Chapter 3
Provisioning of Mussel Seed and Its Efficient Use in Culture

P. Kamermans and J. J. Capelle

Abstract Mussel culture largely depends on seed and feed from the natural environment. This paper focusses on seed provisioning and efficient use of these resources in mussel production. Approaches and technologies for seed supply and efficient use of seed in mussel production are described for the different culture techniques. This includes potential interactions and conflicts with the natural environment. Three methods are used to provide seed: wild harvest, use of suspended collectors and hatchery production. Harvest of wild seed from seaweed (in New Zealand) or natural beds is still a major source for culture in some areas, costs are low but provisioning is often unreliable. Most research concerning spat collection deals with comparison of different types of suspended collectors, settlement cues and problems with biofouling. Hatchery seed is more expensive, but hatcheries provide the opportunity for selective breeding and triploid production giving the product an added value. The challenge is to bring hatchery production costs more in line with the actual sale value of mussel seed. Monitoring genetic diversity can give insight in whether collector seed or hatchery seed growth and survival is negatively affected by reduced diversity. Grow-out occurs in bottom culture, bouchot culture and off-bottom longline and raft culture. In bottom-culture, the focus is on developing better seeding techniques, predator control and optimizing culture practices such as timing of relay, substrate use and harvest. For bouchot culture, technical developments are directed to mechanical methods to increase efficiency in size grading, restocking, harvesting and processing. Innovation in growing-out techniques for longline and raft culture are directed towards the investigation of optimal stocking densities, and on material type and configuration of farms. Production efficiency increases from bottom culture to bouchot culture, to rope and raft culture and are related to the sources of mortality and differences in growth rate. Growth rate of mussels is higher in off bottom culture than in on bottom culture and higher when submerged than in intertidal. Mussels from the *Perna* genus are found to have a higher growth rate but a lower production efficiency than mussels from the *Mytilus* genus. Efficient use of seed in mussel culture should aim at a reduction of mussel

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losses and an increase in growth rates. Important tools are adjusting seeding densities in relation to system design, reducing seeding stress, predator control and applying thinning out or relay.

Keywords Mussels · Seed · Culture · Efficiency

3.1 Mussel Aquaculture Production

Mussels are found in large quantities in coastal areas all around the world. Mussels, often organized in patches or in beds, are easily collected and have been an important protein source (an ecosystem good) for mankind since prehistoric times (Erlandson 1988). Mussels are commonly cultured, all that is needed is protection against dislodgement, by using sheltered sites or attachment substrate and protection against predation, supply of oxygen and seston, which is sufficient in most coastal environments. Mussel culture is carried out according to a variety of techniques, often developed in the course of centuries and adapted to the local culture environment. Mussel culture is based on seed and nourishment from the natural environment. This paper focusses on seed provisioning and efficient use of this resource in mussel production.

Global mussel culture mainly concerns two genera (*Mytilus* and *Perna*) and 9 species (*Mytilus edulis*, *Mytilus galloprovincialis*, *Mytilus californianus*, *Mytilus platensis* (*also called M. chilensis*), *Mytilus unguiculatus*, *Mytilus planulatus, Perna canaliculus*, *Perna perna* and *Perna viridis*). In addition, a small production of *Aulacomya atra* and *Choromytilus chorus* takes place in Chile and Argentina. Mussel production comprises around 1.8 million tonnes with a value of 2.7 billion US dollars (average of 2010–2015, FAO statistics). In 2015, the largest production took place in Asia (1.05 million tonnes), followed by Europe (0.50 million tonnes), the Americas (0.25 million tonnes), Oceania and Africa (0.08 million tonnes) (FAO statistics, www.fao.org). The main mussel producing countries are China in Asia, Spain in Europe, Chile in the Americas, New Zealand in Oceania and South Africa in Africa (Table 3.1). Production in China, Chile and New Zealand started in the seventies of the last century and showed a rapid increase (Fig. 3.1). This levelled off for New Zealand around 2005 and continues to increase in China. In Chile production declined fast around 2011, mainly due to problems with toxic algae (Reguera et al. 2014).

3.2 Culture Techniques and Innovations

Mussels culture is based on recently settled individuals called spat, or juveniles called seed. This resource is collected in different ways depending on the local circumstances and grow-out methods. In general, three methods are used to harvest spat or seed: wild harvest, use of suspended collectors and hatchery production

Table 3.1 Mussel aquaculture production (tonnes) in 2015 per species and per country (FAO statistics, www.fao.org)

