

# **Shellfish Culture and Particulate Matter Production and Cycling: A Literature Review**

**Prepared for:**

**BC Aquaculture Research & Development Committee  
AE 02.03-02.01**

**May 5, 2006**

**Dr. P. Barnes  
Head, Ecological Interactions Research Program  
Centre for Shellfish Research, Malaspina University-College  
900 Fifth Street, Nanaimo, B.C. V9R 5S5**



## TABLE OF CONTENTS

<b>1.0</b>	<b>Introduction</b> .....	<b>3</b>
<b>2.0</b>	<b>Filter Feeding: Filtration and Feces/Pseudofeces Production</b> .....	<b>5</b>
2.1	Particle Capture, Selection and Rejection. ....	5
2.2	Filtration Rates and Clearance Rates in Lamellibranch Bivalves. ....	9
2.2.1	Definitions. ....	10
2.2.2	Methods for Measuring Clearance Rates. ....	11
2.2.3	Endogenous Factors Affecting Bivalve Filter Feeding. ....	15
2.2.4	Exogenous Factors Affecting Bivalve Filter Feeding. ....	18
2.2.4.1	Food Quantity, Quality and Particle Size. ....	18
2.2.4.2	Other Exogenous Factors. ....	26
2.3	Rate of Feces/Pseudofeces Production. ....	28
<b>3.0</b>	<b>Environmental Biodeposition Associated with Suspended Bivalve Culture</b> ..	<b>35</b>
3.1	Bivalve Feces/Pseudofeces Settling Rates. ....	36
3.2	Factors Affecting Biodeposition and Organic Loading. ....	42
3.3	Potential Impacts of Biodeposition. ....	47
3.3.1	Potential Impact on Benthic Biogeochemical and Biological (Infauna) Parameters. ....	47
3.3.2	Potential Impact on Benthic Epifauna and Macrophytes .....	52
3.3.3	Potential Impact on Nutrients. ....	56
3.3.4	Indicators of Impact. ....	61
<b>4.0</b>	<b>Modeling Biodeposition from Suspended Bivalve Aquaculture</b> .....	<b>62</b>
4.1	Particle Tracking Models. ....	63
4.2	Ecosystem Models. ....	69
<b>5.0</b>	<b>Bibliography</b> .....	<b>74</b>



## 1.0 Introduction

The research project, “Shellfish Culture and Particulate Matter Production and Cycling”, investigates the production of particulate material by suspended, deep-water oyster (*Crassostrea gigas*) farms in BC. The project also addresses the fate, and the potential impact on the benthic environment, of this particulate material. This broad research topic involves not only bivalve physiology (e.g. filtration mechanisms and rates, feces and pseudofeces production rates) but also complex ecosystem processes (e.g. biodeposition, biogeochemical and biological benthic impact). *In situ* filtration rates and feces/pseudofeces production rates of filter feeding bivalves are linked to food quality and quantity which are, in turn, affected by site conditions including productivity and hydrography. The deposition of feces/pseudofeces and sloughed material is affected by hydrography, in addition to other site-specific conditions (e.g. bathymetry, water column parameters). Biodeposition has the potential to cause organic enrichment leading to marked changes in sediment biogeochemistry with associated impacts on benthic faunal communities.

Filter feeding of cultured bivalves is, clearly, a vital component of pelagic-benthic relationships that is critical to understanding the potential role of bivalve aquaculture in ecosystem processes. The need for a better understanding of bivalve biodeposition dynamics, particularly biodeposit settling velocities, quality, and erosion characteristics, is emphasized in several sections of this review. While enhanced sedimentation (biodeposition) under bivalve culture has been well researched and documented for suspended mussel culture in many areas of the world, this review demonstrates that this is not the case for either *Crassostrea gigas* suspended culture or Canada’s west coast.

In order to ensure the sustainable development of the bivalve aquaculture industry, a better understanding of the relationship between bivalve production and its influence on the benthic environment is needed. To this end, there is increasing interest in the application of models to predict biodeposition and benthic impacts, as well as other ecosystem effects, associated with bivalve farms. Both ecosystem and particle tracking models are discussed in this review, with emphasis on the latter due to the focus of these models on biodeposition scenarios.

This literature review, like the research project, covers a broad range of topics related to biodeposition associated with suspended bivalve culture. Although the focus of the research project is deep-water suspended oyster culture, it is anticipated that some of the research results may be applicable, at least to some extent, to the suspended culture of other bivalve species in BC. To this end, relevant literature available on filter feeding bivalves in suspended culture, in addition to *C. gigas*, has been incorporated into this review. The diverse topics covered in this review have been grouped into three main sections.



Following this introduction (Section 1), bivalve filtration and feces/pseudofeces production, as well as rates and factors affecting these rates, are reviewed in Section 2. Section 3 reviews the literature on environmental biodeposition associated with suspended bivalve culture, with specific attention to feces/pseudofeces settling rates and to factors affecting biodeposition and organic loading. Also included in Section 3, is a review of the potential impacts of biodeposition from bivalve suspended aquaculture on the benthic environment. The application of modeling techniques to bivalve farm biodeposition scenarios is reviewed in Section 4. Section 5 is the bibliography.



## 2.0 Filter Feeding: Filtration and Feces/Pseudofeces Production

Oysters (Family Ostreidae) and blue mussels (Family Mytiloidea), as well as other cultured bivalves such as scallops (Family Pectinidae), obtain nutrition through filter feeding, a vital component of pelagic-benthic relationships that is critical to understanding the potential role of bivalve aquaculture in ecosystem processes. “Filter feeding” is used throughout this review to mean a type of suspension feeding in which particles are removed from a water current by a filter (Ruppert and Barnes, 1994). Although some of the literature reviewed here refers to “suspension feeding” (a general term, referring to feeding upon particles suspended in water (Ruppert and Barnes, 1994), in all cases the bivalves studied were filter feeders.

Filter feeding bivalves filter particulate material, or seston, from the water column. Seston includes both organic and inorganic fractions; organic portions may include bacteria, phytoplankton, organic detritus, and micro/mesozooplankton (for review see Wong *et al.*, 2003), while the inorganic fraction can include mineral, or silt/sand, grains. Filter feeding is a complex process that can be broken down into phases, including particle capture, particle selection and particle rejection (pseudofeces production), that are discussed in Section 2.1. Also included at the beginning of Section 2.1 is a brief review of gill structure as related to filter feeding. Bivalve filtration and clearance rates, as well as endogenous and exogenous factors affecting these rates, are discussed in Section 2.2. Information on bivalve feces/pseudofeces production rates, and factors affecting these rates, is reviewed in Section 2.3.

### 2.1 Particle Capture, Selection and Rejection

In lamellibranch bivalves, such as blue mussels and oysters, ctenidia (or gill) function has expanded beyond respiration to feeding (Allen, 1985). This group of bivalves, at one time, belonged to the Subclass Lamellibranchia based on this function of the gill. Recently, however, this classification system has been replaced by one based partially on other bivalve morphological characters. “Lamellibranch” is still used, however, as a term for differentiating this group of bivalves based on gill structure and function. In lamellibranch bivalves, enlarged ciliated gills consist of lamellae (sheets of tissue or “gill flaps”) composed of individual filaments connected to each other by interfilamental junctions (cilia or tissue connections) (Newell and Langdon, 1996). Additional structural support is provided by tissue junctions between lamellae (interlamellar junctions) and connections between the tips of the filaments and the mantle or foot (Ruppert and Barnes, 1994). Lamellibranch bivalves can be divided into two main groups, filibranch and eulamellibranch, based largely on the nature of the interfilamental connections. Adjoining filaments are connected via specialized interlocking cilia in filibranchs (mussels and scallops), while gill rigidity is enhanced by rigid tissue junctions in eulamellibranchs (most filter feeding bivalves) (Newell and Langdon, 1996). Members of the family Ostreidae, including *Crassostrea* spp., are called “pseudoeulamellibranch” because the tissue junctions present are not as extensive as those in most eulamellibranch families. Cilia



on bivalve gills are differentiated into specialized structural and functional units and, depending on the bivalve species, functions may include generating water currents through the gill, removing food particles from suspension and transporting particles from the gills towards the mouth (Newell and Langdon, 1996).

Generally, water enters lamellibranch bivalves through a posterior inhalent (infrabranchial) chamber and exits through a posterior exhalent (suprabranchial) chamber (Ruppert and Barnes, 1994). Studies involving visual observations of filter feeding have been hampered due to the difficulties in observing the actual process. Most studies have been performed on surgically altered animals, isolated dissected tissue, or in some cases, on tissue that has been chemically activated (Ward *et al.*, 1993, 1998a, 2000; Ward and Shumway, 2004). Recent studies take advantage of advances in endoscopy to study filter feeding in unaltered and undisturbed animals. Observations of active filter feeding bivalves, including *Mytilus edulis*, *Mytilus trossulus*, *Crassostrea virginica*, *Crassostrea gigas*, and *Pecten maximus*, show that particles in the water column brought in by water flow created by the fronto-lateral cilia make direct contact with the ctenidial filaments. Fronto-lateral cilia simply direct the flow of water and are not necessary for particle capture performed by the filaments of the ctenidia. (Ward *et al.*, 1998 a, b; Levinton *et al.*, 2001; Milke and Ward, 2003; Ward *et al.*, 2003; Beninger *et al.*, 2004; see Ward and Shumway, 2004 for review). Hence, although studies on a variety of mussels and oysters report some differences in detail, basic similarities in particle capture are evident (Ward *et al.*, 1993, 1997, 1998b, 2000; Ward and Shumway, 2004). These results contradict earlier filter feeding theories (Dral, 1967; Foster-Smith, 1975a; Bayne, 1976).

Bivalves filter a wide range of particle sizes with varying capture efficiencies that may be species, or habitat, specific. Much of the literature suggests a trend whereby capture efficiency increases with particle size to an upper threshold and that at the start of this threshold ( $>7 \mu\text{m}$ ), the efficiency becomes species specific (see Ward and Shumway, 2004 for review). The relationships between capture efficiency and endogenous factors and exogenous factors are discussed in Sections 2.2.3 and 2.2.4, respectively.

Once captured, particles are transported, conveyor-belt style, to the front surface of the gill by a mucociliary process, then are further transported by the gills' ventral ciliated groove and/or the dorsal ciliated tract. Which route is used for which purpose appears to be species specific. For example, material is transported in the ventral ciliated groove to the labial palps in *M. edulis* and little material is transported along the dorsal tracts, even at the highest particle concentration (Ward *et al.*, 1993). The small amounts of material in the dorsal tracts are carried anteriorly by cilia-generated currents, however, suggesting some vestigial function for the dorsal tracts in *M. edulis*. In *Mya arenaria*, material is transported along the ventral ciliated groove but observations on the dorsal ciliated tract are lacking (Ward *et al.*, 1993). The sea scallop, *Placopecten magellanicus*, lacks a ventral groove but particles are moved via the ventral



ciliated tract and dorsal tract to the labial palps (Beninger *et al.*, 2004). In *C. gigas* and *C. virginica*, particles are moved via both the dorsal ciliated tract and the ventral ciliated groove towards the labial palps (Beninger and St.-Jean, 1997a; Ward *et al.*, 1998 a, b).

Beninger *et al.* (2004) suggested that potential effectors of particle selection may be macroscopic (gill architecture and filament types) and microscopic (presumably involving sensory detection and decisional behaviour by individual cilia or groups of cilia). Data on microscopic effectors for any bivalve species are lacking but the site of particle selection and macroscopic effectors is the subject of much research. The heterorhabdic (two types of filament) gill, either filibranch (*P. maximus*) or pseudolamellibranch (*C. virginica*, *C. gigas*) is capable of qualitative particle selection (Ward *et al.*, 1998b; Cognie *et al.*, 2003; Beninger *et al.*, 2004). In *P. maximus*, material in the gill ventral tract is of low trophic value and is rejected during valve-clapping, while additional particle selection of material in the dorsal tract occurs on the labial palps (Beninger *et al.*, 2004). In *C. virginica* (Ward *et al.*, 1998a; Milke and Ward, 2003) and *C. gigas* (Ward *et al.*, 1997), material in both the gill's ventral groove and dorsal tract was observed to be transported to the labial palps, but material in the ventral groove is of lesser trophic importance. This material is likely to be rejected as pseudofeces prior to ingestion but may be re-sorted on the palps (Ward *et al.*, 1997, 1998a; Milke and Ward, 2003). Cognie *et al.* (2003) recently demonstrated that oyster labial palps are involved in selection, being the only organs capable of selection for those particles greater in size than the opening of the principal oyster filament. Most species with homorhabdic (one type of filament) gills are not capable of particle selection on the gill. The structure of *M. trossolus* gills does not support particle selection and material transported in the ventral particle groove is unsorted (Ward *et al.*, 1998a). Endoscopy has demonstrated that sorting in *M. trossolus* occurs on the labial palps (Ward *et al.*, 1998a). Similarly, particle sorting occurs on the labial palps in *M. edulis* (Milke and Ward, 2003), and this has been demonstrated using endoscopy (Beninger and St.-Jean, 1997a; Ward *et al.*, 1998b). Regardless of the site within the bivalve where particle selection occurs, the latter may be influenced by exogenous factors such as particle quality, particle size and food quantity (see Section 2.2.4).

Pseudofeces production is integral to the selectivity process in that it permits rejection of less nutritious particles, thereby improving the overall content of material being ingested and assimilated (compensates for poor quality seston in the natural environment) and preventing particle overloading of the ingestion processes (Beninger *et al.*, 1992; Macdonald and Ward, 1994; Bacon *et al.*, 1998). There are three categories of pallial pseudofeces rejection mechanisms into which the four main bivalve gill systems can be grouped (Beninger and St. Jean, 1997a; Beninger and Veniot, 1999). Studies using *M. edulis*, *Mya arenaria* and *Spisula solidissima* have shown that bivalves with siphons plus a ventral particle groove on the gill, including most bivalves with homorhabdic filibranch gills and all bivalves with eulamellibranch gills, have pallial transport of pseudofeces with vertical elevation accomplished via composite cilia (Beninger *et al.*, 1997; Beninger and St. Jean, 1997b; Beninger *et al.*, 1999; Beninger and Veniot, 1999).



A similar mechanism of pallial transport, but with vertical elevation accomplished via mantle ridges, has been observed in the pseudolamellibranch bivalves *C. gigas* and *C. virginica* (Beninger and Veniot, 1999). The scallop, *P. magellanicus*, lacks a ventral groove but material carried on the ventral ciliated tract is usually rejected as pseudofeces. For bivalves such as *P. magellanicus*, which have heterorhabdic filibranch gills, pseudofeces are rejected via valve pulsing (or clapping) (Beninger *et al.*, 1999). Pseudofeces production rates, for most bivalves, increase with increasing seston quantity (particle concentration) (see Section 2.2.4) (Bayne *et al.*, 1993; Shumway *et al.*, 1985; Bacon *et al.*, 1998). However, the ultimate fate (ingested or rejected) of material on the ctenidia depends on both particle concentration and gut fullness (Beninger *et al.*, 1992). When the ctenidia become overloaded with particles or when the ingestive capacity is exceeded, more material is rejected (Ward *et al.*, 1998a).

## 2.2 Filtration Rates and Clearance Rates in Lamellibranch Bivalves

Although numerous studies examine filtration rate and clearance rate in marine bivalves, and in *Mytilus edulis* in particular, this subject continues to be an area of ongoing, significant debate. Subject to controversy are wide-ranging results that appear to be at least partially dependant on methodology used, including type of diet and whether the study was laboratory or field based. These controversial issues are reviewed in depth by Jørgensen (1996), Bayne (1998), Cranford (2001), Riisgård (2001a, 2001b, 2001c, 2004), Widdows (2001), Petersen (2004), and Petersen *et al.* (2004). An explanation of some commonly measured rates associated with filter feeding (Section 2.2.1) and a discussion of the three most commonly used methodologies for determining clearance rate (Section 2.2.2) are presented below. Endogenous factors (Section 2.2.3) and exogenous factors (Section 2.2.4) that might influence filter feeding are also discussed.

### 2.2.1 Definitions

Pumping rate (PR) is the volume of water flowing out the exhalent siphon per unit time (e.g.  $\text{cm}^3 \cdot \text{s}^{-1}$ ). PR can also be expressed as a function of gill area (e.g.  $\text{cm}^3 \cdot \text{s}^{-1} \cdot \text{cm}^{-2}$ ) (Meyhöfer, 1985). “Ventilation rate” has been used as equivalent to pumping rate (Famme *et al.*, 1986; Newell and Langdon, 1996). Direct measurement of pumping rate is technically challenging, as it is difficult to measure water flow from the exhalent siphon without affecting flow rates (Galtsoff, 1926; Hildreth and Crisp, 1976; Famme *et al.*, 1986). A laser (direct) method has been used, albeit rarely, for non-intrusive measurement of the ventilation rates of *M. edulis* (Famme *et al.*, 1986). In contrast, indirect methods estimate rates based on the disappearance of particles in the water, either in a static or a flow-through system, or on the accumulation of biodeposits (feces and pseudofeces combined).

Clearance rate (CR) is commonly defined as the volume of water filtered completely free of particles per unit time (e.g.  $\text{cm}^3 \text{ s}^{-1}$ ) (Cranford and Grant, 1990; Bayne *et al.*, 1993; Bayne, 1998; Hawkins *et al.*, 1996;



Iglesias *et al.*, 1998; Cranford and Hill, 1999; James *et al.* 2001; Riisgård, 2001a; Velasco and Navarro, 2002, 2005). This common definition of CR corresponds to the definition of filtration rate (FR) given in the older literature (e.g. Walne, 1972; Winter, 1973; Thompson and Bayne, 1974). CR is also defined as the volume of water cleared of particles per hour per mussel (James *et al.*, 2001) and as the volume of water cleared entirely of a specific type of particle per unit time per oyster dry tissue weight (Dupuy *et al.*, 2000). Bayne *et al.* (1977), Bacon *et al.* (1998) and MacDonald and Ward (1994) define CR as the volume of water cleared of particles  $\geq 2$   $\mu\text{m}$  per unit time. CR is defined by some researchers as the volume of water cleared of all 100% efficiently-retained particles per unit time (Petersen *et al.*, 2004). If particle retention is 100%, then clearance rate and ventilation rate are equal but because this efficiency is rarely attained, measured clearance rates usually underestimate ventilation rates (Newell and Langdon, 1996).

Filtration rate is most commonly defined in terms of amount of particulate material rather than water volume. For example, FR equals the total particulate matter (or cells) removed from the water per unit time (Navarro and Winter, 1982; Widdows, 1985; Velasco and Navarro, 2002, 2005). Iglesias *et al.* (1998) noted that FR is equal to ingestion rate (IR) (the rate at which seston is ingested by the mouth) when all filtered material is ingested and no pseudofeces are produced. Hawkins *et al.* (1996, 1998) defined FR as (IExTPM)/TIM where IE is inorganic egested rate (for both feces and pseudofeces), TPM is total particulate material and TIM is total inorganic particulate matter.

Selection efficiency, ingestion rate, absorption efficiency and excretion rate are useful measures in filter feeding studies. Selection efficiency, often measured in studies on the effects of food quality on particle selection by bivalve gills, is expressed as a percentage using the equation  $(1-P/F) \times 100$ , where P is organic content of pseudofeces and F is the organic content of the food (particles) (Iglesias *et al.*, 1992; Bayne *et al.*, 1993; Macdonald and Ward, 1994; Hawkins *et al.*, 1996, 1998). Ingestion rate (defined above) and pseudofeces egestion rate (the rate at which pseudofeces are egested (produced) per hour) are used as components of some equations that calculate CR. Absorption efficiency, the net energy gained from food that is ingested and processed as a function of the amount of feces rejected, is measured as a ratio of the organic or inorganic material in food to the organic or inorganic material found in the feces and is expressed as a percentage (Navarro and Thompson, 1994). Excretion rate, the rate at which the dissolved products of nitrogen metabolism are excreted, is measured as  $\mu\text{NH}_4\text{-N}\cdot\text{mussel}^{-1}\cdot\text{hour}^{-1}$  (James *et al.*, 2001).

### **2.2.2 Methods for Measuring Clearance Rates**

Recent reviews of the methods used to measure filtration rates and clearance rates in bivalves include attempts to inter-calibrate the various techniques or, at least, to understand the differences between each technique (Cranford, 2001; Riisgård, 2001a, b, c, 2004; Widdows, 2001; Bayne, 2004; Petersen, 2004; Petersen *et al.*, 2004). The most commonly used methods are indirect: the static (or clearance) method,



the flow-through method and the biodeposition method. Riisgård (2001a) and Petersen *et al.* (2004) provided comprehensive reviews on these methodologies; Iglesias *et al.* (1998) reviewed the biodeposition method only.

The static (or clearance) method measures the CR based on clearance of particles in suspension in a closed chamber. CR can be measured in closed systems by monitoring decreases in particle concentration (Coughlan, 1969), as per Equation 1. Using similar experimental conditions, FR can be calculated as CR x TPM (in mg·h<sup>-1</sup>) (Bayne, 1998; Velasco and Navarro, 2002).

$$[1] \quad CR = (V/t) \ln(C_0/C_t) \quad (\text{Coughlan, 1969; Wright } et al., 1982; \text{ Riisgård, 2001a; Petersen } et al., 2004)$$

Where  $V$  is the volume of water in the experimental chamber;  $t$  is incubation time;  $C_0$  and  $C_t$  are the initial particle concentration and particle concentration at the end of the experiment, respectively. Winter (1973) measured changes in turbidity to determine CR. It has been suggested that measurements of clearance rates for animals in closed systems may be biased, with an apparent decrease in filtration rate over time resulting from the preferential removal of more efficiently captured particles followed by an increase in the proportion of smaller, less efficiently retained particles (Williams, 1982). Determining CR by monitoring the rate at which particles must be added in order to maintain a constant particle concentration reduces this artifact.

