Chapter 9
Feedbacks from Filter Feeders: Review on the Role of Mussels in Cycling and Storage of Nutrients in Oligo- Meso- and Eutrophic Cultivation Areas

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Abstract Cultured and wild bivalve stocks provide ecosystem services through regulation of nutrient dynamics; both by regeneration of nutrients that become available again for phytoplankton production (positive feedback), and by extraction of nutrients through filtration and storage in tissue (negative feedback). Consequently, bivalves may fulfill a role in water quality management. The magnitude of regulating services by filter feeding bivalves varies between coastal ecosystems. This review uses the blue mussel as a model species and evaluates how cultured mussel stocks regulate nutrient dynamics in oligo- meso- and eutrophic ecosystems. We thereby examine (i) the eco-physiological response of mussels, and (ii) the positive and negative feedback mechanisms between mussel stocks and the surrounding ecosystem. Mussel culture in nutrient-poor areas (deep Norwegian fjords) are compared with cultures in other coastal systems with medium- to rich nutrient conditions. It was found that despite differences in eco-physiological rates under nutrient-poor...
conditions (higher clearance, lower egestion, similar excretion and tissue storage rates), the proportion of nutrients regenerated was similar between (deep) nutrient-poor and (shallow) nutrient-rich areas. Of the filtered nutrients, 40–50% is regenerated and thus made available again for phytoplankton growth, and 10–50% of the filtered nutrients is stored in tissue and could be removed from the system by harvest. A priori, we inferred that as a consequence of low background nutrient levels, mussels would potentially have a larger effect on ecosystem functioning in nutrient-poor systems and/or seasons. However, this review showed that due to the physical characteristics (volume, water residence time) and low mussel densities in nutrient-poor Norwegian fjord systems, the effects were lower for these sites, while estimates were more profound in shallow nutrient-rich areas with more intensive aquaculture activities, especially in terms of the negative feedback mechanisms (filtration intensity).

Abstract in Chinese  养殖及野生的双壳类动物通过调节环境营养物质动力学过程来提供生态系统服务：其中包括向环境释放营养物质促进浮游植物生长（正反馈）以及通过滤食将环境中的营养物质转化为软组织进行储存（负反馈）。因此，双壳类可以作为水质调控的工具物种发挥作用。双壳类滤食所产生调节作用与效果因所处不同的近岸生态系统而异。本文以紫贻贝为参考物种，阐述了养殖的贻贝群对不同营养水平的生态系统营养动力过程。内容包括：贻贝的生态生理响应；不同种群数量的贻贝与周围生态系统之间的正负反馈机制。我们对贫营养地区（挪威深海峡湾）的养殖贻贝与其他沿海中等营养水平和富营养状况下的养殖贻贝进行了比较。结果表明，尽管在营养不良条件下，贻贝的摄食生态生理效率存在差异（更高的滤食率，较低的排粪率，相似的排泄和组织储存效率），但是在营养贫乏水域（水深较深）和营养充足水域（水深较浅），贻贝向环境释放的营养物质的比例大致相同。在被滤食的营养物质中，大约40-50%再生并被浮游植物生长利用，大约10-50%的滤食营养物质被储存在组织中，通过收获从生态系统中移出。种种迹象表明，贻贝可能对营养贫乏的生态系统功能有较大的影响。但需要指出的是，尽管挪威海峡湾内的营养较匮乏，但由于其水文特征（水体体积，水滞留时间等）和较低的贻贝养殖密度，贻贝养殖对峡湾的生态环境影响较低，而在浅海营养丰富的水域，由于养殖规模和密度的增加，贻贝强大的滤水能力对生态系统的影响更大。

Keywords  Nitrogen · mytilus · Eco-physiology · Ecosystem interactions · Sink and source

9.1  Introduction

Suspension-feeding bivalves have the potential to influence ecosystem functioning due to their eco-physiological responses and role in nutrient cycling (Dame 1996; Newell 2004). Filtration by bivalves may depress phytoplankton biomass, while at
the same time nutrient regeneration by bivalves may stimulate phytoplankton production (Asmus and Asmus 1991; Prins et al. 1995; Shumway 2011). These processes are regarded as the positive and negative feedback mechanisms of bivalves onto phytoplankton populations (Dame 1996). The capacity to influence ecosystem functioning is particularly evident in areas with concentrated bivalve communities (Smaal and Prins 1993; Dame and Prins 1998), such as in aquaculture settings. Mussels dominate bivalve production in many regions (see Wijsman et al. 2019), hence this paper uses the blue mussel *Mytilus* spp. as model species to discuss the role of bivalve cultivation in nutrient cycling. Whether the feedback processes contribute to a desirable regulation of the system (service) or results in an undesirable effect (impact) depends on the environmental characteristics of a site and the scale of culture activities (Newell 2004). Most mussel cultivation sites are situated in nutrient-rich coastal areas that are influenced by river run-off, thereby taking advantage of high primary production rates to achieve rapid growth (Saxby 2002; Smaal 2002), yet commercial mussel cultivation does exist in oligotrophic ecosystems (Strohmeier et al. 2008; Brigolin et al. 2009). Such differences in ecosystem characteristics indicate that the same process in some systems can be regarded as a regulating ecosystem service while in other systems it is rather a negative ecosystem impact (see Fig. 9.1). Under excessive nutrient availability, filtration of phytoplankton (negative feedback) may help to prevent or overcome eutrophication problems (particularly when coupled with harvesting of the biomass), wherefore this has been recognized as an ecosystem service of mussel aquaculture (Lindahl et al. 2005; Ferreira et al. 2014; Petersen et al. 2014). At the same time, in oligotrophic (nutrient-poor) systems mussel filtration can impose an ecosystem impact when it leads to depletion of phytoplankton and carrying capacity is exceeded. In these nutrient-poor systems, regeneration of nutrients is considered an ecosystem service as it may boost primary production, and result in higher mussel yields.

This paper aims to evaluate the regulating functions of mussel aquaculture through the two major pathways (filtration, nutrient regeneration) as a function of ecosystem trophic status (from nutrient-poor, to nutrient-rich). A relatively large set of literature is available presenting eco-physiological rates measured in nutrient-rich conditions (a.o. Bayne and Scullard 1977; Hawkins and Bayne 1985; Dame et al. 1991; Smaal and Vonck 1997; Filgueira et al. 2010), but because little information

![Feedback loop of filter feeder activity on filter feeder growth linked to potential ecosystem services and ecosystem impacts for nutrient-rich and nutrient-poor systems](image)

**Fig. 9.1** Feedback loop of filter feeder activity on filter feeder growth linked to potential ecosystem services and ecosystem impacts for nutrient-rich and nutrient-poor systems
was available for nutrient-poor conditions, most information in this paper was drawn from oligotrophic Norwegian fjords (Strohmeier et al. 2009; Jansen et al. 2012a, b). The first section provides a review of eco-physiological rates and discusses whether and how the functioning of mussels differs between eutrophic and oligotrophic conditions. Specific emphasis is thereby given to differences between measurements on individuals compared to entire communities. Physiological processes are generally studied at the level of the organism (Dame 1996; Gosling 2015), but extrapolating “average” individual rates to yield population estimates neglects community specific effects such as refiltration or metabolic activity of associated fauna and microbial decomposition of organic material on mussel cultures (Richard et al. 2006; Jansen et al. 2011). The second section of this review evaluates interactions between mussel cultivation and the surrounding ecosystem with particular reference to ecosystem services and impacts. To this end, the positive and negative feedback mechanisms of mussel culture on phytoplankton are compared between areas spanning a gradient from nutrient-poor to nutrient-rich. At last, perspectives on the role of mussel cultivation on nutrient cycling are provided.

9.2 Mussels as Intermediaries in Nutrient Cycling (Eco-Physiology)

The major eco-physiological pathways in which mussels interact with coastal nutrient cycling are; (i) filtration of seston (particulate nutrients) from the water column, (ii) nutrient storage in mussel tissue (assimilation), and growth, (iii) excretion of inorganic metabolic waste products, and (iv) production and mineralization of biodeposits (reviews by Prins et al. 1998; Newell 2004). The mussel *Mytilus edulis* is one of the most studied bivalves in terms of its eco-physiological responses (Bayne 1998; Shumway 2011; Gosling 2015). These studies have shown that mussels tolerate a wide range of environmental conditions, facilitated by a remarkable plasticity of their physiological responses. This physiological plasticity can vary between populations, among individuals of the same population, and due to seasonal changes and variation in the natural environment (Hawkins and Bayne 1992; Shumway 2011). In the following section eco-physiological rates are reviewed for mussels as a function of trophic status of the culture environment, thereby specifically addressing differences between individual and community scale measurements.

