as part of nutrient trading schemes, and offshore. There is, however, little consensus on how to evaluate mussel farming as a mechanism for tackling eutrophication or the likely impacts of moving the industry offshore.

8. Proportionate expansion of the mussel farming industry will produce a sustainable, high-quality, low-carbon, healthy food product that, where appropriately integrated into the coastal zone, will facilitate environmental protection (through exclusion of destructive practices), potentially augment local commercial and/or sport fisheries and provide protected haul-out/ preening sites for a variety of wildlife.

9. *Synthesis and applications*:
   a. Suspended cultured mussel production is rapidly increasing
   b. If unregulated, this expansion may have considerable and/or unknown consequences to the receiving environment.
   c. Proper consideration of the environment will allow the sustainable development of a potentially essential component of global food supply.

1 Introduction

Feeding the expanding human population is one of the preeminent issues facing today's society (Godfray et al. 2010, Smith et al. 2010). Over the last century increasing demand for high quality protein and concomitant technological advances has resulted in the depletion of a majority of the world's fisheries (Pauly et al. 2002) including shell-fisheries (Carranza et al. 2009). In the latter half of the 20th century aquaculture was seen as a possible solution to the fish-supply problem and this industry expanded rapidly producing a high quality fish product at a reasonable cost to western consumers (Asche et al. 2008). However, much fin-fish and crustacean aquaculture is based on feeds that contain a high proportion of wild (forage) fish and is not considered a sustainable solution to global protein provision (Naylor et al. 2000, Pauly et al. 2002).

Unlike fin-fish culture bivalve culture does not require any inputs (feeds, medicines) from the grower (Dumbauld et al. 2009) other than the supporting infrastructure and has the additional advantages of relieving pressure on wild fisheries (Carranza et al. 2009), potentially replacing historically depleted stocks (Kaiser et al. 1998) and being amenable to small-scale, artisanal communities (Piumsombun et al. 2005). Of the bivalves, mussels (family Mytilidae) form the largest group both in terms of cultured tonnage and value (FAO Statistics).

Mussel culture currently occurs, on various scales, in all continents (except Antarctica) and is expanding rapidly, particularly in areas where land and/or freshwater is scarce (e.g. China; Guo et al. 1999) through industry consolidation and technological development (Smaal 2002, Weise et al. 2009).

Mussels have the capacity to radically change their local environment (hence termed 'ecosystem engineers' by Newell 2004) by clearing water of seston and directing it to the seabed in the form of faeces and pseudofaeces (collectively 'biodeposits') and by their physical presence (both living and dead shells)

Mussel farms are characterised by having highly variable impacts on the receiving environment. This makes deriving a common framework for the evaluation of proposed mussel farms, difficult. However, those charged with regulating and managing the coastal strip need to understand both the potential benefits of enhancing the ecological services provided by cultured mussels and the problems that have been associated with their farming. This will better enable the accommodation of mussel farmers, the sustainable (low impact) growth of a potentially important food supply whilst managing demands from various stakeholders.

This review is a broad synopsis of the current status of global mussel culture with a focus on ecological, environmental and sustainability issues and covers relevant mussel physiology, a description of species most widely cultured, culture methods and the resultant global mussel production, the impacts of mussel culture (both benthic and pelagic) with a commentary on the future for mussel farms. It has the objective of informing both policy makers and environmental managers in relation to an expanding industry in an increasingly crowded and competitive coastal margin.

2 Mussel physiology and ecology

Mussels are a key component of many marine and estuarine ecosystems and they have formed the focus of ecologist's attention for many years. Their role in the ecosystem has been extensively studied with several excellent reviews available including Bayne (1976), Smaal (1991) and Dame (1996)

Mussels are active suspension feeders that are commonly found in high densities growing on hard substrata or attached, using byssus threads, to each in clumps (Dame 1996). They are generally intertidal or infralittoral and are characteristically robust with many species able to endure wide salinity and temperature ranges (Hawkins and Bayne 1992)

The diet and feeding mechanism adopted by mussels has attracted more research than almost any other aspect of bivalve ecology and there is a prodigious volume of literature on this subject (reviewed in Dame 1996, Hughes et al. 2005). Mussels pump water through specially adapted gills trapping particles ranging in size from bacteria (~2µm) to zooplankton (several mm) (see §4.3.2). All particles trapped by the gills are wrapped in mucus and either ingested (non-digestible parts are subsequently egested as faeces) or ejected (undigested) as pseudofaeces (collectively 'biodeposits'). The ability of mussels to selectively ingest particular food types, once trapped, remains unresolved (and highly contentious; reviewed in Hughes et al. 2005) but it is clear that, in a majority of locations and times, they feed mainly on phytoplankton (Newell 2004). Mussels thrive in eutrophic conditions and, whilst there is some variability in the minimum mean food concentration required to support different species (varies between ~0.5 and 1.0 µg chlorophyll a per litre; Maire et al. 2007) mussels as a group are limited in their distribution by their food requirements. Mussels continue removing particles from the water column regardless of their own dietary requirements (Newell 2004) and respond to increased food supply by increasing pseudofaecal output rather than reducing feeding rate. Given their ability to filter water, and their frequently high densities, it is not surprising that they are frequently the main herbivore in ecosystems they dominate (Newell 2004).

Biodeposit dispersal patterns reflect local conditions (i.e. current speed and water depth) and the nature of the particle which varies between species and mussel size and diet (which changes seasonally) complicating the understanding and management of mussel farm impacts (Weise et al. 2009). These aspects, and their management implications, are further discussed in §4

3 Introduction to cultured species

Globally, mussel culture is reliant on seven species, four of which are of the genus *Mytilus* (*M. chilensis, M. coruscus, M. edulis* and *M. galloprovincialis*) with three species of *Perna* (*P. canaliculus, P. perna* and *P. viridis*) (Table 3). *Mytilus* is predominantly a temperate water genera with *Perna viridis* being the only farmed warm water species (though with introduction the range of *Mytilus sp* has extended into warmer water, see §4.2.2). The size at harvest depends on species and ranges from about 4 – 7 cm (*M. edulis*) to 10.5 cm (*M. chilensis*), harvesting usually occurring 12 – 24 months following spat settlement (Table 3).

3.1 Mussel culture

Mussels are generally cultured in shallow, non-dispersive coastal sites (Weise et al. 2009), associated with moderate water flow but which are relatively unexposed (Cao et al. 2007) to high levels of turbulence (see below). Culture is usually based either on relaying juvenile mussels (spat) onto the seabed (not further considered here, for a review see Kaiser et al. 1998) or in supported/ suspended culture. Ideally, mussel farms are sited such that the product is free of contamination (by grit and bacterial/viral/algal toxins), where the shell is clean (of epifouling), where site-access time is minimal and where storm-losses do not occur (Hickman 1980, Chaitanawisuti and Menasveta 1987). There also needs to be a local, reliable and sufficient spat supply (see §4.2.2), and a ready labour supply and markets (Chaitanawisuti and Menasveta 1987). Maximising growth rates requires the mussel to be held in a 'reasonable' current flow; 0.22 m s^{-1} is suggested by Lindahl et al (2005) to eliminate water 'recycling' where the same water is sequentially filtered through adjacent mussels (this appears rarely achieved, see Table 3). The upper water-velocity limit for mussel feeding is not reported in the literature but it seems likely to exceed the engineering capabilities of the support structures. Mussels can be supported by bamboo poles (notably in Thailand; Somerfield et al. 2000) and other wooden poles (e.g. 'bouchots' in France; Smaal 2002) or, more commonly, suspended on lines strung between

floats or suspended underneath rafts as used in the major production cnetres fo China, Thailand, Spain and Chile).

The mussel culture cycle is initiated by the collection of 'spat' (from wild stocks or on purpose-made spat collectors) which are then transferred to degradable mesh tubes ('socks') that are then attached to a polypropylene rope ('dropper') which is suspended in the water column. During the first year of growth the mussels attach, using byssus, to the dropper and the mesh disintegrates. The water depth for most farms ranges 3 – 30 m (Table 3) and, where water column is deep, farmers will grow mussels where conditions (e.g. food and the absence of fouling organisms) is optimal (Fuentes et al. 2000). The goal is to maximise the dropper length whilst ensuring that it never touches the seabed as this would allow predators onto the line and contamination by grit. Mussel growth varies considerably on each rope and between rafts/lines with the most current-exposed mussels growing fastest. The mussel encrustation thickens as the crop grows and, without regular or timely harvest, much of the crop would be lost to the seabed (often in clumps), particularly during storms or as a consequence of bird predation. Some mussel farmers thin the mussel lines, removing the smaller shells which are then relayed and grown-on elsewhere (D. Wilson, Inverlussa mussels, personal communication, June 2010).

The sheltered waterways offered by sea loch, rias, estuaries and inlets are highly prized by a broad range of competing stakeholders which include amenity (e.g. tourism, marinas, boat moorings), aquaculture operations (fin-fish, macroalgae), fishing (commercial and sport), waste-discharge (e.g. sewage and commercial effluent) in addition to mussel farming (Jarernpornnipat et al. 2003, Lindahl et al. 2005). Currently, a majority of mussel farms, in all production areas, lie within this coastal strip and are relatively small (e.g. 3 – 5 hectares; Keeley et al. 2009) and, at least in Scotland, commonly stretch across small bays and inlets (personal observations).

