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**REVIEW**

# Characteristics of Suspended Particulate Matter, Benthic Environmental Factors, and Their Relationship to Bivalves

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## Abstract

Bivalves are of great ecological and economic importance across coastal zones around the globe. Their distribution and abundance are affected by various benthic environmental factors, including suspended particulate matter (SPM). The relationship between bivalves and SPM has been studied in various contexts but not recently. Thus, the authors conducted a literature review of SPM found in the marine environment, its characteristics (particle size and density), and how the surrounding benthic environmental factors (salinity, light availability, and current velocity) influence its characteristics. Certain areas were found to lack or require further research, such as on the characteristics of microplastics and the mechanism behind the positive influence of PIM in bivalve diet components not yet discovered. Over the past decades, coastal environments have undergone huge development and change that has affected the SPM components and conditions in coastal marine environments, justifying updated research. The need for this and other information will influence future research, as summarized at the end of the article.

**Discipline:** Fisheries
**Additional key words:** inorganic matter, microplastics, organic matter, suspension feeders, turbidity

## Introduction

Coastal zones play a vital role in the livelihood of humans and marine life around the globe. They provide various ecosystem services, including fisheries, tourism, carbon sinks, nutrient recycling, and moderation of extreme natural events (Begon & Townsend 2021). Coastal fisheries contribute to a nation's economy and are a highly valued part of many communities. For example, coastal production constitutes about 45% of the total fishery production in Japan, accounting for about 60% of all sales because of the many high-value species in these coastal zones (Matiya et al. 2006).

Marine bivalves are a highly targeted, highly valued species and accounted for 14% of the global marine production during 2009-2014. Of this, 89% was from aquaculture and 11% from wild fishery (Wijsman et al. 2019). Their study reported that consumers appreciate the nutritional benefits of marine bivalves as well as their taste.

Although bivalve resources are in high demand, wild bivalve populations have been declining worldwide for decades because of the deterioration in the environments of bivalve habitats, with a severe 85% (Beck et al. 2011). Ongoing research on the causes of this decline and strategies for recovery are areas of increasing research interest.

Suspended particulate matter (SPM) is a key factor that significantly affects the behavior, ecology, and physiology of bivalves (Ward & Shumway 2004). Bivalves filter seawater to obtain food and oxygen from the water column and are exposed to a wide range of living and non-living suspended materials daily. Figure 1 shows a typical benthic environment with influential

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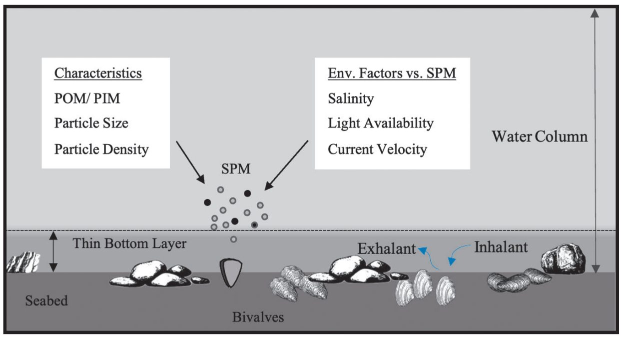


**Fig. 1. Layout of a water column depicting a typical marine bivalve habitat**
POM: particulate organic matter, PIM: particulate inorganic matter, SPM: suspended particulate matter

factors that bivalves are exposed to. As stated by Gosling (2003), bivalves in the wild feed on a variety of SPM, such as bacteria, phytoplankton, micro-zooplankton, detritus, and dissolved organic matter (e.g., amino acids and sugars). In filtering seawater, bivalves also modify the coupling between the seafloor and water column activities, influencing phytoplankton population dynamics and nutrient cycling (Dame 1993). They depend on SPM for growth and survival in a complex relationship. After mixing and resettling occurs in the water column due to tidal changes and wave action, the water immediately above the seabed forms a thin bottom layer that affects them, as shown in Figure 1. This layer has a higher SPM concentration until full SPM settlement.

SPM has diverse characteristics (e.g., origin, size, density, and chemical composition), and this diversity impacts bivalves in many ways. Due to the complex relationship between bivalves and SPM in the natural environment, many studies have increased our understanding of this field. For example, Fox et al. 1937, Korringa 1952, Møhlenberg & Riisgård 1978, Fegley et al. 1992, Bayne et al. 1993, Ellis et al. 2002, and Newell et al. 2002 are some of the many studies that have focused on the bivalve-SPM relationship.

The environment can alter SPM characteristics, affecting bivalves with ongoing environmental changes due to climate, global warming, and infrastructure development. Hence, updated information is needed on how current environmental factors affect SPM and their effects on bivalves. This information is not available in reviews older than 20 years, so this article concentrates on what needs to be updated due to the recent changes in coastal environments. Our focus is on (1) the characteristics of SPM and its effects on bivalves, (2) benthic environmental factors and their influence on SPM, and (3) anticipated research.

## Characteristics of suspended particulate matter

SPM characteristics can affect the physiology, behavior, and ecology of bivalves. Particulate matter, size, and density have the greatest effect and are discussed in this section.

### 1. Particulate organic matter

Particulate organic matter (POM) is a vital component of coastal marine ecosystems, especially for marine filter feeders that depend on it for growth and survival. It originates in seawater from marine plants, river runoff, sediment disturbance, and airborne material of terrestrial origin. POM sources and sinks can be estimated using stable isotopic compositions ($\delta^{13}C$ and $\delta^{15}N$) and geochemical indicators (e.g., the POM C/N ratio) in marine environments (Chen et al. 2021, Dan et al. 2022, Xia et al. 2022). POM also includes discrete biogenic entities formed in situ, including plankton of a wide range of sizes and palatability, bacteria, invertebrate larvae and eggs, and fecal pellets. POM abundance in the marine environment depends on the location. Due to terrestrial runoff and input, POM concentrations near a river mouth are higher than where there are no rivers or development. Armstrong & Atkins (1950) reported POM concentrations of 1.6-1.8 mg $L^{-1}$ in the English Channel, and Widdows et al. (1979) found 1.5-1.9 mg $L^{-1}$ in the Lynher Estuary. The 2-5 mg $L^{-1}$ Griffiths (1980) determined was in False Bay, South Africa. There are several ways to estimate the POM content in the ocean. These include satellite remote sensing and estimating the chlorophyll (living phytoplankton biomass) and particulate organic carbon content (Legendre 1999, Franz et al. 2015). Chlorophyll and the particulate organic carbon content of POM significantly affect the nutritional value of bivalves (Ball et al. 1997, Legendre 1999, Franz et al. 2015, O'Connell-Milne et al. 2020, Newell et al. 2021).

