

Chapter 14

Bivalve Assemblages as Hotspots for Biodiversity



J. A. Craeymeersch and H. M. Jansen

Abstract Many bivalve species occur in aggregations, and locally cover large parts of the seafloor. Above a certain density they provide a distinct, three-dimensional structure and the aggregations are called bivalve beds or reefs. These persistent aggregations form a biogenic habitat for many other species. Bivalve beds, therefore, often have, in comparison with the surrounding areas, a high biodiversity value and can be seen as hotspots for biodiversity. Bivalve have a wide global distribution, on rocky and sedimentary coasts. Different processes and mechanisms influence the presence of associated benthic fauna. This paper reviewed the main drivers that influence the biodiversity, such as the bivalve species involved, the density, the size and the age of the bed, the depth or height in the tidal zone and the substratum type.

Bivalve beds not only occur naturally in many subtidal and intertidal areas around the world, but mussels and oysters are also extensively cultured. Addition of physical cultivation structures in the water column or on the bottom allows for development of substantial and diverse communities that have a structure similar to that of natural beds. Dynamics of culture populations may however differ from natural bivalve reefs as a result of culture site and/or maintenance and operation like harvesting of the bivalve cultures. We used the outcome of the review on the drivers for wild assemblages to evaluate trade-offs between bivalve aquaculture and biodiversity conservation. Studies comparing natural and cultured assemblages proved to allow for a better understanding of the effect of the culture strategies and, consequently, to forward sustainable bivalve cultures. This is illustrated by a case study in the Dutch Wadden Sea.

Abstract in Chinese 多数双壳类是群聚的, 在这些贝类出现的区域, 通常会覆盖海底的大部分地区。当种群数量超过一定密度时, 双壳贝类会形成一种独

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特的三维结构聚合体,这种聚合体被称为双壳贝床或贝礁,这些聚合体为多其他物种提供栖息地。因此,与周边地区相比,双壳贝床具有很高的生物多样性价值,可以被看作是生物多样性的热点区域。双壳贝类是全球性物种,在岩石底质和沉积海岸地区均有广泛分布。不同双壳贝床的形成过程和机制会影响相关的底栖动物群落结构。本文综述了影响双壳贝床/礁生物多样性的主要驱动因素,包括贝类的种类,密度,贝床/礁的大小和年龄,在潮间带所处的深度和高度以及底质类型等。

双壳贝床不仅自然分布于世界各地的潮间带和潮下带,而且还广泛用于养殖,例如贻贝和牡蛎等。在水体内或海底投放的人工养殖结构可以形成与天然贝床结构类似的多种多样的生物群体。但是由于养殖过程中的养殖区域选择、日常维护、收获等人为干扰因素,养殖的双壳贝类的种群动力学过程与自然贝礁并不相同。我们利用野生贝礁作为驱动因素对双壳贝类养殖与生物多样性保护之间的权衡进行了评估。自然和养殖情况下环境状况的对比研究有助于更好地摸清养殖活动的环境效应,研究结果对于贝类养殖业的可持续发展具有非常重要的指导意义。本文将通过荷兰瓦登海的一个研究实例进行说明。

Keywords Bivalves · Biodiversity · Natural beds · Reefs · Aquaculture · Wadden Sea

关键词 双壳贝类 · 生物多样性 · 自然贝床 · 贝礁 · 水产养殖 · 瓦登海

14.1 Introduction

14.1.1 Background

Ecosystem services have become a key focus in resource management, conservation planning and environmental decision analysis. Biodiversity itself is valued by humans in many ways for the key ecosystem services it provides, and thus is important to include in any assessment that seeks to identify and quantify the value of ecosystems to humans (<http://fws-case-12nmsu.edu/CASE/ES>). Although in some cases weak no or even negative correlations were found between biodiversity and ecosystem services (Manhaes et al. 2016), evidence is growing that biodiversity supports ecosystem services delivery. Worm et al. (2006), for instance, found positive relationships between diversity and ecosystem functions and services. High-diversity systems consistently provide more services with less variability and, thus, species diversity has a buffering impact on the resistance and recovery of ecosystem services. Moreover, the authors did not find evidence for redundancy at high levels of biodiversity: the improvement of services (such as fished taxa richness and productivity in catch) was continuous on a log-linear scale. These results fit into the predictions of competition theory that greater diversity leads to greater ecosystem stability and lower species stability, among others due to the so-called portfolio effect (Tilman et al. 2006). Thus, hotspots of biodiversity – i.e. areas with a

relatively high biodiversity value (Johnson 2013) – are likely to provide many ecosystem services.