Species	Country	Tonnes
Mytilus e dulis	France	61,000
	Netherlands	54,100
	Canada	22,725
	United Kingdom	20,112
	Ireland	16,015
	Germany	10,875
	Norway	2731
	United States of America	1788
	Sweden	1525
	Denmark	1229
	Iceland	140
	Senegal	16
	Namibia	10
	Argentina	6
	Argentina	6
	St. Pierre and Miquelon	3
Mytilus galloprovincialis	China	845,038
	Spain	225,308
	Italy	63,700
	Greece	18,628
	France	14,100
	Bulgaria	3373
	Portugal	1315
	South Africa	950
	Croatia	746
	Slovenia	573
	Albania	295
	Russian Federation	207
	Montenegro	189
	Ukraine	70
	Romania	35
	Turkey	3
Mytilus californianus	Mexico	270
Mytilus platensis	Chile	208,707
	Argentina	6
Mytilus plan u latus	Australia	3679
Mytilus unguiculatus	Korea, Republic of	53,536
Perna perna	Brazil	18,364
	Venezuela, Boliv Rep of	1

(continued)

Table 3.1 (continued)

Species	Country	Tonnes
Perna viridis	Thailand	118,775
	Philippines	15,949
	India	8700
	Malaysia	1673
	Cambodia	1500
	Singapore	906
Perna canaliculus	New Zealand	76,811
Aulacomya atra	Chile	1068
	Argentina	4
Choromytilus chorus	Chile	1581

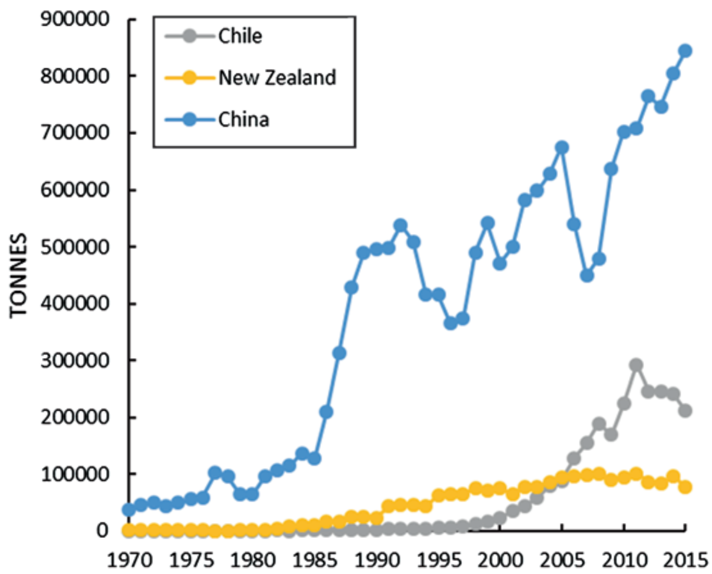

Fig. 3.1 Mussel aquaculture production (tonnes) in Chile, New Zealand and China (FAO statistics, www.fao.org)

(Fig. 3.2). The majority of the grow-out occurs in bottom culture, bouchot culture and off-bottom longline and raft culture (Fig. 3.2).

Each technique to acquire seed has different costs. In general, the least labour-intensive method (wild harvest or fishing) has the lowest cost. Fished seed is mostly used in low-effort grow-out such as bottom culture. However, dredging for seed can result in overexploitation. In New Zealand, this made the industry look for alternatives (Jeffs et al. 1999). Longline and raft culture use collected seed. The system to collect seed is usually the same as what is used for grow-out to make it cost efficient. The most expensive method to acquire seed is hatchery production (Kamermans et al. 2013). This is currently only used in longline culture.

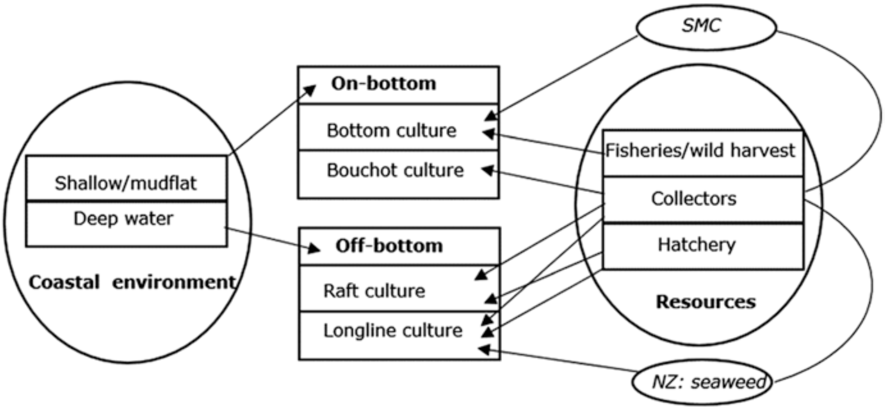

Fig. 3.2 Overview of culture techniques used for mussel production at different environments and for different resources (SMC = Seed Mussel Collectors, NZ = New Zealand)

3.2.1 Bottom Culture

Mussel bottom culture is typically practised on shallow mudflats in areas where there are extensive naturally occurring mussel seed beds (Fig. 3.3d). In the Netherlands, Germany, UK and Ireland, seed fished from natural beds is the main source for bottom culture (Kamermans and Smaal 2002).