3.2 Current status and description of mussel culture industry and production figures

Whilst mussel culture is expanding gaining accurate figures for suspended culture tonnage, by species and country, is difficult because nations combine their seabed-based and suspended cultured mussel production figures when reporting to the FAO (X. Zhou, Fishery Statistician (Aquaculture), FAO, February 2011, personal communication). There are also issues with species identification (for example, the main species cultured in Spain, according to the official return, is *M. edulis* which contradicts all other records in the literature). With these caveats in mind, mussel production is increasing rapidly (Figure 1) with a total output currently standing at approximately 1.6 million tonnes. The main producing nations are, in order, China, Thailand, Spain and Chile and, together these nations account for >75% of global production (Table 1).

China is the biggest mussel producer, and a bulk of this is produced using suspended culture techniques (Lovatelli 1988) and, whilst species are not distinguished in FAO statistics, it will consist of the market preferred *P. canaliculus* and *M. edulis* (personal communication, M. Mei, Marine College of Shandong University, China, July 2010). Thailand is the second biggest producer and, in 2000, a bulk of the P. viridis produced were grown on poles planted in mud in shallow water (Somerfield et al. 2000). However, as Somerfield et al. (2000) notes, the potential for rope-grown mussels in Thailand is considerable and there is increasing interest in moving the sector in this direction (Tunkijjanukij and Intarachart 2007). Spain is by far the largest European producer of mussels and all of these are produced in the rias (flooded river valleys) in the north-west of the country where the production volume is now limited by the carrying capacity in respect of primary production (see §4.3.1). Chile is the biggest south-American producer with fjord grown "Chorito" mussels constituting an important part of the domestic and export (particularly to the EU)

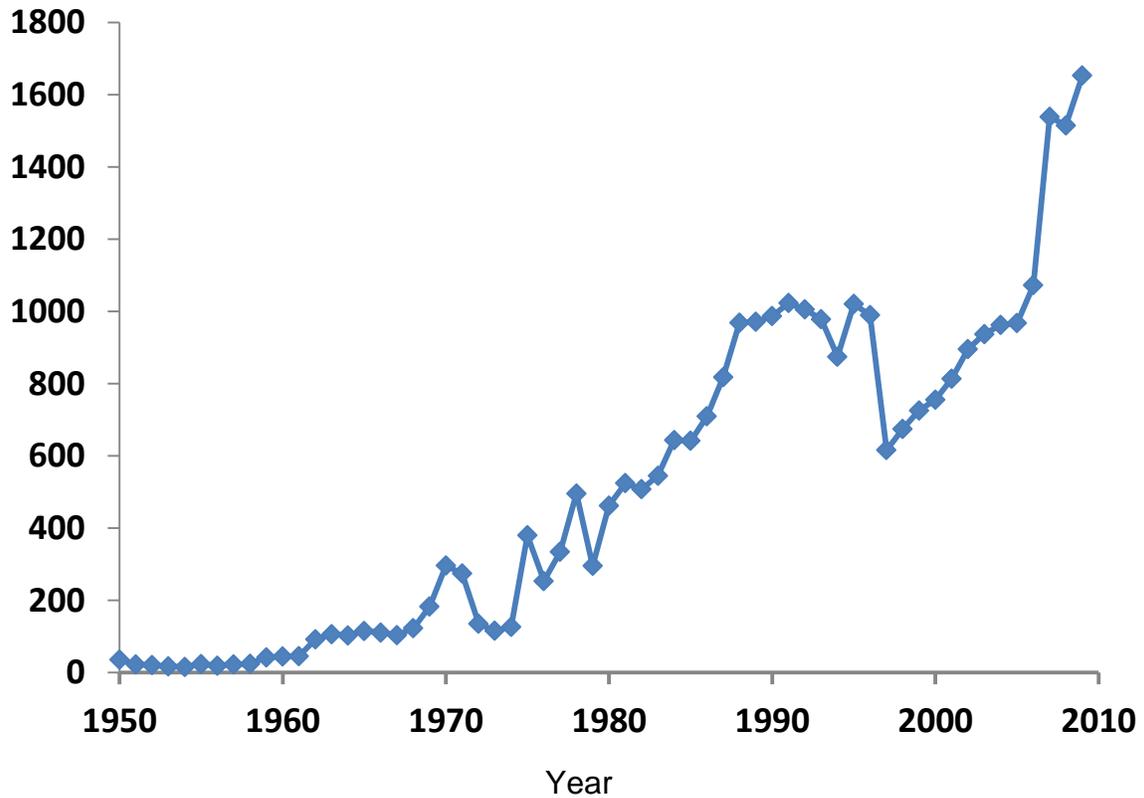markets (Norambuena and Gonzalez 2005).

Figure 1 – Global mussel production (thousands of tonnes, 1950 – 2010).

Source: FAO. Note: whilst this excludes figures from the Netherlands as this is a major producer of seabed-cultured mussels but it may include seabed production from other areas, see note in text.

Table 1 – Mussel production (top 95% in 2009) by country. Source FAO.

Country	Species	Tonnage	%
China	Sea mussels[1]	637373	40
Thailand	*Perna viridis*	227340	14
Spain	Sea mussels[2]	195050	12
Chile	*M. chilensis*	166952	10
New Zealand	*P. canaliculus*	89850	6
Italy	*M. galloprovincialis*	76800	5
France	*M. edulis*	60798	4
Korea (Republic)	*M. coruscus*	55035	3
United Kingdom	*M. edulis*	28000	2
Ireland	*M. edulis*	26502	2
Canada	*M. edulis*	23612	1
Greece	*M. galloprovincialis*	22383	1
Others	mixed	94812	6
Total		1609695	100

Note: 1 – species not specified in FAO statistics, believed to be a mixture of *M. edulis* and *P. canaliculus* (personal communication, M. Mei, Marine College of Shandong University, China, July 2011).

Note: 2 - Species not specified in statistics, but will be *M. galloprovincialis*

Mussel production varies considerably over time in response to global (e.g. the financial crash of 2008) and regional crises (e.g. Chilean tsunami; Rios 2010) but, at least within the European Union, recent projections (for 2025) indicate mussel production will need to exceed >1M tonnes per annum as part of a strategy to close the supply gap between wild fisheries production and the increasing demand for high quality affordable protein (scenario 4, CEC 2009). However, in order to grow the industry must overcome several specific environmental challenges.

4 Environmental challenges facing and limiting the mussel growing industry

There are a number of issues facing the mussel growing industry that need to be met before it can truly realise its growth potential. These issues can be divided into two main types which are 'two sides of the same coin': 1. the impact of the environment on mussels and 2. the impact of mussels on the environment. In respect of how the environment influences mussel culture, the main issues are water quality (presence of toxic algae, microbial and pollutant contamination), the supply of seed mussels (spat) and invasive species associations. In respect of how mussel culture influences the environment, the pelagic and benthic impacts of an expanding industry are most pertinent and form a bulk of this review together with an assessment of stakeholder interactions and the competition for space.

4.1 Assessing the significance of impacts

In discussion with regulators, policy makers and stakeholders (including mussel farmers) we have often been asked to comment on the 'significance' of impacts. Any development (e.g. a mussel farm) will, inevitably, change the receiving environment. Whether this is statistically significant depends on whatever sampling/observation programme is put in place to detect changes and this is usually, at least in part, sample size (and therefore funding) dependent. The biological significance of the inevitable changes that occur following farm emplacement is much harder to define: regulators and policy makers charged with ensuring that no 'significant' change/impacts occur rarely define thresholds beyond which a change would be considered significant; setting such thresholds would require a profound understanding of the temporal and spatial variability and recruitment dynamics of the species in question which is usually not available. This makes defining a 'significant impact' contentious, even between ecologists (Keeley et al. 2009). In the following discussion we use the term significant to identify statistically significant changes (identified by the author) and further comment on the likely biological significance, with a mind to the definition

of acceptable impacts as being 'short-term, reversible and localised' (Fernandes et al. 2001).

The production (per unit area) of mussels, in a given environment, is an obvious driver of the associated impact. In attempting to collate this across different literature sources, it became evident that the basis of the reported metric depended on the production environment. In restricted exchange environments (e.g. fjords and bays) authors generally related the total mussel production (tonnes live weight) to the supporting water body area (km^2). However, in more open systems, where defining the supporting water body area is very subjective, production values were normally related to some measure of the raft or line area making productivity comparisons between different types of production area difficult.

Environmental managers must make informed decisions with regard the environmental consequences of new or scaled-up farms in order to balance the needs of the farmer, other stakeholders and the environment. The following section outlines the major factors limiting the current industry, the mechanisms of mussel farm impact (with comments on why impacts vary widely between sites/ studies) and links this to mussel production.

4.2 The impacts of the environment on mussels

Mussels are useful as environmental monitors because of their ability to bioaccumulate a range of biological and non-biological contaminants such as bacteria, viruses, heavy metals and organic pollutants (Andral et al. 2004). However, the converse is that mussels are liable to pass on toxins to anything, including humans, that consume them. The impact of this is more relevant to the marketing of shellfish in relation to their production environment than there environmental impacts, so is only very briefly considered here, primarily in relation to relocating the industry offshore (see §5.2)

4.2.1 Toxic algae and other contaminants

Toxic algae and microbial contamination rarely have a direct toxic effect on mussels although hypoxia following bloom events definitely can (e.g Davidson et al. 2009). Whilst our understanding of the identity of toxic algal species and the chemical nature of the toxins they produce is relatively well advanced this does not apply to the mechanisms behind why and/or when certain species bloom, what drives the variability in the toxins they contain or, indeed why they produce toxins. Toxic species could form part of a blooming algal community responding to the eutrophication that frequently typifies inshore mussel growing areas. However, there is evidence that that, at least in some areas, toxic algae grow offshore and that they are then advected by currents to the coastal fringe (e.g. Raine et al. 2010) where they may be concentrated. It seems reasonable to speculate that toxic algae advected into warm, eutrophified, restricted exchange environments, may also show rapid *in situ* growth and reach problem concentrations. There are no mechanisms to protect mussel crops from toxic algal contamination and, currently, mussel farmers are best served by monitoring for toxic algae and not harvesting during problem periods (Rhodes et al. 2001). However, there is interest in potentially diverting contaminated mussels to organic chicken feed, a development which would allow harvest to continue (Lindahl et al. 2005) but with, as yet, unknown consequences to either the poultry or profitability. Another solution may be to move the industry outside the coastal fringe into water that is likely to contain a lower concentration of toxic algal species (K. Davidson, personal communication, July 2011).