POM is the primary source of nutrition for bivalves, which contribute to the carbon cycle by transporting carbon to the seafloor (Middelburg 2019). The greatest benefit of POM is its nutritional value and, therefore, it has been used to some degree during the rearing period in almost all experiments that involve rearing bivalves (Widdows et al. 1979, Bricelj & Malouf 1984, Bayne et al. 1989, Bayne et al. 1993, Hawkins et al. 1996).

However, POM also damages the natural environment. Fast-growing aquaculture coastal areas are increasingly affecting POM's source, chemical composition, and fate and vice versa (Sarà et al. 2004, Jean-Marc et al. 2018). Increasing land-based coastal development and agricultural activities have also altered the characteristics, composition, and amount of POM released into coastal waters (Sahavacharin et al. 2022). Recently, harmful algal blooms (HABs) have increased global POM considerably, resulting in the mass mortality of many coastal species and costing aquaculture and the fishery sector millions of dollars (Hallegraeff et al. 2021).

Another consequence of a high abundance of coastal POM is the occurrence of hypoxia, where the dissolved oxygen concentration drops below 2 mg $L^{-1}$ (Zhang et al. 2018). Bivalves in coastal areas are frequently subjected to hypoxia, especially during summer, and their tolerance is highly species-specific (Diaz & Rosenberg 1995). Wu (2002) explained that aquatic organisms respond to hypoxic conditions by (1) attempting to maintain oxygen delivery, (2) conserving energy, and (3) enhancing energetic efficiency and deriving energy from anaerobic sources. An infaunal bivalve found in New Zealand, *Paphies australis*, has evolved efficient strategies for anaerobic energy production (Carroll & Wells 1995), but many species cannot adapt to the warming and hypoxic conditions. For example, a recent study by Tomasetti et al. (2023) showed a reduced performance and survival of *Argopecten irradians irradians* when an eight-day estuarine heatwave coincided with hypoxic conditions. There is reason to believe that the occurrence of hypoxia will only increase and intensify due to the increasing human population, sewage treatment plants' inability to keep up, global warming, agriculture, and deforestation.

This study investigated microplastics, a recent addition to the POM family, which have garnered considerable interest due to their broad applicability and negative impact on marine ecosystems. Thompson (2015) defined microplastics as a collective term that describes a heterogeneous mixture of particles ranging from a few micrometers to several millimeters in diameter and occurring in several shapes, from complete spheres to elongated fibers. In 2010, 4.8-12.7 million metric tons of plastics entered the oceans worldwide, and the yearly input was predicted to increase by an order of magnitude by 2025 (Jambeck et al. 2015). Plastics accumulate in all parts of the oceans: on the surface, in the water column, and in sediments (Moore et al. 2002, Thompson et al. 2004, Barnes 2005). Plastics breaking down into microparticles are becoming part of SPM in the natural environment. Because most plastic particles are < 5 μm in size (Thompson et al. 2004, Claessens et al. 2011), they are taken up by a wide range of marine organisms. However, since most plastics are fragmented and sink to the bottom, benthic invertebrates such as bivalves are most vulnerable to this type of pollution. Microplastic pollution has been an ongoing global issue, so there has been considerable interest in the adverse effects these plastics have on our marine ecosystem. The ingestion of polystyrene microplastics by the Pacific oyster *Crassostrea gigas* affects the development of larvae, endocrine disruptions, and energy usage and storage (Sussarellu et al. 2016). Prolonged exposure to microplastics in *Mytilus edulis* showed notable histological changes and a strong inflammatory response (von Moos et al. 2012).

Microplastics directly affect the physiology of bivalves and indirectly affect them by changing the structure of their sedimentary habitats and delivering persistent organic pollutants (Zhang et al. 2020). Seeley et al. (2020) stated that microplastics altered sediment microbial community composition and the nitrogen cycle in salt marshes. Furthermore, researchers have recently highlighted the possibility of marine microplastics being a potential substrate for pathogens, particularly marine bacteria, such as vibrios, and as carriers of antimicrobial-resistant bacteria (Zettler et al. 2013, Amaral-Zettler et al. 2020, Bowley et al. 2021). Masó et al. (2003) confirmed that drifting plastic debris has been identified as a potential vector for dispersing HAB species. Detailed microscopic examination of plastic debris collected at several places in Costa Brava identified patches of benthic diatoms and small flagellates (< 20 μm), such as resting cysts of *Ostreopsis* sp. and *Coolia* sp. (Masó et al. 2003).

Baroja et al. (2021) stated in a review that most evidence of the impact of microplastics on marine organisms had come from experimental studies under controlled laboratory conditions. However, assessing the effects of plastic pollution requires understanding the relevance of laboratory conditions to those observed in natural marine systems. Their article provided a systematic overview of experimental studies that assessed microplastic effects on bivalves and extracted data on the species of bivalves used, the characteristics of microplastics tested, and the responses monitored during exposure. Baroja et al. (2021) concluded that 23% of bivalve exposure studies did not report critical information on microplastic characteristics like shape and type. To allow reproducibility, future exposure studies must consider the details of the microplastics.

In summary, this section discusses the characteristics and composition of these organic particles, the ongoing changes in coastal environments primarily due to coastal development, how the changes affect these organic particles, and how the organic particles affect the behavior and physiology of marine bivalves.