Mussel seed from wild beds are relayed on bottom plots (lease sites) where the mussels are maintained until harvest. Bottom culture is an extensive culture where the mussels are still, to a large extent, subjected to, and dependent on the environment. The Netherlands are the centre of the bottom culture industry in Europe. In the 1970s most of the hand labour was mechanized leading to bulk production of mussels, limited by external factors such as seed availability and culture area. From the 2000s onwards, system innovation took place resulting in the deployment of seed mussel collectors (SMCs, Fig. 3.2). The first tests with seed mussel collectors started in 2000 (Kamermans et al. 2002) and the method showed a rapid development. In 2016 the total yield was about 20,000 tonnes (Capelle 2017). The main drivers for system innovation through SMCs were: (i) to safeguard a steady supply of seed, (ii) to become more sustainable by reducing bottom dredging, and (iii) pressure from green NGOs.

Mussel farmers in the Netherlands are in a transition process from fishing seed from natural beds to harvesting seed with collectors. A stepwise approach is taken: every 2 years a decision on reduction of seed fishing and expansion of the area reserved for seed collection is made based on the annual yield of the collectors. The shift from fishing to using collectors results in a higher mussel biomass in the system, because areas with natural beds are no longer fished and spat survival is enhanced on the collectors. However, competition for food (phytoplankton) between the extra mussel biomass and natural bivalve populations may result in overgrazing

Fig. 3.3 Mussel culture methods: (**a**) seed fishery, (**b**) seed mussels collectors, (**c**) hatchery production, (**d**) bottom culture, all in The Netherlands, (**e**) Bouchot culture in France (https://reporterre.net/Les-moules-du-Mont-Saint-Michel-etouffent-la-baie-magnifique), (**f**) raft culture in Spain and (**g**) longline culture in New Zealand. Source of pictures: Jacob Capelle (**a** and **d**), Aad Smaal (**e**) and Pauline Kamermans (**b**, **c**, **f**, and **g**)

and possibly affect the production capacity. This can have consequences for the yields of cultured bivalves and for organisms that depend on bivalve stocks for their food such as birds. A recent study used time-series data analysis and model calculations to estimate effects on production capacity (Kamermans et al. 2014). In addition, different indicators, such as meat content and growth rates of bivalves for assessment of changes in production capacity for bivalve shellfish were investigated. Kamermans et al. (2014) concluded that when all reserved space for SMCs is exploited at the envisioned end of the transition, expected effects on total bivalve biomass production will be less than or proportional to the increase in biomass of seed from SMC, depending on the area. In some areas, survival of wild, unfished beds is quite limited, due to predation.

The development of new technology that came with SMCs, increased the costs for the resource and will require innovations in other forms, notably an increase in production efficiency (Capelle 2017). Several research projects have been initiated to investigate this topic. Focus is on developing better seeding techniques (Capelle et al. 2014, 2016), predator control using starfish mops (Calderwood et al. 2016) or crab pots (Calderwood et al. 2015) and optimizing culture practices such as timing of relay, substrate use (Christensen et al. 2015) and harvest (Newell et al. 1998; Ferreira et al. 2007; Newell 2007).

3.2.2 Bouchot Culture

Bouchot culture (pole culture) is conducted exclusively in France, in areas with flat intertidal mudflats and a relatively large tidal range (Fig. 3.3e). In bouchot culture, mussel seed is collected on ropes, that are placed in horizontal racks in the water column when larvae are present. The ropes are then wound around poles in the intertidal zone for grow-out. Bouchot culture dates back to the thirteenth century and the principles and methods remain largely unchanged. Technical developments are very much restricted to mechanical methods to increase harvest efficiency. Amphibious vehicles are used to harvest the bouchots by means of a cylinder that can be lowered over the poles and scrapes off the mussels (Prou and Goulletquer 2002). Processing, size grading and restocking is also mechanized. Spatial conflicts on bivalve culture with other users is limiting the expansion of bouchot culture in France and has stimulated the development of longline cultures (Prou and Goulletquer 2002).

3.2.3 Raft and Longline Culture

In bays with deep waters and bays with rocky shores, rafts and longlines are more commonly used for the grow-out of mussels (Fig. 3.3f, g). Originally developed in the Mediterranean, large-scale raft culture is conducted primarily in Spain, and in more recent times, extensively at the northwest coast of Spain, where local upwelling results in a high food availability (Figueiras et al. 2002). In raft culture, mussels are grown on ropes hanging from rafts. In rope or longline culture mussels are grown on ropes attached to floating buoys at the water surface or submerged buoys. Longline culture is globally the most used culture method for mussels. Countries where high biomasses of mussels are produced on longlines are New Zealand, China, Italy and Chile. Culture practices can be summarized as (1) obtaining seed, (2) stocking and growing on rope, (3) restocking after thinning out and outgrow to consumption size. Major issues in off-bottom culture is resource requirement, density dependent growth and losses and biofouling. Self-thinning occurs when biomass increased through growth and food or space becomes limited (Fréchette and Lefaivre 1995; Guiñez 2005).