9.2.1 Filtration

Bivalve feeding has been extensively studied at the level of individual animals (see review by Cranford et al. 2011). Strohmeier et al. (2009, 2015) showed that mussels can display high feeding rates and high net absorption efficiencies under oligotrophic and low seston conditions despite contradicting feeding paradigms for mussels; Table 9.1 and the review by Cranford et al. (2011) show that clearance rates
Table 9.1: Clearance rates in mussel cultivation areas

| Area | Country | Species     | Food source                  | Clearance rates [L g$^{-1}$ h$^{-1}$] | Ref |
|------|---------|-------------|------------------------------|---------------------------------------|-----|
| Åfjord | NO      | *M. edulis* | Natural seawater             | 5.4 (3.2–8.4)                         | 1   |
| Austevoll | NO    | *M. edulis* | Natural seawater             | 6.4 (3.0–9.6)                         | 2   |
| Oosterschelde | NL    | *M. edulis* | Natural seawater             | (1.4–2.8)                             | 3   |
| Oosterschelde | NL    | *M. edulis* | Natural + *P. tricornutum*    | 1.5 (0.3–3.5)                         | 4   |
| Oosterschelde | NL    | *M. edulis* | Natural seawater             | 2.6 (1.3–3.5)                         | 5   |
| Oosterschelde | NL    | *M. edulis* | Natural + *S. costatum*      | (5.0–8.5)                             | 6   |
| Lynher estuary | UK   | *M. edulis* | Natural seawater             | (1.0–2.5)                             | 7   |
| Aiguillon | FR     | *M. edulis* | Natural + *S. costatum*      | (9.6–11.0)                            | 6   |
| Ria de Arousa | ESP  | *M. galloprovincialis* | Mix sediment & *I. galbana* | 5.0–5.8                               | 8   |
| New Foundland | CA    | *M. edulis* | Natural seawater             | (1.5–2.0)                             | 9   |
| Nova Scotia | CA    | *M. edulis* | Natural seawater             | (1.0–8.0)                             | 10  |
| New Foundland | CA    | *M. edulis* | Natural seawater             | (0.2–3.5)                             | 10  |
| Great Entry Lagoon | CA  | *M. edulis* | Algae mix                    | (3.0–4.5)                             | 11  |
| Amherst Basin | CA   | *M. edulis* | Algae mix                    | (2.5–4.0)                             | 11  |
| Beatrix Bay | NZ     | *P. canaliculus* | Natural seawater            | (0.8–3.9)                             | 12  |
| Sylt      | DEN    | *M. edulis* | Natural seawater             | 1.1                                   | 13  |
| Waddensea | NL     | *M. edulis* | Natural seawater             | 1.5 (0.7–1.9)                         | 14  |
| Oosterschelde | NL   | *M. edulis* | Natural seawater             | 2.2 (1.1–4.8)                         | 5   |
| Marennes- Oleron | FR  | *M. edulis* | Natural seawater             | 1.8 (1.0–2.9)                         | 15  |

*Measurements on communities (benthic mussel beds)*

| Area | Country | Species     | Food source                  | Clearance rates [L g$^{-1}$ h$^{-1}$] | Ref |
|------|---------|-------------|------------------------------|---------------------------------------|-----|
| Åfjord | NO      | *M. edulis* | Natural seawater             | 1.5 (1.0–2.1)                         | 1   |
| Oosterschelde | NL    | *M. edulis* | Natural seawater             | (2.4–30.7)                            | 16  |
| Waddensea | NL    | *M. edulis* | Natural seawater             | 0.8                                   | 17  |
| Havre-aux-Maisons | CA  | *M. edulis* | Natural seawater             | (1.7–6.3)                             | 18  |

Measurements on communities (suspended ropes)

Data were standardized to L g$^{-1}$ tissue DW h$^{-1}$. Weight conversion factors reported by Ricciardi and Bourget (1998) were applied. Values are presented as mean (minimum – maximum), and empty cells indicate that rates were not determined. Country codes (also for following tables): NO Norway, SW Sweden, DEN Denmark, GER Germany, NL The Netherlands, NIR Northern Ireland, UK United Kingdom, FR France, ESP Spain, IT Italy, CA Canada, USA United States, AU Australia, NZ New Zealand, JP Japan

1 (Jansen 2012); 2 (Strohmeier et al. 2009); 3 (Smaal and Vonck 1997); 4 (Smaal et al. 1997); 5 (Prins et al. 1996); 6 (Petersen et al. 2004); 7 (Bayne and Widdows 1978); 8 (Filgueira et al. 2008); 9 (Thompson 1984); 10 (MacDonald and Ward 2009); 11 (Tremblay et al. 1998); 12 (James et al. 2001); 13 (Asmus et al. 1990); 14 (Prins et al. 1994); 15 (Smaal and Zurburg 1997); 16 (van Broekhoven et al. 2014); 17 (Jacobs et al. 2015); 18 (Trottet et al. 2008a)
reported for individual mussels under oligotrophic conditions in Norway were among the highest reported for this species. Jansen (2012) confirmed high feeding rates for individual animals under oligotrophic conditions, but also demonstrated that community-scale rates under field conditions were 2 to 3 times lower (Table 9.1). Prins et al. (1996) showed that community estimates for benthic mussel beds in eutrophic cultivation areas were also lower than measurements on individuals, and Jacobs et al. (2015) concluded that low feeding rates measured on suspended spat collector communities were the result of refiltration within the culture community. Others have also hypothesized that lower community-scale clearance rates could be related to crowding affecting water exchange and/or refiltration (Frechette et al. 1992; Cranford et al. 2011). While the accuracy of various methods for determination of clearance rates for individuals have been the subject of debate during the last decade (Riisgard 2001; Petersen 2004; Petersen et al. 2004; Riisgard 2004; Cranford et al. 2011), there is good evidence for differences in feeding rates between individuals and communities that merit further study.

### 9.2.2 Nutrient Storage in Mussel Tissue

Surprisingly few studies report on the nutrient composition of mussel tissue, but the concentrations reported seem to correspond between the different cultivation areas (Table 9.2). These estimates do no account for nutrient storage in byssus or shell (Hawkins and Bayne 1985). Seasonal changes in nutrient composition are primarily driven by endogenous processes, and seasonal nutrient composition as well as

| Area          | Country | Species         | Carbon [mg g⁻¹] | Nitrogen [mg g⁻¹] | Phosphorus [mg g⁻¹] | Ref. |
|---------------|---------|-----------------|-----------------|-------------------|---------------------|-----|
| Austevoll    | NO      | *M. edulis*     | 438 (402–469)   | 106 (94–123)      | 7 (5–11)            | 1   |
| Whitsand Bay | UK      | *M. edulis*     | 440 (400–470)   | 80 (55–110)       |                     | 2   |
| Oosterschelde| NL      | *M. edulis*     | 448 (113–623)   | 102 (68–126)      | 7 (5–12)            | 3   |
| Oosterschelde| NL      | *M. edulis* spat|                 | 97 (92–104)       | 7.5 (6.6–8.4)       | 4   |
| Ria de Arosa | ESP     | *M. galloprovincialis* | 448             |                   |                     | 5   |
| Western Australia | AU | *M. edulis*     | 333             | 101               | 4                    | 6   |
| Mahurangi Harb.| NZ     | *A. zelandica*  | 396             | 71                |                     | 7   |

Data were standardized to mg element g⁻¹ tissue DW. Weight conversion factors by Ricciardi and Bourget (1998) were applied. Values are presented as mean (minimum – maximum), and empty cells indicate that concentrations were not determined. Country codes given in Table 9.1: 1 (Jansen et al. 2012a); 2 (Hawkins et al. 1985); 3 (Smaal and Vonck 1997); 4 Van Broekhoven (unpublished data); 5(Tenore et al. 1982); 6 (Vink and Atkinson 1985); 7 (Gibbs et al. 2005)
metabolic requirements associated with the reproductive cycle are similar for mussels under both nutrient-poor (Jansen et al. 2012a) and nutrient-rich conditions (Kuenzler 1961; Hawkins et al. 1985; Smaal and Vonck 1997).

9.2.3 Excretion of Inorganic Nutrients

Respiration and nutrient excretion rates of individual mussels measured under nutrient-poor conditions (Table 9.3) are within the range reported for nutrient-rich areas (Table 9.3, see also Burkholder and Shumway 2011), albeit toward the lower end. The slightly lower rates are likely related to the relatively cold and oligotrophic Norwegian fjords, as respiration and excretion rates of mussels are influenced by fluctuations in temperature (Widdows and Bayne 1971; Leblanc et al. 2003) and food supply (Bayne et al. 1993; Lutz-Collins et al. 2009; Jansen et al. 2012a). Ecophysiological models are often used to integrate responses of individual mussels with fluctuations in environmental conditions (Beadman et al. 2002; Dowd 2005). Jansen (2012) applied and validated a model normally used to simulate mussel responses in nutrient-rich areas (Filgueira and Grant 2009), and found that the model accurately predicted excretion rates under nutrient-poor conditions. This demonstrates that metabolic responses in mussels are comparable between cultivation areas of different trophic status, as the model is based on generic equations.

Mussel cultures are complex community structures, which besides the mussels include bacteria, epifauna, epiflora, and trapped biodeposits, which also contribute to nutrient exchange rates (Richard et al. 2006, 2007). The contribution of decomposing biodeposits (see also next section) to community nutrient release rates is particularly evident in the case of bottom cultures, where nearly all egested material is trapped in the community matrix. Indeed, the relatively high release rates for nutrients from bottom cultures are primarily attributed to decomposition of biodeposits (Asmus et al. 1990; Prins and Smaal 1994). Nutrient recycling from the organic matter trapped in suspended cultures is relatively low (Jansen 2012), which seems reasonable as the majority of biodeposits sink to the seafloor resulting in lower biodeposits on suspended mussel culture compared to benthic mussel cultures. Van Broekhoven et al. (2014) concludes that the combined activity of biodeposits decomposition and fauna on mussel spat collectors are either very small or scaled proportionally with mussel biomass or activity, whilst respiration and nutrient release rates are likely dominated by mussel spat activity. Richard et al. (2006, 2007), on the other hand, relate the high nitrate and nitrite fluxes of suspended mussel cultures in Canada to decomposition of organic material trapped in the community matrices.