To calculate clearance rate using the flow-through method, the percentage reduction in particle density from the inflow to the outflow of chambers containing one or more bivalves is measured together with the flow rate through the apparatus (Hildreth and Crisp, 1976; Bayne *et al.*, 1985; Iglesias *et al.*, 1998; Petersen *et al.*, 2004), as per Equations 2 and 3.

$$[2] \quad CR = F(1 - C_{out}/C_{in}) \quad (\text{Riisgård, 2001a})$$

Where  $F$  is the flow rate in the chamber,  $C_{in}$  and  $C_{out}$  are the concentration of particles (e.g. algae) entering and leaving the chamber.

$$[3] \quad CR = [(C_{in} - C_{out})/C_s]Q \quad (\text{Hildreth and Crisp, 1976; Labarta, 1997; Petersen } et al., 2004)$$

Where  $C_{in}$  and  $C_{out}$  are particle concentrations going in and coming out of the chambers,  $C_s$  is the particle concentration surrounding the mussel and  $Q$  is the flow rate. Ideally in flow-through systems, the suspension of particles is assumed to pass the bivalves' inhalant opening only once, ensuring the particle concentration around the opening remains constant. In these cases,  $C_s$  equals  $C_{out}$  (Petersen *et al.*, 2004). Bayne (1998) used a similar formula to calculate filtration rates in flow-through systems:  $FR = F$



$[C_{in} - C_{out}]$ /number of animals. FR is expressed in mg total particulates per unit time per animal. Chamber geometry and regulation of water pressure are important considerations as related to regulation of flow and encouraging inhibition of recirculation of water within the chamber, respectively. Clearance rates may be underestimated due to re-filtration of seawater (Petersen *et al.*, 2004) in volume-limited experimental chambers (Hildreth and Crisp, 1976; Jorgensen, 1976; Winter, 1978; Newell, 1979). Obviously, flow rate and particle size dynamics need to be considered for each experimental species (Riisgård, 2001a) (see Section 2.2.4).

Clearance rates of bivalves can be calculated using the biodeposition method whereby the total amount of inorganic or indigestible material in the biodeposits produced per unit time is divided by the total concentration of the same refractory particulate material in the seston (Jordan, 1987). The accuracy of this method depends on negligible absorption of the refractory particulate material by the oyster.

$$[4] \quad CR = \frac{\text{inorganic biodeposits/unit time (Hawkins et al., 1996; Riisgård, 2001a)}}{\text{conc. of inorganic matter in water}}$$

In this method, ash in the particles may be referred to as a “marker” useful for measuring the rate of particle uptake (see Cranford *et al.*, 1998 and Cranford and Hill, 1999). Similar to CR, FR can also be measured using the biodeposition method. For example, Hawkins *et al.* (1996, 1998) measured FR as total  $\text{mg}\cdot\text{h}^{-1}$  using the equation  $FR = (IE \times TPM)/TIM$ , where IE is inorganic matter egested for both feces and pseudofeces and TPM and TIM are total particulate material and total inorganic material respectively, resulting in FR as total  $\text{mg}\cdot\text{h}^{-1}$ .

In a 2001 review, Riisgård (2001a) cited the failure of some studies to measure maximum filtration rates of the experimental bivalves as one of a number of factors affecting the reliability of some of these methods. Riisgård’s review was met by significant criticism by researchers who questioned the importance of measuring maximum filtration rates and who felt that the review ignored important considerations and findings from the studies reviewed (Cranford, 2001; Widdows, 2001). For rebuttal, see Riisgård (2001b, c). In 2004, Petersen *et al.* used the three methods described above in an attempt to clarify and standardize the methods. Standardizing all external conditions, this study found that the biodeposition method gave lower rates of clearance than either the flow-through method or the clearance method, while the latter two methods gave similar results. The authors suggest, however, that the lower clearance rates given by the biodeposition method may have been an artifact of the experimental design resulting from the clogging of the  $1.2 \mu\text{m}$  filter that collected particulate inorganic material (PIM) in the water so that many particles below the retention efficiency of *M. edulis* ( $4 \mu\text{m}$ ) (Mohlenberg and Riisgård, 1978) were included in the measurement. Hence, an inflated PIM (inclusive of particles not available to the mussel) would lead to a reduced clearance rate ( $CR = (IRR + IER)/PIM$ , where IRR is inorganic



rejection rate and IER is inorganic egestion rate). For more comparative detail on the three methods, refer to Petersen *et al.* (2004).

The importance of details in methodology, equipment employed and consideration of the animals' adaptation to *in situ* or experimental conditions is emphasized in the literature (Riisgård, 2001a; Bayne, 2004; Petersen, 2004; Petersen *et al.*, 2004). In addition, some methods may be more applicable to some bivalve species than others. For example, feces and pseudofeces are easier to collect from oysters than mussels, suggesting that oysters may be better suited than mussels to biodeposition studies (Bayne, 2004).



### **2.2.3 Endogenous Factors Affecting Bivalve Filter Feeding**

Filtration rates and clearance rates of bivalves are not constant within a species or a population and, even for an individual, are variable dependent on the balance between endogenous (e.g. size, reproductive state) and exogenous factors (e.g. temperature, salinity, food density, food quality). Endogenous and exogenous factors may not be independent of each other, with the former often a function of the latter. Gametogenesis, for example, may be partially governed by water temperatures (Bayne, 1976). Understanding how both endogenous and exogenous factors may affect bivalve filtration is critical to interpreting the results of filtration rate experiments and, therefore, to understanding the role of filter feeding bivalves in coastal ecosystems.

Endogenous factors that may affect filtration rate include bivalve size: larger ctenidia associated with larger individuals facilitate greater amounts of water flow and offer a larger capture area for suspended particles. Gross gill area has been positively correlated with FR and CR by Meyhöfer (1985) and Pouvreau *et al.* (1999), respectively. It has been observed, however, that there may be a reduction in the rate of increase in filtration activity for larger animals and this may be partially accounted for by the reduced activity of the gill cilia in old specimens (Schlieper *et al.*, 1958; Winter, 1973). The relative growth rate of the gill also decreases as a bivalve grows larger (and heavier) (Vahl, 1973; Foster-Smith, 1975b).

The maximum filtration rate, partly determined by the gill size of the oyster, is related to tissue weight by the standard allometric equation:

$$[5] \quad FR = aW^b \quad \text{or} \quad FR = aL^b \quad (\text{Bayne, 1976})$$

Where  $W$  is the dry body weight (g),  $L$  is shell length (in mm), “ $a$ ” is a constant and “ $b$ ” is a weight (or length) exponent (Bayne, 1976). While positive relationships between FR (or CR) and shell weight (or length) have been demonstrated for many species of bivalve (Bayne, 1976; James *et al.*, 2001), the weight (or length) exponent,  $b$ , generally decreases as animal size increases (Rao, 1953; Segal *et al.*, 1953; Thompson and Bayne, 1974). The explanation may lie in the relationship between gill area, or possibly the area of the gill ostia, and the dry weight (or length) of the animal (Bayne, 1976; Foster-Smith, 1975b). Petersen *et al.* (2004), using *Mytilus edulis*, found that bivalves with smaller shell lengths had smaller gill surface areas and that these groupings were geographic. Although those mussels with a smaller gill surface area had statistically lower mean clearance rates in all the methods employed, it is important to note that gross gill area only explained 50% of the differences in clearance rates (Petersen *et al.*, 2004).

Clearance rates may be recorded as lower in larger bivalves than smaller bivalves and it has been suggested that this may be related to physiological status, primarily reproductive state (Denis *et al.*,



1999). Increased energy demands associated with the development and ripening of gametes (Bayne and Widdows, 1978; Grant *et al.*, 1993; Hatcher *et al.*, 1997) may cause a negative impact on clearance rate as energy is moved away from feeding and food processing and into reproduction. This impact is likely to be particularly significant when food is of low quality or low quantity (Bayne and Newell, 1983). Cranford and Hill (1999) suggested that the low feeding rates of *in situ* scallops (*Placopecten magellanicus*) and mussels (*M. edulis*) were generally associated with the timing of gamete formation and low food quality. Once reproductive demands were over, both ingestion rates and clearance rates increased for both species (Cranford and Hill, 1999). Clearance rates in *Crassostrea gigas* have been shown to be affected by gametogenesis (Bougrier *et al.*, 1995) and to be particularly depressed during the later stages of gametogenesis (Lefebvre *et al.*, 2000). Since reproductive development and demands vary between species, regions, and also with respect to seasonality, the effects of reproduction on clearance rate need to be considered on a study-by-study basis. The effect of energy demands associated with non-reproductive growth on clearance rate is unclear. Such studies would be confounded by the fact that the same exogenous factors that affect clearance rate, such as temperature, food availability, food quality, habitat positioning and population dynamics, can also impact growth (Bayne, 1976).

Endogenous factors affecting clearance rate include a bivalve's ability to respond to environmental conditions through changes in ventilation rate. Many bivalve species respond to changes in ambient conditions by expanding or contracting the exhalent siphon opening, changing the degree of valve gape and retracting the mantle margin (Foster-Smith, 1976; Jorgensen *et al.*, 1986, 1988). *Crassostrea virginica*, for example, responds to changes in ambient water conditions by fine tuning ventilation activity through adjustment of the space between opposing mantle margins, either at the inhalent or exhalent cavities (Newell and Langdon, 1996). Also, oyster gills have extensive musculature which may lead to direct control of water flow through the gill (Eble, 1996). Muscular contraction would result in both reduction of the width of the interfilamentar space and reduction in ostia size. The former would control the distance between lateral cilia and, therefore, the efficiency with which these cilia can move water. Ostia size may serve to control the resistance of the gill to water flow.

Clearance rates can be integrated with other literature estimates of physiological rate functions into a simulation model of energy flux, and predicted rates of growth compared to actual growth rates. The considerable controversy over the magnitude of clearance rates can be resolved by obtaining concurrent estimates of the physiological rate functions (e.g.: CR/FR, assimilation efficiency, metabolic rate and nitrogen excretion) required to construct a balanced energy budget under close to ambient conditions (Bayne *et al.*, 1985). Although such physiological experiments may be complex and time consuming, they allow the consistency of various rate



functions to be examined within the context of the bivalve's balanced energy budget. For example, Powell *et al.* (1992) used a time-dependent numerical model for population dynamics and energy flow in post-settlement *C. virginica* populations to compare the effect of two "filtration versus size relationships" on simulations of population growth and reproductive effort. Results suggest that an evaluation of measurements of components of the energy budget can only be made within the context of the species' complete energy budget.



## **2.2.4 Exogenous Factors Affecting Bivalve Filter Feeding**

The most significant exogenous factors that affect bivalve feeding behaviour (including clearance rate (CR), filtration rate (FR), particle capture, selection efficiency (SE), ingestion rate (IR), absorption efficiency (AE) and feces/pseudofeces production) are food quality and quantity (Hawkins *et al.*, 1996; see James *et al.*, 2001 for review). Particle size may also affect capture and selection efficiency (Ward and Shumway, 2004). Temporal variability in food characteristics may be influenced by environmental factors such as run-off, tidal currents, primary and secondary production, basin geography/geology, and singular environmental events such as storms (Berg and Newell, 1986). Quality and quantity of food can be assessed through measuring variables, and combinations of variables, such as cell density, chlorophyll a (chl<sub>a</sub>), total particulate matter (TPM), particulate organic matter (POM) and particulate inorganic matter (PIM).

Literature on the feeding behaviour of bivalves, particularly *M. edulis*, is extensive and includes several comprehensive reviews (see Ward and Shumway, 2004). The following text serves to summarize the effects of food quantity and quality, plus particle size, on the feeding behaviour of *Mytilus*, *Crassostrea* and other bivalves (2.2.4.1). The effects of other exogenous factors, including temperature, salinity, exposure and current regimes, on bivalve filtration and related processes are discussed in section 2.2.4.2.

### **2.2.4.1 Food Quantity, Quality and Particle Size**

#### **Mytilus**

*Mytilus edulis* has the ability to adapt feeding behaviour to changes in environmental seston concentration (Bayne, 1972; Riisgård *et al.*, 2003). Laboratory experiments suggest that the FR and CR of *M. edulis* increase when particle concentration increases, regardless of the quality of the particles: increasing the particle concentration of algal suspensions with inorganic particulates (such as silica, silt, intertidal sediments and organic-free ash) resulted in increased FR and CR in *M. edulis* (Kjørboe *et al.*, 1980, 1981; Hawkins and Bayne, 1992; Bayne *et al.*, 1993; Hawkins *et al.*, 1997). Experiments on *Mytilus edulis*, using flowing systems and algal culture dominated by diatoms, demonstrated lower feeding rates (both percent and actual) at low food concentrations (Tenore and Dunstan, 1973). The %carbon removed per g drywt of mussel remained constant as food concentrations increased above natural levels. The response of *M. edulis* CR and FR to an increase in food quantity in the field appears variable, however. While Hawkins *et al.*, (1996, 1998) reported increases in CR and FR in response to increased food quantity (measured as TPM), Cranford and Hill (1999) found large variability in CR in *M. edulis*, using natural seston and field measurements (TPM, chl<sub>a</sub>), even when quantity (and quality) of seston were similar. In field and laboratory experiments, *Mytilus chilensis*, decreased clearance rates



with food of low particle concentration/high quality, while feeding regulation with food of high particle concentration/low quality was regulated by the production of pseudofeces (Velasco and Navarro, 2002).

Feeding behaviour in *M. edulis* has been suggested to respond to both lower and upper thresholds of food quantity. When fed cultured algae in laboratory experiments, *M. edulis* did not filter in dilute suspensions and a critical threshold was required for filtering to occur (Thompson and Bayne, 1972; Bayne, 1976). Riisgård *et al.* (2003) suggested that the lower threshold limit for filtering activity in *M. edulis* may be approximately 630 *Rhodomonas* cells·ml<sup>-1</sup> (or 0.5 µg chl<sub>a</sub>·l<sup>-1</sup>), although valve closure and a reduction in filtration has been observed at <1000 cells·ml<sup>-1</sup> of *Phaeodactylum* (Riisgård and Randløv, 1981). The additional presence of upper thresholds in food quantity, beyond which CR or FR decline, may explain why some studies report decreases in these rates with increasing seston concentration or cell densities. For example, FR of *M. edulis* in laboratory experiments was reported to decrease as concentrations of monocultured algae increased from 10,000 cells·ml<sup>-1</sup> to 20,000 cells·ml<sup>-1</sup> to 40,000 cells·ml<sup>-1</sup>; as cell concentrations doubled, the FR decreased by approximately 50% (Winter, 1973). Interestingly, the field studies of Hawkins *et al.* (1998) on *M. edulis* found no decreases in FR, even at the highest concentrations of 100 mg·l<sup>-1</sup> of natural seston. Without information on the phytoplankton content of natural seston in the latter study, however, the two results are difficult to compare. *Mytilus galloprovincialis*, based on a recirculating flume experiment with algal cultures, demonstrated low CR (0.2-0.4 l·hr<sup>-1</sup>) with high cell concentration (8500-11000 cells·ml<sup>-1</sup>) and much higher CR (0.5-2.5 l·hr<sup>-1</sup>) when cell concentration was low (1300-5800 cells·ml<sup>-1</sup>) (“CR” and “FR” are used interchangeably in this study) (Denis *et al.*, 1999). The CR of *M. chilensis*, in both field and laboratory experiments, decreased exponentially with increasing seston concentrations (TPM) while FR increased. At high seston concentrations (200 mg·l<sup>-1</sup> in the laboratory and 665 mg·l<sup>-1</sup> *in situ*) almost all feeding rates decreased, showing an impairment of food processing (Velasco and Navarro, 2005). Navarro and Winter (1982) postulated that CR in *M. chilensis* will decline at (monocultured algae) cell densities greater than an estimated upper threshold limit of 10<sup>7</sup> cells algae.

Laboratory experiments demonstrated that *M. edulis* increased IR, in response to an increase in food quantity (measured as TPM), with a proportional increase in the rejection of pseudofeces (Bayne *et al.*, 1987; Bayne, 1993; Hawkins *et al.*, 1998). Using *M. edulis* in laboratory experiments, Foster-Smith (1975b) found that even with high concentrations of monocultured algal cells (range of concentrations were <50x10<sup>3</sup> to >800x10<sup>3</sup> cells·ml<sup>-1</sup>), IR stayed high with a corresponding increase in the rate of waste (primarily pseudofeces) production. A similar relationship between IR and food quantity have been shown for *M. edulis* under field conditions (Hawkins *et al.*, 1996, 1998) and *M. chilensis* in both field and laboratory experiments (Velasco and Navarro, 2005). Cranford and Hill (1999), however, found large variability in *M. edulis* IR, using natural seston and field measurements (TPM, chl<sub>a</sub>), even when quantity (and quality) of seston were similar.



Food quality (expressed as POM or OM (organic matter)) has been shown to be positively correlated with *M. edulis* CR and FR under laboratory conditions (Bayne *et al.*, 1987; Hawkins *et al.*, 1998). Newell *et al.* (2005) conducted an *in situ* investigation on feeding behaviour of benthic cultured *M. edulis*. They found that an increase in volume of marine snow (large marine aggregates >0.5mm diameter) during the tidal cycle corresponded with an increase in benthic mussel feeding activity (20% to 60% of maximum exhalant siphon area) and maximum rates of pseudofeces production by the mussels during periods of low tidal current speeds. In contrast, mussels kept in shipboard chambers in surface waters had high pumping rates (80-100% maximum exhalant siphon area). The difference in feeding activity is attributed to lower food quality in bottom waters than in surface waters, due to significantly higher PIM in the former. In contrast, *M. edulis* in a field study conducted by Hawkins *et al.* (1996) found that CR was entirely a function of TPM and even the decrease in OM with increasing TPM had no effect on CR. An *in situ*, natural seston study by Cranford and Hill (1999) also found no clear relationship between OM and CR in *M. edulis*. Laboratory studies of *M. trossolus* (Ward *et al.*, 1998a) demonstrated that CR was affected by food quality and similar studies of *M. galloprovincialis* noted differences in CR associated with different types of algal cells suggesting food preferences, possibly in response to food quality (Denis *et al.*, 1999).

There is generally a strong link between food quality and feeding processes such as particle selection, ingestion, assimilation and production of waste materials (feces and pseudofeces) (Cranford and Hill, 1999). Studies have shown that many species of bivalve can detect food quality, selectively ingesting phytoplankton over inorganic particulates (for review see Ward and Shumway, 2004). In *M. edulis*, material with “usable organic matter” is sorted from inorganic particles that are rejected in the form of pseudofeces (Bayne, 1993; Hawkins *et al.*, 1998). Hawkins *et al.* (1998) found that selection efficiency in *M. edulis* increased with the organic content of the filtered material. Other studies have reported a similar increase in SE with increasing POM for *M. edulis* fed mixtures of natural seston and cultured algae (Bayne *et al.*, 1993; Hawkins *et al.*, 1996). It has been reported that there is a lower threshold of POM for SE and that, for *M. edulis*, the lower threshold limit is POM <20% (Newell *et al.*, 1998). The authors suggest that particle selection has an energy requirement (although not established) so that at <20% POM, this requirement cannot be met. It could also be that in the presence of poor food quality, *M. edulis* will attempt to maximize its nutrient intake by being indiscriminant (i.e. lowering SE). It has been suggested that an upper threshold of particle concentration also exists for SE with and that this threshold exists above the limit at which pseudofeces are produced (Kiørboe and Mohlenberg, 1981; Newell and Shumway, 1993).

Food particle size has been shown to affect capture efficiency in laboratory studies of *M. edulis*, with very high retention efficiencies at the smaller end of the particle range (2-3  $\mu\text{m}$ ) (Vahl, 1972; Mohlenberg and Riisgård, 1978). Incze *et al.* (1980) suggested that for the population of *M. edulis* in their study, the



effectiveness of particle capture in the 3-5  $\mu\text{m}$  range versus larger particles was due to the dominance of nanoplankton-sized phytoplankton that dominated their natural environment. *M. edulis* has also been observed to routinely filter particle up to 100  $\mu\text{m}$  in natural settings (Vahl, 1972). Much of the literature suggests a trend whereby capture efficiency increases with increasing particle size to an upper threshold and that at the start of this threshold ( $>7 \mu\text{m}$ ), the efficiency becomes species specific (Ward and Shumway, 2004 for review). It is also possible that, at the start of this particle size threshold, efficiency may be affected by the size of food particles in the natural environment.

### **Crassostrea**

In field experiments, *Crassostrea gigas* has been shown to increase FR and IR in response to an increase in food quantity (measured as TPM) (Hawkins *et al.*, 1998). Tenore and Dunstan (1973), using flowing systems and algal culture dominated by diatoms, demonstrated that *Crassostrea virginica* exhibited lower feeding rates (both percent and actual) at low food concentrations and that the %carbon removed per g drywt of bivalve remained constant as food concentrations increased above natural levels. In contrast, high CR in *C. gigas* in an oligotrophic lagoon has been related to the low concentration of suspended particulate matter ( $0.65\text{mg}\cdot\text{l}^{-1}$ ) (Dupuy *et al.*, 2000). The presence of an upper threshold in food quantity for *C. gigas*, beyond which CR declines, was reported by Barillé and Prou (1994): in natural conditions CR increased with increasing TPM up to approximately  $50\text{mg}\cdot\text{l}^{-1}$  TPM, after which CR declined. In contrast, the field studies of Hawkins *et al.* (1998) found no decrease in FR of *C. gigas*, even at the highest concentrations of  $100 \text{mg}\cdot\text{l}^{-1}$  of natural seston.