## 2. Particulate inorganic matter

This section discusses the role played by particulate inorganic matter (PIM), the most abundant form of SPM in marine ecosystems. PIM consists of complex mineral, biogenic, and anthropogenic assemblages, including mud, silt, sand, and colloidal aggregates. Terrestrial runoffs during heavy rain and storms are the main contributors to PIM because they include mainly silt and clays, highly charged particles that flocculate on contact with seawater. In addition to terrestrial runoff, PIM enters the marine environment through the air and dry deposition with rainfall (e.g., volcanic ash and dust) (Agarwal 2009). PIM is typically the dominant constituent in estuaries, representing 70%-80% of the SPM by mass (Oviatt & Nixon 1975).

The negative effects of PIM on marine bivalves are discussed in detail in relation to previous studies. Since most marine bivalves, except for deposit-feeding bivalves such as Tellinidae, depend on SPM for nutrients, an increase in PIM concentration in the water column reduces the amount of organic particles ingested by marine bivalves due to the diluted POM and constrains the energy gain (Widdows et al. 1979, Bricelj & Malouf 1984, Bayne et al. 1993, Hawkins et al. 1996). Suspension-feeding bivalves adapt to elevated PIM levels by (1) decreasing clearance rates, (2) selectively ingesting favorable organic food particles, and rejecting PIM through pseudofeces production (Widdows et al. 1979, Griffiths 1980, Bricelj & Malouf 1984). Marine bivalves that ingest inorganic particles with increasing PIM concentrations can reduce gut residence time for food particles and develop low assimilation efficiency (Madon et al. 1998). Thrush et al. (2004) stated that inorganic silts and clays directly affect suspension-feeding animals by clogging feeding structures, such as gills and labial palps, interfering with particle selection, and requiring energy to clear unwanted particles. Most studies have found that PIM has a negative impact on the behavior and physiology of marine bivalves (Bricelj & Malouf 1984, Robinson et al. 1984, Stevens 1987, Iglesias et al. 1996, Navarro & Widdows 1997, Madon et al. 1998, Thrush et al. 2004).

However, some studies have stated that, with the right amount of PIM concentration mixed with POM in the water column, bivalves seem to experience growth through high organic absorption due to higher clearance rates and/or higher absorption efficiency (Winter & Langton 1976; Griffiths 1980; Kiørboe et al. 1980, 1981; Møhlenberg & Kiørboe 1981). For example, Møhlenberg & Kiørboe (1981) studied the influence of natural silt (0-20 mg $L^{-1}$) in addition to unicellular algae cells (0-20,000 cells $mL^{-1}$) on the clearance, growth, and energetics of blue mussel *M. edulis* and found that adding 5 mg silt $L^{-1}$ increased the clearance rate from 32 to 43% over that of a pure algal suspension. Bayne's (1998) theory on regulating filtration and feeding in bivalves could explain these results. If filtration is physiologically controlled by the nutritional needs of the bivalve and the qualitative and quantitative composition of SPM, Bayne's theory states that bivalves in low food environments can increase their absorption of ingested particles during digestion. This theory was proven for mussel *M. edulis* and scallop *Placopecten magellanicus*, where absorption of organic matter was higher when food concentration in SPM was low (Bayne et al. 1993, Cranford & Hill 1999). Contrary to Bayne's theory, Jørgensen's (1996) theory states that bivalve feeding processes are automatic and depend only on the characteristics of certain species. The experimental results of Clausen & Riisgård (1996) supported this theory by showing that, for mussel *M. edulis*, there was no physiological regulation of the filtration rate with nutritional need and that food uptake in nature is characterized by full exploitation of the capacity of the bivalve filter pump. The theory is accurate, but bivalve feeding behavior remains unclear and needs further investigation.

### 3. Particle size

The particle size of SPM is a vital part of the survival of marine filter feeders as these organisms depend on and actively select particles based on their size during filter feeding. As Balasubramanian et al. (2020) emphasized, SPM particle size is an important characteristic essential in the biogeochemical and ecological processes of complex coastal environments. Several studies have shown that particle size distribution impacts ocean processes, such as the settling velocity of particles, carbon fixation, and light availability in the water column (Xi et al. 2014, Qiu et al. 2016, Nasiha et al. 2019). Table 1 summarizes previous studies on the influence of particle size on various bivalve species.

Early studies suggested that bivalves could successfully capture particles in the sub-micron range. However, later studies in the mid-1950s using *M. edulis* demonstrated that capture efficiency for particles < 2.5 μm in diameter was quite low (Fox et al. 1937, Fox & Coe 1943, Korringa 1952, Tammes & Dral 1955). Tammes & Dral (1955) showed that particle capture depends on the particle diameter and that, in mixed suspensions of particles of different sizes, each component is removed separately using a sieving mechanism in the laterofrontal cirri. Later, as shown in Table 1, Møhlenberg & Riisgård (1978) studied the retention efficiency of 13 bivalve species and found that retention efficiency decreased with particle size and the particle diameter at which inefficient retention began was species-specific. All bivalves studied could capture particles > 6 μm in diameter at nearly 100% efficiency.