Abundance and species composition of fauna associated with mussel cultures varies between seasons and farming locations, adding both temporal and spatial components to mussel farming dynamics (Cayer et al. 1999; Khalaman 2001; Richard et al. 2006; Lutz-Collins et al. 2009; Jansen et al. 2011). Jansen (2012) finds that during periods of high fouling abundance, ascidian (Ciona intestinalis)
Table 9.3  Respiration and inorganic nutrient release rates of different species of mussels and culture types in mussel cultivation areas

| Area          | Country | Species           | Temperature [°C] | Respiration [μmol g⁻¹ h⁻¹] | TAN excretion [μmol g⁻¹ h⁻¹] | PO₄ excretion [μmol g⁻¹ h⁻¹] | Si excretion [μmol g⁻¹ h⁻¹] | Ref |
|---------------|---------|-------------------|------------------|-----------------------------|------------------------------|-----------------------------|-----------------------------|-----|
| Measurements on individuals                        |         |                   |                  |                             |                              |                             |                             |     |
| Austevoll    | NO      | M. edulis         | 3–19             | 14.2 (5.7–27.8)            | 0.7 (0.3–1.8)                | 0.07 (<0–0.24)              | –                           | 1   |
| Austevoll    | NO      | M. edulis         | 5–20             | 25.9 (12.6–48.1)           | (1.8–2.6)                    |                             |                             | 2   |
| Åfjord       | NO      | M. edulis         | 12               | 48.9                        |                             |                             |                             | 3   |
| Waddensea    | NL      | M. edulis         | June and Sept    |                             | (0.8–5.0)                    | (0.02–0.17)                 |                             | 4   |
| Waddensea    | NL      | M. edulis         | 3–24             |                             | (10.0–70.0)                  |                             |                             | 5   |
| Oosterschelde| NL      | M. edulis         | 5–18             | 21.3 (10.3–36.0)           | 1.0 (0.2–3.1)                | 0.07 (0–0.13)               | –                           | 6   |
| Oosterschelde| NL      | M. edulis         | 1–20             | 26.3 (15.6–53.1)           | 1.1 (0.9–1.6)                |                             |                             | 7   |
| South        | UK      | M. edulis         | 8–20             |                             | (22.3–71.5)                  | (0.1–2.9)                   |                             | 8   |
| Whitsand Bay | UK      | M. edulis         | 9–15             | 9.8 (3.1–17.2)             | 0.7 (0.1–1.2)                |                             |                             | 9   |
| Whitsand Bay | UK      | M. edulis         | 9–13             | 4.6 (4.2–8.3)              | 0.4 (0.2–0.5)                |                             |                             | 10  |
| Lynher river | UK      | M. edulis         | 11–21            |                             | (0.3–2.7)                    |                             |                             | 11  |
| Lynher river | UK      | M. edulis         | 8–15             |                             | (0.4–1.3)                    |                             |                             | 12  |
| Lynher estuary| UK    | M. edulis         | 5–25             |                             | (18.8–34.8)                  | (0.6–2.8)                   |                             | 13  |
| Swansey Bay  | UK      | M. edulis         |                   |                             |                             |                             |                             | 14  |
| Heacam Bay   | UK      | M. edulis         | 15               |                             | (17.9–44.7)                  | (0.1–0.6)                   |                             | 15  |
| Ria de Arosa | ESP     | M. galloprovincialis | July            |                             | (0.1–0.2)                    |                             |                             | 16  |
| Ria de Arosa | ESP     | M. galloprovincialis | 14–15           |                             | (0.4–0.6)                    |                             |                             | 17  |
| New Foundland| CA      | M. edulis         | 0–15             |                             | (8.9–35.7)                   | (0.1–0.9)                   |                             | 18  |
| Great Entry Lagoon | CA | M. edulis | 20               |                             | (44.7–160.8)                 | (0.7–7.9)                   |                             | 19  |
| Amherst Basin| CA      | M. edulis         | 20               |                             | (35.7–80.4)                  | (0.7–2.5)                   |                             | 20  |
| Nova Scotia  | CA      | M. edulis         | 0–15             | 8.0 (3.3–12.1)             | 1.4 (0.5–2.5)                |                             |                             | 21  |
| Location          | Country | Species       | Temperature Range | Respiration | TAN Excretion | PO4 Excretion | Si Excretion |
|-------------------|---------|---------------|-------------------|-------------|---------------|---------------|--------------|
| Beatrix Bay       | NZ      | P. canaliculus | 11–17             | 31.8 (22.3–38.7) | (1.6–4.4)     |               |              |
| Western Australia | AU      | M. edulis     | 15–20             | 6.7         | 0.02          |               |              |

**Measurements on communities (benthic mussel beds)**

| Location          | Country | Species       | Temperature Range | Respiration | TAN Excretion | PO4 Excretion | Si Excretion |
|-------------------|---------|---------------|-------------------|-------------|---------------|---------------|--------------|
| Baltic            | GER     | M. edulis     | (0.1–3.5)         | (0.01–0.50) |               |               |              |
| Sylt              | DEN     | M. edulis     | 13–19             | 1.2 (0.02–5.0) |               |               |              |
| South             | DEN     | M. edulis     | (0–12.5)          | (0.1–3.2)   | (0.10–0.53)   |               |              |
| Waddensea         | NL      | M. edulis     | June and Sept     | (1.7–14.4)  | (0.08–0.50)   |               |              |
| Waddensea         | NL      | M. edulis     | June-Sept         | 4.4         | 2.5           | 2.3           |              |
| Oosterschelde     | NL      | M. edulis     | (0.9–15.8)        | (0.03–0.68) | (<0–3.0)      |               |              |
| Oosterschelde     | NL      | M. edulis     | M-O-J-O           | (0–7.3)     |               |               |              |
| Narragansett Bay  | USA     | M. edulis     | 15                | 3.1         |               |               |              |

**Measurements on communities (suspended ropes)**

| Location          | Country | Species       | Temperature Range | Respiration | TAN Excretion | PO4 Excretion | Si Excretion |
|-------------------|---------|---------------|-------------------|-------------|---------------|---------------|--------------|
| Austevoll         | NO      | M. edulis     | 3–19              | 16.2 (3.4–28.7) | 0.8 (0.2–1.8) | 0.06 (0.00–0.15) | ~0           |
| Åfjord            | NO      | M. edulis     | 12                | 17.1        | 1.1           | 0.11          |              |
| Oosterschelde     | NL      | M. edulis spat| 18–21             | (72–381)    | (5–70)        | (0.12–6.4)    | (0.1–5.3)    |
| Sacca di Goro     | IT      | M. edulis     | 8–27              | (25.1–26.9) | (3.2–7.6)     |               |              |
| GreatEntry Lagoon | CA      | M. edulis     | 16–19             | (53.0–92.4) | (1.7–11.6)    | (0.22–0.34)   | (0.0–0.7)    |

Rates were standardized to μmol g⁻¹ tissue DW h⁻¹. Where needed weight conversion factors by Ricciardi and Bourget (1998) were used. Values are presented as mean (minimum – maximum), and empty cells indicate that rates were not determined. Country codes are given in Table 9.1.

1 (Jansen et al. 2012a); 2 (Strohmeier 2009); 3 (Jansen 2012); 4 (Prins and Smaal 1994); 5 (Devooy 1976); 6 (Smaal and Vonck 1997); 7 (Smaal et al. 1997); 8 (Bayne and Widdows 1978); 9 (Kreeger et al. 1995); 10 (Hawkins et al. 1985); 11 (Hawkins and Bayne 1985); 12 (Bayne and Scullard 1977); 13 (Livingstone et al. 1979); 14 (Widdows 1978); 15 (Bayne et al. 1979); 16 (Gabbott and Bayne 1973); 17 (Lum and Hammen 1964); 18 (Labarta et al. 1997); 19 (Thompson 1984); 20 (Tremblay et al. 1998); 21 (Hatcher et al. 1994); 22 (Vink and Atkinson 1985); 23 (Kautsky and Wallentinus 1980); 24 (Asmus et al. 1990); 25 (Schütler and Josefsen 1994); 26 (Asmus et al. 1990); 27 (Dame et al. 1991); 28 (Prins and Smaal 1990); 29 (Smaal and Zurzburg 1997); 30 (Nixon et al. 1976); 31 (Jansen et al. 2011); 32 (van Broekhoven et al. 2014); 33 (Nizzoli et al. 2006); 34 (Richard et al. 2006)
metabolism contributes up to 18% of total nitrogen released from suspended mussel culture communities. The contribution of the associated fauna to nutrient cycling cannot, therefore, be ignored. This is also acknowledged by Tang et al. (2011) who estimate that tissue carbon content of fouling ascidians is approximately 6.4% of the carbon production in scallops in Sungo Bay (China). A full understanding and prediction of nutrient regeneration by mussel culture communities requires more information on faunal growth, abundance, and metabolic dynamics within and across cultivation areas.

9.2.4 Biodeposit Release and Mineralisation

Biodeposit production represents a significant pathway in bivalve nutrient cycling (Kuenzler 1961; Prins and Smaal 1994; Cranford et al. 2007). Biodeposition rates under oligotrophic conditions, as measured in the laboratory for individual mussels, are in range with, but not at the maximum rates reported for other areas, whereas the organic matter content (OM) is relatively high (Table 9.4). The latter is likely related to high OM in the food source (~60–70%; Strohmeier et al. 2009, 2015) and the fact that pseudofaeces production is mostly absent under oligotrophic conditions. Seasonal fluctuations in biodeposition rates seem related to changes in food quantity and quality, rather than to temperature (Jansen et al. 2012b). This is consistent with Strohmeier et al. (2009), who suggest that the feeding response to low food concentrations (i.e. oligotrophic conditions) is likely the determining factor for total ingestion, rather than temperature.