In laboratory experiments, a decrease in food quality (OM) led to decreased CR for *C. gigas* (Ward *et al.*, 1998a). In a natural setting, Hawkins *et al.* (1998) found that increasing OM did not increase FR and IR in *C. gigas*. *C. gigas*, like many species of bivalve, can detect food quality (Ward and Shumway, 2004) and is able to selectively remove particulate organic matter (POM) from the total particulate load (TPM), rejecting the inorganics as pseudofeces (Bayne, 1993; Hawkins *et al.*, 1998). When fed different mixtures of algae, *C. gigas* and *C. virginica* responded by rejecting certain material down the ventral track towards the palps (pseudofeces) suggesting a preference for specific algae species (Ward *et al.*, 1998a). Similarly, Levinton *et al.* (2002) used endoscopy to observe microalgae being directed preferentially to the dorsal tract in *C. gigas*, while kelp detritus (ground up to a final cell range overlapping that of the microalgae but considered less nutritious) was directed to the ventral groove for eventual rejection. Levinton *et al.* (2001) suggested that in *C. virginica* and *C. gigas*, there is a tendency for more POM to be rejected by the gills and labial palps, even on short time spans and pulses of high particle concentrations, as the gut fills (Levinton *et al.*, 2001). Selection efficiency in *C. gigas* has been observed to increase with the organic content of the filtered material and with the quantity of seston filtered per hour (Hawkins *et al.*, 1998). Barillé *et al.* (1993), using *C. gigas* in a flow-through experiment with different mixtures of monocultured algae and silt, found that particle retention was dictated more by quantity than quality.



### **Other Bivalves**

Similar to *Mytilus edulis*, both *Cardium edule* (now *Cerastoderma edule*) and *Mya arenaria* have the ability to adapt to the environmental changes in seston concentration and have been shown (in laboratory studies) to reduce the valve gape, and subsequently the filtration rate, in response to concentrations of algal cells lower than a threshold value (Riisgård *et al.*, 2003). Using natural particles in a laboratory experiment, Waite (1989) found that a minimum threshold of chlorophyll concentration is required for the green-lipped mussel *Perna canaliculus* to begin filtering and that clearance rate follows a polynomial relationship with food concentration. However, James *et al.* (2001), observed these mussels actively filtering *in situ*, albeit at a low rate, at concentrations as low as  $0.27 \mu\text{g chl}\cdot\text{l}^{-1}$ .

The response of bivalve CR or FR to food quantity is highly variable between bivalve species, as well as between studies on the same species. In field experiments, the cockle *Cerastoderma edule* increased FR and IR in response to an increase in food quantity (measured as TPM) (Hawkins *et al.*, 1998). Laboratory experiments have demonstrated for the sea scallop, *Placopecten magellanicus*, that increasing the particle concentration of algal suspensions with inorganic particulates (such as silica, silt, intertidal sediments and organic-free ash) resulted in increased FR and CR (Cranford, 1992). Experiments on the hard clam, *Mercenaria mercenaria*, using flowing systems and algal culture dominated by diatoms, demonstrated lower feeding rates (both percent and actual) at low food concentrations (Tenore and Dunstan, 1973). The %carbon removed per gdrywtg of bivalve decreased as food concentrations increased above natural levels (Tenore and Dunstan, 1973). In contrast, Cranford and Hill (1999) measured CR and IR in *P. magellanicus* using natural seston and field measurements (TPM, chl<sub>a</sub>) and often found large variability even when quantity (and quality) of seston were similar. Velasco and Navarro (2005) studied the clam *Mulinia edulis* in both field and laboratory experiments and found that, under both conditions, CR decreased exponentially with increasing seston concentrations (TPM) while FR, IR and AR increased. At high seston concentrations ( $200 \text{ mg}\cdot\text{l}^{-1}$  in the laboratory and  $665 \text{ mg}\cdot\text{l}^{-1}$  *in situ*) almost all *Mulinia edulis* feeding rates decreased, showing an impairment of food processing as observed for *Mytilus chilensis* in the same experiment (Velasco and Navarro, 2005).

As noted in earlier subsections, the presence of upper thresholds in food quantity beyond which CRs decline may explain why some studies report decreases in CR with increasing seston concentration or cell densities. These upper thresholds are rarely defined, however, and may also be species specific. *Perna canaliculus* demonstrated an exponential decline in CR at natural seston levels (measured using chlorophyll a) of  $0.5\text{-}0.6 \mu\text{g chl}\cdot\text{l}^{-1}$  and higher (James *et al.*, 2001). However, the field studies of Hawkins *et al.*, (1998) on *Cerastoderma edule* found no decreases in filtration rate, even at the highest concentrations of  $100 \text{ mg}\cdot\text{l}^{-1}$  of natural seston.



Food quality has been observed to affect feeding behaviour in the sea scallop, *Placopecten magellanicus*. *P. magellanicus* can detect phytoplankton organic compounds with subsequent stimulation of the animal's filtration rate and an increase in particle ingestion rates (Ward *et al.*, 1992). Macdonald *et al.* (1998) suggested that both *Mya arenaria* and *Placopecten magellanicus*, in order to maintain a high AE, regulate ingestion by reducing CR and increasing pseudofeces production when faced with high concentrations of OM. As OM concentrations of the material being ingested decrease, CR increases to offset this decrease (Macdonald *et al.*, 1998). Cranford *et al.* (1998) noted that AE of *P. magellanicus* increased with increasing seston quality. Over a short-term storm event, once seston quality decreased, the AE also decreased but the IR remained high due to increases in CR. Urrutia *et al.* (2001) noted for the cockle, *Cerastoderma edule*, that filtration rates were higher when organic content of the diet was low. Filtration rates of the inorganic, and organic, diet components were highest ( $17.53 \pm 5.06 \text{ mg}\cdot\text{h}^{-1}$ ) and lowest ( $0.91 \pm 0.26 \text{ mg}\cdot\text{h}^{-1}$ ), respectively, with the diet with the lowest POM and chla. Navarro *et al.* (1992) suggested for *C. edule*, this relationship helps to keep AE proportional to organic matter filtration. Bacon *et al.* (1998) measured CR in *M. arenaria* and *P. magellanicus* using treatments with varying seston concentrations (1, 3, 7, and  $14 \text{ mg}\cdot\text{l}^{-1}$ ) and varying proportions of organic matter (25, 50, and 80%). In both species, CR decreased as concentration and organic content increased. When exposed to increasing seston concentrations, scallops reduced clearance rates and increased production of pseudofeces resulting in a maximum IR of  $7 \text{ mg}\cdot\text{l}^{-1}$  while *M. arenaria* similarly reduced clearance rates but maintained low pseudofeces rejection rates, enabling IR to increase to  $14 \text{ mg}\cdot\text{l}^{-1}$  concentration (Bacon *et al.*, 1998).

Under field and laboratory conditions, *P. magellanicus* can select high-quality chlorophyll-a-containing particles and significantly improve the quality of material ingested (Macdonald and Ward, 1994). Scallop selection efficiency (SE) was low when food quality was low and high when food quality was high. Hence, when seston quality is low, scallops appeared to be less efficient at sorting and selecting the high quality particles (chlorophyll a). An increase in seston concentration with no change in quality, led to an increase in pseudofeces production but no increase in selection efficiency (Macdonald and Ward, 1994). Similarly, Bacon *et al.* (1998) studying *P. magellanicus* and *M. arenaria*, reported that the ability of both bivalves to select organic particles over inorganic ones was independent of concentration but selection ability decreased as organic content decreased. Selection efficiency in the cockle *Cerastoderma edule* has been shown to increase with the organic content of the filtered material (Hawkins *et al.*, 1998; Urrutia *et al.*, 1996, 2001). In the latter two studies, however, the positive relationship between increasing selection efficiency and increasing POM concentrations reached a threshold at approximately 40% POM, after which the selection efficiency decreased.

Capture efficiency and particle size have been studied for the mussel *Perna canaliculus* and the scallop *Placopecten magellanicus*. *P. canaliculus* is reported to efficiently filter natural particles up to and larger



than 100  $\mu\text{m}$  (James *et al.*, 2001), while *P. magellanicus* has been shown to retain natural particles ranging from 3 to 40  $\mu\text{m}$  with slightly higher retention efficiency when the majority of particles were <10 $\mu\text{m}$  in diameter (Macdonald and Ward, 1994).

#### **2.2.4.2 Other Exogenous Factors**

In addition to food quality, quantity and particle size, environmental factors such as temperature, salinity, exposure at low tide and current regime may affect bivalve feeding behaviour. The impact of temperature and its effects on bivalve physiology, especially the concepts of critical temperature and mortality, have been well studied and particularly so for *Mytilus edulis* (see Bayne, 1976 for review; Incze *et al.*, 1980). In experiments with *M. edulis* acclimated to a range of temperatures (5°C to 20°C), decreasing and increasing temperature resulted in a decrease and increase, respectively, in FR. This direct response of FR to temperature change held until >20°C when FR decreased (Widdows and Bayne, 1971). Similar relationships between temperature and CR have been found for *Crassostrea gigas* (Walne, 1972; Bougrier *et al.*, 1995). Bougrier *et al.* (1995) reported an upper threshold limit for temperature, at which *C. gigas* CR was maximal, of 19°C; CR decreased at temperatures >19°C. Baines *et al.* (2005) looked at Arctic and temperate populations of *M. edulis*. After acclimation of the two groups, they were put into a flow-through experiment at two temperatures, 2°C and 12°C, and fed algae. Both populations showed reduced FR in the 2°C treatment.

In contrast, James *et al.* (2001) studying *Perna canaliculus* in New Zealand, found that even though summer and winter temperatures had a range difference of ~6°C, there was no difference in CR. Results of studies examining the effects of temperature on FR or CR should be examined with caution, however, as both field and laboratory studies may use only a narrow temperature range or may confound their temperature variables with a secondary variable such as food quality and/or quantity (Hawkins, *et al.*, 1996; Denis *et al.*, 1999; Pilditch *et al.*, 2001).

Marine bivalves, especially those found in the intertidal to shallow subtidal habitats, are often adapted to withstand varying levels of salinity. Bayne (1976) comprehensively reviewed the effects of salinity on bivalve physiology, with oxygen consumption and *M. edulis* being the best-studied physiological process and species, respectively. Despite the considerable information available on the respiratory responses of some bivalves to salinity change, there is little understanding of the physiological processes involved (Bayne, 1976). With respect to filtration, Theede (1963) found that moving acclimated *M. edulis* to different salinities caused a reduction in FR and that while the mussels did acclimate over time, previous levels of filtration were not resumed. It has been suggested, however, that with adequate time (on the order of weeks), FR will return to previous levels (Bohle, 1972).



The effects of various contaminants (e.g. heavy metals, oils, hydrocarbons, PCB) on bivalve physiology are reviewed by Roberts (1976) and presented in more recent papers (Mazzola and Sara, 2001; Burrige, 2003; Grant and Hay, 2003). Although filtration rates of *M. edulis* from locations that carry a heavy contaminant load (largely PAHs, organochlorines and TBT) are often “lower than maximum” and occasionally quite depressed (Widdows *et al.*, 1995; Widdows, 2001), the precise role of contaminants in affecting bivalve filtration is the subject of much debate.

Clearance rates are known to be influenced by a bivalve’s position within the intertidal zone, as well as current regime. For example, CRs of *Mytilus californianus* located low in the intertidal zone were higher than conspecifics in the upper intertidal zone (Segal *et al.*, 1953). There are few *in situ* studies that examine the effect of tidal zone on clearance rates but Marsden and Whitehead (1999) found that *P. canaliculus* individuals in a mid-tide site increased filtration rates in winter while those at the low tide sites did not. The authors postulated that this may be a mechanism by which the mussels maximize their FR to compensate for the increased exposure time and the seasonal demands on physiology during the winter. James *et al.* (2001) studied the same species but found no relationship between FR and temperature regardless of season, suggesting that it is position within the intertidal zone that is most likely regulating the FR.

Cranford *et al.* (1998) found that current velocity was a more critical factor influencing FR in *Placopecten magellanicus* than either food quality or quantity; FR increased with increasing current velocity up to the threshold of  $>9 \text{ cm}\cdot\text{s}^{-1}$ . *Mytilus galloprovincialis*, in a recirculating flume experiment with algal cultures, demonstrated increasing CR with increasing current velocity up to a threshold of  $20\text{-}25 \text{ cm}\cdot\text{s}^{-1}$  (Denis *et al.*, 1999). The authors suggested that flow rate is an important factor affecting FR, demonstrating an adaptive response to variability in the environment. Both these studies support the finding of Newell (1999) that the FR of *M. edulis*, in a flume experiment, was negatively impacted by high current velocities (max  $30 \text{ cm}\cdot\text{s}^{-1}$ ).

### 2.3 Rate of Feces/Pseudofeces Production

Although the deposition of feces and pseudofeces, collectively termed biodeposits, may play an important role in pelagic-benthic coupling, few studies have paid attention to the dynamics of biodeposition. In particular, little is known about biodeposit quality (Navarro and Thompson, 1997), biodeposit production rates (Kautsky and Evans, 1987), as well as their potential for dispersion (Miller *et al.*, 2002; Giles and Pilditch, 2004; Hartstein and Stevens, 2005). Although research that focuses on the production rates of bivalve feces and pseudofeces is relatively uncommon, the need for additional research in this area, particularly in light of the recent interest in depositional models (see Section 4), is clear. This subsection reviews biodeposit production and biodeposit production rates by filter feeding bivalves, with a focus on



bivalves in suspended culture; environmental biodeposition, which combines biodeposit production with the fate of the biodeposits in the environment, is covered in Section 4.

Feces of filter feeding bivalves are primarily organic, composed of organic C and N, silica and chlorophyll-derived pigments (McKinnon *et al.*, 2003), while pseudofeces are generally inorganic plus surplus organic that is not ingested or assimilated (McKindsey *et al.*, 2006). While observations on the size and shape of fecal strings/pellets vary depending on the bivalve species (Moore, 1931; Haven and Morales-Alamo, 1966), pseudofeces are commonly described as amorphous in shape (Miller *et al.*, 2002) or as clumps loosely aggregated with mucus (Haven and Morales-Alamo, 1966).

The early studies on biodeposits of filter feeding bivalves usually reported production rates, with little or no discussion of factors that may be affecting these rates, which were then used to calculate biodeposit production at the commercial scale. For example, individual *Cardium* (now *Cerastoderma*) from coastal France were reported to produce 648mg (wet wgt) of fecal material daily (Damas, 1935). These data were used by Verwey (1952) to calculate total annual deposition by this species, in the Waddenzee, of 100,000 metric tons (dry wgt). Lund (1957) calculated that *Crassostrea virginica* covering an acre of bottom (bottom, not suspended, culture) would deposit 7.58 metric tons of fecal material (dry wgt) in 11 days. A single, 90g Japanese oyster produced a minimum of 0.03 g (dry wgt) feces daily and a raft of oysters, 60m square in Japanese waters, was estimated to annually produce 0.6 to 1.0 metric tons (dry wgt) of fecal material (Ito and Imai, 1955). Haven and Morales-Alamo (1966) suggested that a bed of *C. virginica*, containing 250,000 small oysters and occupying 0.405 hectares of seafloor, may produce up to 981 kg of biodeposits weekly. Tsuchiya (1980) conducted a long-term study on *Mytilus edulis* biodeposit production and estimated that a population living in one square meter produced 9.20 kg of feces and 2.71 kg of pseudofeces per year (dry wgt). More recently, Callier *et al.* (2006) calculated maximum biodeposit production rates for *M. edulis* in Quebec, in August 1992, as  $114.0 \pm 65.2 \text{ mg} \cdot \text{gdrywgttissue}^{-1} \cdot \text{day}^{-1}$ .

The relationship between FR and/or CR and production of feces and pseudofeces is discussed in the previous subsection and, clearly, these physiological processes are linked. Hence, when attempting to identify endogenous or exogenous factors that affect production of biodeposits, it must be remembered that these factors are influencing feeding behaviour in general. Endogenous factors known to affect biodeposit production include size, age and spawning. Tsuchiya (1980) demonstrated that biodeposit production in *M. edulis* decreased during spawning. A positive relationship between biodeposit production and body size has been reported for filter feeding bivalves, including the lamellibranch *Laternula elliptica* (Ahn, 1993) and the oyster *C. virginica* (Haven and Morales-Alamo, 1966). In the latter study, the larger oysters produced twice and four times more feces and pseudofeces, respectively, than the smaller oysters. A long-term study on *M. edulis* demonstrated that although positively correlated to body size, biodeposit production per unit size was higher in small mussels than large mussels (Tsuchiya,



1980). Similar patterns were reported by Callier *et al.* (2006), who studied a fixed number of *M. edulis* held within cylindrical vexar cages fitted into the top of sediment traps for periods of 24 hours. The *in situ* biodeposition by 0+ and 1+ cohorts was a function of mussel size: the 1+ mussels produced, on average, 1.6 times more biodeposits ( $51.5 \text{ mgdrywt}\cdot\text{d}^{-1}\cdot\text{ind}^{-1}$ ) than the 0+ mussels ( $32.4 \text{ mgdrywt}\cdot\text{d}^{-1}\cdot\text{ind}^{-1}$ ). In contrast, the amount of biodeposits produced per unit body weight was greater for smaller mussels ( $72.7 \text{ mgdrywt}\cdot\text{gtissue}^{-1}\cdot\text{d}^{-1}$ ) than larger ones ( $34.7 \text{ mgdrywt}\cdot\text{gtissue}^{-1}\cdot\text{d}^{-1}$ ). A temporally variable, but consistently negative, linear relationship between biodeposit production ( $\text{mgdrywt}\cdot\text{gtissue}^{-1}\cdot\text{d}^{-1}$ ) and mussel tissue (dry wt) was reported (Callier *et al.*, 2006). Physiological rates are an allometric function of body size and thus decline with the relative body surface area available for oxygen diffusion, which decreases with respect to body size as the organism grows (Hawkins and Bayne, 1992).

Several studies have investigated the relationship between biodeposit production and environmental variables, including food quantity and quality and environmental temperature. Seasonal variation in *C. virginica* biodeposit production (mean annual rate  $1.62 \text{ g}\cdot\text{animal}^{-1}\cdot\text{week}^{-1}$ ; maximum rate  $3.92 \text{ g}\cdot\text{animal}^{-1}\cdot\text{week}^{-1}$ ) was positively correlated with water temperature with biodeposit production unmeasurable at temperatures  $<2.8^\circ\text{C}$  (Haven and Morales-Alamo, 1966). Tsuchiya (1980) reported that *M. edulis* produced more biodeposits in the summer than in other seasons and that temperature affected biodeposit production, with the optimum temperature for biodeposit production approximately  $20.0^\circ\text{C}$ . Kautsky and Evans (1987) also showed a positive relationship between *M. edulis* biodeposit production and seasonal temperature; *M. edulis* biodeposit production rates (for an average mussel biomass of  $620 \text{ g m}^{-2}$ ) in the Northern Baltic ranged seasonally from  $0.52 \pm 0.5$  to  $9.76 \pm 4.52 \text{ g}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$  with low rates in the early spring and increased rates with the onset of spring and summer. Research on other environmental variables and *M. edulis* demonstrated a positive relationship with salinity (up to a maximum) (Widdows, 1985) and the production of more biodeposits in the dark than the light (Tsuchiya, 1980).

As has been observed for FR and CR, bivalve biodeposit production may be related to exogenous factors such as food quantity and quality (Tenore and Dunstan, 1973; Navarro and Thompson, 1997). The production of pseudofeces by filter feeding bivalves in media of high phytoplankton concentration is well documented in the literature (Loosanoff and Engle, 1947; Dean, 1957; Galtsoff, 1964; Jorgensen, 1966). In experiments using flowing systems and algal culture dominated by diatoms, the biodeposition rates of *M. edulis*, *C. virginica*, and *Mercenaria mercenaria*, (expressed as  $\text{mg ash-free drywt}\cdot\text{gdrywt meat}^{-1}\cdot\text{d}^{-1}$ ) were shown to increase logarithmically with increasing food concentration as a result of the production of pseudofeces (Tenore and Dunstan, 1973). These experiments also demonstrated that, for all food concentrations tested, *M. edulis* had the highest deposition rates, followed by *C. virginica* and then *M. mercenaria*. *C. virginica* and *M. edulis*, as discussed in the previous subsection, maintain relatively high clearance rates even when seston concentrations increase (Newell and Langdon, 1996; Hawkins *et al.* 1998) through increased production of pseudofeces. Tsuchiya (1980) observed that *M. edulis* produced



more pseudofeces, but a constant amount of feces, when food concentrations increased and that production rate of mussel biodeposits increased with increased flow rate. Such a response to flow is reasonable considering that the food supply to filter feeders is a function of both concentration and flow velocity (Muschenheim, 1987; Cahalan *et al.*, 1989). Dean (1957) found that above  $5 \times 10^5$  cells  $\text{ml}^{-1}$  of *Chlorella*, *C. virginica* initiated significant pseudofeces production. Davids (1964) found a similar maximum for the mussel *M. edulis*. Other species of filter feeding bivalves, such as cockles, clams, and scallops, regulate their ingestion rates primarily by reduction of clearance rates, with some increase, albeit of secondary importance, in pseudofeces production (Hawkins *et al.*, 1998; Grizzle *et al.*, 2001). For example, Winter (1970) found that an increase in food concentration above  $2$  to  $4 \times 10^5$  cells- $\text{ml}^{-1}$  resulted in greater pseudofeces production in *Modiolus modiolus*. The species of bivalves that can exert the greatest influence on benthic-pelagic coupling are those, such as *C. virginica* and *M. edulis*, which maintain high clearance rates and reject large numbers of particles as pseudofeces (Newell, 2004).