Seed for off-bottom culture is obtained mainly with seed collectors. However, when natural settlement is scarce other methods are used. For example, in New Zealand the spat for long-line culture is collected on Ninety Mile Beach in the far North of the North Island, where seaweed covered with recently settled natural spat washes upon a beach. Spat density varies from 200 to 2 million per kg of macroalgae. It is then transported to the culture areas in Coromandel on the North Island and Marlborough Sounds on the South Island (Jeffs et al. 1999).

Most research concerning spat collection deals with settlement cues, comparison of different types of collectors, and problems with biofouling. Understanding the impact of temperature on the rate of larval development is key to predicting the timing of settlement and optimizing mussel seed collection (Filgueira et al. 2015; Jacobs et al. 2014). However, other factors, such as food availability and quality, are important too (Bos et al. 2006; Philippart et al. 2012). Settlement is significantly higher on rough compared to smooth surfaces (Gribben et al. 2011). The most efficient type of SMC has a large surface area, and there is also thought to be a negative relationship between growth and density (e.g. Çelik et al. 2016). Identification and quantification of the presence of mussel larvae is important for optimising the use of suspended seed collectors. With this information timing of deployment can be optimised. Abalde et al. (2003) used mouse monoclonal antibodies to identify *M. galloprovincialis* larvae. The recent development of another identification method involving molecular tools can speed up processing of samples (Ranjith Kumar et al. 2015). After settlement, mussels can show gregarious behaviour on the collector ropes which is influenced by temperature or food availability (e.g. Aghzar et al. 2012). Failure of the collectors, other than insufficient availability of larvae, is mainly due to biofouling. For example, in Canada, the vase tunicate *Ciona intestinalis* reduces mussel production (Ramsay et al. 2008).

Recently, the focus of research on spat collectors extends towards interactions and conflicts with the natural environment. For example, carrying capacity (see box 1) and genetic diversity are a concern. Larraín et al. (2015) showed that blue mussels in southern Chile, raised from wild-caught seed obtained from relatively few collection sites, have lower genetic diversity than in other countries, and limited genetic differentiation among locations. Transplants of seed from other areas can result in mortality due to adaptation problems (Kautsky et al. 1990). Mussel seed has a high adaptive capacity (Widdows et al. 1984; Stirling and Okumuş 1994), but this varies among sources (Tremblay et al. 2011). Thus, adaptation capacity depends on the genetic composition of the stock and local environmental conditions.

Hatchery production of mussels (Fig. 3.3) is not as common as hatchery production of oysters and clams. One of the reasons why hatchery production of mussel seed is less developed for mussels than for other bivalves is that demand for the industry has been limited until now and that very large-scale production is required to make hatchery seed competitive with wild seed. However, commercial hatcheries that produce mussel spat are present (Kamermans et al. 2013). Optimisation of hatchery production is an ongoing process. For example, a recent study by Gui et al. (2016) showed that gill filaments in small *Perna canaliculus* are not fully developed and capture particles between 15–25 μm, while the filaments in bigger mussels are able to capture bacteria-sized particles around 2 μm. This type of information can be used to select the best algal diet for each life stage.

Generally, mussel hatcheries are only feasible when the price of the product allows it and when alternative sources of seed are scarce or unreliable. A pre-feasibility study for the installation of a Chilean mussel seed hatchery showed that seed production in a hatchery was not profitable due to both the low price of Chilean mussels in national and international markets and the high cost of production, mainly associated to the production of microalgae as feed for the larvae (Carrasco 2015). Seed from hatcheries is more expensive, but hatcheries provide the opportunity for selective breeding. Researchers in New Zealand have developed a selective breeding programme for the Greenshell™ mussel (*Perna canaliculus*) (Camara and Symonds, 2014). Innovative tools, such as cryopreservation that enables genetic material from selected stock to be stored, are being developed (Gale et al. 2014; Wang et al. 2014). Another advantage of hatchery production is the ability to produce triploids. Recently spawned mussels cannot be sold due to insufficient meat. Triploids are non-maturing mussels which have the advantage that they can be sold year-round. Two EU projects (BLUE SEED and REPROSEED) looked into hatchery production for mussels in Europe, including triploid production and the use of recirculation systems (Kamermans et al. 2013; Blanco and Kamermans 2015). Recently, a new project was started in Scalloway, Shetland, to test the commercial feasibility of producing mussel spat.

Kamermans et al. (2013) identified some areas where changes could be made to bring hatchery production costs more into line with the potential sale value of mussel seed: (i) use low-tech algal culture; (ii) restrict activities to the natural season and take seed into the field at the smallest size possible; (iii) scale up culture volumes during this restricted period of activity. In addition, production of higher added-value products, such as triploids or selective breeding for specific traits, is needed. Otherwise, the production of seed by hatchery techniques will be not be profitable in most cases compared with the cost of obtaining the wild counterparts.