Although measurements of mussel biodeposits are essential to understand and quantify their contribution to regeneration of nutrients, little has been published on biodeposit quality and their decay rates (reviewed by McKindsey et al. 2011) and more recently reported by Jansen et al. (2012b) and van Broekhoven et al. (2015). Nutrient concentrations in biodeposit depend on the concentration and type of diet the mussels feed on (Miller et al. 2002; Giles and Pilditch 2006) and therefore varies between seasons (Jansen et al. 2012b) and systems (Table 9.4). It has been suggested that mineralization rates of biodeposits are related to the presence of resident gut bacteria that can be voided from the mussel’s digestive system along with the faecal pellets (Harris 1993). However, mineralization rates of fresh biodeposits increase considerably after an initial lag phase of one or two days (Fabiano et al. 1994; Carlsson et al. 2010; van Broekhoven et al. 2015), suggesting that a period of microbial growth may also be due to additional colonization by external microbes during the lag phase (Canfield et al. 2005). Since mineralization rates depend on the presence of microbes on either the benthic or the suspended mussel culture (Giles and Pilditch 2006; Carlsson et al. 2010; Jansen et al. 2012b), decomposition will be more rapid than in the water phase (van Broekhoven et al. 2015). The proportion of carbon and nitrogen decomposed as a function of available (labile) organic nutrients in biodeposits is relatively similar between oligotrophic (Jansen et al. 2012b) and eutrophic environments (Giles and Pilditch 2006; Carlsson et al. 2010; van
Table 9.4  Biodeposition and biodeposit composition in mussel cultivation areas

| Area                      | Country | Species          | Biodeposition [mg g\(^{-1}\) tissue d\(^{-1}\)] | OM [%]     | Carbon [mg g\(^{-1}\) biodep] | Nitrogen [mg g\(^{-1}\) biodep] | Phosphorus [mg g\(^{-1}\) biodep] | Silicon [mg g\(^{-1}\) biodep] | Ref |
|---------------------------|---------|------------------|-----------------------------------------------|------------|-------------------------------|----------------------------------|----------------------------------|-------------------------------|-----|
| Austevoll                 | NO      | M. edulis        | 32 (11–72)                                    | 36 (22–48) | 135 (62–194)                  | 15 (7–23)                       | 1.3 (0.8–1.7)                    | 1                             |     |
| Askö, Baltic              | SW      | M. edulis        | 31 (7–104)                                    | 19 (8–45)  | 129 (50–200)                  | 15 (8–21)                       | 1.9 (1.0–3.0)                    | 2                             | 2   |
| Oosterschelde             | NL      | M. edulis        | Feces Pseudofeces                              | 20 26      | 52 55                         | 4.8 5.4                         | 1.4 1.4                         | 42 31                         |     |
| Bedford Basin             | CA      | M. edulis        | (0–20)                                        | (30–70)    |                               |                                 |                                 | 4                             |     |
| Mahone Bay                | CA      | M. edulis        | (0–80)                                        | (10–70)    |                               |                                 |                                 | 4                             |     |
| GreatEntry Lagoon         | CA      | M. edulis        | 54 (18–114)                                   | 22 (20–25) |                               |                                 |                                 | 5                             |     |
| Logy Bay (NF)             | CA      | M. modiolus      | 5 (1–8)                                       | 17 (13–23) | 69 (47–103)                   | 8 (5–12)                        | 205 (100–335)                   | 6                             |     |
| Queele Estuary            | CH      | M. chilensis     | 21                                             | 60         | 4                             |                                 | 7                               |     |
| Firth of Thames           | NZ      | P. canalicu      | 10                                             | 25         | 3                             |                                 | 8                               |     |
| Mutsu Bay                 | JP      | M. edulis        | (6–116)                                       |            |                               |                                 |                                 | 9                             |     |

Data were standardized to mg DW biodeposit g\(^{-1}\) tissue DW d\(^{-1}\) (biodeposition rates), percentage (organic matter content), and mg element g\(^{-1}\) biodeposit DW (organic nutrient content). Where needed weight conversion factors by Ricciardi and Bourget 1998 were used. Values are presented as mean (minimum – maximum), and empty cells indicate that rates were not determined. Country codes are given in Table 9.1
1 (Jansen et al. 2012a, b); 2 (Kautsky and Evans 1987); 3 (van Broekhoven et al. 2015); 4 (Cranford and Hill 1999); 5 (Callier et al. 2006); 6 (Navarro and Thompson 1997; during springbloom conditions); 7 (Jaramillo et al. 1992); 8 (Giles and Pilditch 2006); 9 (Tsuchiya 1980).
Broekhoven et al. 2015) (Table 9.5). However, under oligotrophic conditions, the amount of nutrient released per gram biodeposit will be higher due to the higher concentrations of nutrients in the mussel biodeposits (Table 9.4). Phosphorus mineralization patterns are inconclusive among studies, likely as a result of the potential for phosphate to bind to sediment and other organic material (Sundby et al. 1992). Profound seasonal differences (up to a factor 80) are observed for silicon release rates by Jansen et al. (2012b), and is assumed to be high when mussel food contains a large fraction of diatoms (Navarro and Thompson 1997). Proportional silicon mineralization rates are 1.4 times higher for feces than pseudofeces, while proportional nitrogen and phosphate mineralization rates were similar for feces and pseudofeces (van Broekhoven et al. 2015). Hypothesized causes are breakdown of the organic matrix by digestive bacterial activity (Bidle and Azam 1999) selection during the feeding process for less recalcitrant diatom frustules, and fragmentation of diatom frustules during the digestive process (as speculated by Dame et al. 1991). Since the proportion of pseudofeces rises with increasing food concentration above a certain level (Foster-Smith 1975; Tsuchiya 1980), the role of mussels in terms of Si regeneration may be proportionally greater at lower food levels (assuming a similar food composition).

9.3 Ecosystem Effects of Nutrient Cycling by Mussels

The previous section demonstrated that mussels contribute to nutrient cycling by translocation, transformation and remineralization of nutrients. These processes related to the mussel’s physiology interact with nutrient cycling in coastal ecosystems through various feedback systems influencing primary production (see reviews by Prins et al. 1998; Newell 2004). Consequently, intensive cultivation of mussels will affect the ecosystem; for example, by altering the carrying capacity (Smaal and Heral 1998; Grant and Filgueira 2011). The feeding activity of mussel communities may influence the abundance of phytoplankton and thereby inhibit primary production (‘top-down’ pathway or negative feedback). Furthermore, Cranford et al. (2009) reported a shift towards a phytoplankton population dominated by picophytoplankton in bays with high densities of mussel cultivation and related this to high grazing activity of the cultured stocks. Meanwhile, mussel excretion and mineralization of biodeposits result in the regeneration of nutrients, which may stimulate primary production (‘bottom-up’ pathway or positive feedback). Not all ingested nutrients are regenerated in a short cycle; a part is retained by the mussel community or in a non-decomposed fraction of biodeposits, and a part may be permanently removed from the system, e.g. when mussels are harvested. Mussel communities can therefore act as a ‘source’ and as a ‘sink’ for nutrients within the ecosystem. The specific pathways contributing to sinks/sources depend on physical features (e.g. depth) of the area and the culture type applied (Table 9.6). Given that phytoplankton use nutrients in specific proportions (Redfield ratio; Redfield et al. 1963), the ‘bottom-up’ stimulation by bivalve nutrient regeneration is influenced by both nutrient availability and stoichiometry of regenerated nutrients. It has been argued
### Table 9.5  Biodeposit remineralization rates in mussel cultivation areas

| Area                  | Country | Species    | Type               | Temp (°C) | Unit     | CO₂ release | TAN release | PO₄ release | Si(OH)₄ release | Ref. |
|-----------------------|---------|------------|--------------------|-----------|----------|-------------|-------------|-------------|-----------------|------|
| Austevoll             | NO      | *M. edulis*| feces              | 5,10,15   | mmol g⁻¹ d⁻¹ | 3.3 (2.0–4.3) | 0.17 (0.12–0.21) | 0.06 (0.01–0.08) | 3.9 (0.1–11.5) | 1    |
| Oosterschelde         | NL      | *M. edulis*| feces pseudofeces  |           | %        | 24% (15–31) | 17% (10–20) |             |                  | 2    |
| Great Entry Lagoon    | CA      | *M. edulis*| biodeposit Jun-Aug | 8-10      | %        | (max 4.5)   | (max 0.3)   | (max 0.02)   | (max 1.0)       | 3    |
| Roskilde & Limfjord   | DEN     | *M. edulis*| biodeposit         | 8-10      | %        | (25–38%)    |             |             |                  | 4    |
| Firth of Thames       | NZ      | *P. canaliculus*| biodeposit         | 20        | %        | 40%         | 18%         |             |                  | 5    |

Data were standardized either to release rate per g biodeposit DW per day or to fraction of initial nutrient content in the biodeposits (e.g. % = TAN/PON*100) for feces or pseudofeces ('biodeposit' indicates that it was unknown whether feces or a mix of (pseudo)feces was incubated). Values are presented as mean (minimum – maximum), and empty cells indicate that rates were not determined. Country codes are given in Table 9.1  
1 (Jansen et al. 2012b); 2 (van Broekhoven et al. 2015); 3 (recalculated from Callier et al. 2009); 4 (Carlsson et al. 2010); 5 (Giles and Pilditch 2006)
Table 9.6 Nutrient source and sink processes by water depth system and mussel culture type

| Depth system | Culture type | Regeneration (source) | Retention (sink) | Removal (sink) |
|--------------|--------------|-----------------------|------------------|----------------|
| Shallow      | Bottom       | Benthic               | Benthic          | Benthic        |
|              |              | \(\text{CO}_2 \text{ (DIC) \& NH}_4\) & \(\text{PO}_4\) excretion mussels \& fauna | \(\text{PO}_4\) binding to sediment | \(\text{N}_2\) from nitrification/ denitrification of \(\text{NH}_4\) |
|              |              | \(\text{CO}_2\) (DIC), \(\text{NH}_4\), \(\text{PO}_4\) \& Si biodeposit mineralization | \(\text{PO}_4\) \& Si biodeposit mineralization | \(\text{PO}_4\) binding to sediment |
|              |              | \(\text{NO}_2/\text{NO}_3\) nitrification of \(\text{NH}_4\) | \(\text{NO}_2/\text{NO}_3\) nitrification from \(\text{NH}_4\) | \(\text{PO}_4\) & Si biodeposit mineralization |
| Shallow      | Suspended    | Pelagic               | Pelagic          | Pelagic        |
|              |              | \(\text{CO}_2\) (DIC) \& NH\(_4\) \& PO\(_4\) excretion mussels \& fauna | \(\text{PO}_4\) excretion mussels \& fauna | \(\text{PO}_4\) excretion mussels \& fauna |
|              |              | Benthic               | Benthic          | Benthic        |
|              |              | \(\text{CO}_2\) (DIC), \(\text{NH}_4\), \(\text{PO}_4\) \& Si biodeposit mineralization | \(\text{PO}_4\) \& Si biodeposit mineralization | \(\text{PO}_4\) \& Si biodeposit mineralization |
|              |              | \(\text{NO}_2/\text{NO}_3\) nitrification of \(\text{NH}_4\) | \(\text{PO}_4\) \& Si biodeposit mineralization | \(\text{PO}_4\) \& Si biodeposit mineralization |
| Deep         | Suspended    | Pelagic               | Pelagic          | Pelagic        |
|              |              | \(\text{CO}_2\) (DIC) \& NH\(_4\) \& PO\(_4\) excretion mussels \& fauna | \(\text{PO}_4\) excretion mussels \& fauna | \(\text{PO}_4\) excretion mussels \& fauna |
|              |              | Benthic (deep fjord basin) | Benthic (deep fjord basin) | Benthic (deep fjord basin) |
|              |              | \(\text{PO}_4\) \& Si biodeposit mineralization | \(\text{PO}_4\) \& Si biodeposit mineralization | \(\text{PO}_4\) \& Si biodeposit mineralization |