Production of biodeposits, linked to feeding physiology, has a seasonal component as a function of phytoplankton production. Callier *et al.* (2006) found that *in situ* biodeposit production of *M. edulis* was greater towards the end of August than in the middle of August and suggested that this difference may be due to differences in seston concentration; both temperature and salinity were relatively stable throughout the sampling period. Although seston concentration was not measured in this study, the hypothesis was supported by the fact that the quantity of naturally sedimented matter (recorded in traps at 1m depth) in mid-august ( $5.6 \pm 1 \text{ mg}\cdot\text{l}^{-1}$ ) was almost twice that at the end of August ( $3.6 \pm 0.5 \text{ mg}\cdot\text{l}^{-1}$ ). Although relationships between environmental conditions and bivalve metabolism have been demonstrated by some studies, the relationship between feeding measurements (such as fecal and/or pseudofeces production or ingestion rates) and environmental factors may be difficult to interpret for *in situ* studies. *In situ* fecal production rates (*in situ*, weight-specific) for the scallop *Placopecten magellanicus* ranged from approximately  $0.35$  to  $1.2 \text{ mg}\cdot\text{g}^{-1}\cdot\text{h}^{-1}$ , with organic content of approximately 45%-85% OM, and corresponding seston levels of approximately  $1.2$  to  $2.7 \text{ mg}\cdot\text{l}^{-1}$  over the course of a tidal cycle (Cranford and Hargrave, 1994). There was no clear relation between these rates and tidal-induced variations in indicators of seston nutritional value, such as organic material, chlorophyll a, POC or PN content. Fecal production rates, similar to ingestion rates, were highest at late flood and ebb tide but were poorly correlated with seston flux: the highest feces production rates were during low particle flux at late flood tide. In a later study, Cranford and Hill (1999) measured seasonal variation in food utilization by *P. magellanicus* and *M. edulis*: weight-specific



fecal production rates were highest in spring and fall but peaked in Oct/Nov at approximately 60 mgdrywt·g<sup>-1</sup>·d<sup>-1</sup> and 80 mgdrywt·g<sup>-1</sup>·d<sup>-1</sup>, respectively. Fecal production rates for the rest of the study (April to September) were usually below 20 mgdrywt·g<sup>-1</sup>·d<sup>-1</sup>. Measured daily seston abundance and composition and environmental parameters, including temperature, could explain only 28% of the variation in the bivalves' daily ingestion rates (Cranford and Hill, 1999) and, presumably, a comparable percentage of variation in associated daily fecal production rates. In a major study of biodeposition by *C. virginica*, no statistical correlation was found between seasonal variation in production of feces and pseudofeces and seasonal variation in total seston (Haven and Morales-Alamo, 1966). Hawkins and Bayne (1992) showed that *M. edulis* excretion (including biodeposit production) may vary greatly over small periods of time (8h) without any apparent relationship with exogenous influences.

Food quality has been demonstrated to affect biodeposit production and the proportion of feces and pseudofeces in many bivalves. Increasing silt and clay content in seston, for example, results in an increase in pseudofeces production by the cockle, *Cerastoderma edule*, and the clam, *M. mercenaria* (Robinson and Langton 1980; Iglesias *et al.*, 1992). Lab experiments on *C. edule* (Urrutia *et al.*, 2001) showed that the lower the organic content of filtered matter, the higher the proportion of matter that was rejected (both total and organic); the proportion of particulate matter rejected ranged from 5% (diet with highest organic content) to 65% (diet with lowest organic content). Miller *et al.* (2002) reported, however, that the pseudofeces component of biodeposits of the clam *A. zelandica* biodeposits stayed at 93-95% (drywt) whether fed either natural seston (20 to 30 mg·l<sup>-1</sup>) or silt/clay additions (up to 600 mg·l<sup>-1</sup>).

The composition of biodeposits, which may affect their potential influence on the environment, has been shown to vary with food supply. POC and PON content of *A. zelandica* biodeposits, fed a phytoplankton diet, were 20.9% and 2.7% respectively but when fed a phytoplankton/silt diet were 6.2% and 0.9%, respectively (Miller *et al.*, 2002). For *P. magellanicus* and *M. edulis*, fecal pellet organic content ranged seasonally from 20% to 70% with the highest values observed during the spring phytoplankton bloom (Cranford and Hill, 1999). In this study, feces generally had a similar organic content as other settled particles, despite containing partially digested organic matter. In contrast, Callier *et al.* (2006) found, in a June to September study in Quebec, that % organic carbon was slightly greater in *M. edulis* fecal pellets than in the naturally sedimented material: 2.4 ± 0.5 % vs. 1.1 ± 0.2 %, respectively. During the same time



interval, the % organic nitrogen in *M. edulis* fecal pellets and the sedimented particulate matter did not differ and both ranged between 0.2 and 0.4 % (Callier *et al.*, 2006). Kautsky and Evans (1987) found that, from April to September in the Northern Baltic, organic content of *M. edulis* biodeposits collected *in situ* was higher than that of naturally sedimenting material (30.4 vs. 24.8%) and, that during this period of high primary production, biodeposits were characterized by comparatively higher levels of organic material, carbon, and nitrogen than at other times.



### 3.0 Environmental Biodeposition Associated with Suspended Bivalve Culture

Bivalve filter feeding results in the packaging of fine suspended material into larger feces and pseudofeces (biodeposits) that contain organic matter (see Section 2.3). Hence, biodeposit production may increase sedimentation rates within bivalve culture sites (Dählback and Gunnarsson, 1981; Hatcher et al., 1994). As noted in Section 2, the dynamics of bivalve feces deposition (biodeposit quality, production rates, settling rates, potential for dispersal, disaggregation rates and resuspension) are poorly understood (Kautsky and Evans, 1987; Navarro and Thompson, 1997; Miller *et al.*, 2002; Giles and Pilditch, 2004; Hartstein and Stevens, 2005) but enhanced sedimentation (biodeposition) under bivalve culture is well documented (Dählback and Gunnarsson, 1981; Tenore *et al.*, 1982; Jaramillo *et al.*, 1992; Hatcher *et al.*, 1994).

Section 3 reviews factors that specifically affect settling rates of bivalve biodeposits (Section 3.1), as well as those factors that affect biodeposition and organic loading more generally (Section 3.2). The potential impacts of this biodeposition associated with suspended bivalve aquaculture are reviewed in Section 3.3. Many of the factors that influence biodeposit settling rates will clearly also influence environmental biodeposition. As a result, a small degree of overlap between Sections 3.1 and 3.2 in discussion of these factors is unavoidable. The great majority of the literature concerns suspended culture of *Mytilus edulis* and, to a lesser degree, other species of mussels (*Mytilus galloprovincialis*, *Mytilus trossulus*, and *Perna canaliculus*) and the eastern oyster, *Crassostrea virginica*. Studies on biodeposition associated with suspended culture of other bivalve species, including *Crassostrea gigas*, are rare, as is research based on the west coast of Canada. While some findings in the literature may be extrapolated, to some extent, to other species or other locations, most results show strong, site-specific influences. Throughout this review, the fact that biodeposition and the impacts of biodeposition are influenced by site-specific factors is emphasized. The need for additional research on Canada's west coast and on *C. gigas* is evident.

#### Section 3.1 Bivalve Feces/Pseudofeces Settling Rates

Although biodeposition may play an important role in pelagic-benthic coupling, few studies have paid attention to the dynamics of biodeposition (see also Section 3.2). In addition to the general lack of data on biodeposit quality (Navarro and Thompson, 1997), production rates (Kautsky and Evans, 1987) and dispersion potential (Miller *et al.*, 2002; Giles and Pilditch, 2004; Harstein and Stevens, 2005), there is a lack of information on biodeposit settling (or sinking) rates (or velocities) and factors affecting this velocity (Callier *et al.*, 2006). Because bivalve biodeposits typically differ from the naturally-occurring seston particles in aggregate particle size and shape, organic content and cohesive properties (Haven and Morales-Alamo, 1966, Kautsky and Evans, 1987; Dame, 1993, 1996), this repackaging of seston into biodeposits induces a downward vertical flux of material from the water column to the seabed. It has



been suggested that because feces and pseudofeces settle out at rates up to 40 times that of nonaggregated particles (Kautsky and Evans, 1987; Widdows *et al.*, 1998). Some data on sinking rates of finfish feed and feces are available from fish farms but sinking rates of biodeposits from bivalve farms are likely to be slower than these, due to the lower density of bivalve feces derived from phytoplankton compared to those of finfish derived from feed pellets (Cromey *et al.*, 2002). The biodeposits produced at bivalve culture sites are expected to disperse farther from their origin than those produced at finfish culture sites because of their slower sinking velocities (Chamberlain *et al.*, 2006). Of course, the area over which biodeposits will settle on the benthos will be strongly influenced by water movement and depth of site (i.e. residence time in the water column).

A better understanding of bivalve biodeposition dynamics, particularly parameterisation of biodeposit settling velocities, quality, and erosion characteristics, is required in order for ecosystem models to make accurate predictions of benthic loading and subsequent effects on the local environment (Henderson *et al.*, 2001; Section 4). Particle sinking rate is a dominant parameter requiring characterization in all particle tracking models (Chamberlain *et al.*, 2006). The sinking rates of particles depend on several properties of the particles including size, density and porosity and are often based on variations of Stokes Law (Hendricks and Eganhouse, 1992; Cromey *et al.*, 1998). However, Stokes Law assumes that particle density and shape are similar across all size ranges and this is not an assumption that is valid for bivalve fecal particles. As a result, bivalve biodeposit sinking rates are poorly estimated by simple sinking rate equations such as Stoke's law, as has been demonstrated by Chamberlain (2002) and Giles and Pilditch (2004). Experiments are required, therefore, to obtain estimates of the sinking rates of these particles. Unfortunately, data on sinking rates of bivalve biodeposits are relatively rare and most relevant data has been generated only recently (Chamberlain *et al.*, 2006). In addition, most available data are relevant to mussels.

Sinking rates for fecal pellets of the mussel, *Mytilus edulis* (4cm), have been reported at  $<0.5 \text{ cm s}^{-1}$  (Chamberlain, 2002; Chamberlain *et al.*, 2001). Sinking velocities for *M. edulis* pseudofeces of  $<0.8 \text{ cm s}^{-1}$  were reported by Chamberlain *et al.* (2001). A sinking rate of  $0.2 \pm 0.02 \text{ cm s}^{-1}$  for flocculent material that was considered to be mussel pseudofeces was reported by Walker *et al.* (2005). It is important to note that in some studies, pseudofeces were either not measured or could not be detected while in other studies pseudofeces and feces could not be distinguished and were measured collectively as biodeposits. Bivalves may produce pseudofeces (particles that are not ingested) under certain environmental conditions such as high suspended particulate material (SPM) concentrations. Bayne *et al.* (1993) suggested a 67:33 feces to pseudofeces production ratio for *M. edulis* under specific ambient seston concentrations. Obviously, pseudofeces production in relation to feces production is dependent on species and environmental conditions, including food quality and quantity (see Section 2.2.5). Pseudofeces tend to have slower sinking rates than fecal pellets because of their fluffy texture (Giles and



Pilditch, 2004) and thus may be dispersed even further than fecal pellets. Different particle types (feces and/or pseudofeces) and their sinking velocities can be modeled in DEPOMOD (see Section 4).

To estimate the dispersal of mussel biodeposits, Callier *et al.* (2006) used experimental studies to characterize biodeposit dynamics, including the size-dependent sinking velocity of feces in a suspended mussel (*Mytilus edulis*) farm in Great-Entry Lagoon, eastern Canada. Mussels (3 to 7 cm) were maintained in cages above sediment traps in the field; fecal pellets were collected after 24 hours and the sinking speed of individual, measured fecal pellets was determined in a cylindrical glass sinking column (45 cm height, 10.5 cm diameter,) filled with filtered (0.7  $\mu\text{m}$ ) seawater ( $21 \pm 1$  °C, 28 psu). No pseudofeces were observed in this study but SPM concentrations in this study ranged from 9.0 to 27.4  $\text{mg l}^{-1}$  and the SPM concentration at which pseudofeces are first produced is approximately 4.5 to 5  $\text{mg l}^{-1}$  (Widdows *et al.*, 1979). Hence, the authors note that they may have been present in low quantities but undetected in the flocculated, sedimented material. Fecal pellets ranged in size: 0.7 to 29.0 mm in length and from 0.3 to 1.8 mm in width. Fecal pellet width was a function of mussel size for mussels in the size range of 3 to 6 cm: larger mussels produced larger fecal pellets. Fecal pellet length is believed to be more a function of current speed than mussel morphology (Giles and Pilditch, 2004). Fecal pellet sinking rate ranged from 0.27 to 1.81  $\text{cm s}^{-1}$  and was best correlated with fecal pellet width (although surface area and length explained significant but lesser proportions of the variance in sinking velocity). Thus, mussel size may be used to predict sinking velocities under varying current regimes, allowing for valid estimates of dispersal in the field.

Giles and Pilditch (2004) quantified the dispersal characteristics (sinking velocity and erosion threshold) of biodeposits of the green-lipped mussel *Perna canaliculus* in New Zealand. Mussels (2.7 to 11.4 cm) were fed one of three diets (natural, algae-dominated and silt-dominated) designed to represent situations such as dense algae blooms that occur in shallow or unmixed eutrophic waters and high concentrations of silt caused by resuspension of sediments or riverine input in coastal ecosystems (Hawkins *et al.*, 1999). Highly significant relationships were derived, for each diet, between biodeposit size (fecal pellet width and pseudofeces area) and sinking velocity: wider fecal pellets, and pseudofeces with greater surface area, sank more quickly. Larger mussels produced larger biodeposits and hence, faster-sinking biodeposits.

Biodeposit sinking velocities also varied significantly with diet (Giles and Pilditch, 2004). Sinking velocities of fecal pellets produced on the algae-dominated diet (0.2 to 1.5  $\text{cm}\cdot\text{s}^{-1}$ ) were approximately 3 to 4x lower than those of pellets produced on the natural (0.9 to 4.3  $\text{cm}\cdot\text{s}^{-1}$ ) and silt-dominated diets (1.1 to 4.5  $\text{cm}\cdot\text{s}^{-1}$ ). Sinking velocities of pseudofeces produced on the algae-dominated diet (0.1 to 0.8  $\text{cm}\cdot\text{s}^{-1}$ ) were approximately 3 to 5x lower than those of pseudofeces produced on the natural diet (0.5 to 2.2  $\text{cm}\cdot\text{s}^{-1}$ ) and 5 to 10x lower than those of pseudofeces produced on the silt-dominated diet (1.1 to 4  $\text{cm}\cdot\text{s}^{-1}$ ). Pseudofeces produced on the natural and algae-dominated diets settled 50 to 70% slower than feces



produced on the same diet, but sinking velocities of silt-dominated diet feces and pseudofeces were similar. *In situ* estimates of biodeposit sinking velocities measured were comparable to those produced on the natural diet. These results emphasize that mussel biodeposit dispersal (and hence the flux to the benthos) depends on the available diet and mussel size and thus could differ significantly between locations, seasons and the size structure of the population.

Hartstein and Stevens (2005) also measured experimental sinking velocities for biodeposits of *P. canaliculus* in New Zealand, reporting an average sinking rate (avg. 6 cm mussel) of  $3.0 \pm 0.41 \text{ cm}\cdot\text{s}^{-1}$ . The authors used 150 randomly collected, freshly egested biodeposits (feces and pseudofeces); each pellet was allowed to sink 0.2 m in a settling tube (0.4 diameter, 1.5 m length) before being timed to fall an additional 1.0 m. Interestingly, Harstein and Stevens (2005) also measured sinking rates of mussel shells and, with a mean of  $37 \pm 2.6 \text{ cm}\cdot\text{s}^{-1}$ , these rates were much higher than those calculated for mussel biodeposits and suggest that shell drop will predominantly accumulate directly beneath, or close to, the mussel long-line.

*Atrina zelandica* is a filter feeding, benthic pinnid bivalve (up to 30cm) common in New Zealand (Powell, 1979; Cummings *et al.*, 1998). Miller *et al.* (2002) measured settling rates of biodeposits of *A. zelandica* in the laboratory (glass cylinder 50 cm x 8cm) in relation to size (length and width) of the biodeposits and diet. *A. zelandica* was fed either cultured phytoplankton (P) or a mixture of phytoplankton and silt (PS) to mimic the natural variation in near-bed seston quality. In this study, feces could not be distinguished from pseudofeces. The chemical composition of biodeposits reflected the diet: P biodeposits had 3 times more organic carbon and nitrogen by weight than those produced on the PS diet. Despite no significant differences in biodeposit shape or size (length or width), PS biodeposits had a settling velocity ( $3.0 \pm 1.3 \text{ cm}\cdot\text{s}^{-1}$ ) twice that of the P biodeposits ( $1.7 \pm 0.8 \text{ cm}\cdot\text{s}^{-1}$ ). Taghon *et al.* (1984) reported, for polychaetes, that diet quality influenced biodeposit settling velocity. This emphasizes the difficulty in predicting settling rate and, ultimately flux, from biodeposit size alone (Miller *et al.*, 2002).

In summary, the average sinking velocity of  $1.0 \pm 0.3 \text{ cm}\cdot\text{s}^{-1}$  for fecal pellets of *M. edulis* (3-7 cm) measured in Callier *et al.* (2006) was about twice that observed by Chamberlain (2002) for *M. edulis* (4.2 cm) individuals but was within the 0.2 to  $4.5 \text{ cm}\cdot\text{s}^{-1}$  range observed for the mussel *Perna canaliculus* (2.7-11.4 cm) (Giles and Pilditch, 2004). De Jong (1994) reported that fecal pellets of *P. canaliculus* settled at a rate of  $1.2 \pm 0.1 \text{ cm}\cdot\text{s}^{-1}$ , but the size of the mussels studied was not given. Hartstein and Stevens (2005) reported that biodeposits from 6 cm individuals of the same species settled at  $3.0 \pm 0.4 \text{ cm}\cdot\text{s}^{-1}$ .

*M. edulis* pseudofeces sinking rates of  $<0.8 \text{ cm}\cdot\text{s}^{-1}$  were reported by Chamberlain *et al.* (2001). Sinking rates of *P. canaliculus* pseudofeces ranged from 0.1 to  $4 \text{ cm}\cdot\text{s}^{-1}$ . Miller *et al.* (2002) found sinking velocities for *A. zelandica* biodeposits ranged from 1.7 to  $3.0 \text{ cm}\cdot\text{s}^{-1}$  but these were from considerably larger bivalves (18.5 – 26 cm) than those used by most other studies. It has been documented that larger



mussels produce larger (wider) fecal pellets (Giles and Pilditch, 2004; Callier *et al.*, 2006) and larger (greater surface area) pseudofeces (Giles and Pilditch, 2004) than smaller mussels. These same studies reported that size of feces and pseudofeces positively affects sinking rate.

Variation in reported sinking rates of bivalve biodeposits may also be affected by diet; food quality affects the density of biodeposits and, hence, settling velocity (Chamberlain *et al.*, 2006). Fecal pellets (Chamberlain, 2002; Giles and Pilditch, 2004) or biodeposits (Miller *et al.*, 2002) from mussels fed on diets with high silt content sank more rapidly than those from mussels fed on diets high in algae or natural diets. A similar relationship between sinking rate and diet was found for mussel pseudofeces (Giles and Pilditch, 2004).

Data on erosion thresholds for bivalve biodeposits is rare but Hartstein and Stevens (2005) found, for *P. canaliculus* biodeposits, that these thresholds were affected by diet but not by mussel size. Ninety percent of fecal pellets produced by *P. canaliculus* on an algae-dominated diet eroded at a bed shear velocity of  $0.28 \text{ cm}\cdot\text{s}^{-1}$ ; this shear velocity is 50% of that required to erode the same percentage of fecal pellets produced on natural and silt-dominated diets. Pseudofeces generally eroded over a similar but wider range of shear velocities and the differences between the 3 diets were less distinctive than for fecal pellets (Hartstein and Stevens, 2005).

The studies reviewed here emphasize that mussel biodeposit dispersal (and hence the flux to the benthos) depends on the available diet and mussel size and thus could differ significantly between locations, seasons and the size structure of the population. Obviously, however, biodeposit dispersal is also dependent on the flow environment, which may be dominated by bi-directional, wave and tidal currents interacting with bottom topography; estimating the length scales for dispersal of biodeposits is complicated in the marine environment. Miller *et al.* (2002) found a weak, but significant, negative relationship between settling velocity of *A. zelandica* biodeposits and distance downstream of the bivalves, suggesting that other variables (e.g. current flow) were important in addition to settling velocity. Furthermore, flow modification due to farm structures is only just being quantified (Plew *et al.*, 2005).

A small variation not only in biodeposit sinking velocity, but also in current velocity or water column depth may have a significant impact on the extent of biodeposit dispersion (Giles and Pilditch, 2004). For example, Callier *et al.* (2006) demonstrated great differences in the potential dispersion of fecal pellets from two *M. edulis* cohorts: 0+ (11 to 14 months old) and 1+ (23 to 26 months old). An average summer current speed of  $5.5 \text{ cm}\cdot\text{s}^{-1}$  is used with sinking velocity data and distance between the mussel lines and the bottom. For the 0+ cohort, the average sinking velocity is  $0.79 \text{ cm}\cdot\text{s}^{-1}$  and the distance between the 0+ mussel lines and the bottom is 1 to 3.5 m; hence, the initial deposition may be estimated to be between 7 and 24.4 m. In contrast, with the same current speed, fecal pellets from the 1+ mussels sank



at an average velocity of  $0.97 \text{ cm}\cdot\text{s}^{-1}$  and the distance below 1+ mussel lines was between 0 and 1.3 m. Hence, the initial deposition is estimated to be between 0 and 7.4 m. The current velocity can reach  $18 \text{ cm}\cdot\text{s}^{-1}$  during strong wind events, however, so that the estimated dispersion of fecal pellets from the 0+ and 1+ mussels may be as much as 79.7 m and 24.1 m, respectively (Callier *et al.*, 2006). This example also demonstrates that, despite the relatively slow sinking speed and even for deeper sites, the time for material to reach the bed will be relatively rapid (min) compared to time-scales of variability important for modelling larger-scale transport processes (e.g. tides) (Harstein and Stevens, 2005).