**Table 1. Previous studies on the effect of particle size on the responses of various bivalve species**

| Bivalve Species | Test Feed | Particle Size vs. Response | Reference |
|---|---|---|---|
| *Mytilus edulis* | Mixed feed*1 | > 6 μm: ≈ 100% RE, 2 μm: 70%-90% RE | Møhlenberg & Riisgård 1978 |
| | Mixed feed*2 | 300 μm: 90% Ingested<br>1mm-1.2 mm: 34% Ingested | Davenport et al. 2000 |
| | *Tapes phillipinarium* larvae | 161 μm: ≈ 90% Ingested | Lehane & Davenport 2004 |
| *Ruditapes decussatus* | Mixed feed*3 | < 3 μm: < 60%-70% RE<br>> 6 μm: 80%-100% RE | Sobral & Widdows 2000 |
| *Cardium echinatum*<br>*Cardium edule*<br>*Modiolus modiolus*<br>*Musculus niger*<br>*Cultellus pellucidus*<br>*Hiatella striata*<br>*Mya arenaria*<br>*Venerupis pullastra* | Mixed feed*1 | > 6 μm: ≈ 100% RE, 2 μm: 70%-90% RE | Møhlenberg & Riisgård 1978 |
| *Pecten opercularis*<br>*Pecten septemradiatus* | ” | > 6 μm: ≈ 100% RE, 2 μm: < 30% RE | |
| *Ostrea edulis* | ” | > 6 μm: 100% RE, 2 μm: 40% RE | |
| *Artica islandica* | ” | > 6 μm: ≈ 100% RE, 1 μm: 60%-70% RE | |
| *Geukensia demissa*<br>*Spisula solidissima*<br>*Brachidontes exustus*<br>*Mercenaria mercenaria* | Mixed feed*4 | > 4 μm: ≈ 100% RE, 2 μm: 35%-70% RE | Riisgård 1988 |
| *Crassostrea virginica* | ” | > 5 μm: 100% RE, 2 μm: 50% RE | |
| *Argopecten irradians* | ” | > 5 μm: 100% RE, 2 μm: 15% RE | |

Mixed feed*1 – a mixture of *Monochrysis lutheri* (2 μm-5 μm), *Dunaliella marina* (5 μm-7.5 μm), *Tetraselmis suecica* (6 μm-9.5 μm), which were all measured using an electronic particle counter
Mixed feed*2 – a mixture of *Artemia* sp. and *Tigriopus brevicornis*
Mixed feed*3 – mixture of fine surface mud and algal cells
Mixed feed*4 – a mixture of bacteria, small particles, and *Isochrysis galbana*, *Cryptomonas* sp.
RE: retention efficiency

However, some species, like the ocean quahog, *Artica islandica*, retained 1 μm particles with an efficiency of about 60%-70%, as shown in Table 1. Generally, the capture efficiency of particles increases non-linearly with increasing particle size to a maximum (Ward & Shumway 2004).

Moreover, *M. edulis* can feed on 3 to 110 μm particles (Newell et al. 1998). However, the species was also recorded to consume zooplankton up to several hundred microns (Davenport et al. 2000; Lehane & Davenport 2002, 2004) and had 100% retention efficiency when feeding on > 6 μm particles (Møhlenberg & Riisgård 1978) and 50% retention efficiency when feeding on 2 μm particles (Newell & Shumway 1993). In addition, a more recent study by Suzuki et al. (2022) reported that larvae shells of dead but incompletely digested zooplankton (bladder moon snail *Glossaulax didyma*) were found in the feces of pen shell *Atrina lischkeana* collected off the shores of Isahaya Bay, Japan. Retention on bivalve gills partially depends on particle size since the ctenidium does not retain the smallest particles with 100% efficiency (Riisgård 1988, Barillé et al. 1993, MacDonald & Ward 1994). Several researchers have observed dissected bivalves, which indicated a rotation of style and beating of ciliated tracts, creating a circulation of fluids within the stomach (Reid 1965, Purchon 1987). Except for protobranchs, crystalline styles are transparent rods found in the digestive system of all bivalves that are instrumental in sorting food particles (Kristensen 1972). For example, in oyster *Crassostrea gigas*, the crystalline style mechanically presses nutritious particles against the absorptive epithelium of the style pouch, and observations showed that when the specimen was held out of water, the crystalline style disappeared and reformed after being submerged an hour later (Bernard 1973). Other studies have reported that the capture efficiency of large particles is lower than that of small particles (Lesser et al. 1991, Bougrier et al. 1997, Pile & Young 1999), which is difficult to explain. A review article by Ward & Shumway (2004) stated that cell shape and flexibility differences significantly influence particle capture. Bayne et al.

(1977) reported that elongated or tri-radiated cells may be more efficiently retained than spherical particles of the same volume. Another possibility is that swimming cells interact with the ctenidium of some bivalve species in different ways. Bricelj et al. (1998) reported that an 11 µm diatom, *Thalassiosira weissflogii*, was entrained in the anteriorly directed slurry in the dorsal ciliated tract, but toxic and non-toxic strains of dinoflagellate (*Alexandrium* spp., 35 µm long) were not retained on the frontal surface of the ctenidium. Particle size selectivity differs among species, so further studies are required for individual particle size selectivity preferences.

## 4. Particle density

Particle density, the amount by weight of suspended particles in a volume of water, is an important characteristic of SPM that needs to be studied since it impacts marine ecology. An increase in SPM density in estuaries or bays is caused mainly by water discharged by rivers and the resuspension of fine sediments during periods of high current velocity on flood and ebb tides and wind-wave activity (Navarro & Widdows 1997). They further explained that while these processes increase total POM, the relative content of POM is reduced because of its higher abundance in resuspended sediments.

SPM concentrations in coastal waters typically range from a few mg $L^{-1}$ to several tens of mg $L^{-1}$ (Oviatt & Nixon 1975). However, some places (e.g., an estuary in New Zealand) experience a rise in suspended sediment concentrations from 10-20 to 1,000 mg $L^{-1}$ during a storm (Fahey & Coker 1992). In countries like Japan, where river outflows are controlled, this influences the SPM particle density (especially POM density) in nearby areas (personal communication). Depending on the tidal conditions at the time of input, sediments will either be transported out of the estuary or deposited. If deposited and available for resuspension, the bottom waters (the thin bottom layer shown in Figure 1) experience high particle density and impact benthic communities, especially such filter feeders as bivalves.