that both feedback control mechanism on phytoplankton can stabilize ecosystems (Herman and Scholten 1990) with ‘top-down’ and ‘bottom-up’ pathways occurring simultaneously. This section evaluates the pathways and magnitude of the feedback mechanisms in different mussel cultivation areas, and assesses if trophic status of the ecosystem is an important driver for defining ecosystem services and ecosystem impacts.

### 9.3.1 Physical and Environmental Characteristics of Mussel Cultivation Areas

The extent to which bivalves influence the ecosystem is largely defined by physical and environmental conditions (Newell 2004), which vary considerably among bivalve cultivation areas (Table 9.7). The majority of mussel cultivation areas are
| Area               | Country | Type                      | Water depth [m] | Volume [10^6 m^3] | Residence time [d] | Ref          |
|--------------------|---------|---------------------------|-----------------|-------------------|-------------------|--------------|
| Lysefjord – total  | NO      | NO Fjord                  | 14              | 880               | 11                | 1            |
| Åfjord – above sill| NO      | NO Fjord                  | 20              | 250               | 5                 | 2            |
| Limfjorden         | DEN     | Estuary with multiple basins |                |                   |                   |              |
| Sylt               | DEN     | Estuary                   | 2              | 7                 | 0.5               | 4            |
| Oosterschelde      | NL      | Estuary                   | 5              | 710               |                   | 3            |
| Wadden Sea         | NL      | Bay                       | 3              | 2740              |                   | 5, 6         |
| Carlingford Louch  | IR      | Estuary                   | 460            |                   |                   |              |
| Bay of Brest       | FR      | Bay                       | (19 max)       | 50 (10–150)       |                   |              |
| Thau Lagoon        | FR      | Lagoon                    | 4              | 1480              |                   |              |
| Marennes-Oleron    | FR      | Estuary                   | 675            |                   |                   |              |
| Ria de Arosa       | FR      | Lagoon                    | 675            |                   |                   |              |
| Bay of Brest       | FR      | Bay                       | 500 (60 max)   | 14                 |                   |              |
| Firth of Thames    | CA      | Lagoon                    | 6              | 117               |                   |              |
| Saldanha Bay       | SA      | Estuary                   | 117            |                   |                   |              |
| Great Entry Lagoon | CA      | Two-lagoon system         | 117            |                   |                   |              |
| Lough Foyle        | IR      | Estuary                   | 2              | 117               |                   |              |
| Loire               | FR      | Lagoon                    | 2              | 117               |                   |              |
| Wadden Sea         | NL      | Bay                       | 3              | 117               |                   |              |
| Bay of Brest       | FR      | Bay                       | (19 max)       | 50 (10–150)       |                   |              |
| Thau Lagoon        | FR      | Lagoon                    | 4              | 117               |                   |              |
| Marennes-Oleron    | FR      | Estuary                   | 675            |                   |                   |              |
| Ria de Arosa       | FR      | Lagoon                    | 675            |                   |                   |              |
| Bay of Brest       | FR      | Bay                       | 500 (60 max)   | 14                 |                   |              |
| Firth of Thames    | CA      | Lagoon                    | 6              | 117               |                   |              |
| Saldanha Bay       | SA      | Estuary                   | 117            |                   |                   |              |
| Great Entry Lagoon | CA      | Two-lagoon system         | 117            |                   |                   |              |
| Lough Foyle        | IR      | Estuary                   | 2              | 117               |                   |              |
| Loire               | FR      | Lagoon                    | 2              | 117               |                   |              |
| Wadden Sea         | NL      | Bay                       | 3              | 117               |                   |              |
| Bay of Brest       | FR      | Bay                       | (19 max)       | 50 (10–150)       |                   |              |
| Thau Lagoon        | FR      | Lagoon                    | 4              | 117               |                   |              |
| Marennes-Oleron    | FR      | Estuary                   | 675            |                   |                   |              |
| Ria de Arosa       | FR      | Lagoon                    | 675            |                   |                   |              |
| Bay of Brest       | FR      | Bay                       | 500 (60 max)   | 14                 |                   |              |
| Firth of Thames    | CA      | Lagoon                    | 6              | 117               |                   |              |
| Saldanha Bay       | SA      | Estuary                   | 117            |                   |                   |              |
| Great Entry Lagoon | CA      | Two-lagoon system         | 117            |                   |                   |              |
| Lough Foyle        | IR      | Estuary                   | 2              | 117               |                   |              |
| Loire               | FR      | Lagoon                    | 2              | 117               |                   |              |
| Wadden Sea         | NL      | Bay                       | 3              | 117               |                   |              |
| Bay of Brest       | FR      | Bay                       | (19 max)       | 50 (10–150)       |                   |              |
| Thau Lagoon        | FR      | Lagoon                    | 4              | 117               |                   |              |
| Marennes-Oleron    | FR      | Estuary                   | 675            |                   |                   |              |
| Ria de Arosa       | FR      | Lagoon                    | 675            |                   |                   |              |
| Bay of Brest       | FR      | Bay                       | 500 (60 max)   | 14                 |                   |              |

Country codes are given in Table 9.1 (Aure et al. 2001); 2 (Aure pers. comm); 3 (Wiles et al. 2000); 4 (in Smaal and Prins 1995, 9 (Smal et al. 2001); 6 (Dame et al. 1991, 7 (Ferrieres et al. 2007); 11 (Ferrieres et al. 2007). A |
in relatively long residence times in terms of months and years for the whole system, whereas residence times are much shorter in terms of days and weeks for the upper and intermediate layers.

Annual primary production rates vary between 73 and 1245 g C m\(^{-2}\) y\(^{-1}\) for the different mussel cultivation areas, with rates reported for Norwegian fjord systems in the lower region (Table 9.8). Background nutrient levels in most areas are influenced by anthropogenic nutrient sources, with the exception of most Norwegian fjord systems (Aksnes et al. 1989). Wassmann (2005) shows that estuaries and coastal ecosystems are now the most nutrient-enriched ecosystems in the world, which he attributes primarily to land-based nutrient sources. Limfjorden (Denmark), for example, receives approximately 20,000 ton N y\(^{-1}\) from land-based sources, and the increased nitrogen input during the most recent decades resulted in high phytoplankton biomass levels, sustaining high densities of mussels up to levels causing hypoxia-induced mortality (Christiansen et al. 2006). The highest primary production rates are reported for Ria-de-Arousa and Saldahna Bay, which are coastal bays that benefit from upwelling of deep nutrient-rich water. The coastal upwelling along the South African coastline (Benguela current system) supplies a flux of approximately 1819 ton NO\(_3\)-N y\(^{-1}\) into Saldanha Bay (Monteiro et al. 1998). Areas that benefit from coastal upwelling are among the most productive and successful mussel farming areas (Figueiras et al. 2002; Saxby 2002).

The pathways for ‘nutrient regeneration’ differ between shallow and deep systems as a consequence of depth, stratification, mixing of the water column, and on the resulting presence or absence of benthic-pelagic coupling (see also Table 9.6). Benthic nutrient regeneration can play an important role in shallow coastal ecosystems with well-mixed water columns, as it may provide up to 80% of the nutrients required for primary production (Jensen et al. 1990; Zeldis 2005; Giles 2006). In contrast, benthic regeneration does not contribute to the nutrient pools in the euphotic zone of Norwegian fjords when the water column is stratified (Aure et al. 1996; Asplin et al. 1999). Euphotic zones of fjord systems are nutrient-limited for extended periods of the year (Paasche and Erga 1988; Sætre 2007), resulting in low Chl \(a\) concentrations (Erga 1989; Aure et al. 2007).