Mussel contamination can also occur when mussels filter and ingest harmful bacteria, viruses (that originate in human and/or animal faeces) or industrial pollutants. Prior to marketing most mussels are depurated (usually in UV sterilised seawater) to reduce microbial contamination (e.g. under the EU-directive 91/492 EEC, July 1991). In the absence of such facilities, mussel marketing will be more challenging (and dangerous to consumers) and, in order to maintain sales, some growers have become important drivers for social-

environmental change (e.g. in Thailand; Jarernpornnipat et al. 2003). However, once again, one solution is to move shellfish production areas further offshore (Somerfield et al. 2000).

4.2.2 Spat supply and invasives

For an expansion of mussel production to occur there must be a reliable source of juveniles (spat). Spat can be collected from the wild or from purpose built spat collectors (commonly some sort of fibrous material facilitating settlement). In Europe, wild spat collection tends to be associated with the relaying and seabed-based operations where it is, in some locations, severely limiting the expansion of the industry (Smaal 2002) particularly where wild mussel beds have a high conservation value e.g. as a seabird feeding resource (Kamermans et al. 2009).

Invasive species, whether introduced by aquaculture activities or not, pose a considerable risk to the mussel farming industry and the environment that sustains them. The role of bivalve mariculture in sustaining and spreading invasive species is excellently reviewed by McKindsey et al (2007) who identifies two main categories of introduction associated with mussel culture, firstly mussels themselves and, secondly, "hitchhiking" species that are vectored into areas via routine mussel culture activities. These are briefly discussed here.

Mussels have been deliberately introduced outside their native range, for reasons of aquaculture, in several regions and, given their role of 'ecosystem engineers' it is not surprising that this has resulted in severe impacts on local populations. Perhaps best described is the impact of *M. galloprovincialis* introduced to Saldhana Bay, South Africa in the mid to late 1970s. The introduced mussel is considered 'out of control' by Hockey and Schurink (1992) and is spreading into, and dominating, native *P. perna* mussel beds (Robinson et al. 2007). The mussel *P. perna* is, however, itself an invasive species, this time on the Uruguayan coast where it dominates intertidal native mussel species but only at certain beach levels (Carranza and Borthagaray 2008). Although not an

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aquaculture species, *M. trossulus* (native of the Baltic Sea and US) has recently and for unknown reasons, rapidly come to dominate mussel lines in Loch Etive, Scotland (Dias et al. 2009). It is not known how this species arrived (i.e. whether it is an invasive or relict population) but it is characterised by low meat contents and weak shells, results in a crop that is unsalable, and has effectively closed the sector in Loch Etive. Whilst an 'invasive' in Loch Etive, in other areas it is *M. trossulus* being challenged, for example, the invasive *M. galloprovincialis* is displacing it on the west coast of the US, particularly in warmer water (Lockwood and Somero 2011).

The adoption of appropriate legislation /guidelines (e.g. Pinnell 2008, Hambrey et al. 2009) should prevent the deliberate introduction of non-native mussels (albeit too late in many circumstances). The more modern problem is the relationship between normal mariculture practice, such as seed transfer, and the spread of 'hitchhiker' invasives: in New Zealand the large-scale transport of mussel seed from North Island to the growing areas of South Island is threatening to spread invasive tunicates (reviewed in Keeley et al. 2009), already a major problem to mussel growers in Prince Edward Island, Canada (Gittenberger 2009). Invasive species, including potentially toxic microalgal species, can also be transported inside the digestive systems of mussels (Kaiser et al. 1998).

Whilst overgrowth by invasive species is a major problem, mussel mariculture is also affected by native fouling organisms. These include polychaetes such as the keel worm *Pomatoceros triqueter* which, in one Scottish sealoch, is reported to have increased in abundance over time, a phenomenon that was attributed to the increased substratum available in the form of dead shells and mussel infrastructure (Douglas Wilson, Inverlussa mussels, personal communication, June 2010).

4.3 Impacts of mussel farming on the seston

Mussels are highly competitive, fast growing and exceptionally efficient at removing particles from the water column with varying proportions either being assimilated (as growth) or reaching the seabed as faeces /pseudofaeces. This biomass and nutrient transfer from the wider pelagic to localised benthic environments (if accumulation occurs) will have a number of direct and indirect effects on other mussels in culture and non-commercial species. Even where significant reductions in the bioseston do not occur, mussels may alter the balance in the bioseston with ecological implications.

4.3.1 Carrying capacity and bioseston depletion

Cultured mussels have the potential to reduce local seston by a number of mechanisms, including direct consumption and by reducing water exchange in restricted environments (e.g. fjords) which limits plankton recharge and the import of nutrients.

Gross depletion of seston in the presence of very high densities of mussels is to be expected because of their capacity to filter seawater: Tenore et al (1982) estimates that a volume of water equivalent to 80% of the entire volume of Ria de Arosa could be filtered every day by the cultured mussels in that ria. Given the filtration capacity of mussels and the density of some cultures it is, therefore, perhaps no surprise that reductions in chlorophyll *a* (a proxy for phytoplankton) has been observed at a range of scales. For example, using airborne imaging Grant et al. (2007a) demonstrated seston depletion at the km scale whilst, at smaller scales and using fluorescence, Petersen (2008) demonstrated an 80% reduction in phytoplankton concentration down-current of a mussel raft. Indeed, the mussel induced reduction in phytoplankton around a New Zealand (Beatrix Bay) farm was sufficient for Ogilvie et al. (2000) to suggest augmenting the water with a nitrogenous fertiliser to boost primary, and subsequent mussel, productivity.

The flux of seston in response to changes in mussel culture density is well suited to mathematical modelling and this is a potentially useful tool for environmental managers. These models have been used to suggest limiting further expansion of mussel culture in some locations, e.g. Trecardie Bay, Prince Edward Island, Canada (Grant et al. 2008), and that an expansion (at least in respect of seston) of the industry in La grande Entrée, Quebec (Grant et al. 2007b) would be sustainable.

Commercial mussel farms are necessarily extensive and, in places, dominate the surface of many production areas (e.g. >50% in Trecardie Bay, PEI, Canada (Grant et al. 2007a), and the Ria Arousa, Spain (this major sea-use change is very clearly seen using Google Earth™). Mussels are grown throughout the water column with droppers usually stopping just above the seabed (see §3.1), effectively forming 'curtains'. These curtains of mussels can be a significant barrier to water flow: Boyd (1998) showed the mussel rafts deflect the majority of flow around them with current velocities decreased from 7.5 cm s^{-1} to 1.25 cm s^{-1} within individual rafts whilst Plew et al. (2005) and Strohmeier et al. (2005) demonstrated a 36 – 70% reduction in current speed within the farm structure. This has important implications both for the lateral dispersion of the faecal and pseudofaecal material (see §4.4.2) and the supply of nutrients and food to other parts of the production area. Mussel farms located close to the entrance of restricted exchange environments are likely to be particularly contentious as they reduce water exchange or mixing (up to 40% predicted for Sungo Bay, China; Grant and Bacher 2001) limiting food and/or nutrient supply to other farms and native filter feeders alike. This is likely to be particularly important where local (e.g. within bay or fjord) production is limited. Furthermore, Plew et al. (2005) demonstrated moderate, and frequency dependent, attenuation of wave energy across a 650 m wide farm which may have particular implications for intertidal communities and reduce wave-driven currents and mixing.

Seston depletion is an inevitable consequence of mussel feeding and justifying a suitable threshold that simultaneously protects the environment and allows for mussel production is difficult. Rodhouse and Roden (1987) modelled carbon flux within Killary Harbour, Ireland (a 7.7 km^2 embayment) and estimated that an extraction of ca. 260 tonnes km^{-2} yr^{-1} (equating to approximately half the estimated primary production) would have major ecological consequences with the implied recommendation that mussel production should be limited to that figure. Other modelling approaches have also been used, eg. Jiang and Gibbs (2005), using the mass-balance energy flow model (ECOPATH™), suggested that a production rate of about 300 tonne km^{-2} is the upper threshold for mussel production in embayments (100% food particle consumption by cultured mussels), setting a limit of 65 tonne km^{-2} (~22%) as being ecologically sustainable. This sustainable production figure (65 tonne km^{-2}) is exceeded by farms currently in operation, culturing several different species (Table 2) including in Trecardie Bay (Canada) where overproduction is stated as occurring (Waite et al. 2005). However, Tenore et al. (1982) states that 10% of the primary production in the Spanish Rias yields ~700 tonnes km^{-2}, clearly indicating considerable site differences in potential and ecologically sustainable mussel yields.

Table 2 – Range in mussel production (tonnes km^{-2} yr^{-1})

Species	Location	Production	Reference
M. edulis	Trecadie Bay, Prince Edward Island, Canada	150	(Grant et al. 2008)
M. gall.	Ria Arousa, Spain,	700	(Tenore et al. 1982)
P. canaliculus	Beatrix Bay, New Zealand	170	(Christensen et al. 2003)

Notes: *M. gall. – M. galloprovincialis.*

Clearly, setting upper production limits based on maintaining an adequate background seston concentration, will require a thorough understanding of local

hydrography, particularly external recharge and nutrient supply in restricted exchange environments.