Grow-out with hatchery seed is uncertain when it comes to the origin of the harvested strain. This can be the initially seeded hatchery material or wild recruits. Díaz-Puente et al. (2016) used multiplexed microsatellites to trace back the individual origin of a batch of harvested mussels and showed that 98.3% of the adult harvest came from the original hatchery full-sib family while only 1.7% of the mussels were recruited from the wild. A microsatellite genetic analysis of *M. edulis* on the west coast of Canada showed significant reduced genetic diversity in cultured populations compared to the wild population (Gurney-Smith et al. 2017). According to the authors, this is partially due to small effective breeding groups during hatchery propagation, creating genetic drift over successive generations. These results indicate the need for pedigree programs. The European network GENIMPACT evaluated genetic impact of aquaculture activities on native populations. Beaumont et al. (2006) concluded for mussels that it is essential to precisely characterize the true distributions of *M. edulis*, *M. galloprovincialis* and their hybrids in all European regions, but especially where mussel aquaculture takes place. Based on such a survey, a series of sites should be identified that are to be genetically monitored on a regular basis to identify any changes in species composition over time. As far as we are aware such monitoring has not started yet. Effects of climate change, such as ocean acidification, may have a serious impact on larval production. A recent study by Waldbusser et al. (2015) showed that larval shell development and growth in *Mytilus galloprovincialis* are dependent on aragonite saturation state, and not on carbon dioxide partial pressure or pH. With increasing acidification the aragonite saturation state decreases resulting in malformations and reduced growth of D-larvae. Hatcheries have the possibility for chemical manipulation of the seawater in larval tanks.

Innovation in grow-out techniques for longline and raft culture are mainly directed towards the investigation of optimal stocking densities and farm configuration. A few examples are: growing mussels without the need for thinning (Pérez-Camacho et al. 2013), using size grading (Cubillo et al. 2012), stocking as a function of food availability (Fréchette and Bacher 1998; Grant et al. 2008; Cranford et al. 2008; Strohmeier et al. 2005), and investigating the effect of spacing of mussel ropes (Drapeau et al. 2006; Aure et al. 2007). Effect of the culture structures on food provisioning to the mussels, can reduce mussel quality when scaling up (Rosland et al. 2011). Innovation in raft design is directed to deal with harsh environmental conditions, that results for example in submerged raft designs (Wang et al. 2015) and in optimizing food availability by raft design and orientation (Newell and Richardson 2014).

Biofouling on mussels grown on ropes or nets reduces mussel growth and quality (Sievers et al. 2013). In Canada up to 50% mortality was observed under heavy tunicate fouling (Locke and Carman 2009). Biofouling organisms that are causing major problems are ascidians, especially *Ciona intestinalis,* but may also consist of conspecific mussels or other species of mussels, for instance in New Zealand *M. galloprovincialis* is causing large fouling problems on the more valuable *P. canaliculus*. Forrest and Atalah (2017) used a 4-year dataset to calculate that *M. galloprovincialis* cover caused a 5 to 10% decrease in annual yield of *P. canaliculus*. Woods et al. (2012) reported an average of 54% biofouling organisms of the total rope biomass after 6 months. The reseeding of ropes reduced the amount of biofouling to 15% of the total rope biomass 6 months later. Innovations to reduce fouling are directed at reducing settlement. This can be done for instance by occupying 100% of the rope with mussels, or by manual removal of fouling or by using anti-foulants (Fitridge et al. 2012).

Space restrictions in the coastal zone and developments such as off-shore wind-farms, have speeded up developments towards off-shore mussel farms (Buck et al. 2004; Plew et al. 2005; Brenner et al. 2007; Ferreira et al. 2009; Van den Burg et al. 2017). However, off-shore conditions are much more challenging, also from a regulatory perspective (Corbin et al. 2017) and is an important driver of innovation in system design such as on the mooring of the systems (Ögmundarson et al. 2011), material use (Buck 2007) float design and food availability (Stevens et al. 2008).

3.3 Efficient Use

Culture efficiency is defined as how many units of end product (marked sized mussels) are harvested from one unit of resource (mussel seed). The index of culture efficiency is the average physical product APP (Ferreira et al. 2007), the Harvest to Seed Ratio (Newell 2007) or the relative biomass production (RBP) (Capelle et al. 2016). Efficient use is defined as by what means mussels growers can maximize their culture efficiency. Culture efficiency is biologically defined by the dynamics of growth and survival between resource and end product. There are several stages in the mussel culture cycle where management measures are or can be taken to improve growth and survival. These are: at seeding or stocking of seed, at relaying or thinning out and by predator control.

Survival of cultured mussels is dependent on the environment and on stress experienced in culture. In bottom mussel culture, large losses were found associated with seed handling (Calderwood et al. 2014; Capelle et al. 2016). Mussels are gregarious, but high mussel densities will increase competition and may result in substantial losses, that are witnessed in bouchot culture (Soletchnik et al. 2013), rope culture (Fréchette and Bacher 1998; Lauzon-Guay et al. 2005), but also in bottom culture (Capelle et al. 2014). In rope culture mussel losses can peak as a result of secondary settlement, when mussels that were initially attached (primary settlement), detach from the ropes in search for a different attachment substrate (South et al. 2017).