Table 2 summarizes previous findings on the effect of particle density on various bivalve species. Increased concentrations of PIM (e.g., clay and silt) in suspension may increase pseudofeces production, which would decrease the amount of organic food ingested and could damage the gills of filter feeders and limit bivalve growth (Bricelj & Malouf 1984, Robinson et al. 1984, Stevens 1987, Iglesias et al. 1996, Navarro & Widdows 1997, Snyder et al. 2017, Palmer et al. 2020). Furthermore, Robinson et al. (1984) previously showed that suspended sediment concentrations as low as 100 mg $L^{-1}$ negatively

**Table 2. Previous studies on the effect of particle density on the responses of various bivalve species**

| Bivalve Species | Particles | Particle Density | Response | Reference |
|---|---|---|---|---|
| *Mytilus edulis* | fine surface sediments | 0-350 mg $L^{-1}$ | CR – negative relationship as particle density increased within this range | Widdows et al. 1979 |
| | Mixture feed*1 | 0-5 mg $L^{-1}$ | 32%-34% incr. in CR and 30%-70% incr. in GR relative to control | Kiørboe et al. 1981 |
| | natural sediments | 0.15-0.43 mg $L^{-1}$ | 4-6 L $g^{-1}$ $h^{-1}$ CR | Strohmeier et al. 2009 |
| *Atrina zelandica* | Mixture feed*2 | 10 mg $L^{-1}$<br>20 mg $L^{-1}$<br>80 mg $L^{-1}$ | 0.70-1.10 L $h^{-1}$ CR<br>0.61-0.95 L $h^{-1}$ CR<br>0.40-0.60 L $h^{-1}$ CR | Ellis et al. 2002 |
| *Mercenaria mercenaria* | Mixture feed*3 | 20 mg $L^{-1}$<br>40 mg $L^{-1}$ | 31% decr. in CR relative to control<br>52% decr. in CR relative to control | Bricelj & Malouf 1984 |
| *Cerastoderma edule* | natural sediments | 5 mg $L^{-1}$<br>30 mg $L^{-1}$ | > 5 mg $h^{-1}$ FR, ≈ 2.5 mg $h^{-1}$ IR<br>> 20 mg $h^{-1}$ FR, 5 mg $h^{-1}$ IR | Navarro et al. 1992 |
| | Mixture feed*4 | 1.6 mg $L^{-1}$<br>526 mg $L^{-1}$ | Highest CR (1.79 ± 0.20 L $h^{-1}$)<br>Lowest CR (0.060 ± 0.026 L $h^{-1}$) | Navarro & Widdows 1997 |
| *Placopecten magellanicus* | *Chroomonas salina* | $10^6$ cells $L^{-1}$ | Highest CR (13.71 L $h^{-1}$) | Wildish et al. 1992 |
| | Mixture feed*5 | 1-14 mg $L^{-1}$ | CR decr. from 5.0-2.0 L $h^{-1}$ | Bacon et al. 1998 |
| *Mya arenaria* | Mixture feed*5 | 1-14 mg $L^{-1}$ | CR decr. from 3.0-1.5 L $h^{-1}$ | Bacon et al. 1998 |
| *Pecten maximus* | natural sediments | 0.15-0.43 mg $L^{-1}$ | 9-12 L $g^{-1}$ $h^{-1}$ CR | Strohmeier et al. 2009 |

Mixture feed*1– a mixture of natural silt and *Phaeodactylum tricornutum*
Mixture feed*2 – a mixture of sediment slurry, *Chaetoceros* sp., and *Isochrysis* sp.
Mixture feed*3 – a mixture of bottom sediments and *Pseudoisochrysis paradoxa*
Mixture feed*4 – a mixture of fine surficial sediment and *Isochrysis* galbana
Mixture feed*5 – a mixture of *Chaetoceros muelleri* and silica. CR: Clearance rate; FR: Filtration rate; IR: Ingestion rate; GR: Growth rate; SL: Shell length; decr.: decrease; incr.: increase

affected bivalve energetics. Bricelj & Malouf (1984) also showed evidence that fine-grained sediment concentrations as low as 40 mg $L^{-1}$ reduced the clearance rate by 52% relative to the control and inhibited the growth of hard clam *Mercenaria mercenaria* (Table 2). The results of a laboratory experiment by Ellis et al. (2002) showed that sediment concentrations as low as 80 mg $L^{-1}$ had adverse effects on the *Atrina zelandica* horse mussel.

A decreased filtration rate is the main reason high-density particulates adversely affect bivalves, but this has yet to be clarified. Observations on dissected bivalves indicate particle density may be a factor in sorting in the bivalve stomach (Reid 1965), but this has yet to be studied in intact bivalves. Jørgensen (1996) reported that increased particle density can also adversely affect the feeding behavior of suspension-feeding bivalves. To address this gap in research, Brillant & MacDonald (2000) conducted an experiment to determine whether sea scallop *Placopecten magellanicus* can sort particles within the gut based on density alone and found that light polystyrene beads were retained longer than the heavier glass beads.

However, the effects of particle density are strongly affected by the lab-outdoor difference, acclimation of experimental animals to experimental conditions, and size distribution of particles (Fréchette & Grant 1991, Cole et al. 1992, Jørgensen 1996). Therefore, when evaluating a report on laboratory experiments, it is essential to ensure that the experiment validates the situation and conditions of the natural environment. Thus, several studies have been conducted under field conditions to study bivalve responses to increasing concentrations of natural SPM. Results suggested that continuous, interrelated changes in feeding physiology can help maintain nutrient acquisition rates independent of short-term fluctuations in SPM composition (Hawkins et al. 1996, 1999; Urrutia et al. 1996; Ellis et al. 2002). An example that covers every aspect of the natural conditions is the study by Ellis et al. (2002), which focused on the physiological conditions of horse mussel *A. zelandica* when exposed to different suspended sediment concentrations. This study had three parts: a laboratory experiment, a field survey, and a field experiment. Across all fields and experimental conditions, results demonstrated a negative relationship between suspended sediment concentrations and the physiological conditions of *A. zelandica* (Ellis et al. 2002).