**9.3.2 Nutrient Sinks and Sources**

Physiological processes such as inorganic nutrient excretion, biodeposition (and subsequent remineralisation processes), and growth of tissue material (see also previous section) interact with physical features of the area and the culture type applied (Table 9.6) to drive the fraction of ingested nutrients that becomes regenerated, and thus becomes available as a source of nutrients to the ecosystem. Figure 9.2 (left panels) provides an overview of the relative importance of the physiological processes involved in nutrient cycling by mussel cultures. The processes have been expressed as fractions, with the sum of the three processes giving 100%. It is thereby assumed that the sum of the three processes equals ingestion (in accordance with
Table 9.8  Biochemical characteristics of mussel cultivation areas

| Area          | Country | Trophic classification | Time     | PP [g C m\(^{-2}\) y\(^{-1}\)] | SPM [mg l\(^{-1}\)] | Chl \(a\) [μg l\(^{-1}\)] | POC [mg l\(^{-1}\)] | PON [mg l\(^{-1}\)] | DIN [μM] | PO\(_4\) [μM] | Si [μM] | Ref |
|---------------|---------|------------------------|----------|-------------------------------|---------------------|--------------------------|-------------------|-------------------|---------|-------------|---------|-----|
| Austevoll     | NO      | Oligotrophic           | Annual   | 0.4 (0.2–1.1)                 | 1 (0–8)             | 0.2 (0.1–0.6)            | 0.02 (0.01–0.05)  | 2.1 (0–7)         | 0.2 (0–0.6) | 2.4 (0–8.5) |       | 1   |
| Lysefjord     | NO      | Oligotrophic           | Annual   | 100–140 (0.8–4)               | 1–1.5 (0.9–6.5)     | 0.15–05                  | 0.01–0.02         | 0.2 (0–0.6)       | (0.02–0.03) | (1–5)       |       | 2   |
| Åfjord        | NO      | Mesotrophic            | Seasonal | 1.2 (0.1–4.0)                 | 0.3 (0.1–1.5)       | 0.04 (0.01–0.2)          | 2.4 (0.5–7.3)     | 0.3 (0.1–0.5)     | 3.2 (0.9–5.5) |           | 3   |
| Sylt          | DEN     |                        | July–Aug | 73 (17–202)                   | 1.0 (0.3–7.5)       | 0.15 (0.05–0.6)          |                   |                   |         |             |        | 4   |
| Limfjorden    | DEN     | Eutrophic              | Annual   | 284 (0–1460)                  | >10 (0–50)          |                         |                   |                   | 37 (0–100) | 0.5 (0–9)  |       | 5   |
| Oosterschelde | NL      | Eutrophic              | Annual   | 200 (115–456)                 | 6 (5–6)             | 5                        | 1                 | 0.1               | 30      | 1.5 (1–6)   | 15 (1–40) | 6   |
| W. Waddenzee  | NL      | Eutrophic              | Annual Springbl | 200 (6–120) | (3–13) |                         |                   |                   | 17 (0–64) | 0.5 (0.5–3) | 0.8    | 7   |
| Carlingford Lough | UK  | Eutrophic              | Annual   | 7.6                            | 2.3                 |                         |                   |                   | 8.1     | 0.6         |        | 9   |
| Lough Foyle   | UK      | Eutrophic              | Annual   | 15.5                           | 3.2                 |                         |                   |                   | 35.1    | 1.1         |        | 9   |
| Thau Lagoon   | FR      | Eutrophic              | Annual   | 400 (0.5–5)                   | (0.5–20)            | 0.3 (0.1–0.7)            | 0.04 (0.01–0.13)  | 1.8 (1–12)        |         |             |       | 10  |
| Ria de Arousa | ESP     | Eutrophic              | Seasonal | 99 (0–1351)                   | 1.1 (0.5–2.6)       | 4.6 (0.1–34)            | 0.3 (0.01–0.07)   | (2–12)           |         |             |       | 11  |
| N. Adriatic Sea | IT    | –                      | Annual   | 0.4 (0.4–16)                  | 0.2                 | 0.03 (0.02–0.1)          |                   |                   |         |             |       | 12  |
| Tracadie Bay  | CA      | Eutrophic              | Seasonal | 318 (18–1204)                 | 3.3                 | 2.9 (1–12)              | 0.1               | 5 (1–14)         | 0.3 (0.1–0.6) | 2 (0.2–6) | 13  |

(continued)
Table 9.8  (continued)

| Area                  | Country | Trophic Classification | Seasonality | Primary Production (PP) | Suspended Particulate Material (SPM) | Organic Material (OM) | Chlorophyll a (Chl a) | Particulate Organic Carbon and Nitrogen (POC, PON) | Dissolved Inorganic Nitrogen (DIN) | Phosphate (PO₄) | Silicate (Si) |
|-----------------------|---------|------------------------|-------------|-------------------------|--------------------------------------|-------------------------|-----------------------|---------------------------------------------------|-----------------------------------|----------------|--------------|
| Great Entry Lagoon    | CA      | Oligotrophic           | Jun–Oct     | (50–220)                | (4–27)                               | 1.8 (0.8–3.1)           | 0.4                   | 0.3 (0.1–0.5)                                    | 1.1 (0.4–2.5)                    | 14             |              |
| New Foundland         | CA      | Seasonal               |             |                         | 4.3 (2.2–6.5)                        | (0.2–5)                 |                       |                                                   |                                   | 15             |              |
| Saldanha Bay          | SA      | Eutrophic              | Seasonal    | 1240 (581–5875)         | 3.6 (Feb)                            | 8.6 (0.4–5.9)           |                       | (0–35)                                           |                                   | 16             |              |
| Firth of Thames       | NZ      | Mesotrophic            | Annual      | 168 (69–384)            | (3–10)                               | 1.5                     | 0.3                   |                                                   |                                   | 17             |              |

Trophic classification according to Nixon (1995). Primary production (PP), Suspended Particulate Material (SPM), Organic Material (OM), Chlorophyll a (Chl a), Particulate Organic Carbon and Nitrogen (POC, PON), Dissolved Inorganic Nitrogen (DIN), Phosphate (PO₄) and Silicate (Si). Values are presented as mean (minimum – maximum). Country codes are given in Table 9.1:
1 (Strohmeier 2009, Jansen et al. 2012a); 2 (Aure et al. 2001, 2007, Strohmeier unpubl data; values provided for upper 10 m); 4 (Asmus et al. 1990, Smaal and Prins 1993); 5 (Olesen 1996, Wiles et al. 2006, Maar et al. 2010); 6 (Smaal and Vonck 1997, Smaal et al. 2001, Wetsteyn et al. 2003); 7 (Dame et al. 1991, Philippart et al. 2007; waterbase NL); 8 (Philippart et al. 2007); 9 (Ferreira et al. 2007); 10 (Souchu et al. 2001, Plus et al. 2006); 11 (Smaal and Prins 1993, AlvarezSalgado et al. 1996b, Figueras et al. 2002, 2010); 12 (Brigolin 2007); 13 (Bates and Strain 2006, Cranford et al. 2007, Cranford unpubl data, Harris unpubl data); 14 (Tremblay et al. 1998, Callier et al. 2006, Trottet et al. 2007); 15 (Thompson 1984, Navarro and Thompson 1997); 16 (Monteiro et al. 1998, Pitcher and Calder 1998, Probyn unpubl data); 17 (Zeldis 2005)
Under oligotrophic conditions, less than 50% of the captured nutrients are expelled with biodeposits, which is lower than the other areas where more than 50% and, in certain cases, up to 80% of the ingested nutrients are expelled with biodeposits (Fig. 9.2). The right hand panels of Fig. 9.2 present the fractions of ingested nutrients either recycled as a source of nutrients, or retained or removed as sinks of nutrients (sum is 100%). Whether remineralisation of biodeposits acts as a source of nutrients available for phytoplankton growth depends on the system
Excretion of inorganic nutrients always acts as a source, while nutrient removal when mussels are harvested is always considered a sink. Biodeposition can result in both nutrient sources and sinks, depending on interactions with benthic processes: nutrients are either returned to the water column, buried in the sediment, or released in gaseous form ($N_2$). In deep fjords, biodeposits sink to the seafloor and as a consequence of limited benthic-pelagic coupling it is assumed that remineralized nutrients will not be available for phytoplankton growth. The estimates presented in Table 9.2 do not account for loss of mussels from the culture structures (Frechette 2012), nor for nutrient storage in byssus or shell (Hawkins and Bayne 1985); so that harvest values will be either slightly over or underestimated.

Firstly, measurements are considered for individual mussels (Fig. 9.2, upper panels). It is estimated that in deep fjord systems, approximately half of the ingested carbon and phosphorus, and 25% of nitrogen is regenerated (Fig. 9.2). Lower regeneration values for nitrogen are related to the capture and storage of nitrogen in tissue material (Jansen et al. 2012a). Mineralization of biodeposits does not significantly contribute to the source of recycled nutrients in deep fjord systems, because the majority of nutrients sink to the seafloor and regenerated nutrients are not returned to the euphotic zone of fjord systems within short time intervals due to stratification of the water column. For on-bottom and suspended cultivation of mussels in shallow areas, benthic biodeposit decomposition has been shown to significantly contribute to total nutrient regeneration (Asmus et al. 1990; Baudinet et al. 1990; Hatcher et al. 1994; Prins and Smaal 1994; Giles et al. 2006; Richard et al. 2007). Combining nutrients released by biodeposit remineralisation with those released by direct excretion results in relatively similar ‘source’ values for carbon and nitrogen regeneration in oligotrophic fjords and shallow eutrophic areas. All regenerated carbon is assumed to contribute to the source of recycled nutrients. This assumption is reasonable for Norwegian fjord systems which are generally considered to be weak absorbers of atmospheric CO$_2$, whereas in some eutrophic estuaries CO$_2$ might be released to the atmosphere since these systems often have oversaturated pCO$_2$ levels (Frankignouille et al. 1998). In these estuaries, release of CO$_2$ by eco-physiological processes represents a sink process, and values presented in Fig. 9.2 might underestimate the carbon sink for these cases (see also Filgueira et al. 2019).

Secondly, measurements are considered for mussel communities (Fig. 9.2, lower panels). Nutrient regeneration rates for suspended cultures are defined in a similar manner as for individuals (see subscript Fig. 9.2). Regeneration by benthic communities is defined as the difference between uptake of organic material and release of inorganic nutrients, and has been determined using benthic tunnel measurements in the Oosterschelde (Netherlands) and Sylt (Denmark). A high degree of variability between measurements has been observed with occasionally higher release rates than uptake rates (source >100%), likely induced by mineralization of biodeposits or dead mussels trapped within the culture structures. An extensive seasonal study on nutrient cycling by oyster *Crassostrea virginica* reefs in the North Inlet estuary (South Carolina; Dame et al. 1989), using similar benthic tunnel measurements, indicate that 66% of nitrogen and 8% of phosphorus taken up by the reef is regenerated as ammonia and phosphate, respectively. Studies performed on benthic cultures
(Dame et al. 1989; Asmus et al. 1990; Prins and Smaal 1994) also pointed out that sediment processes may bind, and thus retain, phosphate, and that denitrification processes may lead to a loss of gaseous nitrogen from the system by the formation of N₂. The effects of bivalve cultures on denitrification rates have not been fully characterised (Newell 2004) and previous studies of sediments underlying suspended mussel cultures have been inconsistent, showing either increase (Kaspar et al. 1985; Giles et al. 2006) or decrease (Christensen et al. 2003).