3.3.1 Stocking Density

Stocking mussels at optimal densities will enhance the culture efficiency. High mussel densities will increase competition and might result in substantial losses in bouchot culture (Soletchnik et al. 2013) and rope culture (Fréchette and Bacher 1998; Lauzon-Guay et al. 2005). Stocking in lower densities typically increases efficiency in rope culture (Cubillo et al. 2012), as well as in bottom culture (Capelle et al. 2016). Mussel size at stocking is an important parameter that effects culture efficiency: smaller mussels show higher losses (Lauzon-Guay et al. 2005), but have a higher biomass production potential (Petraitis 1995). However, stocking in low densities will expose more substrate for other species to settle on and enhances biofouling (South et al. 2017; Cubillo et al. 2015). Furthermore, when costs are considered higher biomass production at higher densities might compensate a reduction in quality and survival (Pérez-Camacho et al. 2013; Capelle et al. 2017). In several reports, mussel losses were attributed to seed handling. In bottom culture these losses are density dependent and can be reduced by applying a more homogeneous seeding pattern (Capelle et al. 2014) and by limiting the handling time (Calderwood et al. 2014). In rope culture, losses of 54% were observed within 1 month after stocking (South et al. 2017).

3.3.2 Relaying and Thinning Out

Selecting the best site, with high food availability, may substantially increase culture productivity in mussel bottom culture (Herman et al. 1999; Ferreira et al. 2007). Feeding rates may increase up to a flow velocity of 0.8 m s^{-1} (Widdows et al. 2002); at a certain threshold, mussels may be dislodged, and as such, mussel farmers need to optimize production within this range. In bottom mussel farming, relaying is common practice. Mussels are often kept on sheltered plots over winter and relayed to plots with good growing conditions in spring. Mussels might also be relayed from intertidal plots to deeper plots, to stimulate survival and growth (Beadman et al. 2003). Mussels that are transplanted between areas may require physiological adaptations. Especially in the size of the gills that are used to capture particles and in the size of the labial palps that are used to sort particles into edible and not edible (Bayne 2004). In areas with high turbidity, gills are small and labial palps are large (Theisen 1982). In mussels, an adaptation in the gill-to-palp ratio was observed after transplantation to sites with different turbidity values (Essink and Bos 1985; Payne et al. 1995). After a transplantation experiment between two systems in southern England, it took 2 months for the mussels to adapt the gill-to-palp ratio to the new environment (Widdows et al. 1984).

Ropes or nets have limited attachment area, hence mussels will start to fall off when mussel densities are too high. Self-thinning occurs when mussel biomass increases and space or food becomes limiting, causing a reduction in growth and survival (Alunno-Bruscia et al. 2000; Guiñez et al. 2005). Manual thinning out on ropes in raft culture in Galicia Spain occurs after 4–7 months of growing when the mussels reach 4–5 cm (Cubillo et al. 2012). In the thinning process mussels are detached from the ropes and re-socked in a lower density around a new rope. During the thinning process size grading can take place that will result in a more uniform mussel size at harvest and in less mussel discards (Pérez Camacho et al. 1991). The thinning process in Spain was associated with mussel losses (Pérez Camacho et al. 1991, 2013).

3.3.3 Predator Control

Mussels are not only providing goods for human consumption, but also for a range of other species, some of which depend on them as a food source. Several management measures to prevent predation in *bouchot culture* are described by Dardignac-Corbeil (1975): (1) Crabs (*Carcinus meanas, Maja brachydactyla*) which predate on the bouchot mussels, can be prevented by placing a sheet around the bouchots. (2) Predation by birds (e.g. gulls or molluscivorous ducks) on mussels on bouchots can be reduced by using nylon threads to prevent the birds landing. (3) When starfish and mollusc drilling snails (*Nucella lapillus*) are present in high densities and predation levels are high they need to be manually removed.

Predation may exert a top down limitation on production. Especially, in *bottom culture*, because mussel plots are accessible for benthic predators as well as for fish and birds. Intertidal mussels are preyed upon by shore crabs and birds (oystercatchers, herring gulls), while subtidal mussels are preyed upon by shore crabs, sea stars and molluscivorous (diving) ducks. The number of sea stars on culture plots is reduced by freshwater treatment and there is a selective fishery on sea stars with sea star mops (Netherlands, United Kingdom, Germany, and Ireland) and purse-seines (Denmark Petersen et al. 2016). Freshwater treatment is applied before seeding when mussels are in the vessels' hold; the process consists of the joint exposure of mussels and associated sea stars to freshwater for several hours Mussels will keep their shells shut, while sea stars are unable to protect themselves against osmotic stress and will not survive. Sea star mops are made of fuzzy rope entwined around small chains that are towed over the mussel plots, which ensnares the sea stars thereby enabling removal. The efficiency of sea star removal by mops was estimated in a case study in Belfast Lough in Northern Ireland. The results show a large variation in the catch efficiency (4–78%), while the mean sea star reduction applying this method was 27% (Calderwood et al. 2016).