Several bivalve species occur in aggregations, and locally cover large parts of the surface. Above a certain density they provide a distinct, three-dimensional structure and the aggregations are called bivalve beds (Cohen et al. 2007). Mytilid mussels form aggregations by attaching byssal threads to the substratum and conspecifics (Buschbaum et al. 2009; Ysebaert et al. 2009; Lancaster et al. 2014). Oysters are another important group of aggregating species living attached to hard substrata, including living and old shells and conspecifics. The larvae get attached to the substratum by a kind of ‘cement’ produced by a gland in the foot (Walne 1974). These persistent aggregations form – in contrast to aggregations of more mobile bivalve species such as sea scallops (Brocken and Kenchington 1999) – a biogenic habitat for many other species. Bivalve beds, therefore, often have a relatively high biodiversity value compared to surrounding areas and can be seen as hotspot for biodiversity (Bruno et al. 2003; Johnson 2013). Indeed, several authors report that mussel beds on rocky shores and sedimentary coasts harbour more diverse communities than surrounding rock or tidal flats (see e.g. Buschbaum et al. 2009 and the references therein). The magnitude differs depending on a number of biological, ecological or bio-geographical aspects.

Bivalves have a wide global distribution, on rocky and sedimentary coasts, and not only abundance of wild populations is significant, but also of cultured stocks. Though aquaculture is frequently judged for its ecological impacts, it is increasingly recognized that cultured bivalve stocks can also provide a variety of ecosystem services. From a biodiversity perspective, fisheries of natural bivalve stocks can negatively impact biodiversity, while at the same time biodiversity can be high at culture plots or suspended longlines, suggesting that ecosystems may also benefit from aquaculture activities.

14.1.2 Scope and Aim of Review

Biodiversity, and the associated ecosystem services, are not only provided by natural bivalve assemblages but also by aquaculture communities. To assess the role of bivalve aquaculture in biodiversity conservation it is essential to understand the drivers that determine settlement and succession of associated species on bivalve beds. On the one hand are drivers linked to natural processes in each cultivation area (i.e. geographical location, water temperature, depth etc), on the other hand cultivation activities (i.e. seed collection, relay/resocking, harvest, predation control) may also interfere with biodiversity succession. Studies on biodiversity development on aquaculture structures often have a limited temporal resolution, we therefore evaluate the natural biodiversity drivers for wild assemblages and use this to evaluate trade-offs between bivalve aquaculture and biodiversity conservation. The final section of this chapter presents a case study from the Dutch Wadden Sea where the effects of both mussel seed fisheries and bottom cultivation on biodiversity reduction and/or stimulation were evaluated on a bay wide scale.

14.2 Drivers for Biodiversity in Natural Bivalve Assemblages

Persistent bivalve beds are highly structured compared to the surrounding areas, physically change the environment and, thus, create unique habitats (Buschbaum et al. 2009; Ysebaert et al. 2009). Different processes and mechanisms influence the presence of associated benthic fauna. Relative importance of each mechanism will determine the (combined) outcome of the ecosystem engineering effect of the mussels (Ysebaert et al. 2009).

In sedimentary environments, epibenthic bivalve beds provide a major hard substratum on the sediment surface (Buschbaum et al. 2009). Biogenic habitat also offers shelter and predator refuge for mobile epibenthos, which might be predators of the mussels themselves (e.g. crabs and starfish), and are thus also attracted by the mussels as prey (Beadman et al. 2004; Ysebaert et al. 2009). In the intertidal zone, the complex structure provides refuge from tidal stress, and the habitat created is much cooler and more humid than elsewhere during low tides (Cole 2010; Arribas et al. 2013; Jungerstam et al. 2014).

Biodeposition caused by the bivalves will locally change the sediment composition, due to an enrichment of the sediment. As a result, several studies observed a decline in polychaetes, or shift from a community dominated by polychaetes to one dominated by oligochaetes (Commito and Boncavage 1989; Dittmann 1990; Ragnarsson and Raffaelli 1999; Ysebaert et al. 2009) within the bivalve beds. The increased supply of mussel deposits and organic matter may also be an additional food source within bivalve patches: the associated fauna depends on mussel deposition for 24 to 31% of its energy demand (Norling and Kautsky 2007). As a result, biodeposition may have an additional positive effect on diversity (Buschbaum et al. 2009). Thus, bivalve beds provide ecosystem services to the benthic community beyond the physical habitat provided by shells alone (Spooner and Vaughn 2006).

Activity by bivalves themselves might influence the settlement of other species. Dense suspension-feeding bivalves reduce the probability of successful larval settlement by any larvae, including their own. Several authors hypothesize that infaunal species that form cocoons, brood, fragment asexually, or disperse at large postlarval stages may be relatively more abundant in mussel beds than species with planktonic larval dispersal, although this enhancement might also simply be related to the higher spatial complexity of the bivalve bed (Dittmann 1990; Dolmer 2002; Thiel and Ullrich 2002; Ysebaert et al. 2009).

Thus, modification of the physical environment by habitat-forming species may have cascading effects on the associated fauna, in most cases increasing species diversity (Cole and McQuaid 2010; Arribas et al. 2013). On sediment dominated tidal flats as in the Wadden Sea, *Mytilus edulis* beds are seen as ‘islands of biodiversity’ (Buschbaum and Nehls 2003 in Markert et al. 2010). Higher biodiversity has been reported with increasing structural complexity even within the same species (Tsuchiya and Nishihira 1986; Markert et al. 2010). Some invasive engineers, however, may decrease the complexity of habitats by replacing more heterogeneous

native species or assemblages, resulting in decreased species diversity as shown for plantations (Crooks 2002).