Many studies show the relationship between SPM concentrations and the physiological effect on marine bivalves (Navarro et al. 1992, Iglesias et al. 1992, Bayne et al. 1993, Navarro & Widdows 1997). High filtration rates are more favorable to increase energy gain during turbid conditions because marine bivalves can process more particulate matter. Since most of these studies were carried out in the late 1900s, it is necessary to perform similar experiments or modify them to confirm whether the response of bivalves to different SPM concentrations is the same as the experimental conditions used decades ago. Dafforn et al. (2015) stated that over 50% of the world's coastline has been modified by hard engineering, including seawalls, groins, and breakwaters, which are constructed for land reclamation, fishery practice, coastal protection from erosion, flooding, and storm strikes. For example, a dike was built to help prevent coastal flooding in Isahaya Bay, Japan in 1997, and this resulted in a 1,500 ha loss of tidal flats, which not only destroyed the nursery ground for many fish and microbenthic invertebrates but also decreased the purification ability of the ecosystem (Sasaki 2017). Sasaki (2017) further stated that benthic species could have been a natural water purification system before land reclamation. However, without the tidal flats, the concentrations of total nitrogen (TN), total phosphorous (TP), and chemical oxygen demand (COD) in the regulating reservoir sometimes now exceed the environmental quality standard. Four months after the enclosure, Sato (2001) reported the mass deaths of 73 ind. $m^{-2}$ of bivalve *Tegillarca granosa* (3 cm-5 cm in shell length) that inhabited the muddy tidal flats in the inner part of the bay. The reason for the need of updated investigations is that coastal areas have undergone much development and huge modification over the past decades, and these changes have greatly influenced and changed SPM components in coastal marine environments.

## Benthic environmental factors vs. suspended particulate matter vs. bivalves

This section focuses on how benthic environmental factors, such as salinity, light availability, and current velocity, influence SPM compositions and how these influences on SPM affect the behavior and physiology of bivalves (Fig. 1). These factors might directly affect bivalves. However, for this review, we do not focus on the direct effects but rather on the effect of these benthic environmental factors on SPM characteristics and composition. These factors have considerable influence on SPM characteristics and composition in coastal areas.

### 1. Salinity

This section discusses the effect of salinity on SPM characteristics and how SPM impacts bivalve physiology. Coastal areas are known for their remarkable spatio-temporal fluctuation in environmental factors, one being the huge variation in salinity due to river flow inputs of freshwater, which decreases salinity levels as they mix well through various physical processes, such as tidal changes and wave action. It is essential to further investigate the effects of salinity on SPM characteristics within coastal zones to find how this would later impact marine bivalves.

According to previous studies, through competitive, complexing, electrostrictive effects on seawater ions (Bourg 1987, Gschwend & Schwarzenbach 1992), and modification of sorptive properties of SPM by interactions between the particle surface and substances dissolved in seawater (Turner & Rawling 2001), salinity affects the partitioning of trace chemical constituents. Salinity influences SPM by aggregating suspended particles in the natural environment. Salinity in the environment influences flocculation and aggregation of SPM, which affects particle size and surface area and, therefore, settling velocity. For example, the higher the salinity, the greater the SPM flocculation; the bigger the flocs, the faster the settling velocity (Kranck 1973, 1981; Lick et al. 1992). Priya et al. (2015) stated that a particle settling in a water column is affected by the density of the water, which is a result of salinity stratification, which influences its settling velocity. This study further stated that a higher salinity gradient caused a higher density at the bottom, causing more viscosity and forming flocs. The flocs, lighter than the denser water at the bottom, remained in suspension and decreased the settling velocity. In southern Japan, Nishimura et al. (2011) reported that the concentration-based settling velocity of suspended mud increased with an increase in salinity at the tidal river of the Chikugo River. In another study, Joen et al. (2011) studied the influence of salinity and organic matter on the distribution coefficient ($K_d$) of perfluorooctane sulfonic acid (PFOS) and perfluorooctanoic acid (PFOA) in a brackish water clay system. Results showed that the distribution coefficients ($K_d$) for PFAs onto inorganic clay surfaces increased with salinity, providing evidence for electrostatic interaction for the sorption of PFAs. In contrast, the relationship between $K_d$ and organic carbon content ($f_{oc}$) suggested that hydrophobic interaction is the primary driving force for the sorption of PFAs onto organic matter. Enhanced sorption of PFAs onto particulate matter at high salinity can evoke potential risks to benthic organisms in estuarine areas. These studies show that salinity and other factors (e.g., seawater temperature) play a considerable role in the distribution of SPM, especially POMs in coastal estuarine environments.

The influence of salinity on SPM further affects marine bivalves in terms of changes in (1) particle size, (2) settling velocity, and (3) electrical characteristics (Kranck 1973, 1981; Bourg 1987; Gschwend & Schwarzenbach 1992; Lick et al. 1992; Hernroth et al. 2000). Therefore, when considering the effects of SPM on bivalves, a holistic approach should be taken to understand the complex relationship between environmental factors such as salinity, their effects on the SPM characteristics, and consequently, how the SPM changes affect benthic organisms, such as bivalves.

**2. Light availability**

Light availability has a profound effect on a wide variety of aquatic processes. However, for this review, we focus mainly on the effects of light availability on SPM in the marine environment. According to Wofsy (1983), light availability may be the most critical factor controlling biomass-specific productivity. The most studied area is the primary role of light availability as a source of energy for phytoplankton photosynthesis. Phytoplankton falls under the POM category, so light availability indeed affects the abundance of POM in the natural marine environment. In addition, in terms of its effects on SPM, light availability affects water transparency (Scheffer 1998), algal competition (Huisman & Weissing 1994, Huisman et al. 1999, Reynolds 2006), phytoplankton biodiversity (Reynolds 1998, Stomp et al. 2004), and seston stoichiometry (Hessen 2006).