When Davies et al. (1980) tested the effect of exclusion of shore crabs in newly formed intertidal mussel beds on a scale of 800 m^2; they found that exclusion of shore crabs resulted in a 400–500% increase in yield over a period of 2 years. Experiments have been conducted on selective crab fisheries in a comparative study on culture plots in the Wadden Sea, but no differences in survival between culture plots where crabs were removed vs. where no crab fishery took place could be found (Kamermans et al. 2010). Therefore, exclusion of shore crabs seems to be more effective than a selective fishery.

Rope or net culture of mussels have the advantage above bottom culture that benthic predators cannot reach the mussels directly. Predation by mobile predators on mussels in raft or longline culture are therefore limited to molluscivorous birds and fishes. However, predators with pelagic larvae can settle between the mussels. Sea stars commonly settle in long-line farms and marine flatworms (*Turbellaria* or *Plathyhelminthes*) can infest the mussels and cause substantial losses (Galleni et al. 1980; Robledo et al. 1994). Ducks such as eider ducks that primarily feed on mussels can cause extensive damage to longline mussel cultures (Dunthorn 1971;

Żydelis et al. 2009). In Maine (USA) mussels are protected by nets placed around the mussel rafts (Newell and Richardson 2014). Mussel ropes and nets are very attractive for a range of fish species (Šegvić-Bubić et al. 2011). In the Mediterranean, sea breams are considered a pest that is very difficult to handle and may require nets as physical barriers (Prou and Goulletquer 2002).

3.3.4 Other Loss Factors

Sometimes environmental events result in mussel losses and the only option mussel growers have are mitigation measures. Environmental factors such as harmful algal blooms (HABs) (Peperzak and Poelman 2008) or diseases and parasites (mainly limited to *Myticola intestinalis* in *Mytilidea* (Bower et al. 1994) and *Bucephalus sp.* in *Perna* (da Silva et al. 2002), on bouchot mussels heat stress might increase losses up to 70% (Soletchnik et al. 2013). Ice scour is a catastrophic event for intertidal mussel populations (Donker et al. 2015) However, not all mussel losses can be explained. In recent years, abnormal high mussel losses were observed at mussel production sites in the Atlantic coast in France (2014–2016) and at the Oosterschelde estuary in the Netherlands (2016). Mussel meat at sites with abnormal mortality rates contained higher densities of granulomas, inflammatory inclusions at the Atlantic coast in France, suggesting that the mussels experienced stress (Robert and Soletchnik 2016). In a follow-up study, climatic events tied to climate change that affected abiotic conditions, but also algal compositions and timing of blooms were linked to higher mortality events, although a conclusion is still lacking (Travers et al. 2016; Soletchnik et al. 2017). Elevation of atmosphere and sea surface temperatures resulted in shifts of the geographical distribution of mussels to colder areas (Berge et al. 2005) and catastrophic summer mortalities at intertidal sites due to heating stress (Jones et al. 2010).

3.3.5 Differences in Efficiency Between Species and Culture Methods

Reported culture efficiencies are shown in Table 3.2, expressed as Relative Biomass Production (RBP): the biomass of harvestable product from one biomass unit of seed. It appears from this table that bottom culture is the least efficient, which can be explained by the high density dependent losses, predation pressure and dislodgement vulnerability for the mussels in this type of culture. Major improvements are expected in reducing handling stress and density dependent losses (Capelle et al. 2017). Production efficiencies of mussels from the *Perna* species are around 5 kg of harvestable product from 1 kg of seed, despite having the largest growth rates. It seems that survival rates for *Perna* mussels are lower than for other rope or raft

Table 3.2 Differences in mussel culture efficiency including growth and mortality, expressed as Biomass Production Rate (RBP) between countries, systems and species