The effect on biodiversity might differ between species, the density and the size of the bed or the age of the assemblage. There might also be differences between intertidal and subtidal beds, the position on the (soft) sediment (epibenthic vs endobenthic), and regional or local conditions. In the next paragraphs we will review these aspects.

14.2.1 *Bivalve Species*

A few studies compared beds of different species in the same region. Markert et al. (2010) compared established *Crassostrea*-reefs and native *Mytilus*-beds. The authors report higher diversity values in oyster beds, and these findings are discussed in terms of differences in ecosystem engineering by *C. gigas* versus *M. edulis*. The *Crassostrea*-reef might have influenced the frequency of epibenthic organisms by providing a more complex habitat matrix with an extended hard substrate surface. The geometry of *Crassostrea* shells offers various cryptic microhabitats most suitable for colonization by several vermicular organisms. In contrast to mainly horizontal surfaces which occur in *Mytilus*-patches, vertically oriented *Crassostrea* shells show complex patterns of current flow. Several species, such as suspension-feeding organisms like *Polydora*, may benefit from these conditions, thus resulting in a higher diversity of the epibiont community. Compared to a *Mytilus*-bed, the superficial structure of a *Crassostrea*-reef increases bottom roughness and water turbulences. Thus, more biodeposits could have been exported from *Crassostrea*-patches than from *Mytilus*-patches. *M. edulis* are more frequently affected by burial. The mussels themselves are able to move back to the surface but attached organisms may suffer. In *Crassostrea*-patches, there is a permanently sediment-free upper shell surface, which may have contributed to the richer epibenthos in *Crassostrea*-patches.

Arribas et al. (2013) compared beds of 2 coexisting mytilids on intertidal rocks. *Brachidontes rodriguezii* and *Perumytilus (Brachidontes) purpuratus*, along the northern Argentinian coast. Although these species are very similar in their biological and ecological function, the fauna associated with their matrices are very different. Some species were found associated with only 1 species of mussel, e.g. the bivalve *Lasaea adansoni* with *Perumytilus purpuratus*, or *Mytilus edulis* with *Brachidontes rodriguezii*.

Jungerstam et al. (2014) on the other hand did not find evidence of a strong mussel species effect on associated communities in rocky shore mussel assemblages in South Africa.

When comparing biodiversity of bivalve beds of different regions, the degree of diversity may depend strongly on the regional spectrum of species and the ability of these species to adapt to the engineered conditions within mussel beds. Soft bottom mussel beds may constitute physically similar habitats through the world but the

responses of other benthic species may not be the same, and thus the arising mussel bed communities arise by site-specific rules (Buschbaum et al. 2009). In a study comparing mytilid beds in the North Sea (*M. edulis*), the southern Chilean coast (*Perumytilus purpuratus*, *M. chilensis*), the Yellow Sea (*Musculista senhousia*), and the coast of southern Australia (*Xenostrobus incostans*), these authors did find higher diversity than surrounding areas for mussel beds in the North Sea and at the Chilean coast. For mussel beds in the other regions the number of associated species were only slightly higher (Australia) and even somewhat lower (Yellow Sea) than in adjacent sediments. Comparisons might, however, not only be hampered by regional species' pools, but by differences in e.g. bivalve density, patch sizes, age of the bivalve bed, tidal height and substrate type.

14.2.2 *Bivalve Density and Patch Size*

Some studies related differences in diversity to the bivalve density at the time of the sampling (Commito 1987; Dittmann 1990; Murray et al. 2007), but more recent studies did not find increased diversity at higher bivalve densities, or expressed their doubt. Faunal assemblages associated with ribbed mussel beds along the South American coast varied independently of the density of mussels (Sepúlveda et al. 2016). Asmus (1987) found no correlation between the density of blue mussels and the species number of associated epifauna. The mussel density encountered within a bed at the time of sampling requires careful consideration in view of the fact that the mussel bed will change dynamically due to mussel growth and mortality. As a result, the infaunal assemblages encountered at the time of sampling may reflect not only the mussel density at that time but also the initial mussel stocking density. The latter may have a long-term influence through the biodeposition that has occurred prior to invertebrate sampling (Beadman et al. 2004). In conclusion, any positive (and negative) correlations are thus likely to depend on local physical conditions and larval dispersions, and no general assertions can be made (Murray et al. 2007).

Cole (2010) experimentally compared engineered and unmodified habitat, and different configurations of engineered patches of the marine intertidal mussel *Trichomya hirsuta*. Regularly spaced solitary mussels had more edge and consequently more species, unique species (mostly macroalgal species but also several molluscs, arthropods and polychaetes) and densities of generalists. The findings suggest that the configuration of patches of a habitat is a crucial factor affecting mussel bed biodiversity, and fragmentation of habitat into regularly spaced patches may have a positive influence on biodiversity due to the positive response of other species to habitat edges. The experimental design, however, poorly reflects natural complex structure as described above. Factors affecting the structure of the habitat (bed thickness, age distribution, cover, ...) probably have larger effect than patch size itself. Not surprisingly, thus, in literature different relationships are found between patch size, even within a single study area, although always either positive

or not significant (see e.g. Tsuchiya and Nishihira 1986; Norling and Kautsky 2008; Koivisto et al. 2011; Jungerstam et al. 2014; Sepúlveda et al. 2016).