Incorporating sinking rates of feces/pseudofeces into depositional models is complex. Chamberlain *et al.* (2006) note that sinking, as well as diffusion and advection, all require a separate estimate or model of physical processes and that sinking is particularly problematic, for the loss side of index models, since particles undergo aggregation (flocculation), disaggregation, deposition and resuspension. While turbulence initially favours aggregation by increasing the encounter rate of particles, above some level it causes disaggregation (Cranford *et al.*, 2003). These behaviours have the additional complexity of boundary layer physics which regulate their fate. Some models, including DEPOMOD, have been successful at making these predictions on a local scale, but prediction of sedimentation rate for a whole bay is a significant task (Chamberlain *et al.*, 2006). These issues are discussed in more detail in Section 4.

### 3.2 Factors Affecting Biodeposition and Organic Loading

The extent and magnitude of biodeposition around suspended culture of bivalves depends on a number of factors, including the size and nature of the farm. The culture species, stocking density, overall production and biomass, culture methods and fouling community may all affect biodeposition. Site characteristics, including hydrography, bathymetry, primary productivity and food availability will also affect biodeposition (Asmus and Asmus, 1991; Jaramillo *et al.*, 1992; Mazouni *et al.*, 1998; Black, 2001; Chamberlain *et al.*, 2001; Cranford *et al.*, 2003; Hartstein and Rowden, 2004; Hartstein and Stevens, 2005; McKindsey *et al.*, 2006; ICES, 2004).

Chamberlain *et al.* (2001) reported that even slight differences in the physical properties of sites can result in marked differences in biodeposition. Similarly, Giles and Pilditch (2004) suggested that a small variation in biodeposit sinking velocity, as well as small variations in current velocity or water column depth, may have a significant impact on the extent of biodeposit dispersion. In the Gulf of St. Lawrence region of Canada, mussel farms are usually established in relatively shallow coastal areas (e.g. 3-5m, Grant *et al.*, 2005), as compared to other areas (e.g. >8m in New Zealand (Hartstein and Stevens, 2005) and B.C. (Barnes, unpubl. data). The mussel farm sites in eastern Canada are also characterized by low current velocities (Grant *et al.*, 2005). All things being equal, the accumulation of biodeposits will be



higher in these types of farms than in ones established in areas with deep waters and strong currents (Hartstein and Stevens, 2005). Grant (2000) identified estuaries in Prince Edward Island (PEI), with relatively small tidal exchange and a high percentage of the total estuarine volume under culture, as having the greatest risk of biodeposition effects. Indeed, while sediments under mussel farms in estuaries in PEI (Grant *et al.*, 2005) and northwest Spain (Leon *et al.*, 2004) showed significant increases in organic matter content, similar increases were not observed in fjords in Newfoundland (Anderson *et al.*, 2003).

Callier *et al.* (2006), studying suspended *M. edulis* farms in Quebec, also reported that farm biodeposits are not dispersed broadly with dispersion limited to about 12m around the mussel farm. In fact, most studies that have evaluated biodeposit dispersion based on biodeposit settling velocity, water depth and current velocity (Chamberlain, 2002; Giles and Pilditch, 2004; Hartstein and Stevens, 2005) have suggested that dispersion is limited to within about 50 m of the farm site. Callier *et al.* (2006) suggest that the combination of the observed low initial dispersal of biodeposits and the fact that the labile component of mussel biodeposits degrades very quickly (Fabiano *et al.*, 1994) means that the potential effects on benthic communities would be expected to be quite localized. Once again, however, generalizations are difficult given variation in site characteristics and the benthic impacts of organic biodeposits under suspended mussel culture operations have been shown, globally, to have benthic impacts ranging from local to inlet-wide (Dahlback and Gunnarsson, 1981; Tenore *et al.*, 1982; Mattsson and Lindén, 1983; Kaspar *et al.*, 1985; Shaw, 1998; Mirto *et al.*, 2000). Biodeposition under bivalve farms may also demonstrate temporal variation related to bivalve biodeposit production and settling rates, as discussed in Sections 2.3 and 3.1 respectively, as well as seasonal and tidal variations in hydrographic conditions (Hatcher *et al.*, 1994; Cranford and Hargrave, 1994; Cranford and Hill, 1999).

Biodeposition in the vicinity of suspended bivalve culture may be encouraged by the physical interference posed by bivalve installations (e.g. rafts for deep-water, suspended culture) that alter current flow patterns. Acting as a sediment curtain, suspended cultures can slow current speed through the farm and increase sedimentation rates within its boundaries (Cranford *et al.*, 2006). Plew *et al.* (2005) measured a 36-63% reduction in current speed through a New Zealand mussel farm while Graf and Rosenberg (1997) have estimated that the interception of laterally advected material by the farm, and the increase in deposition of organic material, may double the food supply to the benthos. Biodeposition from fouling communities attracted to the raft structures, including organisms such as polychaetes, starfish, and hydrozoans, may also contribute to observed sedimentation rates at bivalve farm sites (Callier *et al.*, 2006). Stenton-Dozey *et al.* (2001) found that organic loading and anoxia from *M. galloprovincialis* raft culture in South Africa was due not only to the mussels but also to their main biofouler, *Ciona intestinalis*, a tunicate that produces similar waste material.



Additional benthic loading may result from the, potentially, considerable mortality and fall-off of cultured bivalves and fouling organisms in suspended culture (Cranford *et al.*, 2003). For example, a daily average of 130 g·m<sup>-2</sup> of mussels (whole mussels only, not including broken shells or empty shells in traps) fell daily to the bottom under mussel lines in the Magdalen Islands, Quebec in the end of July 2004 (Leonard, 2004). Iglesias (1981) and Freire and González-Gurriarán (1995) noted an abundance of mussels, shell and shell fragments under mussel farms in the Ría de Arosa, Spain, while Inglis and Gust (2003) found that living mussels and mussel shells covered 55% of the bottom within farm sites in New Zealand but were absent from non-farm sites. De Jong (1994) reported that the most noticeable visual impact of mussel farms is the reef-like structure that develops beneath them. In that study, clumps of mussels up to 20-30 cm thick covered 38 % of the seafloor beneath mussel line and reached a density of 250 mussels·m<sup>-2</sup>.

Given the number of factors that may influence sedimentation, or biodeposition, in the vicinity of suspended bivalve farms, and that many of these factors are site specific, it is no surprise that data reported in the literature are highly variable. In addition, data on biodeposition rates in the literature are limited; because sedimentation rates are largely site specific, many researchers focus on biodeposit production rates and/or the impacts of biodeposition rather than using sediment traps to measure biodeposition directly. Hartstein (2003) reported sediment flux rates beneath *Perna canaliculus* farms (8 to 42m water depth) in New Zealand ranging from 133 +/- 22 g·m<sup>-2</sup>·d<sup>-1</sup> to 77.18 +/- 13 g·m<sup>-2</sup>·d<sup>-1</sup> at times of maximum productivity. Hatcher *et al.* (1994) studied sedimentation associated with *M. edulis* and *M. trossulus* sites in Nova Scotia (3 to 7m water depth) and found that sedimentation rates were always significantly higher by at least a factor of 2 at the mussel line site than reference site. Annual mean sedimentation rates of 88.7 g·m<sup>-2</sup>·d<sup>-1</sup> were recorded at the mussel farm site and 36.4 g·m<sup>-2</sup>·d<sup>-1</sup> at the reference site. Although mussel farm sedimentation rates were as high as 177 g·m<sup>-2</sup>·d<sup>-1</sup> in late summer/autumn, rates still were low compared to the 553 g·m<sup>-2</sup>·d<sup>-1</sup> rate measured under a shallow water mussel culture site in Spain (Jaramillo *et al.*, 1992). Hatcher *et al.* (1994) reported that potential input of carbon through sedimentation at both sites was within the range reported in Hargrave (1994) for the same area: 45-1875 mmolC·m<sup>-2</sup>·d<sup>-1</sup>, with input at the mussel site was approx 3.5 times that at the reference site. Grant *et al.* (1995) reported similar sedimentation rates for *M. edulis* sites in eastern Canada, with an annual average of 88.9 g·m<sup>-2</sup>·d<sup>-1</sup>. Rates under *Crassostrea gigas* farms in Baynes Sound BC, in September 2002, were reported to average 39.54 +/- 4.2 g·m<sup>-2</sup>·d<sup>-1</sup> in comparison with 7.95 +/- 2.19 for reference sites (Hay and Co., 2003). Callier *et al.* (2006) studied sedimentation rates at *M. edulis* farms in Quebec and found that their results, similar to those reported in Hatcher *et al.* (1994), showed that suspended mussel culture can increase sedimentation by a factor of 1.3 to 5.5. Comparable results were reported by Stenton-Dozey *et al.* (1999). Cranford and Hill (1999), however, reported that *M. edulis* farms (Nova Scotia) increased natural sedimentation rates by an average factor of 26.



A study on seasonal variation in biodeposition from *M. edulis* farms (11m water depth) in the Adriatic Sea, reported considerably lower sedimentation rates (Danovaro *et al.*, 2004) than those above. Sedimentation rates ranged from 4.5 +/- 1.5 to 17.0 +/- 5.5 g·m<sup>-2</sup>·d<sup>-1</sup> at mussel sites in winter and spring, respectively. The authors found no significant differences in sedimentation rates between the mussel and reference sites. Similarly, there were no significant differences in organic content of the vertical flux between the mussel site and reference site and organic content was relatively constant throughout the year (947.6 +/- 379.3 to 968.2 +/- 216.2 g·m<sup>-2</sup>·d<sup>-1</sup>). The authors suggest that continuous resuspension and/or export of mussel biodeposits may be responsible for the low sedimentation rates recorded (Danovaro *et al.*, 2004). The low sedimentation rates reported by Danovaro *et al.* (2004) are comparable, however, with those reported for *Crassostrea gigas* and *Mytilus planulatis* (native blue mussel native) farms in Tasmania (Crawford *et al.*, 2003). Crawford *et al.* (2003) recorded sedimentation rates that ranged from 7.2 g·m<sup>-2</sup>·d<sup>-1</sup> to 14.5 g·m<sup>-2</sup>·d<sup>-1</sup> at farm sites (8 to 12m water depth). These sedimentation rates are similar to those of Hayakawa *et al.* (2001) under *C. gigas* longline culture in Japan, even though the average oyster density in the latter study was much higher (1100 individuals·m<sup>-2</sup>). Crawford *et al.* (2003) suggest that the lower sedimentation rates they recorded may be due to the timing of their study in mid-late summer, noting that the higher rates reported for other studies (e.g. Grant *et al.*, 1995) occurred during later summer/autumn.

The results summarized above emphasize that bivalve farm biodeposition may be highly site and farm specific. The potential impacts of biodeposition from suspended bivalve culture are also, therefore, highly specific to both site and farm. Given the complexity of factors affecting both feces and pseudofeces production (Section 1) as well as the environmental factors affecting deposition of this material, much of the information in the following review must be considered to represent potential scenarios, rather than predictable scenarios. Prediction of biodeposition and related impacts, through modelling, is discussed further in Section 3.



### 3.3 Potential Impacts of Biodeposition

This subsection reviews the potential impact of biodeposition associated with suspended bivalve aquaculture on benthic biogeochemical and biological parameters (Section 3.3.1). In Section 3.3.1, “biological parameters” refers to infaunal organisms. The potential impacts on benthic epifauna and macrophytes, and on nutrients, are covered in Section 3.3.2 and Section 3.3.3 respectively. Finally, in Section 3.3.4, indicators of benthic impact that can be used to detect the effects of biodeposition from suspended bivalve culture are summarized.

#### 3.3.1 Potential Impact on Benthic Biogeochemical and Biological (Infaunal) Parameters

Most studies on the environmental impacts of biodeposition from suspended bivalve culture involve research on some combination of sediment organic content, total sulphides and oxidation-reduction potential (redox), which have been shown to be indicators of increased organic matter loading (Hargrave *et al.*, 1997). Much research also includes effects on faunal (and floral) communities.

One of the first studies demonstrating a link between increased sedimentation rates under a bivalve lease (relative to a control site), accumulation of organic matter and greater sulfate reduction and sulphide accumulation was carried out for *M. edulis* in Sweden by Dählback and Gunnarsson (1981). A similar increase in benthic sulfate reduction was reported by Tenore *et al.* (1982) for mussel farms in Spain. In a Nova Scotia study, sediment oxygen consumption was found to be highest at sites of suspended culture of *Mytilus* spp., with peaks during phytoplankton blooms (Hatcher *et al.*, 1994). In a study based on the east coast of Canada, Chamberlain *et al.* (2001) found that, in comparison to the sites characterized by fast water velocity, slow-water sites had thick layers of mussel feces, lower redox values, lower benthic diversity, and that the community composition was dominated by opportunistic polychaetes.

The influence of suspended bivalve (mostly mussel) culture on benthic infaunal communities is one of the best studied of all the environmental influences associated with bivalve aquaculture. Where effects have been observed, they have largely followed the typical eutrophication response model outlined by Pearson and Rosenberg (1978). Briefly, as the level of organic input is increased, typical soft sediment communities dominated by large filter feeders are replaced by smaller, more deposit-feeding organisms, starting with small polychaetes (notably, the



opportunistic *Capitella* spp.), shifting to nematodes, and finally ending up with anoxic conditions and mats of the bacteria *Beggiatoa* spp. (see review in Rosenberg, 2001).

One of the earliest studies documenting the benthic effects of bivalve aquaculture on faunal communities looked at long-line culture of *M. edulis* on the Swedish coast and found not only anoxic conditions with hydrogen sulphide production in the upper sediment layers, but also that the mollusk and ophuroid community had been replaced by opportunistic polychaetes (Mattsson and Lindén, 1983). The authors suggest that impacts are long-term, as they observed little recovery of disturbed communities eighteen months after mussels were harvested. Recently, benthic communities under mussel farms in Quebec have been reported to be dominated by opportunistic species (Callier *et al.*, 2004).

Examining *M. galloprovincialis* raft culture in a sheltered bay in South Africa (with an extensive history of bivalve farming and an average current of  $7 \text{ cm}\cdot\text{s}^{-1}$  from tidal forcing), Stenton-Dozey *et al.* (2001) found that sediment POC and PON were higher at farm sites than at reference sites. At some farm sites, bottom waters and sediments were anoxic with total reduced sulphides in the sediments greater than at reference sites. Raft locations had significantly less biomass (5-15% less than reference sites) and a greater proportion of detritivores and carnivores than filter feeders (abundance and biomass of filter feeders was reduced). The authors reported that farm position, rather than age of a raft, correlated with the degree of community disturbance and that impact was localized. Interestingly, this study reports similar observations four years after an intensive mussel raft culture operation was removed, suggesting long-term effects (Stenton-Dozey *et al.*, 1999).

The sediments beneath *Perna canaliculus* farms in Pelorus Sound, New Zealand (tidal flushing rate of  $4 \text{ km}\cdot\text{hr}^{-1}$ ) have been reported to be characterized by lower diversity of benthic fauna: polychaetes dominate at farm stations while reference stations were shown to have bivalves, ophuroids and crustaceans (Kaspar *et al.*, 1985). Hartstein and Rowden (2004) examined three *P. canaliculus* long-line farms in Pelorus Sound with different hydrodynamic regimes. Significant differences were found between the macrofaunal assemblages of samples taken inside and outside the farms at low energy sites but no significant differences were reported between samples taken inside and outside the farms at high energy sites. Sediments near low energy farms were dominated by polychaetes, while sediments at high energy sites were abundant in ophuroids (Hartstein and Rowden, 2004). The authors found that although no single variable explained the trends, sediment total organic matter was higher inside than outside the farms at low energy sites but there was no difference in total organic matter, inside or outside the farms, at high energy sites. They note that if the sinking rate of *P. canaliculus* feces is approximately  $3.45 \text{ cm}\cdot\text{s}^{-1}$ , then the low energy sites would be unable to disperse them.



Mirto *et al.* (2000) studied mussel long-line farms in the Tyrrhenian Sea to assess the use of microbial activity and meiofaunal composition as indicators of impact. In comparison to control sites, farm sites had deeper sediment redox boundaries, higher chlorophyll values, higher proteins concentrations, and were also characterized by higher total bacterial numbers and shifts in bacterial composition to predominantly cyanobacteria. Overall, meiofaunal total densities were lower at farm sites.

Other bivalve culture methods may produce similar impacts, dependent on the specifics of the farm and site. For example, studies on sediments beneath beds of *M. edulis* beds cultivated directly on the sediment in Wales reported that infaunal communities in sediments, in comparison to sediments devoid of mussels, had decreased species composition, decreased total number of individuals, decreased abundance of species, and decreased species richness (Beadman *et al.*, 2004). A study by Smith and Shackley (2004) in the same area demonstrated large and significant changes in sediment grain size characteristics (with a shift to a higher percentage of mud) in the mussel sites accompanied by changes in the benthic community: the total number of species declined and did the overall number of individuals (Smith and Shackley, 2004). Similar to other studies, the shift in the benthic fauna community was away from surface deposit feeders and filter feeders to deep-deposit feeders and predators.

The influence of bivalve farm and site characteristics, biodeposition can be such that biodeposition have a “positive” environmental impact. Limited organic matter input can enhance benthic production, both primary and secondary and can result in improvements in sediment quality for consumption. For example, Thorne (1998) found a higher diversity and total number of benthic species plus a higher number of total individuals at oyster culture sites than at sites without culture activities. These results suggest that the oyster sites were indicative of “mild organic enrichment” (Pearson and Rosenberg, 1978). Large scale effects on the benthos should also be considered. For example, Pillay (2004) suggested that although there might be an area of reduced biomass directly below aquaculture sites, there would also be a transition zone some distance from aquaculture sites, in which enhanced organic enrichment would stimulate the growth of the benthos.

Some studies have detected no biodeposit-related responses at bivalve culture sites (Crawford *et al.*, 2003; Danovaro *et al.*, 2004). The benthic environments under and near three farms (combinations of *M. edulis* long lines and *Crassostrea gigas* trays) in Tasmania were compared with the benthic environments outside the farms. The farms had long-term, high levels of production and average current speeds between 3.4-3.8 cm·s<sup>-1</sup>. Sediment deposition, redox values, sediment sulphide concentrations, organic carbon content and water turbidity levels near the bottom were significantly different between the farms but not significantly different between sites outside each farm and sites within each farm. Benthic infauna did not show clear signs of organic enrichment and benthic infauna were not significantly different between sites inside and outside each farm, although they were different between the three farms. One



site did have dense coverage of fine filamentous algae, thought to have fallen off the mussel longlines, and patchy bacterial mats while another site had dense seagrass beds under oyster trays and outside the farm (Crawford *et al.*, 2003).

Danovaro *et al.* (2004) looked at Central Mediterranean mussel long-line culture and found that for sediments at farm sites versus sediments at reference sites, there was no significant difference in the depth of the redox boundary layer, total mass flux, organic matter flux, chloropigment concentrations, phaeopigment concentrations, meiofaunal abundances, total bacterial counts or frequency of cell division. The study showed that seasonal differences were significant but not with respect to farm versus control; for example, total organic matter was only slightly higher at farm sites but it was higher at control sites in the spring. Unfortunately, however, the study did not report information on site characteristics.

McKinnon *et al.* (2003) compared sediments and fauna beneath suspended long-line culture of *M. edulis* in Port Phillip Bay Australia with those between 5, 25 and 50 m distance from the farm. While the percentage of sediments  $<63\mu\text{m}$  decreased significantly with distance from the farm, there were no significant trends in %total organic carbon or redox potential with distance from the farm. The lowest redox potential values were recorded beneath the farm, however. Spatial differences in infaunal communities did not indicate that communities beneath the farm were distinct from those further from the farm although infaunal species diversity and richness were greatest beneath the farm and decreased significantly with distance from the farm. Epifaunal species of bivalves and starfish were also abundant at farm sites. The authors concluded that environmental impacts from long term mussel farming in Port Phillip Bay were small and restricted to the immediate vicinity of the farmed area. They suggest that the low impact of this mussel farm compared to impacts of farms in other regions may be due to the relatively low production of farms in Port Phillip Bay ( $\leq 15\text{-}30\text{t}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$ ).



### **3.3.2 Potential Impact on Benthic Epifauna and Macrophytes**

The majority of research on the influence of suspended bivalve culture, as summarized above, has largely concentrated on benthic processes (physical, chemical and biological) as they relate to increased organic loading associated with biodeposition (Carroll *et al.*, 2003). With respect to the biological component, typically only infaunal communities are assessed. Tenore and Dunstan (1973) found that elevated levels of biodeposition associated with aquaculture of *M. edulis*, *C. virginica*, and *M. mercenaria* enhanced detrital food-chains, thereby augmenting the standing stock of benthic invertebrates and ultimately fisheries species. Increased biodeposition may increase the abundance of certain large, epifauna taxa (McKindsey *et al.*, 2006). For example, Olaso (1979, 1982) reported a greater abundance of sea cucumbers (deposit-feeders) in mussel culture sites than outside of them. Tenore and González (1976) also found that there was little unworked mussel biodeposits in the sediments underlying the mussel rafts; most had been reworked by the community there, including sea cucumbers (Costelloe and Keegan, 1984).

Winter flounder (*Pseudopleuronectes americanus*), one of the dominant fish species in the lagoons of the Magdalen Islands, appears to have an increased abundance within mussel farms (McKindsey *et al.*, 2006). Winter flounder shift their diet with ontogenetic stage; the smallest sizes depending mostly on small polychaetes (Stehlik and Meise, 2000) which often dominate under mussel aquaculture sites because of increased nutrient loads (Mattsson and Lindén, 1983). Not surprisingly, only the smallest size classes of winter flounder are more abundant under mussel lines (Callier, unpubl. data). Winter flounder are particularly susceptible to predation by sand shrimp (*Crangon septemspinosa*), which are ubiquitous in most coastal areas in NE Canada, including the Magdalen Islands, and this susceptibility is size-dependent (Taylor, 2003). The faster the flounder grow and attain a size refuge from predation, the greater their contribution to overall productivity. Hence, there is some evidence that mussel aquaculture in the Magdalen Islands may lead to increased productivity of this fish species (McKindsey *et al.*, 2006).