In areas of high water exchange, and/or sufficient in situ production, and where farms are sufficiently small compared to their supporting water body it is unlikely that ecologically meaningful impacts in the overall seston concentration will occur. Under such circumstances direct impacts, through competition with other filter feeders won't be important but consideration should still be given to the influence of cultured mussels on the balance between different members of the planktonic community.

4.3.2 The influence of mussel on the bioseston balance

Mussels can change the balance of bioseston in a number of ways, including selective feeding, should this occur (Ren et al. 2006) or particle size (see below) and by their own reproductive efforts (see below).

Mussels have the competitive advantage over zooplankton, in temperate waters, of being 'ready and waiting' to feed in the spring as soon as temperatures allow compared to many zooplanktors which have low overwintering populations (Newell 2004). This means that in areas of high-farm density mussels can not only replace zooplankton as the major herbivore but also become a major predator of them (including egg and larval stages of commercially important species; Newell 2004).

Like all filters, mussels have a lower particle size threshold beneath which particle retention efficiency starts to drop (Dame 1996). This threshold is varies between species; in the case of the relatively large species *P. canaliculus,* it is approximately 5 μm meaning much of the picophytoplankton (<2μm) are not available as food (Safi and Gibbs 2003) whilst for *M. edulis*, retention efficiencies of approximately 30% have been reported for particles of 1μm (Riisgard 1988) making picophytoplankton and some bacteria available. Selective feeding of this

type has two important consequences, firstly, it will increase the relative proportion of smaller plankton (within unknown ecological consequences) and, secondly, it indicates that a crude measure of chlorophyll *a* is not necessarily a good measure of how much food is available to either the mussel crop or its competitors (Safi and Gibbs 2003).

The ability of mussels to selectively direct captured food to the mouth or reject it as pseudofaeces is an aspect of mussel physiology that has raised considerable, occasionally acrimonious, debate (reviewed in Hughes et al. 2005). In terms of planktonic consequences, selective ingestion can only alter the balance in the planktonic community if organisms ejected in pseudofaeces are able to survive and re-enter the water column. Whilst the prognosis for pseudofaecal entrapped phytoplankton is not known, bacterial acidification of the pellet is likely to make it unsuitable for their growth and reproduction (Dr J. Day, Culture Collection for Algae and Protozoa, personal communication June 2011) even to those phytoplankton that are able to move to heterotrophic metabolism.

Whilst mussels are generally considered herbivorous there are several records of them growing successfully on heterotrophs. This includes the ciliates that dominate the plankton in Grande-Entrée Lagoon, Magdalen Islands, Canada where mussels have been cultured for >25 years (Trottet et al. 2008). Larger, multicellular heterotrophs, including zooplankton, are also known to be taken by a variety of mussel species including *P. canaliculus* (Zeldis et al. 2004), *M. edulis* (cyprids, nauplii and copepods taken; Lehane and Davenport 2006), *M. galloprovincialis* (26 -77% size-dependent depletion of zooplankton; Maar et al. 2008) and microzooplankton (Lam-Hoai and Rougier 2001). Whether active ingestive-selection of zooplankton, by mussels, occurs is not known but size selectivity is influenced by water hydrography with larger zooplanktors being more susceptible to capture in more turbulent water (Maar et al. 2007) presumably as such turbulence reduces the effectiveness of their escape response. The fate of soft-bodied zooplankton is largely unknown (Lehane and

Davenport 2006) but crustacean larvae (up to 6 mm) that are ejected in pseudofaeces have been reported as either dead or moribund (Davenport et al. 2000). Zooplankton communities around mussel farms can also be changed by the reproductive effort of the cultured mussels themselves (Keeley et al. 2009) and by the propagules of species associated with the mussel farm (including starfish and crabs; Tenore et al. 1982).

Whilst there can be little doubt that disproportionately intensive mussel farming could change planktonic balance the ecological consequences of these changes are poorly understood (Keeley et al. 2009). It is plausible that they may either mask or exacerbate larger-scale changes in plankton occurring, *inter alia*, as a consequence of fishing (on both target and non-target species; Lynam et al. 2010) or climate change (Boyce et al. 2010, Lynam et al. 2010).

4.4 Impacts of mussel farming on the benthos

There are a number of ways in which cultured mussels change the benthic habitat and, consequently, benthic communities. These changes are linked to the accumulation of mussel biodeposits, the supply of living shells (food) to the benthos, the subsequent accumulation of empty shells (shell debris) and the role of the supporting structures as artificial reefs.

4.4.1 Methods of detecting benthic changes around mussel farms

The assessment of the impact of mussel farms on the surrounding environment has been approached in a number of ways and draws on experience gained from monitoring other maritime activities particularly fish-farming. However, monitoring around mussel farms poses unique challenges. These challenges include (i) the sometimes considerable lateral movement of mussel supporting structures (we have measured at least 18 lateral displacement in one sea loch based farm) (ii) unpredictable crop losses that result in a short-term food pulse for predators and a new debris field and (iii) the highly variable nature of biodeposits over both space and time (iv) the variations in impact attributable to

husbandry practice (e.g. line spacing). These (and other) sources of variation may account for much of the contrasting data summarised in Table 4. All sampling programmes are, inevitably, a compromise between budget and experimental power (see §4.1) and, with this in mind, it is worth assessing the most useful methods for detecting mussel farm impacts.

Numerous studies (including many of those reviewed here) report results from a pseudoreplicated design (sensu Hurlbert 1984) and most of the studies do not attempt to show the extent of impact, rather they attempt to address whether a difference between the mussel site and one or more control stations is/are detectable, itself not necessarily a particularly interesting question (Gigerenzer 2004) (see §4.1). Linking cause (i.e. mussel farm) and effect is best achieved using a before-after-controlled-impact (BACI) design with numerous control sites (Underwood 1994) and, preferably, several farm sites. The choice of response variable is important as they will reflect impacts on different aspects of the ecosystem and will show varying degrees of temporal and spatial dependency.

The mechanism by which cultured mussels impact the benthic environment suggests several approaches to monitoring. The accumulation of biodeposits will, in most cases, result in a change in the sedimentary organic carbon content and carbon/nitrogen ratios. Monitoring organic carbon content is relatively cost-effective and several researchers (e.g. Callier et al. 2008, Cranford et al. 2009) have found significant changes attributable to farms. The major impact occurring as a consequence of the accumulation of biodeposits occurs if the material causes changes in the sedimentary nutrient cycles, particularly if degradation is associated with lowered sedimentary oxidative capacity. This can be readily and cost-effectively measured using redox probes (provided sample collection is possible), and, although these tend to be somewhat erratic (personal observations), they are a standard method in relation to monitoring fish-farm impacts in the UK (SEPA 2005). An alternative method, offering considerable

potential for the high-resolution mapping of the redoxcline, is to use REMOTS technology (O'Connor et al. 1989).

The changing benthos will include both indicator species (of limited inherent 'value') and species of high conservation interest (e.g. those named in conservation legislation). Meiofauna respond rapidly to environmental change making them potentially useful bioindicators but are relatively difficult to identify and, because they recolonize superficial layers quickly, may not be particularly sensitive indicators of an ongoing degraded status deeper in the sediment (reviewed in Coull and Chandler 1992).

Sediment samples for both sediment carbon content/redox analysis or meiofaunal analyses, can be collected using a coring device. While this works well in fine sediments, in coarser sediments or, more particularly, where the sediment contains (or consists of) shell debris, sample collection can be difficult or impossible. This can be tackled by using longer cores (to penetrate the overlying mussel debris into a more cohesive sediment and ballasting the corer appropriately; personal observations) but standard cores of ca. 60 mm diameter are never likely to sample shell debris/mud/sand mixtures effectively and, in the case of monitoring mussels, this is likely to occur in the most interesting (i.e. impacted) areas.

Megafauna are often logistically difficult to sample (Crawford et al. 2001) and are patchily distributed (D'Amours et al. 2008) with low abundances (1 per 10m2 is classified as 'common' on the 'SACFOR' scale; Hiscock 1998) making statistical analysis challenging (or unyielding) without a very large sample size (personal observations). Many megafaunal species likely to be observed around mussel farms are robust, opportunistic, vagile benthic scavengers and are unlikely to indicate either a high-quality or degraded sedimentary status making then only a crude indicator of environmental change (Crawford et al. 2001).

The most commonly used group in monitoring benthic impacts, and potentially the most useful, are the macrofauna. These are readily sampled (using a grab), are relatively easy to identify (at least to a certain taxonomic level and this is often sufficient to demonstrate change e.g. to family; Olsgard et al. 1997, Thompson et al. 2003, Lampadariou et al. 2005) and the nature of macrobenthic species changes in relation to organic enrichment is relatively well understood (under the Pearson and Rosenberg 1978 paradigm). Grab sampling offers the advantage over sampling using a coring device of being sufficiently robust to penetrate and close around mussel shell debris (personal observations) making sampling alongside/ in between mussel lines, even in the presence of very high levels of shell debris, straightforward.

Point sampling, for example the collection of cores or grabs, is invariably spatially limited. The inevitable spatial limitation of point sampling devices can be overcome, at least in part, by using acoustic techniques, such as side-scan (for seabed texture) or multibeam (for high resolution seabed bathymetry). Side-scan and mulitbeam sonar imaging, at resolutions <0.1 m, offer considerable potential in monitoring the extent of change around mussel farms provided the impact is associated with an acoustically distinguishable phenomenon. This has been shown by Hartstein (2005) who mapped the shell debris field around a New Zealand farm but may not be so suitable in highly heterogeneous environments (John Howe, unpublished data, 2011), where shell-debris has a similar acoustic impedance compared with the background or where the hanging mussel lines impede acoustic visualisation.