14.2.3 Age and Size Structure of the Bivalve Assemblage

With the aging of the mussel assemblage, mussels require more space for attachment and some individuals in the periphery of the patch are pushed out while some inside the patch are shifted. This results in a multi-layered bivalve bed. It also results in more space and larger amounts of sediments and shell fragments (Tsuchiya and Nishihira 1986). As mentioned above, this mostly results in an increase in species diversity. However, if recruitment fails, the patch might become mono-layered and poorer in species richness (Tsuchiya and Nishihira 1986).

In the study of Tsuchiya and Nishihira (1986) patches of different age also differed in size: older patches consisted of larger mussels. The size of mussels is, however, not necessarily related to their age (Buschbaum and Saier 2001). To separate the effects of size and age, O'Connor and Crowe (2007) manipulated the age of mussel patches of *Mytilus edulis* and the size of mussels within them to test experimentally the effect of size on the associated assemblages. At one of the two locations, the size of the mussels did affect the abundance of some species, but did not affect species richness. Cole and McQuaid (2010) found the same results in beds of *Mytilus galloprovincialis* and *Perna perna*. Sepúlveda et al. (2016), on the other hand, did not find any significant association of both richness and abundance of the associated fauna with the size or density of ribbed mussels *Aulacomya atra*.

14.2.4 Substrate Type and Stability

Benthic species show distinct distribution patterns in relation to the type of substratum (see e.g. Wood 1987; Künitzer et al. 1992; Reiss et al. 2010) and substrate stability (Arribas et al. 2013). On hard substrates, bivalve beds are obviously epibenthic. Soft bottom mussel beds may be endobenthic, with a diversity of transitions between endobenthic and epibenthic mode. In endobenthic beds, most individuals are positioned below the sediment surface. Thus, diversity may depend on the epi- versus endobenthic traits (Buschbaum et al. 2009). Low substrate stability consequently results in unstable habitat for the associated fauna, directly as a consequence of increased susceptibility of the bivalve bed to dislodgment, or indirectly as a consequence of differences in the amount of sediment trapped. On rocky substrates along the northern Argentinian coast, a relationship was found between rock hardness, the amount of sediment trapped and the biological assemblage. Species composition was different and total abundance was lower at the shore with the lowest rock hardness and the smallest amount of sediment trapped. Diversity, however, was not

significantly different (Arribas et al. 2013). Ysebaert et al. (2009) hypothesized that a decrease of number of endobenthic species due to an increased organic flux to the sediment to be stronger in a low-flow environment than in a high-flow environment where most biodeposition was expected to be swept away with currents. However, this hypothesis was rejected by their results. Apparently (pseudo) fecal material is also deposited nearby the mussel bed (*M. edulis*) under a strong current regime. The physical structure of the dense bed leads to protected conditions. Moreover, the strong hydrodynamic forces lead to much higher suspended matter concentrations in the water and thus increase the biodeposition rates of mussels as compared to the quiet clearer waters in calm conditions.

In literature both a rich associated assemblage of species of bivalve beds are reported as well as similar or reduced diversity in comparison to the surrounding sedimentary environments. This suggests that mussel beds in sedimentary environments may not invariably be hot diversity spots.. Buschbaum et al. (2009) found, for instance, enhanced species richness and diversity in epibenthic *Mytilus edulis* beds, and lower in *Musculista senhousia*. Other studies showed the opposite: higher species richness inside *M. senhousia* beds, decreased diversity in *M. edulis* beds (Crooks 1998; Commito et al. 2005). Apparently the response is not dependent on the species, but the effects on the associated species are site specific (Buschbaum et al. 2009).

14.2.5 Tidal Versus Subtidal

Bivalves in the intertidal zone experience different abiotic conditions than their subtidal conspecifics. Mussels in the intertidal zone experience extremes in temperature, from baking in the sun in summer to freezing in winter. They are subject to freshwater exposure during rainstorms, to risk of being dislodged by waves or battered by logs during storms, and to periodic interruption of feeding, gas exchange, and excretion through tidal cycling (www.asnailsodyssey.com). And, of course, there is a difference in tidal emergence. This might have influence on bivalve bed characteristics, such as growth of the animals, the density or the three-dimensional structure (AIN 2001; Saier et al. 2002). Moreover, species composition changes too along the tidal gradient and, consequently, this may result in differences in the associated species.

The literature mentioned above compared either mussel- and non-mussel covered areas or different bivalve beds, but comparisons were only made within intertidal or subtidal areas. We are only aware of one study comparing intertidal with subtidal. Saier et al. (2002) compared studies of intertidal and adjacent shallow subtidal mussel beds in the northern Wadden Sea. They concluded that intertidal and subtidal sites were ecologically different with respect to the mussel bed structure as well as associated organisms. The studies revealed higher densities in intertidal beds

of smaller mussels. Subtidal mussels were less fouled. Several sessile species are found only on either intertidal or subtidal beds. Finally, higher diversity and species richness on non-attached epifauna (mobile invertebrates living within the mussel bed matrix) was found subtidally.