Biodeposition, in the form of fall-off, from bivalves in suspended culture operations and their associated fauna, may enhance the amount of food available to benthic predators. As noted earlier, the fall-off of mussels and other bivalves in suspended aquaculture may be considerable. A marked increase in the abundance of large mobile predators (rock crab, lobster, and starfish) under mussel lines in the Magdalen Islands (McKindsey *et al.*, unpublished data) was associated with a daily average fall-off of whole mussels of 130 g m<sup>-2</sup> in July 2004 (Leonard, 2004). A number of other authors have also reported a



greater number and/or biomass of benthic predators, that likely prey directly on bivalves fallen from suspended culture, within culture sites relative to control sites. These include starfish (Saranchova and Kulakovskii, 1982) and crabs (Miron *et al.*, 2002). Urchins are attracted to the fast growing kelp falling from mussel lines in eastern Canada (MR Anderson pers. obs.) and, in the Mediterranean, benthivorous fish have also been documented feeding on mussel fall-off (Gerlotto *et al.*, 2001). Gerlotto *et al.* (2001) measured an increase in fish density and production around mussel lines in the Mediterranean that they attributed directly to the increased prey availability at the farm site.

Romero *et al.* (1982) studied the spatial distribution of crabs with respect to the location of suspended mussel culture sites in Ría de Arosa in Spain. Over 4 seasons, they found that both the abundance and biomass of 3 dominant crab species were greatest within mussel farms, relative to control sites. In fact, there was on average more than twice the number of crabs within mussel sites relative to control sites. In the same area, two species of crab fed preferentially on mussel fall-off when found at culture sites (Freire *et al.*, 1990; Freire and González-Gurriarán, 1995). Olaso (1979, 1982) studied the distribution of echinoderms in the same ría and observed 10 times the biomass of echinoderms (mostly starfish) within mussel sites relative to control locations, the starfish feeding on the mussels that had fallen from the rafts overhead. In an ongoing study, D'Amours *et al.* (2005) found the abundance of several macroinvertebrate and fish species to be greater within a series of mussel culture sites than in control locations in PEI. Mussels fall-off on the seafloor reportedly serve to aggregate the predatory starfish *Coscinasterias muricata* under mussel lines in Pelorus Sound, New Zealand; mean density of the starfish population at farm sites was 39x that at non-farmed sites and was strongly related to mussels abundance (Inglis and Gust, 2003). The authors suggest that this food source likely increases the starfish's reproductive output by enhancing growth and gonad maturation rates. Taken together, it seems quite likely that the productivity of this species may be increased by the presence of bivalve aquaculture.

Bivalves and associated fauna that fall from suspended bivalve operations may not only serve as food, but may also provide a physical structure that acts as habitat for species normally associated with hard-bottom communities. Hence, suspended bivalve culture may lead to a soft-bottom benthic community changing into a hard-bottom benthic community. Inglis and Gust (2003) found that the benthic physical structure within farm sites in New Zealand was substantially increased by the living mussels and mussel shells that covered 55% of the bottom. The reef-like structure that develops beneath New Zealand mussel farms, consisting of clumps of mussels up to 20-30 cm thick covering 38 % of the seafloor beneath mussel lines, has been reported as the most noticeable visual impact of the farms (de Jong, 1994). Iglesias (1981) and Freire and González-Gurriarán (1995) found an abundance of mussels, shell and shell fragments in the Ría de Arosa and suggested that the additional physical structure in the system provides "habitat refuge" for associated species.



Hard-bottom communities are generally more diverse, have a greater biomass (Ricciardi and Bourget, 1999) and are more productive (Cusson and Bourget, 2005) than soft-bottom communities. Thus suspended bivalve culture may have indirect positive effects on local ecosystem diversity and productivity. Kaspar *et al.* (1985) found that the build-up of live mussels and shell material under a mussel farm in New Zealand allowed for the development of a community with tunicates, calcareous polychaetes and sponges, species normally associated with hard-bottom reefs. Iglesias (1981) discussed the importance of the increase in habitat heterogeneity, due to the physical structure under mussel rafts, in augmenting the diversity of fishes and the abundance of active predators relative to control sites. Greater fish abundance, diversity and biomass have been reported for mussel sites than control sites, albeit with temporal variations in trends by Iglesias (1981) and Chesney and Iglesias (1979).

While mechanisms of interactions between natural aggregations of suspension-feeding bivalves and macrophyte communities have been clearly demonstrated (for review see McKindsey *et al.*, 2006), the same is not true for bivalves in suspension culture. No known published studies have addressed the issue of ecological interactions between suspended bivalve aquaculture and macrophyte communities in a rigorous and scientifically defensible fashion (McKindsey *et al.*, 2006). This is particularly surprising in light of the expansion of suspended bivalve culture internationally, increased recognition of the critical ecological roles of macrophyte communities, and observed global declines of seagrasses.

The available literature on interactions between other forms of bivalve aquaculture (e.g. off-bottom culture) and macrophytes is summarized in McKindsey *et al.* (2006) and is only briefly mentioned here. Two studies comparing recent data and historical records, came to different conclusions in regard to the effects of extensive off-bottom culture of oysters and mussels in Thau Lagoon, France. Deslous-Paoli *et al.* (1998) concluded that *Zostera* spp. have extended their distributions from shallow regions to areas up to 5m depth in some areas of the lagoon and attribute this to reduced turbidity in culture regions as a result of bivalve filter feeding. In contrast, De Casabianca *et al.* (1997) concluded that over the past 100 years, macrophyte communities have shifted from dominance by *Zostera* to dominance by opportunistic algae due to elevated levels of nitrogen and increased turbidity resulting from bivalve culture-driven eutrophication. Stake and rack culture of *C. gigas* in the Pacific northwestern United States has resulted in significant reductions in percent cover ( $\leq 75\%$ ) and shoot densities of *Zostera marina* (Carlton *et al.*, 1991; Pregnall, 1993). Similar results were found by Everett *et al.* (1995) who suggested that density declines of *Z. marina* were the result of sedimentation, in combination with erosion and substrate disturbances during set-up and harvesting of oysters in stake and rack plots.



Suspended bivalve culture could potentially result in negative as well as positive influences on macrophyte assemblages via mechanisms related to bivalve filtering capacity (decreasing turbidity and subsequently stimulating photosynthesis) and/or enhancing benthic-pelagic coupling (enhancing nutrient concentrations and cycling rates) through deposition of feces and pseudofeces (reviewed by Newell, 2004; Deslous-Paoli *et al.*, 1998); also see Section 3.3.3 following). Most arguments put forth in the literature are derived from studies of natural bivalve assemblages (for review see McKindsey *et al.*, 2006) or from anecdotal observations obtained during studies of benthic fauna. For instance, tangential to examining benthic macrofaunal communities in and around Tasmanian bivalve farms, abundant seagrass communities were observed under oyster off-bottom leases in certain regions (Crawford *et al.*, 2003).

### **3.3.3 Potential Impact on Nutrients**

There is an extensive literature describing how high numbers of filter feeding bivalves can alter nutrient dynamics in their environment (for reviews see McKindsey *et al.*, 2006; Dame, 1996; Cranford *et al.*, 2003). High concentrations of bivalves can influence dissolved concentrations of inorganic forms of nitrogen, phosphorus and silicate: ammonia and phosphate are excreted, and ammonia, phosphate and silicate are released from benthic environments by the decomposition of bivalve biodeposits (Dame *et al.*, 1991; Smaal and Prins, 1993; Prins and Smaal, 1994; Strain, 2002). Nutrient cycling rates and availability may also be increased in the presence of suspended culture through the mineralization of the large amounts of feces and pseudofeces trapped within the holding structures (e.g. mussel socks). This permits nutrients to be released at shallower, more nutrient-depleted depths than occurs if the nutrients are regenerated in the sediments (Strain, 2002). Because nitrogen is usually considered to be the nutrient limiting primary production in coastal ecosystems, the most attention has been paid to nitrogen cycling. However, bivalve culture also has the potential to affect N:P and N:Si ratios, with possible consequences for phytoplankton dynamics (Cranford *et al.*, 2003).

At bivalve aquaculture sites, increased organic matter sedimentation, from both cultured species and fouling organisms, can act to retain nutrients in the coastal region (Dählback and Gunnarsson, 1981; Kaspar *et al.*, 1985; Feuillet-Girard *et al.*, 1988; Barranguet *et al.*, 1994; Grant *et al.*, 1995). A shortened cycle of nutrients between the benthos and phytoplankton (for example, the rate of nitrogen cycling is greatly increased) can increase local nutrient availability as less material is exported (Jordan and Valiela, 1982; ICES, 2004) greatly increasing rates of nitrogen cycling. Nutrient regeneration rates under bivalve farms are some of the highest measured in marine environments (Prins and Smaal, 1994). Even at sites where natural deposition is high and sediments are already organically rich, mussel farms can significantly enhance the release of inorganic nutrients from the sediments. In coastal fjords of Newfoundland, where natural sediments may have up to 35% organic matter, sediments under mussel farms can release 5 to 10 times more ammonium than nearby reference sites (Strang, 2003). The efflux



of ammonium from the sediments in the presence of bivalve culture is also reported by Hatcher *et al.* (1994). Phosphate release is also enhanced under farms when redox conditions are suitable for phosphorus mobilization (Strang, 2003).

The reducing conditions under bivalve cultures may increase denitrification (Kaspar *et al.* 1985), a process that represents a net loss of nitrogen from the system to the atmosphere. Newell (2004) suggests that enhancement, by bivalve biodeposition, of the burial of N and P and removal of N from the ecosystem via denitrification (Newell *et al.*, 2002; Newell *et al.*, 2005) may be often overlooked. However, the system will shift to dissimilative nitrate reduction in the presence of sulphide with increased organic loading and denitrification rates will then be reduced (Christensen *et al.*, 2003). In addition, factors such as the abundance of microphytobenthos also affect nutrient transformations and regeneration (Sundbäck and Graneli, 1988; Sundbäck *et al.*, 2000); microphytobenthos reduce the rates/amounts of sediment-water transfer of nutrients (Christensen *et al.*, 2003). Increased biodeposition has been shown to reduce the abundance of microphytobenthos under mussel farms in New Zealand, leading to an increase in ammonium efflux (14x that of sites with higher levels of microphytobenthos) (Christensen *et al.*, 2003).

The effect of regenerated nutrients from the sediments on the water column and primary productivity will depend on several factors primarily related to the hydrological regime of the system. In shallow lagoons and well mixed coastal areas, nutrient regeneration may enhance primary production of phytoplankton or macrophytes (Bartoli *et al.*, 2001). At other sites, however, stratification may prevent return of nutrients to the upper water column.

In addition to the nutrients supplied as a result of efflux from the sediments, bivalves excrete ammonia directly into the water column. While mineralization of biodeposits has been suggested to be a more important nutrient source for phytoplankton production than direct excretion (Asmus and Asmus, 1991; Prins and Smaal, 1994), it has also been suggested that the high flux of excreted ammonia from dense bivalve populations can have a major effect on phytoplankton and exert a controlling influence on nitrogen concentrations in some coastal regions (Maestrini and Spano, 1986; Dame *et al.*, 1991; Dame, 1996; Strain, 2002).

Feedback between bivalves, phytoplankton and nutrients (released from sediments and ammonia excreted directly into the water column) have been well-studied (see Dame, 1996 for review). Release of nitrogen compounds associated with dense bivalve populations can promote primary productivity in environments where nitrogen may be limited (Kaspar *et al.*, 1985; Asmus and Asmus, 1991) and may potentially alter phytoplankton community composition (leading to effects on grazer species composition and abundance) and contribute to more frequent algal blooms (Bates, 1998; Bates *et al.*, 1998; Philippart



*et al.*, 2000). Pietros and Rice (2003) used mesocosm experiments to study *C. virginica* in the northeastern United States and found that, when compared to control treatments (no oysters), oysters not only impacted phytoplankton species composition but also contributed to the regeneration of phytoplankton through the rapid scavenging of dissolved inorganic nitrogen products. In France, Souchu *et al.* (2001) found that the high density of oysters in the Thau Lagoon were not food-limited during the summer because of the great rate of nutrient fluxes from the benthos stimulating the growth of phytoplankton. Using *in situ* enclosure experiments in summer and winter, Ogilvie *et al.* (2003) studied the influence of the cultured mussel *Perna canaliculus* on the abundance of phytoplankton in Pelorus Sound, New Zealand. In summer, mussels caused an increase (11–17%) in phytoplankton biomass, possibly by converting particulate nitrogen to ammonium, making the nitrogen available for phytoplankton utilisation. A significant increase of chlorophyll a was also observed in enclosures with no mussels to which nitrogen was added, indicating that the phytoplankton were nitrogen-limited. However, in the winter, the highest chlorophyll concentrations were found during periods of high ambient nitrogen, suggesting that phytoplankton in the winter are light-limited, not N-limited (Gibb and Vant, 1997). In the winter, the mussel-only enclosures actually reduced phytoplankton biomass through grazing (5-14%).

Not all studies demonstrate a nitrogen link between bivalve aquaculture and phytoplankton. La Rosa *et al.* (2002) looked at the impact of mussel and finfish farms on water column nutrients. Dissolved inorganic nitrogen (DIN) was found to be higher in the mussel culture but this did not seem to alter the chlorophyll concentrations to the phytoplankton population. Mazouni (2004) investigated the availability of nitrogen production to phytoplankton from a long-line culture site that had pre-existing high levels of primary production but were ultimately N-limited. Peaks in dissolved inorganic nitrogen in the water column were coincident with high DIN releases from the cultures and also high nitrogen flux from the sediments. The main species of DIN was ammonium and efflux was highest in the summer-autumn, likely a result of high temperatures and higher metabolic activities (Mazouni, 2004). Renewal of N was greater at the culture-water interface than the benthos interface and the efflux of ammonium was higher in sediments under the culture (Mazouni, 2004). However, there was no correlation between chlorophyll-a trends and DIN concentrations suggesting that renewal and regeneration of DIN from the sediments was insufficient for primary production.

A concern with excess nitrogen compounds (whether excreted or effluxed from the sediments) is that it is a precursor condition to eutrophication, especially in sheltered or poorly tidally flushed locations. Souchu *et al.* (2001) studying the Thau Lagoon system suggested that the oyster and mussel culture, in addition to poor flushing rate, may be a factor that is predisposing this area to eutrophication. In contrast, however, mussel farms have been suggested to limit the impact of eutrophication in ongoing aquaculture operations in Prince Edward Island (Landry, 2002) and for eutrophication-targeted operations in Sweden



(Haamer, 1996). Bivalve culture may also have another influence on eutrophication inasmuch as the bivalves themselves act as a sink for nitrogen and other elements that are removed at harvest. Harvesting of nutrients via removal of bivalves may be used to alleviate the local effects of nutrient addition by fish farms (ICES, 2004). A number of salmon farms in Scotland and Canada are combining the culture of mussels and salmon on an experimental basis (Robinson *et al.*, 2003; Cook *et al.*, 2003). In the case of more oligotrophic systems, such as off-shore in New Zealand, this may have a negative effect on the system as nutrients may be limiting there (Kaspar *et al.*, 1985) but there is little direct evidence of environmental effects (ICES, 2004).

Although the enumeration of the processes through which high concentrations of bivalves can influence nutrient dynamics is straightforward, and field studies have confirmed that these mechanisms operate, predicting the net impact of these processes on nutrient levels is problematic. Ultimately, the balance between nutrient excretion back to the water column and nutrient removal via sedimentation and harvesting will depend on numerous scaling factors including hydrographic features of the system, nutrient supply and seasonality and the biomass of the bivalves on the farm(s) (McKindsey *et al.*, 2006). Further research is needed to assess the ability of different coastal regions to resist or assimilate the effects of increased organic enrichment through a variety of physical and biogeochemical processes. For some locations, different types of ecosystem models are available and are starting to give us a picture of how intense bivalve aquaculture can modify whole ecosystems. Such models contribute significantly to our understanding of interactions between cultured bivalves and the environment, and will inform bivalve aquaculture management. But they are not yet capable of suggesting attributes of the nutrient cycle that would be suitable for monitoring, or thresholds of such variables that could be used to trigger management actions (Cranford *et al.*, 2006).

#### **3.3.4 Indicators of Impact**

The extensive global work on the benthic impacts of bivalve aquaculture has led to the development of a number of indicators of impact that, while obviously varying in intensity depending on the specific situation, can be generalized (Cranford *et al.*, 2006). Chemical indicators include a low-negative oxidation-reduction potential (redox) and a deep redox boundary layer in sediments; anoxic conditions with high oxygen consumption rates and high levels of hydrogen sulphide; higher levels of organic material, carbon and nitrogen, efflux of dissolved inorganic nitrogen from the sediments and finer grained sediments. C:N ratios may be altered and there may be higher rates of denitrification in the sediments, but these latter two indicators are inconsistent. Biological indicators include reduced diversity, species richness, total number of individuals or abundance, and meiofaunal density. Additional biological indicators are increases in total bacterial numbers, the presence of *Beggiatoa* spp. and a shift from filter



feeding/surface deposit feeders to predator/carnivore species, deep burrowers, and opportunistic polychaetes (e.g. *Capitella capitata*) (Cranford *et al.*, 2006).

The above biogeochemical measures and infaunal community assessments address only a component of the ecosystem, however, and cannot be used in some situations (e.g. hard substrates) or may be of questionable value when working in protected coastal areas where organic loading is already very high (McKindsey *et al.*, 2006). Macroinvertebrate epifauna and fishes, some of which are important commercial or recreational species, are important components of the ecosystem that are often not considered in studies of the potential impacts of bivalve aquaculture or in management decisions. These ecosystems are complicated and a “negative” effect in one component may also result in a “positive” effect in another. For example, for suspended bivalve culture no literature was found that reported net “negative” effects on macrofauna and fishes (McKindsey *et al.*, 2006).



## 4.0 Modeling Biodeposition From Suspended Bivalve Aquaculture

Over recent years, modeling effort with regard to bivalve aquaculture has focused primarily on predicting and exploiting capacity rather than environmental interactions (although the two are closely linked) (Chamberlain *et al.*, 2006). Historically, modeling the benthic effects of suspended bivalve farming has received little attention. Bivalve aquaculture may be generally perceived as having less dramatic environmental effects than finfish aquaculture, for example, as feed is not added to the environment and bivalves are grown at comparatively low biomass per unit area (Callier *et al.*, 2006). However, because of the increasing number and size of commercial bivalve farming operations, there is increasing interest, however, in application of models to predict biodeposition and benthic impacts, as well as other ecosystem effects, associated with bivalve farms. In order to ensure the sustainable development of the bivalve culture industry, a better understanding of the relationship between bivalve production and its influence on the benthic environment is needed.

Generally, the accuracy of model predictions will be determined by the suitability of the model to the test environment, how the model is configured and the quality of the data used in parameterization (Chamberlain *et al.*, 2006). Also, the scale at which the effects of bivalve aquaculture may occur (localized to far field) means that different processes have to be taken into account within models, depending on the type of effect being simulated. Recent and ongoing research focuses on the application of particle tracking models, such as DEPOMOD (Cromey *et al.*, 2002), that can be applied to predicting (organic) flux from culture sites to a localized area of seafloor for bivalve farming scenarios (Chamberlain, 2002; Hartstein and Stevens, 2005; Chamberlain *et al.*, 2006). With these models, a quantitative relationship between flux and a benthic community descriptor may be developed to predict the influence of different levels of aquaculture on benthic status (Chamberlain, pers. comm.; Henderson *et al.*, 2001). Because these models provide *a priori* assessment of the potential nature and scale of effect of individual aquaculture operations on their near-field benthic environment, they are of increasing interest and utility to habitat management and operators alike (Chamberlain *et al.*, 2006). In addition to particle tracking, or waste sedimentation models, which focus on localized deposition, ecosystem models that take a broader approach also have been applied to predicting rates, and impacts, of biodeposition from bivalve aquaculture (Dowd, 2005; Grant *et al.*, 2005). It has been suggested that a carefully designed ecosystem model and supporting measurement program can provide an understanding of not only how a coastal ecosystems works, but under what conditions significant aquaculture impacts might be expected (Chamberlain *et al.*, 2006).

Following are discussions of the application of particle tracking models (Section 4.1) and ecosystem models (Section 4.2) to biodeposition associated with bivalve aquaculture.



#### 4.1 Particle Tracking Models

Until recently, modeling the processes and effects of enhanced sedimentation in the marine environment has concentrated on sources where the quantity and nature of material being discharged can be calculated and, to some degree, regulated. Sewer outfalls, pulp mill effluents and cage finfish farms are readily amenable to waste sedimentation/particle tracking modeling. Silvert and Cromey (2000) reviewed modeling approaches to finfish farming. Spatially explicit hydrodynamic-dependent particle tracking models, such as DEPOMOD, predict (organic) flux from culture sites to the bottom and a quantitative relationship between flux and a benthic community or biogeochemical descriptor may be developed to predict the influence of different levels of aquaculture on benthic community structure (Henderson *et al.*, 2001).

A variety of particle tracking models, all of which use the same basic algorithm, are available for use with finfish farm scenarios (Chamberlain, pers. comm.). For finfish farm situations, these models simulate the trajectory of particles (feces and waste feed pellets) as they are released from a cage structure and settle through the water column, to give a prediction of the magnitude and spatial extent of the deposition of material on the seabed (Chamberlain *et al.*, 2006). Further predictions, linking the flux of material to changes in the biological structure and/or chemical status of the seabed may be achieved through the use of field measurements and semi-empirical models (e.g. Cromey *et al.*, 2002). The fundamental forcing parameters used in these models were initially reported by Gowen *et al.* (1989) as the hydrographic regime, depth of water and settling velocity of the waste material. To be effective, the overall model must represent all the important processes (e.g. advection, deposition, resuspension) that affect, or cause, benthic impact. A detailed analysis of a number of finfish waste sedimentation models is presented in Chamberlain *et al.* (2005).