9.3.3 Stoichiometry of Regenerated Nutrients

The previous section pointed out that mussel communities can act as a source of regenerated nutrients. The nutrients are regenerated in different proportions (stoichiometry), which may differ to varying degrees from the stoichiometry of the inorganic nutrient pool in the ambient water (Prins et al. 1998; Jansen et al. 2011). On a large scale, the average stoichiometric composition of phytoplankton is described by Redfield’s ratio (Redfield ratio 106C:16Si:16 N:1P; Redfield et al. 1963). However, the stoichiometric composition of individual phytoplankton species, and therefore their nutrient requirements, may deviate from this ratio (Falkowski 2000). Changes in stoichiometry of available inorganic nutrients may affect phytoplankton growth (Goldman et al. 1979), and in this way could potentially induce a shift in the composition of phytoplankton species.

Figure 9.3 presents dissolved inorganic N:P ratios in the water at various mussel cultivation areas, and for the purposes of this review we assume that ratios below Redfield’s ratio (N:P = 16) are indicative of more nitrogen-limited systems, whereas ratios above this ratio are indicative of more phosphorus-limited systems. Most of the mussel cultivation areas show a N:P ratio < 16, which is consistent with the common observation of nitrogen limitation in marine environments (Nixon et al. 1996). The assumption that phosphorus is generally sufficiently available in coastal waters (Nixon et al. 1996), does not seem to hold for all of the coastal waters used for shellfish cultivation; the Wadden Sea during spring bloom, Lough Foyle, and the Northern Adriatic Sea have been reported to be phosphorus-limited (Ferreira et al. 2007; Philippart et al. 2007; Brigolin et al. 2009).

N:P ratios of regenerated nutrients determined for individual mussels and for mussel communities are presented in Fig. 9.3 by broken and by solid lines, respectively. There are no cases where the N:P ratio of the net release by individual mussels or by mussel communities exceeds the Redfield’s ratio, indicating that mussel activity is not likely to increase the ratio of N:P in the water. In most cases the N:P ratios of the regenerated nutrients (lines) differ from the ambient water (bars). The N:P ratios of nutrients released by suspended mussel communities (Austevoll, Great Entry Lagoon) are higher than ratios of nutrients released by benthic communities (Oosterschelde, Sylt; Fig. 9.3). In one case, the Oosterschelde estuary in the Netherlands, measurements have been made for both suspended mussel communities and mussel beds. The suspended community releases N and P in a ratio of
approximately 7, whilst the ratio of N and P released from mussel beds is lower (Fig. 9.3). Removal of nitrogen through denitrification processes has been suggested as a cause for the low N:P ratio measured in mussel beds (Asmus et al. 1990; Prins and Smaal 1994).

Measurements of phosphate dynamics over sediments underneath mussel farms have shown release in some cases (Baudinet et al. 1990; Souchu et al. 2001; Richard et al. 2007), and an apparent balance or an uptake in others (Hatcher et al. 1994; Mazouni et al. 1996; Giles and Pilditch 2006). Asmus et al. (1995) attributed differences in phosphorus fluxes to site-specific environmental characteristics. A balance or an uptake of phosphate can be related to the buffering capacity of sediments, caused by absorption of phosphate by iron hydroxides or calcite occurring in the oxidized surface layer of marine sediments (Sundby et al. 1992). This suggests that phosphate dynamics vary according to the location where decomposition takes place. Benthic mineralized phosphate may become trapped in the sediment, while pelagic mineralized phosphate is likely to become available in the water column.

Silicon does not play a role in physiology of mussels (Prins and Smaal 1994; Jansen et al. 2012a), and, therefore, all ingested silicon is expected to be egested with biodeposits. Decomposing biodeposits show high release rates of silicate (Jansen et al. 2012b; van Broekhoven et al. 2015, see also Table 9.5). In contrast to nitrogen and phosphorus, silicon mineralisation from biodeposits is thought to be driven primarily by chemical dissolution rather than microbial processing (van Broekhoven et al. 2015). In deep stratified systems, biodeposits (including all of the captured silicon, but not all of the carbon, nitrogen, and phosphorus) are transported to the bottom of the basin and regenerated nutrients, including silicon, do not become regenerated in the euphotic zone. This may potentially suppress the devel-

**Fig. 9.3** Annual N:P [DIN:DIP] stoichiometry in the water at various mussel cultivation areas (bars), with release rates measured for individual mussels (broken lines) and mussel communities (solid lines). Horizontal dotted line indicates the Redfield ratio (N:P=16). References are given in Table 9.3.
opment of siliceous phytoplankton diatoms and favour development of non-siliceous phytoplankton such as flagellates and dinoflagellates (Turner et al. 1998). In shallow estuaries, biodeposit remineralization contributes to the pool of regenerated silicate (Asmus et al. 1990; Prins and Smaal 1994), which reduces the potential of silicate limitation in those areas (Prins et al. 1995).

9.3.4 Significance at Ecosystem Scale

The previous sections have discussed the potential effects of mussel communities on nutrient cycling in coastal ecosystems, irrespective of mussel abundance or dimensions of the system. In order to be able to evaluate system-wide interactions, estimates for the bivalve standing stock are an essential parameter (Table 9.9); although the majority of these values are associated with a large uncertainty. Combining standing stock estimates with dimensions of the systems (Table 9.7) provides area and volume-based biomass density estimates (Table 9.9). The Wadden Sea (NL) and several systems in France are important mussel cultivation areas in terms of total harvest quantities. However, these systems are also characterized by co-culture or co-existence of several bivalve species (e.g. Crassostrea gigas or Ensis sp.). As the current review focusses on mussels, systems where mussels comprise a minor proportion of total bivalve biomass were excluded from the analysis of mussel-ecosystem interactions. Mussel biomass density is highest in the eutrophic estuaries in Tracadie Bay (Canada) and the small coastal inlet Sylt (Germany), whereas biomass density in oligotrophic fjord systems is among the lowest reported.

Interactions are firstly evaluated by the total food uptake relative to the total food available (Fig. 9.4a, Smaal and Prins 1993; Dame and Prins 1998), which can also be described as an indicator for the ‘top-down’ influence on phytoplankton or ‘negative feedback mechanism’. In the Norwegian fjords (Åfjord and Lysefjord) clearance times (CT) are longer than water residence times (RT) and primary production times (PPT) despite oligotrophic conditions, indicating that mussel cultures do not dominate food dynamics in these fjord systems. This is different from many other systems where clearance times are shorter than residence times (CT/RT <1). This confirms studies by Smaal and Prins (1993), Dame and Prins (1998) who report that clearance times are shorter than the residence times for most mussel cultivation areas. However, for most areas primary production is faster than mussel feeding (CT/PPT>1) indicating that the food source is renewed faster than it is filtered. Limfjorden has the longest residence times (almost one year), and a high mussel biomass which together result in high food uptake relative to residence times (CT/RT<<1) indicating that the system is potentially regulated by mussel filtration. However, high nutrient loading in this system results in high primary production rates (Maar et al. 2010) which subsequently indicates that mussels do not overgraze phytoplankton populations (CT/PPT>>1).

Secondly, mussel-ecosystem interactions were evaluated by nitrogen (DIN) turnover time (Dame 1996) relative to the residence time (Fig. 9.3b). This indicator can
| Area            | Country | Species              | Culture type | Harvest (WW) [ton y⁻¹] | Standing stock (DW) [ton] [g m⁻²] [g m⁻³] | Ref |
|-----------------|---------|----------------------|--------------|------------------------|----------------------------------------|-----|
| Lysefjord       | NO      | *M. edulis*          | Rope         | 94                     | 2.1 [0.1]                              | 1   |
| Åfjord           | NO      | *M. edulis*          | Rope         | 1200                   | 109 [7.8] [0.4]                        | 2   |
| Limfjorden       | DEN     | *M. edulis*          | Bottom       | 90,000                 | 2509 [1.6] [0.4]                       | 3   |
|                 |         | *C. gigas*           |              | 580                    | 6 [0.0] [0.0]                          |     |
| Sylt             | DEN     | *M. edulis*          | Bottom       | 189                    | 26.3 [4]                              | 4   |
| Oosterschelde    | NL      | *M. edulis*          | Bottom       | 25,000                 | 6061 [17.3] [2.2]                      | 5   |
|                 |         | *C. gigas*           | Bottom       | 2424                   | 2.4 [0.3]                             |     |
|                 |         | cockles              | Bottom       | 848                    | 6.9 [0.9]                             |     |
| Wadden Sea       | NL      | *M. edulis*          | Bottom + rope| 5018                   | 3.6 [1.3]                             | 6   |
|                 |         | *M. arenaria*        | Natural      | 8419                   | 6.0 [2.1]                             |     |
|                 |         | *Ensis*              | Natural      | 12,880                 | 9.1 [3.2]                             |     |
|                 |         | Other bivalves       | Natural      | 5799                   | 4.1 [1.4]                             |     |
| Carlingford Lough| UK      | *M. edulis*          | Bottom + rope| 2500                   | 209 [4.3] [0.5]                       | 7   |
|                 |         | *C. gigas*           | Trestles     | 320                    | 27 [0.6] [0.06]                       |     |
| Belfast Lough    | UK      | *M. edulis*          | Bottom       | 15,318                 | 1281 [1.7]                            | 8   |
|                 |         | *C. gigas*           | Trestles     | 50                     | 4 [0.006]                             |     |
| Bay of Brest     | FR      | Various              |              | 13,275                 | 90 [8.9]                              | 9   |
| Thau Lagoon      | FR      | *C. gigas + M. edulis*|              | 13,500                 |                                          | 10  |
| Marennes-Oleron  | FR      | *M. edulis*          |              | 242                    | 0.4 [11]                              |     |
|                 |         | *C. gigas*           |              | 2424                   | 3.6 [6]                               |     |
|                 |         | Other bivalves       |              | 788                    | 1.2 [12]                              |     |
| Ria de Arosa     | SP      | *M. galloprovincialis*| Raft         | 172,500                 | 4809 [19.6] [1.1]                      | 12  |
| Tracadie Bay     | CA      | *M. edulis*          | Rope         | 1943                   | 261 [15.9] [6.4]                       | 13  |
| Great Entry Lagoon| CA | *M. edulis*          | Rope         | 180                    | 15 [0.5] [0.1]                        | 14  |
| Firth of Thames  | NZ      | *P. canaliculus*     | Rope         | 9000                   | 251 [0.2] [0.02]                      | 15  |