The distribution of water turbidity and light transmission in coastal areas are strongly influenced by sediment moving from land-based sources through rivers and estuaries (Bell et al. 2015). Knowledge of seawater properties such as turbidity and light transmission is essential to understanding the conditions of coastal environments (Azis Ismail & Prayitno 2020). The relationship between light availability and suspended POM in the water column is mutual (Azis Ismail & Prayitno 2020). Though, the same cannot be said for light availability and suspended PIM. Light availability might not have much influence on PIM. However, inversely, PIM greatly influences light availability because as PIM concentrations increase directly after massive freshwater inputs through rivers from heavy downpours or changes in tides, coastal water turbidity levels increase sharply, lowering light availability. On the other hand, light penetrating through the water column allows primary production by light-dependent phytoplankton that increases POM densities in the water column and hence drives the microbial food web that takes place down to depths of the euphotic zone (Gameiro et al. 2011). Gameiro et al. (2011) reported that light availability was the principal limiting factor for low primary production despite high nutrient concentrations from high freshwater input and strong tidal currents in the Targus estuary on the west coast of Europe. Maung-Saw-Htoo-Thaw et al. (2017) reported comparable results when the monsoon season off the coast of Myeik City, Myanmar, delivered heavy precipitation and brought significant amounts of terrestrial nutrients to the coast. However, turbidity affected coastal waters, which limited light penetration into the water column and decreased primary production.

Over the recent years, HABs have been an area of growing interest as they have cost fisheries, and the aquaculture sector many millions of dollars. Since they contribute to the overall density of POMs and light availability is one of the contributing factors, they should be studied in more detail to help control HABs.

## 3. Current velocity

This section reviews how current velocity strongly influences SPM characteristics (e.g., SPM density). As shown in Table 3, several studies have reported the effects of current velocity on bivalves (e.g., filtration rates and clearance rates) (Wildish & Miyares 1990, Newell et al. 2001, Widdows et al. 2002). However, the effects of current velocity focusing on SPM characteristics and composition have been poorly studied.

Current velocity near the seabed is likely to affect SPM availability and the feeding behavior of bivalves. For example, high-speed currents can detach bivalves from their substrates, stagnant conditions cause particle settlement with high SPM densities directly above the seabed, and optimal current speeds provide the best conditions for maximum feeding. Bottom high-speed currents may result in a direct physical impact on mussel performance or the erosion or disturbance of the underlying sediment. In contrast, the mussels can influence their surrounding environment at reduced current velocities by depleting food downstream (Fréchette & Bourget 1985a, Fréchette et al. 1993). At higher current velocities directly above a natural mussel bed, phytoplankton depletion was low compared to mussels elevated in the water column above the food-depleted zone, which grew faster than those near the bottom (Fréchette & Bourget 1985a, b).

Moreover, currents caused by continuous tidal changes trigger the resuspension of benthic sediments, resulting in a higher SPM density in a water column that barely causes resettlement due to ongoing tidal changes. On the other hand, currents caused by high winds and wave action are not continuous and happen occasionally, resulting in resuspension of benthic sediments. Once the driving force of these currents weakens, sediments resettle to the bottom, often accumulating on the surface of bivalves at various thicknesses, disrupting their filtering activity. In a laboratory experiment, Yurimoto et al. (2008) tested the influence of resuspended sediments and their surface accumulation on pen shell *A. pectinata*. Results from this study stated that resuspended sediments are an efficient food source for pen shells. However, accumulation of sediments (resettlement) over 10 mm thick increased glycogen consumption and fatality risk to the organism avoiding burial. Sediment accumulation experiments that might cause suffocation and influence

**Table 3. Previous studies on how current velocity influences the responses of various bivalve species**

| Bivalve Species | Current Velocity | Response | Reference |
|---|---|---|---|
| *Mytilus edulis* | 0.2-0.6 m $s^{-1}$<br>> 0.6 m $s^{-1}$ | CR decr. continuously within this range<br>CR = 0 L $h^{-1}$ ind. $^{-1}$ | Nielsen & Vismann 2014 |
| | 0-0.8 m $s^{-1}$<br>> 0.8 m $s^{-1}$ | CR – highest<br>decr. in CR | Widdows et al. 2002 |
| | 0.1-0.3 m $s^{-1}$ | decr. in FR | Newell et al. 2001 |
| | 0.06-0.22 m $s^{-1}$<br>> 0.25 m $s^{-1}$ | decr. in FR<br>FR < 10% | Wildish & Miyares 1990 |
| *Placopecten magellanicus* | 0.02-0.1 m $s^{-1}$<br>> 0.1 m $s^{-1}$ | Optimum Growth<br>Inhibited Growth | Wildish et al. 1987 |
| | ≈ 0.1 m $s^{-1}$ | Optimum Growth | Wildish et al. 1992 |
| *Crassostrea virginica* | 0.04-0.07 m $s^{-1}$<br>0-0.005 m $s^{-1}$ | Growth – highest<br>Growth – lowest | Lenihan et al. 1996 |
| *Ruditapes decussatus* | < 0.08 m $s^{-1}$<br>> 0.17 m $s^{-1}$ | CR – highest<br>decr. in CR | Sobral & Widdows 2000 |
| *Argopecten irradians concentricus* | 0.017-0.039 m $s^{-1}$<br>0.014-0.172 m $s^{-1}$ | Growth – unaffected<br>decr. in Growth | Eckman et al. 1989 |
| *Pinctada maxima* | 0.08 m $s^{-1}$ | FR & IR – highest | Supii et al. 2012 |

CR: clearance rate; FR: filtration rate; IR: ingestion rate; decr.: decrease the physiological state of bivalves should be clarified.