We recommend that managers overseeing the implementation of a sampling regime appropriate to the monitoring of benthic impacts of mussel farming should focus on determining the extent of the mussel debris field (e.g. Wong and O'Shea 2011) (using drop-down camera or side-scan sonar) and stratified (distance), randomised, grab sampling approach to assessing the extent of macrobenthic

change and this should be visualised using multiple dimensional scaling (MDS) (Clarke and Ainsworth 1993). Where community analysis is not possible, the moderate organic enrichment found around a majority of the surveyed farms assessed in this review (where an impact was occurring) is likely to be associated with an increase in macrofaunal abundance or biomass (e.g. Stenton-Dozey et al. 2001 and unpublished data) and a decrease in the depth of the redoxcline which can be visualised using sediment profiling (Callier et al. 2008). We recommend that sampling should be conducted at the time of maximum mussel productivity (and potential impact) (Danovaro et al. 2004) and that managers should be aware of the considerable effect that the employed husbandry practice (e.g. stocking density) may (e.g. Drapeau et al. 2006) or may not (e.g. Miron et al. 2005) have on the local and regional impacts of mussel farms. In highly dispersive, open sites (typical of Table 4, Part II) it is likely to be difficult to detect changes (within a reasonable budget) potentially negating any purpose, or need, for monitoring (Crawford 2003).

4.4.2 Biodeposit accumulation and subsequent impacts

The benthic impact of mussel biodeposits will depend on the extent and nature of any accumulation and these two aspects are both closely linked to the water column in which the mussel is feeding. Mussel biodeposits reflect the supporting water column; for example as the silt fraction increases, the biodeposits become increasing dense (and so sink quicker) and, commensurately, become increasing less labile (Giles and Pilditch 2004). The inherent variability in water quality that occurs spatially and temporally (e.g. proximity to rivers carrying silt following heavy rain and seasonal upwelling events; Tenore et al. 1982) results in biodeposits that are highly variable over time and between locations (e.g. Hatcher et al. 1994). Even at the same time and location different mussel species have been reported to produce biodeposits that vary significantly (Jaramillo et al. 1992).

Biodeposit size also influences sinking rates, with larger mussels producing larger, faster sinking, biodeposits (Callier et al. 2006) but there are also striking differences in sinking rates between faecal and pseudofaecal material (e.g. by a factor of five in M. edulis; Callier et al. 2006 , Weise et al. 2009). Whilst smaller (younger) mussels produce smaller biodeposits, with greater dispersal potential, they also produce a greater volume of biodeposits (per unit biomass; Weise et al. 2009) meaning that, potentially, biodeposit accumulation can be greatest underneath crops in their first year of growth. The nature and extent of biodeposits is further complicated by the role of farm-associated fouling organisms (Tenore and Gonzalez 1976), for example McKindsey et al (2009) predicted that biodeposition rates would be doubled under mussel lines that were heavily fouled with the nuisance tunicate *Ciona intestinalis* (see §4.2.1).

The lateral transport of the biodeposits depends on current flows (as influenced by the mussel structures themselves (see §4.3.1) and water depth but their accumulation also depends on their resuspension from the seabed. Denser, faster sinking biodeposits (as above) have higher resuspension velocities (double reported for P. canaliculus fed on diets containing silt; Giles and Pilditch 2006) but near-bed resuspension velocities are highly influenced by the nature ('roughness') of the seabed. For example, Hall-Spencer et al. (2006) showed that structurally-complex maerl trapped fish-faecal material, thereby decreasing dispersion, and it seems likely that mussel shells (dead or alive) on the seabed will enhance the accumulation of mussel biodeposits in the same way.

The variability in quality, quantity and accumulation of mussel deposits, both in time and space, may help account for the very wide range of benthic impacts reported around mussel farms (summarised in Table 4). However, it should be noted that clear impacts are only demonstrated on farms located in enclosed bays, and albeit with several exceptions, subject to lower current speeds. In these conditions, we predict impacts commensurate with moderate (e.g. enhanced biomass) to severe organic enrichment (e.g. presence of sulphate

reducing bacteria). In a majority of cases, these impacts included the impoverishment of the macrobenthic community which constitutes a loss of biodiversity at the local scale. There is little information on the extent of these impacts, and their duration: Mattsson and Linden (1983) and Wong and O'Shea (2011) both recorded macrobenthic impacts that extended up to 20 m from the surveyed farm whilst Hartstein (2005) measured organic enrichment up to 30 m from a mussel farm. However, on a Thai farm (*P. viridis*), Somerfield et al. (2000) provided evidence that meiobenthic impacts that did not extend much beyond the farm periphery whilst, in terms of impact duration, recovery (in terms of carbon/nitrogen balance and macrobenthos) has been estimated at four and 1.5 years Mattsson and Linden (1983) and Stenton-Dozey et al (1999) respectively.

4.4.3 Effects of live mussel shells and shell debris

Mussel farming can also change the receiving environment through the accumulation of shells which fall from the supporting structure onto the seabed. Shells end up on the seabed through natural attrition (Mattsson and Linden 1983), disturbance by predators (e.g. birds) or during storms, through deliberate dumping (e.g. of low-valued, small or biofouled shells) during harvest operations (Hartstein 2005) or through the cleaning of farm superstructure (which frequently includes mussels) onto the seabed (Hartstein 2005).

The deposition of live shells will feed and enhance megabenthic predator/scavenger populations with the resultant empty shells accumulating and potentially changing the physico-chemical nature of the sediment.

Most of the literature, personal observations and discussions with mussel farmers indicate that, in most circumstances, dropped live shells are quickly consumed by predators. It, therefore, seems unlikely that new benthic mussel communities will develop under mussel farms as a consequence of the loss of living shells. Given that the number of shells dropped can be large, for example

3000+/-1000 shells m^{-2} year^{-1} according to Mattsson and Linden (1983), it is not surprising that benthic predators/scavengers (mainly crabs and starfish) are commonly observed as being very abundant around farms (e.g. Tenore et al. 1982, Inglis and Gust 2003) and that the seabed around farms is frequently covered with shell debris (up to 50% Inglis and Gust 2003 and more (personal observations)). Whether enhanced benthic predators/scavengers associated with dropped shells should be viewed as negative depends on perspective; Tunkijjanukij and Intarachart (2007) comment that some commercial fish and crab species were more abundant in association *P. perna* detritus (in Thailand) to the benefit of static gear fishermen and Mattsson and Linden (1983) reported good fish catches next to mussel rafts. However, this effect is not found at every location, for example Clynick et al (2008) found little evidence of enhanced productivity in association with mussel lines in the Magdalen islands (Quebec, Canada). Whilst living mussel beds are associated with high levels of biodiversity (e.g. Norling and Kautsky 2007, 2008) the biodiversity implications of the dead shells that are most frequently reported under mussel farms is less clear although Kaspar et al. (1985) noted that similarly biodiverse communities existed on both suspended-living and seabed-located dead shells and attributed this to the fact that both offered a hard substratum for attachment of epifauna/ flora.

In most mussel farm situations the independent effects of shell-debris will be hard to determine as live shells sink quickly (we estimate 0.2 m s^{-1}) and are likely to accumulate directly under the farm (personal observations). In more quiescent locations, under mussel lines, mussel shells are likely to be associated with biodeposits (actually exacerbating accumulation, see above) and be shaded from light by overlying mussel lines. There is little known about the long-term fate of mussel shells deposited under farms though anecdotal evidence (W. Spiers, Muckairn Mussels, Scotland, personal communication, June 2010) suggests that in shallow (<5 m), brackish water they slowly dissolve though whether this also occurs in deeper, fully saline water and/or when shells are entrained in sediment,

is not known. Should burial in organically enriched detritus occur (likely under a mussel farm) then it seems plausible that the reducing conditions that normally develop in cases of organic enrichment (Pearson and Rosenberg 1978) may be buffered by the calcium carbonate present in the shell.

Evidence from the oil and gas industry indicates that in more offshore environments (where the mussel growing industry may move, see §5.2) the delivery of mussel shells to the seabed has much the same effect as that reported for around inshore mussel farms. For example, freshly removed fouling mussels (consisting of *M. californianus* and *M. galloprovincialis*) from offshore oil platforms (California, USA) that were dumped onto the seabed reportedly attracted a novel predators/scavenger assemblage (including some commercially important species; Page et al. 1999) which evolved into a differently altered (compared to background) state following the removal of the platform (Bomkamp et al. 2004) but one that still contained species of commercial value. However, this didn't apply to other groups at the same location, for example Love et al. (1999) noted that whilst fish abundance increased in association with mussel mounds under oil platforms there was no change in assemblage structure.

4.4.4 Reef effects

Any structure that is placed, either floating or attached to the seabed, into the marine environment will have an immediate influence on the water column and, through their physical presence, immediately attract fish and other motile fauna: this 'reef effect' has been extensively reviewed in relation to oil and gas platforms (Baine 2002, Seaman 2002), offshore renewable energy structures (Gill 2005 , Inger et al. 2009, Langhamer et al. 2009) and purpose built reefs (e.g. Pickering 1996, Pickering and Whitmarsh 1997, Baine 2001). Artificial reefs are often associated with increased biodiversity which is normally attributed to the additional habitat complexity they offer (Eriksson et al. 2006). In the case of mussel farms, where a bulk of the infrastructure is not in contract with the

seabed, they should be considered *de facto* fish-aggregating devices (FADs) with a similar functionality to artificial reefs (Hower 1998).