Country	System	Species	Typical Growth rate	Typical Mortality rate	Typical annual mussel production	Yield (RBP)	Source
Spain, Galicia	Raft	*M galloprovinciales*	87.6 mg/day	33–36% seed	150 kg m^{-2}	27.6	Figueras (1990), Pérez Camacho et al. (1991) and Figueiras et al. (2002)
			0.13 mm/day	Thinning: 14–15%			
				Grow out: 19–20%			
Italy, PO Delta	Rope	*M. galloprovinciales*	0.12 mm/day	59–82%	–	–	Ceccherelli and Barboni (1983)
UK, Menai Strait	Bottom, intertidal	*M. edulis*	0.04 mm/day	82–90%	12.8 kg m^{-2}	0.89–1.45	Dare and Edwards (1976)
India, Goa	Raft	*P. viridis*	0.27 mm/day	–	48 kg m^{-2}	–	Qasim et al. (1977)
India, Vizhinjam	Raft	*P. viridis*	0.10 mm/day	–	15 kg m^{-2}	5–11	Appukuttan et al. (1980)
Ireland, Killany	Rope	*M. edulis*	–	4–48%	5 kg m^{-1} ~ 250 kg m^{-2}		Rodhouse et al. (1985)
Loughs, Northern Ireland, UK	Bottom	*M. edulis*	20 mg/day, 0.06 mm/day	70% (prod. cycle, 26 months)	0.15–2.9 kg m^{-2}	1–4	Ferreira et al. (2007)
France	Bouchot – naturally settled	*M. edulis*	6 mg/day		6.07 kg m^{-1}	–	Boromthanarat and Deslous-Paoli (1988)
Marennes-Oleron	Bouchot Transplants		1.1 mg/day		10.78 kg m^{-1}	2.9	
Agadir, Maroc	Rope	*M. galloprovincialis*	–	87–88 % (prod cycle, 12 months)	9.1 kg, m^{-1}	2.8–5.7	Idhalla et al. (2017)

(continued)

Table 3.2 (continued)

Country	System	Species	Typical Growth rate	Typical Mortality rate	Typical annual mussel production	Yield (RBP)	Source
NZ	Rope	*P. perna*	–	86% (prod cycle, 12 months)	16.4 kg, m^{-1}	3.9–6.5	
NZ	Rope	*Perna canaliculus*	0.20 mm/day	54% (1 month), 81% (5 moths)	2.03–3.91 kg, m^{-1}	4.5–6.9	South et al. (2017) and Jeffs et al. (1999)
NL	Bottom	*M. edulis*	0.04 mm/day	–	–	–	Unpublished data
Oosterschelde			20 mg/day				
Wadden Sea	Bottom	*M. edulis*	0.07 mm/day	42% (1 month)	4.9 kg m^{-2}	1.0–1.9	Capelle et al. (2016)
			30 mg/day	77% (cycle)			
France	Bouchot	*M. edulis*	0.023 mm/day	–	–	–	Garen et al. (2004)
Pertuis Breton	Longline		0.034 mm/day				
	Bottom		0.016 mm/day				
	Intertidal						

grown mussel families, and are in fact comparable with mussel bottom culture. Note that RBPs of *Perna* mussels are higher than for mussel bottom culture, caused by faster growth rates of *Perna* mussels. It is reported that detachment from ropes is a major problem during the grow out of *Perna* mussels (South et al. 2017; Petes et al. 2007). Bouchot culture is slightly more efficient than bottom culture but less efficient than rope culture. This can be explained by the low growth rates which are experienced in this type of intertidal culture, and the fact that bouchot mussels are more vulnerable to benthic predators than rope cultured mussels. Raft culture of *M. galloprovincialis* in Spain is a very effective culture. High yields are reached because the culture starts with small seeds which increase in weight tenfold when they are thinned out and the mussel seed is re-socked in a lower density over three new ropes (Pérez Camacho et al. 1991).

3.4 Conclusions

The starting material for mussel culture is wild harvest of seed, use of SMC or hatchery production. Fished seed is mostly used in bottom culture, while longline and raft culture predominantly use seed collectors. Hatchery seed is only used in longline culture. Most research concerning spat collection deals with comparisons of different types of seed collectors, settlement cues and problems with biofouling. Optimising the timing of deployment of the collectors and the timing of harvest can increase the yield of seed collectors. Hatchery seed is more expensive, but hatcheries provide the opportunity for selective breeding and triploid production giving the product an added value. The challenge is to bring hatchery production costs more in line with the potential sale value of mussel seed. Monitoring can give insight in whether genetic diversity of collector seed or hatchery seed is negatively affected.

Efficiency in use of mussel seed shows large differences between species, regions and culture techniques. Survival rates seem higher for mussels from the *Mytilus* genus, than for mussels from the *Perna* genus. Several key processes were identified that can explain these differences. Losses differ because of different predation pressures or because of differences between substrate and the relationship between food, space and density. Other sources of losses can be related to anomalous, environmental events, such as storms or heat stress. Losses due to such events might become more common in the near future, for example, with the effects of climate change. Growth rates differ between species and between production systems. In general, mussels form the *Perna* genus display higher growth rates than mussels from the *Mytilus* genus. Rope and raft culture is more efficient in terms of yield than bouchot, while bouchot seems a little more efficient than bottom culture.

For bottom culture, seed from SMCs has gradually become an important seed source complementary to seed from wild harvest. However, seed is more expensive from SMCs than from wild harvest and several research programs were carried out towards methods to increase efficient use. Technical developments in off-bottom culture mainly concern optimizing system designs and are particularly innovative in the way in which they relate system design to optimal feeding rates and dealing with harsh hydrodynamic conditions. Spatial conflicts in traditional culture areas may provoke the development of off-shore culture implying risk of exposure to hydrodynamic stress.

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