As shown in Table 3, Wildish & Miyares (1990) reported that *M. edulis* experienced a decreased filtration rate with increasing current velocities from 0.06 to 0.22 m $s^{-1}$ and flows > 0.25 m $s^{-1}$ resulted in filtration rates < 10%, remaining this way up to flow speeds of 0.38 m $s^{-1}$. Later, Newell et al. (2001) results indicated that *M. edulis* decreases its filtration rates as current speeds increase from 0.1-0.3 m $s^{-1}$, probably due to unfavorable hydrodynamics (a pressure differential). Current velocities ranging from 0.1-0.3 m $s^{-1}$ had a highly significant linear decrease in exhalant siphon area but no effect on valve gaping of *M. edulis* (Newell et al. 2001). A study by Sobral & Widdows (2000) reported that an infaunal bivalve species, *Ruditapes decussatus*, recorded a maximum clearance rate up to a current speed of 0.08 m $s^{-1}$. As current speeds surpassed 0.17 m $s^{-1}$, the clearance rate decreased with sediment erosion and movement (Table 3). Using annular flumes to determine the influence of current velocity on infaunal deposit-feeding bivalve, *Macoma balthica*, Widdows et al. (1998) stated that *M. balthica* was found to increase the sediment resuspension (due to burrowing or feeding activity) fourfold, at densities similar to those recorded at the Skeffling mudflat (Humber estuary) (i.e., > 1,000 ind. $m^{-2}$). There was a significant correlation between sediment resuspension and *M. balthica* density (r = 0.99; ***$P$ < 0.001), which supported previous in-situ field observations indicating bioturbation by *M. balthica* enhanced sediment erodibility.

The movement of water and the speed of movement are very important in transporting nutrients, oxygen, and other SPMs in the aquatic environment, especially for sessile organisms like bivalves, which greatly depend on water currents to deliver nutrients within their reach. There are upper and lower tolerance limits to current velocities (Widdows et al. 2002), which have been studied in some bivalve species, as shown in Table 3. Finding the upper and lower limits of current velocity for each species is an area of interest.

## Future research

After carrying out a literature review on studies and research related to SPM, benthic environmental factors, and bivalves, the authors point out certain ideas and specific areas for further investigation in this section.

First, most previous studies to examine the effects of SPM on bivalves used artificial diets, and very different responses were observed in bivalves when fed natural suspensions of lower organic content (Foster-Smith 1975, Navarro et al. 1992, Iglesias et al. 1992, Cranford & Gordon 1992, Bayne et al. 1993). When bivalves were fed natural suspensions of lower organic content, physiological responses included increased pseudofeces production (Iglesias et al. 1992), filtration rate, and selection efficiency with high pseudofeces production (Bayne et al. 1993). Cranford & Gordon (1992) reported that the filtration rate of sea scallop *Placopecten magellanicus* decreased when bentonite concentrations exceeded 6 mg·$dm^{-3}$ and those levels lower than 1.0 mg·$dm^{-3}$ enhanced filtration rates. Furthermore, Doering & Oviatt (1986) mentioned that when different models of feeding behavior are applied to field populations of bivalves, data collected from experiments using natural suspensions of particulates agreed with observed processes. Therefore, future experiments should be performed in the natural environment or in a way that best mimics the natural environment where changes and fluctuations of feed concentrations and availability, salinity, and seawater temperature reflect natural environmental conditions.

Second, the mechanism that is involved in the positive effects of PIM addition to bivalve diets. The main reason is that adding silts and other inorganics can overload the filtering mechanism and limit the dilution of the ingested material (Jørgensen 1966, Widdows et al. 1979). However, it has been proven that adding silt to artificial algal diets enhanced growth in suspension-feeding bivalves (Winter & Langton 1976; Griffith 1980; Kiørboe et al. 1980, 1981; Møhlenberg & Kiørboe 1981). As mentioned, in Section 1.3 Particle Size, several studies have examined the crystalline styles that play an essential role in particle sorting and selection (Kristensen 1972, Bernard 1973). However, further investigation of the mechanism causing the positive effect of PIM inclusion is an interesting and challenging area.

Third, the temporal variation pattern of SPM characteristics affects the response of bivalves. Newell & Shumway (1993) and Hewitt & Norkko (2007) explained in detail the importance of investigating the effects of stress duration variations on bivalves. After investigating the stress effects of increased sediment concentration on suspension-feeding bivalves (*Austrovenus stutchburyi* and *Paphies australis*) through short-term laboratory and long-term field transplant experiments, Hewitt & Norkko (2007) found that short-term (two-day) feeding responses did not reflect feeding or biomass responses. However, strong biomass responses were observed after three months in the field. The effect of exposure duration and method of exposure (gradual exposure) are thus necessary for future laboratory and field experiments.

In addition, individuals of the same species in the same experiment show significant differences in response to identical treatment. Widdows et al. (1979) stated that high variance in clearance rate data due to individual variation made it difficult to mask the effect of particle concentration over the narrower range of concentration studies in laboratory experiments. For example, Figures 5 (Ellis et al. 2002) and 6 (Hawkins et al. 1999) show significant variations in individual data. Strohmeier et al. (2009) also reported a considerable variation in clearance rates (Fig. 4). Therefore, it would be advantageous to investigate the reason for these variations and how they impact the results or conclusions for exposure experiments.

Another area of current research is marine microplastics. Plastic concentration in the oceans is continuously increasing, poisoning many of our marine organisms. There may still be unknown effects plastics might have on the marine ecosystem (Wang et al. 2018, Alimba & Faggio 2019, Baroja et al. 2021, Wang et al. 2021). Plastic debris has entered diverse invertebrate and vertebrate species, eliciting varieties of toxicological effects (Gall & Thompson 2015), and the potential for plastic debris to transport organic and inorganic hazardous chemicals from land to the marine environment and humans via feeding pathways has reached alarming proportions across the globe (Teuten et al. 2009, Holmes et al. 2012). Past studies have demonstrated the urgent need for a better understanding of microplastic characteristics, microplastic toxicology, and multiple effects of microplastics on aquatic systems to develop adequate mitigation and prevention strategies for this global issue (von Moos et al. 2012, Baroja et al. 2021).

Last, developing a method or technology to serve as a health indicator when carrying out exposure experiments without killing the bivalve would be groundbreaking. A recent study by Martinović et al. (2022) evaluated the effect of short-term hyposalinity on the physiological state of pen shell *Pinna nobilis* using a non-invasive heart rate recording sensor. Another is a biosensor developed by Wu et al. (2022) that records real-time remote stress in fish. Hopefully, a similar design could be modified for bivalves. Such technological advancement would allow researchers to conduct experiments over more extended periods and provide more precise data without sacrificing the test animals.

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