14.2.6 Other Factors

When comparing studies on biodiversity aspects of bivalve beds, one should keep in mind that the degree of diversity may strongly depend on the biogeographical/regional species pool. Even if the mussel beds constitute physically similar habitats the responses of other benthic organisms may not be the same, hence, the associated mussel bed communities arise by site-specific rules (Buschbaum et al. 2009). Sepúlveda et al. (2016), for instance, showed that the mussel-associated fauna along the northern Argentinean coast differed between the northern (Peru and Northern Chile) and southern area (Southern Chile). The differences reflect the well-known Peruvian and Magellanic provinces and show that the associated fauna is highly sensitive to biogeographic signals, despite the fact that the fauna make use of similar bioengineered habitat throughout their geographic ranges..

In conclusion, there seem to be some generic drivers, but one should realize that the influence of the mentioned drivers depend strongly on the local hydrodynamic, topographic and biogeographic conditions.



Fig. 14.1 Mussel aquaculture on bottom plots (left) and suspended ropes (right) demonstrating that cultures include a rich community of flora, epifauna and mobile fauna (crabs, fish) species. ©J. Capelle (left) and T. Strohmeier (right)

14.3 Biodiversity Trade–Offs in Cultured Bivalve Assemblages

Bivalve beds naturally occur in many subtidal and intertidal areas around the world, but mussels and oysters are also extensively cultured (Wijsman et al. 2019). Mussel aquaculture is done by means of bottom cultures (by seeding intertidal or subtidal beds), but also by suspended cultures (using rafts or longlines), and cultures on bouchots (Smaal 2002; Beadman et al. 2004) (Fig. 14.1). Addition of physical cultivation structures in the water column or on the bottom allows for development of substantial and diverse communities that have a structure similar to that of natural reefs (Callier et al. 2017): the biogenic structure offers habitat for numerous species, infaunal and epibenthic, hard substrate species, as well as shelter and predator refuge for mobile epibenthos. Apart from the reef building function in the water column, suspended cultures may also create rich fauna communities in the benthic environment through fall-off and enrichment by biodeposition (McKindsey et al. 2011; Callier et al. 2017) similar to enrichment effects observed in direct proximity of natural bivalve reefs (Dittmann 1999, van der Zee et al. 2012, Ysebaert et al. 2019, and references mentioned above). Moreover, some of the epibenthic species, including the cultured bivalves, are attracted by the bivalves as prey. Dynamics of culture populations may however differ from natural bivalve reefs as a result of culture site and/or maintenance and operation of bivalve farms (Callier et al. 2017). Consequently, differences may be expected in the processes that are dominant for driving biodiversity development, and thus in the faunal communities of natural and cultured beds. We can expect this to be the same in cultured bivalve assemblages (Table 14.1).

14.3.1 *Mussel Fisheries on Wild Beds*

Mussel seedbeds, where spatfall, the settling and attachment of young) to the substrate has occurred, are often exploited by dredging the young seed mussels and moving them to areas where growing conditions are more favourable. Surprisingly few studies are available describing the impacts of this type of bivalve dredging on

Table 14.1 Expected influence of cultured bivalve assemblages on biodiversity

Aquaculture strategy	Expectation based on natural beds
Choice of cultured species	Biodiversity varies with species
Density of species	Multi-layered, more complex beds have higher diversity
Predator control	Disturbance limits complexity and diversity
Relay and harvesting	Disturbance limits complexity and diversity
Age when harvested	Young, less complex, beds have lower diversity
Site selection	Local conditions are most important driver

changes in the abundance of associated species. A meta-analysis on the effects of different types of trawling and dredging by Collie et al. (2000) concluded that data on impacts and recovery of epifaunal structure-forming benthic communities are indeed lacking.

Dolmer (2002) demonstrated that dredging on commercial-sized mussels negatively influence fauna communities on the short-term, especially for polychaetes. Furthermore, after 4 months the effects of dredging on epibenthos were still evident and included a reduction in density of a number of taxa (sponges, echinoderms, anthozoans, molluscs, crustaceans, and ascidians). A large scale study in the Dutch Wadden Sea suggested that impacts can in certain seasons last up to 1.5 years, while for other seasons it was hard to define any impact at all (see case study below). Collie et al. (2000) concluded that recovery from dredging may take several years.

By collecting spat to stock cultivation sites new habitats are created that will support some of the animals present on the seedbeds (Smaal and Lucas 2000; Murray et al. 2007).