Structures placed in the sea rapidly become colonised (unless expensive and often toxic preventative measures are adopted) usually by unique animal and plant assemblages (Brown 2005). Whilst mussel farms are operated to produce a 'clean' monoculture product (which attracts the best price) they can enhance local biodiversity through habitat provision, for example, Tenore and Gonzalez (1976) reports that over 100 species were found in amongst mussels in suspended culture in the Spanish Rias. Whilst sustaining and increasing biodiversity is usually considered beneficial the additional diversity associated with artificial reefs is not always representative of the local assemblage and is, at least in the short-term, influenced by the substratum (Brown 2005) and varies between locations (Cook et al. 2006). New or newly cleaned mussel infrastructure constitutes a 'disturbed' community, potentially facilitating the growth of invasive species (Stachowicz et al. 1999) and their spread along coastlines (by acting as 'stepping stones' Bulleri et al. 2006) (see §4.2.2).

5 The future for mussel farming

Mussel farming is a relatively extensive (cf. intensive) farming method and the primary issue facing expansion of mussel farming is space. Space occupancy will almost always incur a cost (e.g. from a licensing authority or seabed owner) but this is likely to vary according to competition from other stakeholders.

The two major avenues for the expansion of mussel culture are considered to be in restricted exchange environments as part of a bioremedial/polyculture nutrient trading scheme and offshore, in more exposed environments, to reduce stakeholder conflict. Offshore operation is challenging and the move into that arena might prove more economical when combined with other major infrastructure e.g. marine renewable energy sector.

5.1 Bioremediation and polyculture

Mussel culture operations are often located in enclosed, sheltered waters in close proximity to population centres (see § 3.1). Such locations are frequently linked with the build-up of inorganic nutrients (principally nitrates and phosphate) resulting in eutrophication and the uncontrolled growth of phytoplankton (Tett et al. 2003). Such occurrences have been associated with the global expansion of 'dead zones' (Diaz and Rosenberg 2008) in coastal seas that are frequently associated with intensive, unregulated aquaculture in areas including the largest aquaculture operator, China (Cao et al. 2007, Xiang 2007).

One solution to eutrophication is to reduce the nutrient concentrations in the afflicted water body. This is relatively straightforward if the nutrients stem from a point sources (e.g. a particular factory or sewage treatment works with a direct isolated input to the sea), but much more difficult where the source is diffuse, e.g. agricultural run-off (Newell 2004) or where the source is located in the eutrophified water body itself (i.e. a fish-farm). Bioremediation using mussels and polyculture (of a nutrient supplier and mussels) are, conceptually, closely linked both involving the balance between nutrient input and nutrient extraction (using mussels).

Nitrogen (as ammonium, nitrite or nitrate) and phosphorous (as phosphate) are the major nutrients that determine overall phytoplankton abundance. Silicon (as silicate) also plays a role as it is a dietary requirement for diatoms and the balance between it and other nutrients is an important determinant of planktonic composition (Tett and Lee 2005). Mussels, both naturally occurring and farmed, are potentially major players in determining the recycling, and elimination, of these nutrients, from the environment. Mussel culture has the potential to remove nutrients through three main mechanisms: (i) mussel harvest, (ii) microbially mediated biodeposit mineralisation and (iii) simple burial of biodeposits.

Balancing nutrient inputs (e.g. fish-farms) and elimination using mussels (polyculture) has been suggested as a potential solution to concerns regarding the impact of fish-farms in a number of countries included China (Cao et al. 2007) and there is some basis for considering such an approach economically viable (Whitmarsh et al. 2006). Farmed *M. edulis* contain approximately 1 g nitrogen and 0.6 – 0.8 g phosphorus per kg live weight (Haamer 1996) and, by harvesting, these nutrients are removed (as noted for Trecadie Bay, PEI; Grant et al. 2007a). The harvest of *P. viridis* has been deemed successful in removing fish-farm nutrient inputs around Hong Kong (Gao et al. 2008). However, nutrient removal through harvesting is only likely to be a relatively minor way of dealing with eutrophication, for example, a 1500 tonne (biomass) fish-farm may release 104 tonnes of nitrogen per annum whilst a standard mussel harvest (nominally 200 tonnes per annum) would only capture about 1.5 – 15 tonnes nitrogen (Paul Tett, unpublished data, July 2011). However, this may still have value in terms of nutrient trading (Gren et al. 2009a).

In eutrophic water where the bioseston has a very high density, a majority (up to 80%; Tenore and Dunstan 1973) of the filtered particulate material is rejected as pseudofaeces (see §2). This means that, in eutrophic conditions, the fate of the nutrients contained in the biodeposits is likely to have the greatest influence on the nutrient concentrations in the supporting water body (Newell 2004) and, thereby, the efficacy of using mussels in bioremediation.

Biodeposits contain fixed (organic) nitrogen (e.g. amino acids and proteins) and phosphorous (e.g. phosphorylated nucleosides). This material is labile and rapidly broken down by benthic bacteria operating at the sediment/water interface (Grenz et al. 1990). In aerobic conditions, aerobes will oxidise such material to ammonium (NH_4^+) and phosphate (PO_4^-) with the ammonium being either lost to the water column or further oxidised to nitrate which then diffuses either into the water column or is advected (actively via bioturbators, see below, or via diffusion) further into the sediment (Newell 2004). This is the critical part in

using mussels as a tool for tackling eutrophication as nitrates can form the terminal electron sink for anaerobic bacteria operating on the aerobic/anaerobic boundary ('redoxcline'), where they reduce (dentritfy) the nitrate to nitrogen gas effectively removing it from the system (see Figure 1; Newell 2004). The optimal depth of aerobic sediment isn't specified in the literature but what is clear is that the presence of benthic infauna has a profound effect on nutrient fluxes in sediment, including those impacted by mussel biodeposits. The importance of large polychaetes in enhanced denitrification has been shown by Hansen and Blackburn (1992) and Hansen and Kristensen (1998) but this also applies to smaller polychaetes (e.g. Capitella sp; Heilskov and Holmer 2001) and oligochaetes (Riise and Roos 1997). However, research by Lindqvist et al (2009) has indicated that the meiobenthos also make an important contribution to denitrification, possibly through their role in advection.

The requirement for a sedimentary redoxcline to facilitate denitrification limits the situations where using mussel to facilitate nitrogen mineralisation can be used. For example, in conditions where the sediment is already under oxygen stress using mussels to reduce nutrient levels is likely to be less effective (Christensen et al. 2003). It also indicates, as found by Sloth et al (1995), that overloading the benthos with organic material (e.g. biodeposits) will result in a decrease in denitrification as the sedimentary biological oxygen demand exceeds supply and the redoxcline moves towards the sediment's surface. What is more, mussel farms resulting in localised (in time and/or space) sediment surface anoxia, in an otherwise oxic sedimentary environment, will tend to increase nitrogen and phosphorous recycling, with potentially major nutrient pulses occurring both as the sediment becomes anoxic (see below) and as, and if, it recovers (Hansen and Kristensen 1997, Newell 2004). Richard et al (2007a) observed increased nutrient fluxes to the water column, from oxygen starved sediments, underneath mussel farms (2 year old mussels only) in Grande-Entree lagoon (Quebec, Canada) and it seems plausible that, where inappropriately located, mussel

farms may actually exacerbate eutrophic conditions rather than alleviating them (Hatcher et al. 1994, Nizzoli et al. 2005)

The cycling of nutrients as described above is based on sediments that do not support benthic algae (i.e. where sediments lie beyond the photic zone). However, in many mussel growing areas benthic primary producers (e.g. diatoms) are likely to occur around farms and, when actively growing, form a sink for bioavailable nitrogen and, in the short term, reduce the amount that can be advected downwards and denitrified. The longer-term role of benthic primary producers in nutrient cycling is less clear, for example, they may die and then decay in the autumn as light levels drop potentially releasing nutrients, although eutrophication problems associated with an autumnal release are likely to be site specific. In assessing the importance of benthic primary production in nutrient cycling, it should be remembered that the compensation depth may significantly increase if the water clarity increases (e.g. through plankton grazing by cultured bivalves; Newell 2004) and that the microphytobenthic density is highly variable in space and time Azovsky et al. (2004) and Berninger and Huettel (1997) (respectively) further complicating our understanding of their potential role in nutrient cycles in association with mussel farms. Regrettably, another complicating factor will be the potential replacement of the microphytobenthos with opportunistic macroalgal species (such as *Ulva sp, Cladophora sp*) which have the potential to bloom then die and decay with unknown consequences to nutrient cycling (Newell 2004).

Whilst marine sediments have the capacity, through denitrification, to reduce overall amount of nitrogen in the system through nitrification there is no comparable mechanism for phosphorous which can only be lost to the system through isolation from the overlying water column (through, for example, burial). In aerobic conditions, phosphates (from whatever origin) bind to metal oxides and, in this form, are not bioavailable but this process is reversible and the development of anoxic conditions results in phosphate release. The assimilative

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capacity of sediments will depends on their metal ligand content but, ultimately phosphates released in reducing conditions will follow the redoxcline as it moves towards the surface and be released back into the water column, potentially in quite major fluxes (Newell 2004). While several authors note increased phosphate fluxes under mussel farms in various locations (e.g. Ria de Vigo, Spain; Alonso-Perez et al. 2010), Gulf of Fos, France (Baudinet et al. 1990) and the Adriatic (Nizzoli et al. 2005) it is not clear if this represents a net increase in phosphate recycling (compared to farm-absent conditions) and other authors have found mussel farms to have a negligible role in the phosphorous cycle (Hatcher et al. 1994, La Rosa et al. 2002). Silicate flux has been found to be greater under mussel farms compared with control sites (Baudinet et al. 1990, Alonso-Perez et al. 2010) although this may vary over time, for example, (Prins and Smaal 1994) found sediments to be a silicate sink during the spring (plankton bloom) but that the accumulated silicate was slowly regenerated throughout the rest of the year. This contrasts with the findings of Richard et al. (2007a) who reported that the greatest silicate flux occurred during summer when water temperatures were at their greatest and that this was driven by benthic mineralisation of biodeposits (Richard et al. 2007b), a process influenced by bioadvective processes (Lindqvist et al. 2009).