Waste sedimentation/particle tracking models designed for finfish farms are now being adapted for bivalve aquaculture (Chamberlain pers. comm.; Chamberlain *et al.*, 2006).

Factors that may contribute to the effect of bivalve farms on their local environments, and that must be considered in the model, include the quantity and quality of material exiting the farm, dispersion of this material and the fate of waste material post-deposition (e.g. resuspension). While the processes acting on the particles as they settle through the water column will be the same for bivalve farms as for finfish farms, and can be simulated through modeling, aspects of model parameterization and data input of the finfish farm models require modification for the bivalve farm scenario. Specifically, food loading/excretion rate values (unlike finfish farms, no additional feed is added to the system), settling rates of bivalve biodeposits (feces and pseudofeces) and farm structure configuration require modification. Chamberlain *et al.* (2006) provided a detailed discussion on these parameters and their associated variability in regard to bivalve farm scenarios and, therefore, these issues are summarized only briefly here.



Unlike finfish farms, determining food loading and excretion rate values for bivalve farms is not straightforward and cannot be calculated using known quantities of food supplied to the farm together with feed conversion and wastage rate estimates. Production rate of biodeposits from bivalve farms, as discussed in Section 1.3, is both highly site specific and temporally variable and is dependent on a range of complex and interrelated factors including: supply of suspended material (concentration and rate), quality of suspended material (organic content, silt content), feeding behaviour of mussels (rate, assimilation), and biomass of mussels (stocking density) estimates (Chamberlain *et al.*, 2006). Some of these factors, such as quantity and rate of food delivered to the farm site, are relatively simple to measure and model, but other factors, including bivalve feeding behaviour and excretion rates, are not so well understood. For example, daily seston availability and several environmental parameters could only explain 28% of the variation in daily ingestion rates of *Mytilus edulis* (Cranford and Hill, 1999). The application of feed conversion parameters to a known food loading in order to derive environmentally-realistic bivalve biodeposit quantity estimates, and to produce model results comparable to field measurements, is extremely difficult (Chamberlain, 2002). Although the application of a generic conversion factor for feed input to biodeposit output for whole farm scenarios is not considered possible at present (Chamberlain *et al.*, 2006), measuring and/or calculating the actual rate of quantity of material released from a bivalve farm site can be used as an alternate strategy for defining the feed load/excretion rate parameter for modeling. This strategy removes the requirement to parameterize and model all the above factors and to calculate the rate of quantity of material released, the measured *in situ* biodeposit production rate of bivalves at a farm site can be extrapolated to the spatial scale of interest (e.g. raft, line or whole farm). Chamberlain *et al.* (2005) noted that although there is significant potential for the introduction of errors in such a scaling calculation, such estimates and calculations may not be unreasonable if the biodeposit production measurements are conducted under actual site conditions.

Particle settling rate is a dominant parameter requiring characterization in all particle tracking models. Available information on the settling rates of bivalve biodeposits is reviewed, in detail, in Section 3.1. Fecal settling rates are variable with some of the variation likely due to size and composition (density). Reported settling rates of biodeposits may also differ from those for feces as a result of the incorporation of pseudofeces; the latter have a fluffy texture and, as a result, usually have slower settling rates than fecal pellets (Giles and Pilditch, 2004) and may thus be dispersed even further than fecal pellets. However, different particle types with different sinking velocities can be modeled in DEPOMOD (Chamberlain *et al.*, 2006). As noted in Section 3, and as recognized by DEPOMOD, the area over which biodeposits will settle on the benthos will be strongly influenced by residence time in the water column, dependent on water movement and site depth. Most particle tracking models require the location of the particles' start position to be defined and, for finfish farms, this generally involves defining the location and dimensions of the cages, after which the particles are then released at random points within



the structure. For the suspended bivalve culture scenario, the 'cage' may be defined as the whole farm, individual lines or single droppers (Chamberlain *et al.*, 2006).

Similar to particle tracking models used in finfish farm scenarios, those used in bivalve farm scenarios all use the same algorithm (Chamberlain, pers. comm.). To date, however, case studies and application of particle tracking models to bivalve farm scenarios have been attempted by only a small number of researchers and all studies to date are on mussel (*Mytilus edulis* or *Perna canaliculus*) farms. Chamberlain (2002) first explored techniques for applying DEPOMOD to bivalve farm scenarios, using mussel farms in Scotland and Ireland. In this study, the outputs were quantified as predictions of a benthic community descriptor, the Infaunal Trophic Index (ITI)<sup>1</sup> (Word *et al.*, 1978) values. ITI values were generated from a semi-empirical model, a sub-module within DEPOMOD, validated for finfish farms in Scotland. ITI values were compared with field measurements but difficulties were encountered in quantifying the feed load/excretion rate values. The author found that the model tended to over-predict the degree of impact when food loading and feed conversion estimates were applied, whereas estimations of the quantity of material exiting the farm structures resulted in underestimates of effect. Chamberlain (2002) concluded that there were processes involved that were not taken into account in the modeling process and that further research was necessary before realistic predictive capability could be attained.

Hartstein and Stevens (2005) combined current meter data, biodeposit settling velocity, turbulent diffusivity and water depth to model the initial depositional distribution of biodeposits at three mussel (*Perna canaliculus*) farm sites in sheltered to exposed environments (Marlborough Sounds, New Zealand). Rather than attempting to model the

<sup>1</sup> The validity of ITI is the subject of controversy and it has been suggested that more recently-developed indices, although also not fully validated, may be more appropriate than the ITI (ICES 2005). explicit hydrodynamics of the sites, the authors chose to drive the model with the observed variability and then conduct a sensitivity analysis of the controlling parameters.

Comparison of the modelled dispersal pattern and seabed identification of mussel biodeposits, using sedimentological data, indicated a very close association at sheltered sites. Both were found to reduce to natural levels approximately 30–50 m from the farm site (Hartstein and Stevens, 2005). The similarity between the model and observed distribution of the mussel biodeposits suggested that, once deposited on the seabed, the biodeposits remain immobile due to the low hydrodynamic energy of the sites. The exposed site, in contrast, had only a poor correlation between the dispersal model and identification of mussel biodeposits on the seabed. While the dispersal model indicated that the majority of mussel biodeposits initially accumulated within 50 m of the farm, observations found no sign of any mussel biodeposits in sediment up to 200 m from the farm boundary. Lack of biodeposits at the exposed site was



interpreted to mean that there is, at times, sufficient energy for resuspension and for dispersion of these deposits over a wide enough area to result in little impact on the natural sediment (Hartstein and Stevens, 2005). The authors note, however, that a number of processes have been ignored in the simplified model, including the distortion of flow through the farm due to the long-lines (Plew *et al.*, 2005) and that New Zealand-style long-lines subjected to strong current and/or wind are often deflected up to 10 m thereby widening the potential dispersal in comparison to a static long-line. The simplified model also ignored waves, the effect of seabed variability and that flow will, in reality, be spatially variable. Resuspension was also ignored. Limitations and assumptions of particle tracking models are discussed in more detail later in this Section.

Chamberlain *et al.* (2006) used data from a suspended *Mytilus edulis* culture site in the Magdalen Islands, Quebec as a case study for the application of DEPOMOD. The model input parameters were based on *in situ* measurements (some extracted from the literature) of biodeposit production rate, fecal pellet settling rate and hydrographic data. Model outputs were compared with field measurements of sedimentation. The model predicted the main area of deposition was directly beneath the farm site, a reflection of the very shallow nature of the site. Model predictions of solids flux compared favourably with observed flux, although the model tended to underpredict the scale of sedimentation when compared to field data. This may have been due to the model or it may have been a capture device artefact (Chamberlain *et al.*, 2005).

The final component required in this modeling process, particularly for applicability to management, is the prediction of scale of change or effect to the benthic status - generally measured as alteration to the benthic community structure (e.g. ITI) and/or sediment quality - as a result of the increased flux or accumulation of waste (Chamberlain *et al.*, 2006). A number of semi-empirical models have been developed that predict measures of benthic impact such as the benthic enrichment index in sediments (Hargrave, 1994) or indices of benthic diversity (Cromey *et al.*, 2002). Preliminary field trials examining the relationship between dose (biodeposit flux) and response (benthic community index/geochemical measure) have already been conducted to assess the effect of a range of biodeposition rates on seabed conditions (Callier *et al.*, 2004). When such relationships can be demonstrated to be significant, model predictions of the degree and spatial extent of benthic impact may be made at other locations having similar substrates, oceanographic and hydrodynamic conditions (Chamberlain *et al.*, 2006). Hence, these models can be used as a management tool to aid mussel growers and regulators in selecting bivalve culture sites, defining site limitations, optimizing production as well as designing and implementing monitoring programs.

In summary, results of the preliminary application of a particle tracking model to mussel culture sites (Quebec, Scotland, Ireland) shows promise with regard to predictive capability (Chamberlain, pers.



comm.). The physical processes affecting the deposition of particulate waste from bivalve sites are well parameterized in the model but the uncertainty in the feed load/excretion rate parameter is a significant concern, as it is a critical input into the model, affecting all subsequent predictions (Chamberlain *et al.*, 2006). There are new and promising modeling techniques to better define this input parameter, although the application of a generic conversion factor (food input to biodeposit output) is still premature (Chamberlain *et al.*, 2006). Model performance, and the ability to assess predictive capability, will similarly be improved by coupling biodeposit flux and changes in the benthic status (biology/chemistry) with linkage to model outputs (Chamberlain *et al.*, 2006).

Particle tracking models, like all models, have assumptions and limitations. Chamberlain *et al.* (2006) noted that a number of processes not yet incorporated into these models could potentially have significant effects on the fate and impact of biodeposits. These processes include the effects of the physical structure of the farm on water movement and post-deposition modification of particles, including resuspension and degradation. The resuspension of sedimented material is complex (depends on sediment type, cohesiveness, flocculation, degradation, etc.) and clearly varies both spatially and temporally. More studies are required to validate the current default values used in DEPOMOD (e.g.. critical erosion threshold, consolidation time) for bivalve culture (ICES, 2005). Additional limitations include the effects of application of a spatially homogenous horizontal flow field within the model domain and the effects of turbulence on the integrity of fecal and pseudofecal particles (Chamberlain *et al.*, 2006). There are a number of studies currently underway, in Quebec and in Europe, to examine the application of particle tracking modeling techniques to predict the effect of increased sedimentation from suspended bivalve farms on the benthic environment (Chamberlain, pers. comm.). As more information becomes available, confidence in the predictive capability of these models will increase.

#### **4.2 Ecosystem Models**

In addition to particle tracking models that focus on localized deposition, ecosystem models also have been applied to predicting rates, and impacts, of biodeposition from bivalve aquaculture. Ecosystem models emphasize a process-oriented understanding of the system under consideration. Index models, simplified ecosystem models, are based on the premise that a biological term which alters the ecosystem in some way (e.g. filtration of seston, waste production) is alleviated by tidal or other exchange mechanisms (which replace seston or remove wastes) (Chamberlain *et al.*, 2006). For example, Dame (1996) compared filtration of seston with its tidal renewal in a simple ratio but the same concept has also been applied to production of biodeposits (Grant *et al.*, 2005). This approach addresses far-field, or bay-wide, impacts because conditions are averaged throughout the whole ecosystem.



From the standpoint of an index of waste removal model, particle depletion and production of biodeposits may be coupled as complementary bioenergetic aspects of mussel feeding. The bioenergetics of many cultured animals are well known and, hence, a theoretical determination of waste output is reasonably easy to obtain. Examples of these calculations may be found in Grant and Bacher (1998), Grant *et al.* (2005), and Gillibrand and Turrell (1997). Dowd (1997) cautions, however, that from a mathematical perspective, the nonlinear functional relationships used to describe bivalve bio-energetics have often led to poor model predictions due to their high sensitivity to inadequately known physiological parameters. Chamberlain *et al.* (2006) also suggest that (*in situ*) bivalve feeding behaviour and excretion rates may not be well understood. For an ecosystem model, it is necessary to scale estimates for individual animals up to the entire cultured population and so, biodeposit production is multiplied by “culture density”. The latter is derived from typical farm density diluted by the volume of the entire bay (Chamberlain *et al.*, 2006). This value thus incorporates the size of the culture, established or proposed, as well as the size of the receiving waters, an essential mode of scaling for a one-box model. If desired, adjustments could also be made for animals of different sizes using allometry (Chamberlain *et al.*, 2006).

While index models are appealing in that the comparisons they engender are easily understood, the loss side of the equation is problematic. Loss occurs as a result of several physical processes (diffusion, advection and/or sinking) which all require a separate estimate, or model. Not only are these processes poorly understood but boundary layer physics, which regulates their fate, must be considered (Chamberlain *et al.*, 2006). Some particle tracking models have been successful at making these predictions on a local scale but prediction of sedimentation rate for a whole bay is a significant task. The degradation of organic input by the benthos is another, equally complex, loss term. Benthic carbon demand varies as a result of many factors including temperature, sediment type, and oxygen conditions. An average estimate of benthic respiration for a bay could be provided but this would require matching to an input term (organic deposition) that, as noted above, is uncertain at best. Comparing waste production to tidal exchange, by considering the mass of biodeposits prior to deposition, avoids some of these problems (Grant *et al.*, 2005). This approach still provides an index of waste removal but does not require the uncertainty of modelling sedimentation.

Grant *et al.* (2005) applied this approach, employing a simplified model of suspended mussel culture that balances production of feces and pseudofeces versus physical exchange, to mussel culture in eastern Canada. Biodeposit production rates were calculated using a bioenergetic submodel and tidal flushing was determined with a tidal prism method. Comparing model predictions with results from a short-term field study, the authors found that although the model could be used to make relative comparisons between estuaries, input of levels of ambient suspended particulate material would be helpful for comparison with field estimates of biodeposition. In addition, accurate knowledge of mussel culture density and longline spacing was obviously critical for model input (Grant *et al.*, 2005).



In addition to indices which contrast waste production with tidal renewal, it is possible to calculate a variety of indices for ecosystem health (Jorgensen *et al.*, 2005) although many of these are retrospective, utilizing empirical data. They are not intended for prediction or incorporation of “potential scenario” data such as culture density. The advantages and disadvantages of other indices, specifically assimilative capacity, seston depletion, oxygen consumption and trophic indices, are reviewed by Chamberlain *et al.* (2006).

To avoid the problems with loss terms, additional qualitative predictions of impact in the form of simulation models may be more useful (Chamberlain *et al.*, 2006). Box models (e.g. Dowd, 2005) allow variables such as biodeposition and nutrient concentration to be examined as a function of bivalve stocking density and a large range of numerous scenarios, including time-dependent scenarios, are possible. However, box models incorporate spatial delineation and, also, simple tidal prism calculations will not suffice; a numerical model of circulation is required to quantify exchanged process in different areas of a bay. As a result of the physical exchange requirements, as well as that of boundary time series, there may be considerable development time with box models (Chamberlain *et al.*, 2006). From a management perspective, the progress to spatial models from index models may be required where there are multiple lease applications in a given bay and/or continued culture development through time.

Index models do not specify space, so they cannot be used to consider the interaction between farms but they can be used to set a maximum on the proposed culture area. Index models have been suggested as valuable screening tools for relative ranking of different systems (Grant *et al.*, 2005). If a site requires further study, examination of impacts at a smaller and more detailed spatial scale using a tool such as a particle tracking model (Chamberlain, 2002) would be a logical next step. In addition, further efforts might include comparison with other impacts (nitrogen cycling) as well as with other habitat indices (e.g., benthic enrichment index; Hargrave, 1994) and even community-based measures of ecosystem health (Deegan *et al.*, 1997). Chamberlain *et al.* (2006) suggest that a survey of various indices (Meeuwig *et al.*, 1998; Yokoyama, 2003) should be undertaken to designate the most robust examples in terms of predictive capability, ease of calculation, sources of error, and data requirements.

Marine ecosystem models have made many advances in recent years and are being widely applied in coastal marine systems (Chamberlain *et al.*, 2006). Dowd (2005) suggested that a well established mathematical modeling framework exists for the lower trophic levels of marine ecosystems, and that this framework is readily adapted to assess the extent to which bivalve aquaculture interacts with, and affects, the supporting ecosystem. Hence, a carefully designed ecosystem model and supporting measurement program can provide an understanding of not only how a coastal ecosystem works, but also serves as a quantitative tool for looking at the effect of different levels of bivalve aquaculture on ecosystem



processes. Formulation and application of such models must be done on a site-specific basis, however, and these models require a long term commitment, continual refinement, and application and testing on a variety of cases if they are to be useful (Chamberlain *et al.*, 2006).



## 5.0 Bibliography

- Ahn, I.Y. 1993. Enhanced particle flux through biodeposition by the Antarctic suspension-feeding bivalve *Laternula elliptica* in Marian Cove, King George Island. *Journal of Experimental Marine Biology and Ecology* 171: 75-90.
- Allen, J.A. 1985. The recent Bivalvia: their form and evolution. *In*: Truman, E.R., and Clarke, M.R. (eds.), The Mollusca, Volume 10. Academic Press, New York. pp.337-403.
- Anderson, R.S., Kraus, B.S., McGladdery, S., and Smolowitz, R. 2003. QpX, a pathogen of quahogs (hard clams), employs mucoid secretions to resist host antimicrobial agents. *Journal of Shellfish Research* 22: 205-208.
- Asmus, R.M., and Asmus, H. 1991. Mussel beds: Limiting or promoting phytoplankton? *Journal of Experimental Marine Biology and Ecology* 148: 215-232.
- Bacon, G.S., MacDonald, B.A. and Ward, J.E. 1998. Physiological responses of infaunal (*Mya arenaria*) and epifaunal (*Placopecten magellanicus*) bivalves to variations in the concentration and quality of suspended particles. I. Feeding activity and selection. *Journal of Experimental Marine Biology and Ecology* 219: 105-125.
- Baines, S.B., Fisher, N.S. and Kinney, E.L. 2005. Influence of temperature on dietary metal uptake in Arctic and temperate mussels. *Marine Ecology Progress Series* 289: 201-213.
- Barillé, L., Prou, J., Heral, M. and Bougrier, S. 1993. No influence of food quality, but ration-dependent retention efficiencies in the Japanese oyster *Crassostrea gigas*. *Journal of Experimental Marine Biology Ecology* 171: 91– 106.
- Barillé, L. and Prou, J. 1994. Modeling Japanese oyster physiological processes under natural tidal variations in suspended particulate matter. *ICES-CM/F* 22: 1-12.
- Barranguet, C., Alliot, E., and Plante-Cuny, M.R. 1994. Benthic microphytic activity at two Mediterranean shellfish cultivation sites with reference to benthic fluxes. *Oceanologica Acta* 17: 211-221.
- Bartoli, M., Nizzoli, D., Viaroli, P., Turolla, E., Castaldelli, G., Fano, E.A., and Rossi, R. 2001. Impact of *Tapes philippinarum* farming on nutrient dynamics and benthic respiration in the Sacca di Goro. *Hydrobiologia* 455: 203-211.
- Bayne, B. L. 1972. Some effects of stress in the adult on the larval development of *Mytilus edulis*. *Nature* 237: 459.
- Bayne, B.L. (ed.) 1976. Marine Mussels: Their Ecology and Physiology. Cambridge University Press, Cambridge, U.K. 506 pp.
- Bayne, B. L., Widdows, J., and Newell, R.I.E. 1977. Physiological measurements on estuarine bivalve molluscs in the field. *In*: Proceedings of 11th European Marine Biology Symposium, Pergamon Press, London pp. 57-68.
- Bayne, B.L. and Widdows, J. 1978. The physiological ecology of two populations of *Mytilus edulis* L. *Oecologia* 37: 137-162.



- Bayne, B.L. and Newell, R.I.E. 1983. Physiological energetics of marine molluscs. *In*: Saleudin, A.S.M., and Wilber, K.M. (eds.), The Mollusca, Volume 4, Physiology, Academic Press, New York pp. 407-515.
- Bayne, B.L., Brown, D.A., Burns, K., Dixon, D.R., Ivanovici, A., Livingstone, D.R., Lowe, D.M., Moore, M.N., Stebbing, A.R.D., and Widdows, J. 1985. The Effects of Stress and Pollution on Marine Animals. Praeger, New York.
- Bayne, B.L., Hawkins, A.J.S., and Navarro, E. 1987. Feeding and digestion by the mussel *Mytilus edulis* L. (Bivalvia: Mollusca) in mixtures of silt and algal cells at low concentrations. *Journal of Experimental Marine Biology and Ecology* 111(1): 1-22.
- Bayne, B.L. 1993. Feeding physiology of bivalves: time-dependence and compensation for changes in food availability. *In*: R.F. Dame (ed.), Bivalve Filter Feeders in Estuarine and Coastal Ecosystem Processes. NATO ASI Series G33, Springer-Verlag, Berlin, pp.1-24.
- Bayne, B. L., Iglesias, J. I. P., Hawkins, A.J.S., Navarro, E., Heral, M., and Deslous-Paoli, J.M. 1993. Feeding behaviour of the mussel, *Mytilus edulis*: responses to variations in quantity and organic content of the seston. *Journal of Marine Biology, Association of the United Kingdom* 73: 813-829.
- Bayne, B.L. 1998. The physiology of suspension feeding by bivalve molluscs: an introduction to the Plymouth "TROPHEE" workshop. *Journal of Experimental Marine Biology and Ecology* 219: 1-19.
- Bayne, B.L. 2004. Comparisons of measurements of clearance rates in bivalve molluscs. *Marine Ecology Progress Series* 276: 305-306.
- Bates, S.S. 1998. Ecophysiology and metabolism of ASP toxin production. *In*: Anderson, D.M., Cembella, A.D., and Hallegraeff, G.M. (eds.), Physiological Ecology of Harmful Algal Blooms. Springer-Verlag, Heidelberg. pp.405-426.
- Bates, S.S., Garrison, D.L., and Homer, R.A. 1998. Bloom dynamics and physiology of domoic-acid-producing *Pseudonitzschia* species. *In*: Anderson, D.M., Cembella, A.D., and Hallegraeff, G.M. (eds.) Physiological Ecology of Harmful Algal Blooms. Springer-Verlag, Heidelberg. pp.267-292.
- Beadman, H.A., Kaiser, M.J., Galanidi, M., Shucksmith, R., and Willows, R.I. 2004. Changes in species richness with stocking density of marine bivalves. *Journal of Applied Ecology* 41(3): 464-475.
- Beninger, P.G., Ward, J.E., MacDonald, B.A., and Thompson, R.J. 1992. Gill function and particle transport in *Placopecten magellanicus* (Mollusca: Bivalvia) as revealed using video endoscopy. *Marine Biology* 114: 281– 288.
- Beninger, P.G., Dufour, S.C., and Bourque, J. 1997. Particle processing mechanisms of the eulamellibrach bivalves *Spisula solidissima* and *Mya arenaria*. *Marine Ecology Progress Series* 150: 157-169.
- Beninger, P.G. and St.-Jean, S.D. 1997a. The role of mucus in particle processing by suspension-feeding marine bivalves: unifying principles. *Marine Biology* 127: 389-397.