14.3.2 *Benthic Cultivation Plots*

As for natural beds, it is expected that by increasing mussel biomass through cultivation, the species richness, abundance, and biomass of the associated macrofauna would also increase compared to the surrounding, bare areas. An increase in the number of epibenthic species indeed was found for mussel culture plots in the Oosterschelde (the Netherlands) but not in Limfjorden (Denmark) (Ysebaert et al. 2009). In the latter system, however, epifaunal species are rare, and although no increase in diversity was observed within the mussel plot, species richness was higher at sites with mussels compared to sites with none or almost no mussels. Trianni (1996) observed higher diversity for cultivation sites of on-bottom oyster culture relative to surrounding muddy bottom areas due to increase abundance of epifauna associated with the oyster shells.

Mussel farmers will attempt to lay mussels at a density and tidal height that will realize highest growth and the greatest financial return upon harvest. At high mussel densities multi-layering is likely to occur, which will increase mussel bed complexity (see e.g. Beadman et al. 2004; Smith and Shackley 2004; Ysebaert et al. 2009), providing habitat for a large number of associated species. If so, the seeding practice might influence the number of species found on a commercial bivalve bed. This conclusion is also made by Murray et al. (2007) based on the findings of Tsuchiya en Nishihira (1986) in natural beds that mussel patch size is positively correlated with species richness. However local differences do exist as on intertidal mudflats in north Wales, UK, highest number of species was found at beds with low mussel cover (Beadman et al. 2004). These beds have habitats suitable for both the typical mudflat fauna and the typical mussel bed fauna by the extra microhabitats provided within the isolated clumps of mussels. Species richness declined with increased

area of mussels, hence the more positive benefits of increased habitat complexity are apparently out-weighted by negative factors, such as a highly anoxic environment and competition for food and space. Murray et al. (2007) investigated mussel and fauna biomass on rafts, and intertidal and subtidal bottom cultures in Maine (USA). They observed both significant positive and negative, as well as no correlations between mussel biomass and associated faunal biomass. This indicates that, as for natural beds, the biodiversity associated to bivalve cultures is likely to a large extent driven by local conditions. Ysebaert et al. (2009) also suggests that the impact on the benthic community due to biodeposition is influenced by local topographic and hydrodynamic conditions.

Regular relay and harvesting of cultured beds may, on the other hand, prevent the age and size of the mussel patches increasing above a certain point. It may also make the bed structure less layered and complex. Thus, harvesting is expected to limit the diversity of the associated fauna (Tsuchiya and Nishihira 1986; Smith and Shackley 2004). Though under certain circumstances, a lower cover might result in a higher diversity (Beadman et al. 2004), as mentioned before. Little is known about the temporal dynamics of succession in associated species on commercial bottom plots and how culture practices influence these processes. Questions still remain to be answered include e.g. how much fauna is transported together with seed to the bottom plots, how quickly will a plot be colonised by opportunists and the more resident fauna species, and what are the effects of relaying and predator control?

In bottom cultures predation by starfish and crabs can be significant (Capelle et al. 2016a) and measures are taken to remove starfish with special adapted trawls that basically 'mob' the bottom plots removing part of the starfish population. Yet the efficiency of this method is debated.

14.3.3 *Suspended Cultures*

The ecological effect of the habitat created by bivalve farming is well-recognized for bottom cultures. Forrest et al. (2009) suggests that there is also evidence of a comparable role for suspended culture structures, intertidal trestles or other intertidal structures used for bivalve cultivation.

In suspended cultures, the physical infrastructures themselves (buoys, ropes and anchors) already provide substrate for many organisms (Murray et al. 2007; Ysebaert et al. 2009), as well as the bivalve populations itself. The settlement of different ascidian, polychaete and crustacean genera reported by Jansen et al. (2011) on suspended mussel ropes, reflected a significant increase in taxonomic richness throughout an annual cycle. This agrees with Taylor et al. (1997), Richard et al. (2006) and Lutz-Collins et al. (2009), which showed that number and composition of fauna associated to bivalve cultures are dependent on culture duration. Intra-annual variation in associated faunal abundance is also observed in suspended oyster culture (Mazouni et al. 2001). Temperature is thought to be an important driver for abundance of associated species, especially for filter-feeding species that attach to the suspended cultures (Khalaman 2001). The average number of fauna genera associ-

ated with mussel ropes ranged between 7–10 genera (Richard et al. 2006; Jansen et al. 2011). The proportion of the fouling biomass relative to mussel biomass ranges from 0 to 10% (LeBlanc et al. 2007; Jansen et al. 2011). The presence of deposit-feeding polychaetes, such as *Capitella* and *Neoamphitrite*, indicate that mussel ropes contain large amounts of organic material, thereby indicating that suspended ropes serve as a sediment compartment in the water column (Jansen et al. 2011 and references therein).

The mussel stocking densities used (i.e., the number of mussels per unit length within a sock) influence the growth rate of the mussels and, simultaneously, determine the amount of surface area available for the epifaunal organisms to colonize (Tsuchiya and Nishihira 1986; Thompson and MacNair 2004). Lutz-Collins et al. (2009) studied the effect of mussel density on colonization by polychaetes in Prince Edward Island (Canada). Polynoid worms of the genera *Harmothoe* and *Lepidonotus* were by far the most abundant taxa colonizing mussel socks. Although there were sharp density variations associated with stocking density, these differences were inconsistent and no trends across stocking densities were observed: an increase in stocking density did not seem to be causally related to an increase (or decrease) in the total specific epifaunal densities. Because of this apparent lack of influence, stocking density was considered to be irrelevant. Date along the growing season was in this study the most obvious factor influencing the overall epifaunal composition.