This lack of a common pattern with regard nutrient cycling under mussel farms probably reflects, once again, the complex, interrelated, highly spatially and temporally variable interaction between mussels and their receiving environment. As a consequence the potential for mussels in removing nutrients from eutrophified water bodies is normally quantified through harvest removal only (though Haamer 1996 suggested physically removing biodeposits as a means of enhancing nutrient removal). The expansion of mussel farms, as part of nutrient trading schemes, has been identified as showing considerable potential (Folke and Kautsky 1992) with mathematical models suggesting economic viability (Ferreira et al. 2009) and such an approach has been suggested for application

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to the Baltic Sea (Lindahl et al. 2005) with the resultant crop being used for human consumption, chicken food and agricultural fertilizer.

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5.2 Space competition and the potential for offshore expansion

Competition for space is now limiting expansion of the mussel aquaculture sector in all production areas e.g. Europe (Smaal 2002), Australia (Anon 2011), Canada, India (Appukuttan et al. 1980), Thailand (Somerfield et al. 2000) and China (Guo et al. 1999, Xiang 2007).

In many mussel growing areas the broader surrounding water body is productive (i.e. nutrient rich), and the move offshore is only limited by the technological, cultural (farmer attitude) and cost issues related to a move offshore.

The type of competition faced by an expanding mussel farming sector tends to divide on the basis of the local human population pressure and the naturalness of the production areas. In areas of low surrounding population density and in areas of high scenic and naturalness value mussel farms can be associated with a reduction in amenity value. Users potentially affected by a change of use of this space include those involved in the tourism industry and, if aquaculture is spatially limited by a regulatory authority, other aquaculture ventures (fish or shellfish). Mussel farms located inshore have not been implicated in many megafaunal interactions except with birds; bird predation is a major problem in some areas necessitating remedial action (Ross et al. 2001, Anon Unspecified) though the impact is more on the mussel farm than the birds.

In areas of high surrounding population density e.g. many estuaries and rias, space competition is with alternative space users. These include the aquaculture sector, leisure, angling, yacht anchorages (Smaal 2002, Lindahl et al. 2005),

marine reserves, research (Stenton-Dozey et al. 2001) and waste-water disposal (Jarernpornnipat et al. 2003, Boyd et al. 2005, Cao et al. 2007).

Untreated waste water (e.g. untreated sewage) disposal into shellfish growing area results in contamination of the shellfish with obvious negative implications for product sale. In areas of high coastal population density e.g. India and Thailand, both a lack of expertise and microbial pollution of near shore waters is limiting the industry (Jarernpornnipat et al. 2003, Boyd et al. 2005). Whilst a move offshore would alleviate this problem (Somerfield et al. 2000) conflict with fishermen is likely to continue (Gibbs 2004) and the necessary capital investment might not be available to many of the potential artisanal growers that benefit from the existing inshore industry (Piumsombun et al. 2005).

The offshore environment poses considerable technological and logistical challenges to mussel farmers: waves can damage infrastructure potentially causing loss of the crop to the seabed, limit harvesting opportunities and hence reliability of supply to markets and also make maintenance difficult (Linley et al. 2007). Despite these issues, in New Zealand, there are plans for several large scale offshore mussel farms (2,465 ha in Hawke Bay 3,800 ha offshore from Opotiki with others planned) These sites represent a major expansion of the mussel farming industry in New Zealand (Keeley et al. 2009) but require costly bespoke boats and machinery.

One potential way of limiting the capital expenditure required to establish large-scale offshore mussel farms is to combine them with other offshore operations. Such an approach offers the advantages of not only sharing infrastructure (for example, mooring devices; Buck et al. 2006) but also the exclusion zone. Sharing the exclusion zone reduces the total area lost to other activities, notably towed gear fishing (Buck et al. 2004, Michler-Cieluch et al. 2009), and mussel culture may actually benefit other fishing activities (e.g. sport fishing and commercial static gears; Tunkijjanukij and Intarachart 2007). Offshore mussel

culture already operates in collaboration with oil production in the US (Mee 2006) and, within the Baltic, heavy mussel encrustations have been observed on wind-turbine supports suggesting possible suitability for a dual offshore power and mussel culture site (Maar et al. 2009) where epibiotic mussels are already associated with increased numbers of small demersal fish (Wilhelmsson et al. 2006).

Whilst offshore mussel culture is necessary because of space limitations it has several inherent advantages over inshore sites. These advantages include the production of a superior product (fewer parasites; Buck et al. 2005), better growth rates (Holmyard 2008) and reduced benthic impacts (Keeley et al. 2009). However, expansion of the mussel culture industry offshore may have implications for migrating animals, for example, concerns regarding the trapping of marine mammals, is limiting the expansion of the offshore industry in Rhode Island Sound, Massachusetts, USA (Walter 2000). Whilst storm damage will inevitably causes losses to the mussel grower it may also release a considerable amount of plastic detritus into the sea forming litter which will either get washed onto local shores within unknown ecological consequences (Hinojosa and Thiel 2009) or add to the plastic reservoir that characterises some areas of our oceans.

6 Conclusions

Mussel culture is a global business that produces a high-quality food product, the demand for which is set to grow in response to an expanding human population and the further decline of wild fisheries. The current mussel industry, based on seven mussel species with a current annual production of >1.5 million tonnes, is located in a broad range of environments from boreal enclosed waters, deep water lochs, shallow, warm estuaries to more open-ocean conditions and operates at a range of scales, from small artisanal operations to the 1000+ hectare farms that are being developed in New Zealand. The husbandry techniques employed by this broad range of growers is also diverse, ranging

from simple, near-shore pole supports to farms that are designed for mechanisation. As it currently stands, the common factor in mussel production is the location of farms in sheltered, highly productive waters.

This review identified a dozen cases each where significant impacts and no, minor or positive ecological impacts around/underneath mussel farms were found (Table 4). Non-significant impacts were usually attributed to there being sufficient dispersal of biodeposits but, as Somerfield et al.(2000) (attributed to O'Conner et al 1989) points out, the absence of detectable local impacts does not necessarily mean that the broader environment is not impacted. The most intuitive, broader impact that could occur around extensive mussel farms is one of benthic starvation. Whilst this has never (to our knowledge) been demonstrated, it seems plausible that littoral and infralittoral benthic communities, located shoreward of mussel farms, will suffer reduced productivity in situations where the ecosystem is at maximum mussel yield (e.g. the Spanish rias) and, potentially, at much lower levels. This impact will be exacerbated in situations where the presence of mussel farms significantly reduces the water flow to affected communities, such as occurs when mussel lines are strung across bays.

The possibility of selective particle capture in mussel feeding, or the ability of some phytoplankton groups to evade capture, has profound implications for the impact mussel farms would have on the phytoplankton balance. This is a major gap in our understanding and has implications for the expansion of the industry particularly in enclosed areas e.g. for purposes of bioremediation or polyculture.

All human activities will have an impact on the receiving environment and ecologists can ascertain the nature and extent of such impacts given sufficient resources. Deciding whether statistically detected impacts have an ecological significance is much harder and the major challenge to the regulatory authorities is to define impact thresholds (e.g. seston depletion, relative footprint size).

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Where possible, this should be done within the framework of existing legislation (e.g. the Urban waste-water treatment directive in Europe) and the challenge (to ecologists) would then be to develop a conceptual model that incorporated all major elements (site hydrography to species and husbandry technique) that determine mussel farming impact and the scale of that impact (Tett 2008) in order to meet Fernandes et al.'s (2001) recommendations re. aquaculture impacts.

Whatever the impacts of mussel farms, and whether or not these impacts are deemed acceptable, the sheltered water that currently characterises the industry is under increasing pressure from a range of stakeholders. The generally agreed solution to such overcrowding is to move the mussel culture industry offshore. This has numerous advantages in addition to space availability including product quality, and there may financial benefits from cooperating with other offshore operations (e.g. with the offshore renewable energy industry). However, the expansion of the industry offshore poses several new ecological questions, some of which are already being addressed by the nascent offshore renewable energy industry sector.

The global expansion of mussel farming can be sustainable provided it is proportionate to relevant, local-scale ecological processes. Where this occurs mussel farming can deliver a sustainable, high-quality, low-carbon food product. Furthermore, where mussel farms are integrated into a well-managed marine spatial plan, they can be used to increase local habitat heterogeneity (and subsequent biodiversity), reduce anthropogenic eutrophication, limit destructive fishing practices in fragile environments (e.g. trawling), increase local fisheries (commercial and sport) and provide protected sites for a variety of birds and mammals.