Density is expressed in terms of harvest rate (ton WW y⁻¹), and in standing stock for the whole system (ton DW), per unit area (g DW m⁻²) and per unit volume (g DW m⁻³). For the Norwegian fjords, only the water volume above the sill was used in the calculations. Asterisk (*) indicates that standing stock was reconstructed based on harvest, length of the production cycle and WW/DW conversion factors by Ricciardi and Bourget (1998). Country codes are given in Table 9.1 1 (Strohmeier et al. 2005; pers. comm Strohmeier); 2 (pers. comm. M. Hoem and A. Koteng); 3 (Dolmer and Geitner 2004); 4 (in Smaal and Prins 1993); 5 (Smaal et al. 2001); 6 (Philippart et al. 2007, Schellekens et al. 2014); 7 & 8 (Ferreira et al. 2007); 9 (in Smaal and Prins 1993); 10 (Thouzeau et al. 2007); 11 (Smaal and Zurburg 1997); 12 (Figueiras et al. 2002); 13 (Cranford et al. 2007); 14 (Trottet et al. 2008b); 15 (Zeldis 2005)
Fig. 9.4 Mussel-ecosystem interactions expressed by indicators for negative and positive regulation of primary production, calculated according to Dame and Prins (1998), Smaal and Prins (1993) and Dame (1996) based on the following parameters

Residence time (RT) = Time to exchange water body
Clearance time (CT) = Time to filter the water body

\[ CT = \frac{\text{system volume}}{CR \times \text{mussel biomass}} \]

Primary production time (PPT) = Time to renew phytoplankton (Bp/P)

\[ PPT = \frac{\text{POC}_{\text{phytopl.}} \times \text{volume system}}{\text{Primary production} \times \text{Area system}} \]

with the assumption: 40 mgPOC_{\text{phytopl.}} mgChla^{-1}

Nitrogen turnover time (NTT) = Time to renew DIN

\[ NTT = \frac{\text{DIN} \times \text{system volume}}{\text{DIN Release} \times \text{Mussel biomass}} \]

The extent to which mussel populations have a regulating function in the ecosystem is evaluated by the ratios between the parameters:

- CT/RT > 1: no/minor regulation
- CT/RT < 1: phytoplankton potentially regulated by mussel filtration
- CT/PPT > 1: no/minor regulation
- CT/PPT < 1: phytoplankton is overgrazed
- NTT/RT > 1: no/minor regulation
- NTT/RT < 1: mussels potentially driving nutrient cycling

References are given in Tables 1-9. Asterisk (*) indicates that community-scale rates were applied.
describe the potential extent of ‘bottom-up’ stimulation of phytoplankton production or the ‘positive feedback mechanism’. The total DIN pool in the ambient water was lowest in Åfjord, Lysefjord and the Firth of Thames, so that a quantity of regenerated nitrogen from mussel cultures could make a proportionally greater contribution to its availability. However, mussel density in these areas is also low (<0.4 g DW m\(^{-3}\)). As a result, nitrogen turnover times remain long relative to water residence times (NTT/RT>40), indicating a limited effect of mussels on nutrient cycling. Low DIN concentrations are reported for Great Entry Lagoon resulting in a high NTT value, suggesting a relatively high effect on the DIN pool (NTT/RT<1). However, this outcome may be skewed because ambient values are based on the period June-October, thus excluding the higher winter values. Besides Great Entry Lagoon, the relative effect of regeneration processes (NTT/RT) is most pronounced in the Oosterschelde estuary and Tracadie Bay, indicating that mussels may influence nutrient cycling although NTT/RT values did not fall below 1. These are shallow estuaries/bays with high mussel cultivation activity, as indicated by the high relative mussel density (2-6 g DW m\(^{-3}\), Table 9.9).

This analysis of positive and negative feedback mechanisms of mussels acting on phytoplankton growth (Fig. 9.4) addresses some consequences of mussel populations for ecosystem functioning, but it is based on a static approach. However, marine systems are complex, and suspended organic matter and inorganic nutrient concentrations are subject to physical, biochemical and eco-physiological processes and fluctuate over both temporal and spatial scales. It should be noted that the literature presented here represents integrated annual values, whereas in fact most of the parameters fluctuate over temporal scales. Prins and Smaal (1994) address the importance of seasonality in terms of the contribution of mussels to nutrient regeneration in the Oosterschelde, demonstrating that mussel beds could account for almost half of the total DIN regeneration of the system, but only during summer when nutrients are limiting. Similarly, Jansen et al. (2011) demonstrate that at the scale of one mussel farm in a Norwegian fjord, the contribution of mussels to the inorganic nutrient pool is insignificant during winter conditions but substantial during summer. This is a result of the combination of low nutrient concentrations (nutrient limitation) in the ambient water, high metabolic activity of the mussel population, and high biomass and metabolic activity of fouling organisms.

9.4 Perspective on the Regulating Services of Mussels in Nutrient-Poor and Nutrient-Rich Cultivation Areas

The extent to which bivalve suspension feeders fulfil a regulative role varies between coastal ecosystems (Dame and Prins 1998). Trophic status (nutrient-poor to nutrient-rich) of a system influences the regulating potential for mussels in two ways: (1) the eco-physiological response may vary as a function of ambient nutrient (and thus food) concentrations, and (2) nutrient regeneration has a proportionally greater effect when ambient concentrations are low.
9.4.1 Physiological Response

The high feeding rates observed in oligotrophic areas suggest that the physiological response of mussels under low nutrient conditions may differ from areas with higher nutrient concentrations. As model results indicated that metabolic responses are comparable between cultivation areas, this suggests that the slightly lower rates observed for oligotrophic areas are simply a result of low food concentrations rather than a specific response related to the trophic status of the system. Also, nutrient composition of the mussel tissue is similar in oligo- and eutrophic areas, and appears to be endogenously regulated and driven primarily by reproductive processes. Mussels are able to efficiently use the low-concentration but high-quality food sources in oligotrophic systems, resulting in low biodeposit production (in absolute and in relative terms). In eutrophic areas, up to 95% of the filtered nutrients can be expelled with biodeposits in certain cases, which is partly due to pseudofaeces production, while in oligotrophic areas less than 50% of all ingested nutrients is expelled with faecal material.

9.4.2 System Feedbacks

Differences in eco-physiological rates under oligotrophic as compared to eutrophic conditions (higher clearance, lower egestion, approximately similar excretion, and similar storage in tissue) may lead to distinct mussel-ecosystem interactions. Proportionally more nutrients are excreted as metabolic waste products under oligotrophic conditions (e.g. NH₄), potentially resulting in a higher positive feedback and thus enhanced primary production. In deep fjord systems, the pool of nutrients available for phytoplankton growth is only supplied by directly excreted inorganic metabolic waste products, while in shallow areas remineralization of biodeposits may also contribute to the pool. Ecosystem interactions are here defined as the fraction of ingested nutrients either recycled and again available for primary production (source) or permanently removed from the system (sink). The current review showed that through these mechanisms the ecosystem interactions are comparable between deep oligotrophic and shallow eutrophic systems. This indicates that the theoretical role of mussels in nutrient cycling and positive feedback processes is relatively similar across mussel cultivation areas. Furthermore, stoichiometry of regenerated nutrients (C>N>P) is generally different from that observed in the ambient water and from the Redfield ratio. This indicates that mussel cultures have the potential to influence phytoplankton community composition by causing shifts in the proportional availability of C, N, P, and Si. The oligotrophic fjord systems are examples where silicate limitation, potentially induced by mussel activity, may suppress diatoms while favouring (dino)flagellate development, while in shallow estuaries this phenomenon is expected to be of less importance due to the contribution of regenerated silicate through biodeposit decomposition.
Evaluation of the regulating potential of mussel cultures at the ecosystem level is based on indicators for negative (CT/RT and CT/PPT) and positive (NTT/RT) feedback processes on primary production. These indicators for mussel-ecosystem interaction demonstrate that despite low background nutrient levels, mussel aquaculture in Norwegian fjord systems at present has limited effects owing to low mussel densities and physical characteristics of the fjords (large volume, short residence times of the upper water layer). Estimates for mussel-ecosystem interactions are more profound in shallow nutrient-rich areas with high mussel biomass, especially in terms of the negative feedback mechanisms through filtration of phytoplankton. The significance of the positive feedback mechanism (nutrient regeneration) has a strong seasonal component as many mussel cultivation systems are nitrogen-limited during summer periods when mussel activity is high. These comparisons between cultivation areas suggest that physical characteristics of the site in combination with mussel density better define the feedback to the ecosystem, and hence the regulating potential of mussel cultures, rather than trophic state.

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