In many cultivation areas mussel lines are at least once being resocked during the culture cycle to grade the mussels and thin densities to prevent drop-off. During this process most of the associated biota will be removed, however, no information on the effects of those management activities are reported in literature.

It should be noted though that fostering biodiversity in suspended cultures might seem somewhat paradoxical from an commercial perspective, as fouling species are in many cases the bane of the aquaculture industry (Durr and Watson 2010; Fitridge et al. 2012). Fouling species might interfere, compete for food sources with the bivalves (e.g. tunicates) or they might predate on the bivalves itself (e.g. star fish or crabs). Particularly in case of suspended cultures methods have been developed to remove the fouling organisms. Generally, control of biofouling in aquaculture is achieved through the avoidance of natural recruitment, physical removal and the use of antifoulants (Fitridge et al. 2012). Methods to remove ascidians, a fouling species that can become dominant on mussel ropes and competes for space and food resources, include freshwater and acid treatments (Carman et al. 2016).

Mussels from rafts or longlines not only have effects on the fauna associated with the cultivation structure but also on the fauna of the sedimentary environment below them. Drop-off from mussels mostly enhances species such as star fish, sea cucumber and crabs (Romero et al. 1982; McKindsey et al. 2011). McKindsey et al. (2011) reviewed the extensive literature on the effects of biodeposition on infauna communities and suggest that, for the most part, community responses follow the Pearson en 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. Though the latter is not

frequently observed under mussel farms. Biomass and species richness may increase with limited organic loading whereas abundance may increase with moderate loading as smaller, opportunistic, species come to dominate.

14.4 Case Study: How Do Benthic Mussel Culture Activities Affect Subtidal Biodiversity in the Western Wadden Sea

Mussel culture in the Dutch Wadden Sea is dominated by bottom cultivation, and mussel seed is traditionally collected from wild subtidal mussel beds, though a shift towards suspended systems for spat collection is implemented. Seed fisheries and management of bottom plots may each have specific effects on reduction or enhancement of biodiversity of associated species. To assess these effects, an integrated approach was applied which provided an ecosystem wide evaluation on the effects of mussel culture activities on biodiversity of infauna and epifauna communities in sublittoral areas of the Dutch Wadden Sea.

14.4.1 Fisheries Impacts on Biodiversity

Mussel seed generally settles in the south-western part of the Wadden Sea, yet the total area of mussel seed beds varies strongly from year to year. Approximately 50% of the beds are characterised as instable, indicating that they will not survive the winter as a result of storms and/or predation. Fisheries takes place two times a year; in autumn the classified instable beds are open to fisheries, and in spring stable beds may be fished, given that there is enough total mussel biomass for birds to feed on (Capelle 2017).

The effect of mussel fishery on mussels, epifauna and infauna species was investigated over a period up to 6 years comparing adjacent plots with and without mussel seed fishery (Craeymeersch et al. 2013; Glorius et al. 2013; Van Stralen et al. 2013) (Fig. 14.2). Only 4 of the 21 areas were fished more than once during the research period. Short to medium-term (weeks to months) effects of fishery activities were observed in terms of total density and in species composition of fauna populations. As most species were positively correlated to the presence of mussels (associated species), changes in species communities were assumed to be correlated to the removal of mussels. Reduction in abundance of anemones was linked to removal or damage by fishing nets. Long term (> 1.5 year) effects were not observed, thereby assuming that mussels that remained on the fished plots provided enough structure for development of associated fauna populations. Observed effects, i.e. different development in open and closed plots, were more profound for plots fished during spring than during autumn because closed (no fishery) plots also changed considerably in terms of mussel and thus associated fauna biomass during winter storms, making it difficult to detect any fishery related impacts.

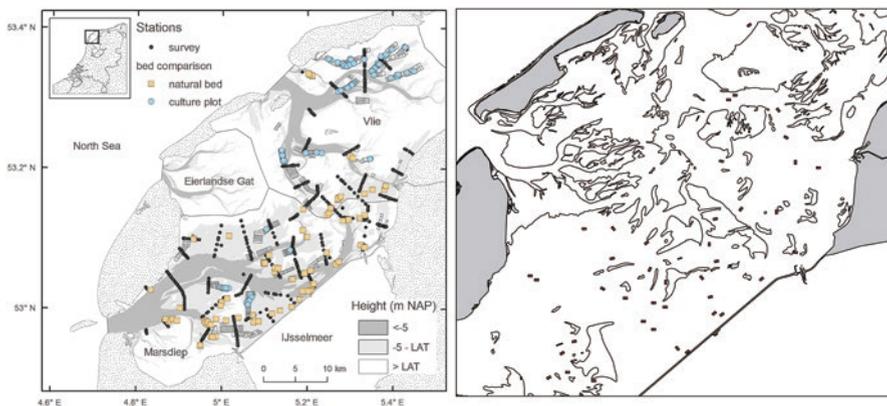


Fig. 14.2 Maps of the western Dutch Wadden Sea. Left: sampling stations of benthic survey in 2008 and from a study comparing natural mussel beds and mussel culture plots (Drent and Dekker 2013b). Right: locations used in studies on the impact of mussel seed fisheries (Craeymeersch et al. 2013)

The study also confirmed large heterogeneity of associated fauna composition within a mussel bed, and large year-to-year variation in species composition, independently of any human impact. It was therefore concluded that overall, any fishery effects seemed to be less important in determining species composition than external factors controlling mortality and recruitment.