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Table 3 – Basic description of commonly cultured mussel species

Species	Common name	ATH	Conditions where cultured	Location	Reference
Choromytilus chorus (Molina, 1782)	Choro mussel		Cold temperate	Chile	(Winter et al. 1984)
Mytilus chilensis (Hupé, 1854)	Chilean or Chilean blue mussel	nk	Temperate	eastern Pacific (notably Chile)	(Chaparro and Winter 1983) (Carranza et al. 2009)
M. coruscus	Korean mussel, thick shelled mussel	24	Temperate	Korea and China	http://www.iiasa.ac.at/Research/EEP/yssp/Wang2009.pdf
M. edulis (L., 1758)	blue or common mussel	18-24	Cold temperate Cold temperate	Baltic Baltic	(Lindahl et al. 2005) (Gren et al. 2009b)
M. *galloprovincialis* Lamark,1819 *	Mediterranean mussel	12 - 18	Warm temperate	Atlantic	(Tenore et al. 1982, Babarro et al. 2003) }
Perna canaliculus (Philipsson, 1788)	New Zealand green lipped mussel.	12 - 24	Warm temperate	New Zealand	(Hickman 1979)
P. perna	Brown mussel	5 - 8	Tropical	India	(Appukuttan et al. 1980)
P. viridis (L. 1758)	Green lipped or Asian green mussel	6	Tropical	India	(Rajagopal et al. 1998, Tunkijjanukij and Intarachart 2007)

Notes: ATH – age to harvest (in months), nk- not known

Table 4 – Examples of mussel farms –environment interaction indicating location, cultured species, nature of the receiving environment and farming duration and the type and consequence of impact

Note: Key to species column: M. gallo – M. galloprovincialis, P. canal. – P. canaliculatus. Key: Site – type of environment (enclosed or open). Sub. – substratum, Op. – years of operation. Note: several studies describe and compare impacted and un-impacted sites and are these are split and summarised accordingly.

Part I – significant impacts

Location	Species	Nature of receiving environment	Type of impact, consequence and notes	Reference
Tjarno Island, Sweden	*M. edulis*	Depth: 8 -13 m. Current: 3 cm s^{-1} Site: Enclosed Sub.: Mud/ clay Op.: ca. 1 y (not certain)	Organic enrichment resulting in reduced conditions substantial *Beggiatoa sp.* Smell of H_2S was recorded.	(Dahlback and Gunnarsson 1981)
Tjarno Island, Sweden	*M. edulis*	Depth: 15 m Current: 3 cm s^{-1} Site: Enclosed Sub.: mud/ sand, Op.: ca. 3 y	Significant organic material accumulation associated with replacement of large benthic infauna by opportunists. H_2S noted in sediments from under the farm with limited recovery following cessation of farming.	(Mattsson and Linden 1983)
Great-Entry lagoon, Magdalen Islands, Canada.	*M. edulis*	Depth: 5 - 7 m Current: 5 - 18 cm s^{-1} Site: Enclosed Sub.: mud/silt; Op.: 23 y	Accumulations of organic material underneath farms led to growth of *Beggiatoa sp* indicating major impacts. Dominance by opportunistic species. Impact greatest under younger mussels	(Callier et al. 2007)
Prince Edward	*M. edulis*	Depth: 2.5 – 6 m	Algal and bacterial (*Beggiatoa sp*) films associated	(Hargrave et al.

Location	Species	Site parameters	Observations	Reference
Island, Canada		Current: <0.5 cm s^{-1} Site: Enclosed Sub.: mud to fine sand Op.: ca. 10 y	with highest mussel culture intensity. Redox and free sulphur both indicated impacted status associated with mussel culture.	2008)
Saldanha Bay, South Africa	*M. gallo.*	Depth:12 – 15 m Current: 8 cm s^{-1} Site: Enclosed Sub.: Fine/medium sand. Op.: 10 y	Organic enrichment, anoxia, high C:N ratios. Reduction in macrofaunal biomass and change in assemblage. Under some rafts biodeposits 20 cm deep with evidence of sulphide production. High degree of macrobenthic disturbance. Marginal recovery four years after raft removal	(Stenton-Dozey et al. 1999, Stenton-Dozey et al. 2001)
Ria da Arosa, Spain.	*M. edulis*	Depth: 19 m Current[1]: 4 – 8 cm s^{-1} Current[2]: 20 – 25 cm s^{-1} Site: Enclosed Sub.:, Op.: 40 y	Mussel aquaculture has resulted in the benthic environment becoming a low diversity polychaete dominated assemblage from previously diversity equilibrium assemblages	(Tenore et al. 1982), similar results fro Ria de Vigo, see (Ysebaert et al. 2009)
Beatrix Bay, South Island, NZ.	*P. canal.*	Depth: 20 m Current: 6- 12 cm s^{-1} Site: Enclosed Sub.: muddy sand	Low macrofaunal diversity, hypoxic sediments, high sedimentary ammonia efflux, low denitrification was associated with high sulphide concentrations.	(Christensen et al. 2003)
south south-west coast of Ireland	*M. edulis*	Depth: 13 – 14 m Current: 2.6 cm s^{-1} Site: Enclosed Sub.: mud	Reduction in macrofaunal diversity. Reduced macrofaunal diversity associated with organic enrichment	(Chamberlain et al. 2001)

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		Op.: >8 y.		
Tyrrhenian Sea, Western Mediterranean, Italy.	Not specified, probably *M. gallo.*	Depth: 10 m Current: not specified Site: Open Sub.: mud/sand Op.: not specified	Microbial and meiobenthic community changed underneath farms, also found chloroplastic pigments proteins and lipids change, attributable to biodeposit accumulation (this is a non-replicated study)	(Mirto et al. 2000)
Pelorus Sound, New Zealand	*P. canal.*	Depth: 11 m Current: >1 ms^{-1} (max) Site: Enclosed Sub.: mud/sand Op.: up to 5 y.	Significant organic (including nitrogen) enrichment, lowered CN ratios. Decreased macrofaunal diversity was observed under the farm when compared to control sites.	(Kaspar et al. 1985)
Catherine Cove, Marlborough Sound, New Zealand.	*P. canal.*	Depth: 10 – 30 m Current: 3 – 4 cm s^{-1} Site: Semi-enclosed Op.: 15 y, Sub.: mud	Macrobenthic change with dominance by opportunistic polychaetes within the farm boundary associated with moderate organic enrichment.	(Hartstein and Rowden 2004)
Part II minimal impacts				
Hauraki Gulf, New Zealand.	*What species of Perna??*	Depth: Current: Site: Open Op.: Sub.:	Species richness and density (of non-impact indicators) increased under the farm, attributed to increased structural diversity offered by shell hash. Footprint limited to 20 m from farm edge.	(Wong and O'Shea 2011)
New South-Wales, Australia	*M. edulis*	Depth: 6 – 10 m Current: >10 cm s^{-1}	Minimal impact attributed to low stocking density and rapid dispersal of biodeposits but also the operation	(Lasiak et al. 2006)

		Site: Semi-enclosed Op.: 1.5 y	time.	
Southeast Brazil	*P. perna*	Depth: 3 m Current: 25 cm s^{-1} Site: Open Sub.: mud/sand. Op.: 12 y	Greater diversity found under the farm compared to control locations. No measured increase in organic load. No accumulation of shell debris, negligible impact attributed to sufficient water flow.	(da Costa and Nalesso 2006)
Ireland (SW coast)	*M. edulis*	Depth: 12 -15 m Current: 3 cm s^{-1}. Site: Enclosed Sub.: silt/mud Op.: 8 y	No significant impacts detected, attributed to a high residual (not mean) current speed	(Chamberlain et al. 2001)
East and SE Tasmania, Australia.	*M. edulis* and pacific oyster (mixed)	Depth: ca 10 m Current: 3 – 4 cm s^{-1} Site: Sub.: silts and clays Op.:2 – 16 y	Minimal change in sediments around farms, attributed to low stocking density. Any impact was attributed to decomposition of farm-derived fouling macroalgae (and was minor). (Note: these were long-line based mixed oyster and mussel farms).	(Crawford et al. 2003). Note that the species was not specified, assumed *M. edulis*
Prince Edward Island, Canada	*M. edulis*	Depth: up to 6 m Current: weak Site: Enclosed Sub.: Mud Op.:10 - 16 y	Little change in mud /organic content, redox potential, sulphide concentration or species diversity	(Miron et al. 2005)
Blowhole Point, Marlborough	*P. canal.*	Depth: 10 – 30 m Current: 10 cm s^{-1}	No significant change in macrobenthic community or organic enrichment (note the operation time was only	(Hartstein and Rowden 2004).

Sound, New Zealand.		Site: Open Sub.: mud; Op.:3 y	3 years).	See also (Keeley et al. 2009) for a major review of farms within the same region
Adriatic Sea, Italy	*M. gallo.*	Depth: 11 m Current:10 cm s^{-1} Site: Open Sub.: sandy-mud Op.: 6 y.	1. Limited impact, possible increase in deposit feeders underneath farm at expense of filter feeders unable to compete. 2. No significant change in biochemical indicators (organic content, phaeopigments) or meiobenthic community structure. Slightly enhanced bacterial counts under the farm.	(1. Fabi et al. 2009) (2.Danovaro et al. 2004)
Gulf of Thailand, (east coast), Thailand	*P. viridis*	Depth: 3 m Current: 20 – 40 cm s^{-1} (predicted) Site: Open Sub.: mud/sand Op.: 5 y	Impact limited to immediate area underneath farm, and increase in sediment coarseness noted.	(Somerfield et al. 2000)

[1]- (Blanco et al. 1996), positions of current meters not supplied, estimates of current speed throughout Ria da Arosa.

[2] - (Voorthuysen 1973) – current speeds estimated from foram test presence, represent approximate maxima.

Notes: current speeds are means in cm s^{-1} (to two significant figures).