14.4.2 Biodiversity on Culture Plots

Moving seed mussels to bottom culture plots enhances the total mussel biomass in the Wadden Sea by 27% compared to a situation where no fisheries exists (Wijsman et al. 2014; Capelle et al. 2016b). This is a consequence of mussel seed fisheries on instable mussel beds, and subsequent transport to bottom plots where the mussels have higher survival rates and where reduction of predators (starfish, crabs) is achieved through effective management strategies.

It is well known that bivalve populations serve as a suitable habitat for a number of species, resulting in high biodiversity within bivalve aggregations (see Sect. 14.2). A field study was performed to test if this also holds for biodiversity on culture plots (Drent and Dekker 2013a). Approximately three times higher total biomass of associated fauna was observed for wild beds (i.e. beds originating from natural spatfall) compared to culture plots, mainly caused by high biomass of endobenthic species on wild beds (Fig. 14.3). However, the total number of species recorded was significantly higher for culture plots (102 for plots, versus 84 for beds), indicating that culture plots do serve as an unique habitat for biodiversity development. A complicating factor for direct comparison is however the spatial distribution; culture plots are mostly located in the north, while wild beds survive best in the South-West of the Wadden Sea, indicating that not only the origin (wild

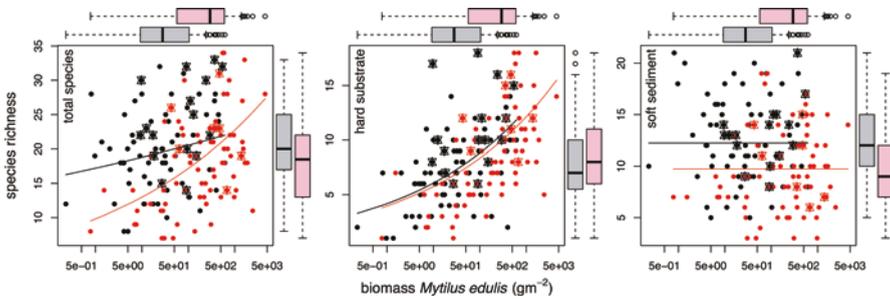


Fig. 14.3 Relationship between total species richness (left), species richness of hard substrate species (middle) and species richness of soft sediment species (right), in a 0.06 core sample and biomass of *Mytilus edulis* in the same sample. Black dots are for cores outside mussel culture plots and red dots for cores inside mussel culture plots. Lines are fitted GLM model results for inside and outside mussel culture plot observations. Boxes in the margins show the distribution of the observations. Stations with *Crassostrea gigas* are indicated with stars (Drent and Dekker 2013a)

bed vs culture plot) but also local environmental conditions, like salinity, might drive biodiversity development within the mussel aggregations. Culture plots are situated in higher salinity zones near tidal inlets connecting the Wadden Sea with the North Sea, wild beds in lower salinity zones landwards of the tidal basins. Comparison of culture plots and wild beds located in proximity of each other show higher species richness for wild beds, indicating that environmental conditions may indeed affect biodiversity development. The overall conclusion of this study was that wild beds and culture plots differ in fauna communities (species and densities), but both form a unique habitat for a diverse population of benthic fauna.

14.4.3 Integrated Assessment

These studies show that the effects of different mussel culture activities vary; seed fisheries on wild beds may have a direct negative impact on biodiversity (short term), but at the same time leads to an increased survival and thus higher total biomass of mussels on the culture plots. High mussel biomass in turn leads to high biodiversity, also on culture plots. Quantitative comparison between those processes is difficult, due to large temporal and spatial differences of the activities. Nevertheless, those results provide valuable guidance for further development of management strategies for nature conservation and sustainable bivalve culture in the sublittoral areas of the Dutch Wadden Sea.

14.5 Concluding Remarks

The influence of different drivers such as the kind of bivalve species, bivalve density, substrate type, tidal zone, etc. ... on associated species appear generic while local hydrodynamic, topographic and biogeographic conditions strongly define

which driver is dominant for each specific area. This holds for both natural as cultured bivalve assemblages. Even within a small waterbody, such as the western Wadden Sea, differences in biodiversity are found that can partly explained by natural drivers, such as salinity or depth, and another part is the result of local spatial variability. Nevertheless, studies comparing natural and cultured assemblages allow for a better understanding on the effect of the culture strategies and, consequently, to forward sustainable bivalve cultures.

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