- Beninger, P.G. and St.-Jean, S.D. 1997b. Particle processing on the labial palps of *Mytilus edulis* and *Placopecten magellanicus* (Mollusca: Bivalvia). *Marine Ecology Progress Series* 147: 117-127.
- Beninger, P.G., Veniot, A., and Poussart, Y. 1999. Principles of pseudofeces rejection on the bivalve mantle: integration in particle processing. *Marine Ecology Progress Series* 178: 259-269.
- Beninger, P.G., Decottignies, P., and Rincé, Y. 2004. Localization of qualitative particle selection sites in the heterorhabdic filibranch *Pecten maximus* (Bivalvia: Pectinidae). *Marine Ecology Progress Series* 275: 163-173.
- Berg, J.A. and Newell, R.I.E. 1986. Temporal and spatial variations in the composition of seston available to the suspension feeder *Crassostrea virginica*. *Estuarine, Coastal and Shelf Science* 23: 375-386.
- Black, K.D. 2001. Environmental impacts of aquaculture. CRC Press, Boca Raton.
- Bøhle, B. 1972. Effects of adaptation to reduced salinity on filtration activity and growth of mussels (*Mytilus edulis*). *Journal of Experimental Marine Biology and Ecology* 10: 41-49.
- Bougrier, S., Geairon, P., Deslous-Paoli, J.M., Bacher, C., and Jonquières, G. 1995. Allometric relationships and effects of temperature on clearance and oxygen consumption rates of *Crassostrea gigas* (Thunberg). *Aquaculture* 134(1-2): 143-154.
- Burridge, L.E. 2003. Chemical use in marine finfish aquaculture in Canada: A review of current practices and possible effects. *In: A scientific review of the potential environmental effects of aquaculture in aquatic ecosystems*. Canadian Technical Report of Fisheries and Aquatic Sciences 2450: 131p.
- Cahalan, J.A., Siddall, S.E., and Lukenbach, M.W. 1989. The effects of flow velocity, food concentration, and particle fluxes on the growth rates of juvenile bay scallops, *Argopecten irradians*. *Journal of Experimental Marine Biology and Ecology* 129: 45-60.
- Callier M.D., Richard, M., McKindsey, C.W., Archambault, P., and Desrosiers, G. 2004. Level of biodeposition supportable by a sandy benthic community: an *in situ* benthocosm experiment. *Aquaculture Canada*, October 17-20, Quebec (QC), Canada.
- Callier, M.D., Weise, A.M., McKindsey, C.W., and Desrosiers, G. 2006. Sedimentation rates in a suspended mussel farm (Great-Entry Lagoon, Canada): biodeposit production and dispersion. *Marine Ecology Progress Series*. *In press*.
- Carlton, J.T., Vermeij, G.J., Lindberg, D.R., Carlton, D.A., and Dudley, E.C. 1991. The first historical extinction of a marine invertebrate in an ocean basin: the demise of the eelgrass limpet *Lottia alveus*. *Biological Bulletin* 180: 72-80.
- Carroll, M.L., Cochrane, S., Fieler, R., Velum, R., and White, P. 2003. Organic enrichment of sediments from salmon farming in Norway: environmental factors, management practices, and monitoring techniques. *Aquaculture* 226: 165-180.



- Chamberlain, J., Fernandes, T.F., Read, P., Nickell, T.D., and Davies, I.M. 2001. Impacts of biodeposits from suspended mussel (*Mytilus edulis* L.) cultured on the surrounding surficial sediments. *ICES Journal of Marine Sciences* 58: 411-416.
- Chamberlain, J. 2002. Modelling the environmental impacts of suspended mussel (*Mytilus edulis* L.) farming. PhD Thesis, Napier University, 200p.
- Chamberlain, J., Stucchi, D., Lu, L., and Levings, C. 2005. The suitability of DEPOMOD for use in the management of finfish aquaculture sites, with particular reference to Pacific Region. DFO Canadian Science Advisory Secretariat Research Document 2005/035. 53p.
- Chamberlain, J., Weise, A., Dowd, M., and Grant, J. 2006. Modelling approaches to assess the potential effects of shellfish aquaculture on the marine environment. DFO Canadian Scientific Advisory Secretariat Research Document. 2006/032.
- Chesney, E.J. Jr., and Iglesias, J. 1979. Seasonal distribution, abundance and diversity of demersal fishes in the inner Ria de Arosa, northwest Spain. *Estuarine Coastal Marine Science* 8: 227-239.
- Christensen, P.B., Glud, R.N., Dalsgaard, T., and Gillespie, P.A. 2003. Impacts of longline mussel farming on oxygen and nitrogen dynamics and biological communities of coastal sediments. *Aquaculture* 218(1-4): 567-588.
- Cognie, B., Barillé, L., Massé, G., and Beninger, P.G. 2003. Selection and processing of large suspended algae in the oyster *Crassostrea gigas*. *Marine Ecology Progress Series* 250: 145-152.
- Cook, E.J., Black, K.D., and Sayer, M.D.J. 2003. In-situ bio-filters at commercial salmon farms in Scotland - How effective are mussel lines as biological filters? *In: Beyond Monoculture*, Abstracts of Aquaculture Europe Symposium 2003: 148-149.
- Costelloe, J., and Keegan, B.F. 1984. Feeding and related morphological structures in the dendrochirote *Aslia lefevrei* (Holothuroidea: Echinodermata). *Marine Biology*, Berlin, Heidelberg 84(2): 135-142.
- Coughlan, J. 1969. The estimation rate from the clearance of suspensions. *Marine Biology* 2: 356-358.
- Cranford, P.J., and Grant, J. 1990. Particle clearance and absorption of phytoplankton and detritus by the sea scallop *Placopecten magellanicus* (Gmelin). *Journal of Experimental Marine Biology and Ecology* 137: 105-121.
- Cranford, P.J., and Gordon, D.C. Jr. 1992. The influence of dilute clay suspensions on sea scallop (*Placopecten magellanicus*) feeding activity and tissue growth. *Netherlands Journal of Sea Research* 30: 107-120.
- Cranford, P. J., and Hargrave, B.T. 1994. *In situ* time-series measurement of ingestion and absorption rates of suspension-feeding bivalves: *Placopecten magellanicus*. *Limnology and Oceanography* 39(3): 730-738.
- Cranford, P.J., Emerson, C.W., Hargrave, B.T., and Milligan, T.G. 1998. *In situ* feeding and absorption responses of sea scallops *Placopecten magellanicus* (Gmelin) to storm-induced changes in the



- quantity and composition of seston. *Journal of Experimental Marine Biology and Ecology* 219(1-2): 45-70.
- Cranford, P.J., and Hill, P.S. 1999. Seasonal variation in food utilization by the suspension-feeding bivalve molluscs *Mytilus edulis* and *Placopecten magellanicus*. *Marine Ecology Progress Series* 190: 223-239.
- Cranford, P.J. 2001. Evaluating the 'reliability' of filtration rate measurements in bivalves. *Marine Ecology Progress Series* 215: 303-305.
- Cranford, P.J., Dowd, M., Grant, J., Hargrave, B.T., and McGladdery, S. 2003. Ecosystem level effects of marine bivalve aquaculture. *In: F.A.O. Canada (ed.), A Scientific Review of the Potential Environmental Effects of Aquaculture in Aquatic Ecosystems, Volume 1. Canadian Technical Report for Fisheries and Aquatic Sciences. Fisheries and Oceans Canada. pp.51-95.*
- Cranford, P.J., Anderson, R., Archambault, P., Balch, T., Bates, S.S. Bugden, G., Callier, M.D., Carver, C., Comeau, L., Hargrave, B., Harrison, W.G., Horne, E., Kepkay, P.E., Li, W.K.W., Mallet, A., Ouellete, M., and Strain, P. 2006. Indicators and thresholds for use in assessing shellfish aquaculture impacts on fish habitat. *DFO Canadian Scientific Advisory Secretariat Research Document. 2006/034.*
- Crawford, C.M., Macleod, C.K.A., and Mitchell, I.M. 2003. Effects of shellfish farming on the benthic environment. *Aquaculture* 224: 117-140.
- Cromey, C.J., Black, K.D., Edwards, A., and Jack, I.A. 1998. Modelling the deposition and biological effects of organic carbon from marine sewage discharges. *Estuarine Coastal Shelf Science* 47: 295-308.
- Cromey, C.J., Nickell, T.D., and Black, K.D. 2002. DEPOMOD-modelling the deposition and biological effects of waste solids from marine cage farms. *Aquaculture* 214: 211-239.
- Cummings, K.S., Mayer, C.A., and Szafoni, R.E. 1998. Endangered freshwater mussels (Mollusca: Unionidae) in the North Fork Vermilion River, Illinois with comments on the federally endangered clubshell, *Pleurobema clava* (Lamarck, 1819). *Transactions of the Illinois State Academy of Science* 91: 91-102.
- Cusson, M., and Bourget, E. 2005. Global patterns of macroinvertebrate production in marine benthic habitats. *Marine Ecology Progress Series* 297: 1-14.
- Dahlbäck, B. and Gunnarsson, L.A.H. 1981. Sedimentation and sulfate reduction under a mussel culture. *Marine Biology* 63: 269-275.
- Damas, D. 1935. Le role des organismes dans la formation des vases marins. *Annls. Society of Geology, Belgium* 58: 143-151.
- Dame, R., Dankers, N., Prins, T., Jongasma, H., and Smaal, A. 1991. The influence of mussel bed on nutrients in the western Wadden Sea and eastern Scheldt estuaries. *Estuaries* 14(2): 130-138.



- Dame, R.F. 1993. The role of bivalve filter feeder material fluxes in estuarine ecosystems. *In*: Dame, R.F. (ed.), Bivalve Filter Feeders in Estuarine and Coastal Ecosystem Processes. NATO., ASI Series, Volume G33, Springer-Verlag, Berlin. pp.245-269.
- Dame, R.F. 1996. Ecology of Marine Bivalves: An Ecosystem Approach. CRC Press, Boca Raton, FL.
- D'Amours, O. and Archambault, P. 2005. Monitoring fishes and macroinvertebrates to determine indirect influence of bivalve aquaculture on ecosystem. *In*: AquaNet V. Victoria, BC, October 18-21, 2005. pp.E61.
- Danovaro, R., Gambi, C., Luna, G.M., and Mirto, S. 2004. Sustainable impact of mussel farming in the Adriatic Sea (Mediterranean Sea): evidence from biochemical, microbial and meiofaunal indicators. *Marine Pollution Bulletin* 49: 325-333.
- Davids, C. 1964. The influence of suspensions of micro-organisms of different concentrations on the pumping and retention of food by the mussel (*Mytilus edulis* L.) *Netherlands Journal of Sea Research* 2: 233-249.
- De Casabianca, M.L., Laugier, T., and Collart, D. 1997. Impact of shellfish farming eutrophication on benthic macrophyte communities in the Thau Lagoon, France. *Aquaculture International* 5(4): 301-314.
- de Jong, R.J. 1994. The effects of mussel farming on the benthic environment. MSc Thesis, University of Aukland, Aukland. 145p.
- Dean, D. 1957. The experimental feeding of oysters. Ph.D Thesis, Rutgers University. 228p.
- Deegan, L.A., Finn, J.T., Ayvazian, S.G., Ryder-Kieffer, C.A., and Buonaccorsi, J. 1997. Development and validation of an estuarine biotic integrity index. *Estuaries* 20(3): 601-617.
- Denis, L., Alliot, E., and Grzebyk, D. 1999. Clearance rate responses of Mediterranean mussels, *Mytilus galloprovincialis*, to variations in the flow, water temperature, food quality and quantity. *Aquatic Living Resources* 12(4): 279-288.
- Deslous-Paoli, J.M., Souchu, P., Mazouni, N., Juge, C., and Dagault, F. 1998. Relationship between environment and resources: impact of shellfish farming on a Mediterranean lagoon (Thau, France). *Symposium on the National Coastal Oceanography Program (PNOC)*. 21(6): 831-843.
- Dowd, M. 1997. On predicting the growth of cultured bivalves. *Ecological Modelling* 104: 113-131.
- Dowd, M. 2005. A biophysical coastal ecosystem model for assessing environmental effects of marine bivalve aquaculture. *Ecological Modelling* 183(2-3): 323-346.
- Dral, A.D.G. 1967. The movement of the latero-frontal cilia and the mechanism of particle retention in the mussel (*Mytilus edulis* L.). *Netherlands Journal of Sea Research* 3: 391-422.
- Dupuy, C., Vaquer, A., Lam-Höai, T., Rougier, C., Mazouni, N., Lautier, J., Collo, Y., and Le Gall, S. 2000. Feeding rate of the oyster *Crassostrea gigas* in a natural planktonic community of the Mediterranean Thau Lagoon. *Marine Ecology Progress Series* 205: 171-184.
- Eble, A.F. 1996. The eastern oyster: *Crassostrea virginica*. Maryland Sea Grant Publications. 750p.



- Everett, R.A., Ruiz, G.M., and Carlton, J.T. 1995. Effect of oyster mariculture on submerged aquatic vegetation: An experimental test in a Pacific Northwest estuary. *Marine Ecology Progress Series* 125(1-3): 205-217.
- Fabiano, M., Mistic, C., and Danovaro, R. 1994. Chemical and microscopic study of particulate proteins in Ligurian coastal waters. Proceedings of the 10th Meeting of the Italian Association of Oceanology and Limnology, Allasio 4-6 November 1992 and proceedings of the Italian Association of Oceanology and Limnology (1991-1992). pp.355-366.
- Famme, P., Riisgård, H. U., and Jørgensen, C.B. 1986. On direct measurement of pumping rates in the mussel *Mytilus edulis*. *Marine Biology* 92: 323-327.
- Feuillet-Girard, M., Heral, M., Sornin, J.M., Deslous-Paoli, J.M., Robert, J.M., Mornet, F., and Razet, D. 1988. Nitrogenous compounds in the water column and at the sediment-water interface in the estuarine bay of Marennes-Oleron: Influence of oyster farming. *Aquatic Living Resources* 1(4): 251-265.
- Freire, J., Fernandez, L., and Gonzalez-Gurriaran, E. 1990. Influence of mussel raft culture on the diet of *Liocarcinus arcuatus* (Leach) (Brachyura: Portunidae) in the Ria de Arosa (Galicia, NW Spain). *Journal of Shellfish Research* 9(1): 45-57.
- Freire, J. and Gonzalez-Gurriaran, E.F. 1995. Feeding ecology of the velvet swimming crab *Necora puber* in mussel raft areas of the Ria de Arousa (Galicia, NW Spain). *Marine Ecology Progress Series* 119(1-3): 139-154.
- Foster-Smith, R.L. 1975a. The role of mucus in the mechanism of feeding in three filter-feeding bivalves. *Proceedings of the Malacological Society, London* 41: 571-588.
- Foster-Smith, R.L. 1975b. The effect of concentration of suspension and inert material on the assimilation of algae by three bivalves. *Estuarine, Coastal and Shelf Science* 34: 393-421.
- Foster-Smith, R.L. 1976. Some mechanisms for the control of pumping activity in bivalves. *Marine Behaviour and Physiology* 4: 41-60.
- Galtsoff, A.M. 1964. The American oyster *Crassostrea virginica* Gmelin. *Fishery Bulletin, Fish and Wildlife Service, United States Department of the Interior* 64: 480p.
- Galtsoff, P.S. 1928. Experimental study of the function of oyster gills and its bearing on the problems of oyster culture and sanitary control of the oyster industry. *Bulletin of the Bureau of Fish, Washington* 44: 1-39.
- Gerlotto, F., Brehemer, P., Buestel, D., and Sanguinéde, F. 2001. A method of acoustic monitoring of mussel longline ground using vertical echo sounder and multibeam sonar. *ICES CM 2001/R:01*: 14pp.
- Gibb, M.M. and Vant, W.N. 1997. Seasonal changes in factors controlling phytoplankton growth in Beatrix Bay, New Zealand. *New Zealand Journal of Marine and Freshwater Research* 31(2): 237-248.



- Giles, H. and Pilditch, C.A. 2004. Mussel biodeposit dispersal. *Marine Ecology Progress Series* 282: 205p.
- Gillibrand, P.A. and Turrell, W.R. 1997. The use of simple models in the regulation of the impact of fish farms on water quality in Scottish sea lochs. *Aquaculture* 159: 33-46.
- Gowen, R.J., Bradbury, N.B., and Brown, J.R. 1989. The use of simple models in assessing two interactions between fish farming and the marine environment. *In: de Paux E.J. and de Paux, N.W.N (ed.), Aquaculture - A Biotechnology in Progress*. Bredene, Belgium. European Aquaculture Society. pp.1071-1080.
- Graf, G. and Rosenberg, R. 1997. Bioresuspension and biodeposition: a review. *Journal of Marine Systems* 11: 269-278.
- Grant, C.M. and Hay, B.E. 2003. A review of issues related to depletion of population of selected infaunal bivalve species in the Hauraki Gulf Marine Park. Report prepared for the Hauraki Gulf Forum, 99p.
- Grant, J., Dowd, M., Thompson, K., Emerson, C., and Hatcher, A. 1993. Perspectives on field studies and related biological models of bivalve growth and carrying capacity. *In: Dame, R.F. (ed.), Bivalve Filter Feeders in Estuarine and Coastal Ecosystem Processes*. NATO ASI Series, Springer-Verlag, Berlin. pp.371-420.
- Grant, J., Hatcher, A., Scott, D.B., Pocklington, P., Schafer, C.T., and Winters, G.V. 1995. A multidisciplinary approach to evaluating impacts of shellfish aquaculture on benthic communities. *Estuaries* 18(1A): 124-144.
- Grant, J. and Bacher, C. 1998. Comparative models of mussel bioenergetics and their validation at field culture sites. *Journal of Experimental Marine Biology and Ecology* 219: 21-44.
- Grant, J. 2000. Method of accessing mussel culture impacts for multiple estuaries (15) and associated culture sites for PEI. Unpublished report prepared for Habitat Management Division, Fisheries and Oceans Canada, 34p.
- Grant, J., Cranford, P., Hargrave, B., Carreau, M., Schofield, B., Armsworthy, S., Burdett-Coutts, V., and Ibarra, D.A. 2005. A model of aquaculture biodeposition for multiple estuaries and field validation at blue mussel (*Mytilus edulis*) culture sites in eastern Canada. *Canadian Journal of Fisheries and Aquatic Sciences* 62(6): 1271-1285.
- Grizzle, R.E., Shumway, S.E., and Bricelj, V.M. 2001. Physiology and bioenergetics of *Mercenaria mercenaria*. *In: Kraeuter, J.N. & Castagna, M. (eds.), The Hard Clam, Mercenaria mercenaria*. Amsterdam, Elsevier. pp.305-382.
- Haamer, J. 1996. Improving water quality in a eutrophic fjord system with mussel farming. *Ambio* 5: 356-362.
- Hayakawa, Y., Kobayashi, M., and Izawa, M. 2001. Sedimentation flux from mariculture of oyster (*Crassostrea gigas*) in Opfunato estuary, Japan. *ICES Journal of Marine Science* 58: 435-444.



- Hargrave, B.T. 1994. A benthic enrichment index. Canadian Technical Report of Fisheries and Aquatic Sciences 1949: 79-91.
- Hargrave B.T., Phillips, G.A., Doucette, L.I., White, M.J., Milligan, T.G., Wildish, D.J., and Cranston, R.E. 1997. Assessing benthic impacts or organic enrichment from marine aquaculture. Water, Air and Soil Pollution 99: 541-650.
- Harstein, N.D. 2003. Supply and dispersal of mussel farm debris and its impacts on benthic habitats in contrasting hydrodynamic regimes. PhD thesis, University of Auckland.
- Hartstein, N.D. and Rowden, A.A. 2004. Effect of biodeposits from mussel culture on macroinvertebrate assemblages at sites of different hydrodynamic regime. Marine Environmental Research 57: 339-357.
- Hartstein, N.D., and Stevens, C.L. 2005. Deposition beneath long-line mussel farms. Aquacultural Engineering 33(3): 192-213.
- Hatcher, A., Grant, J., and Schofield, B. 1997. Seasonal changes in the metabolism of culture mussels (*Mytilus edulis* L.) from a Nova Scotia inlet: the effects of winter ice cover and nutritive stress. Journal of Experimental Marine Biology and Ecology 217: 63-78.
- Haven, D.S. and Morales-Alamo, R. 1966. Aspects of biodeposition by oysters and other invertebrate filter feeders. Limnology and Oceanography 11(4): 487-498.
- Hawkins, A.J.S. and Bayne, B.L. 1992. Physiological interrelations and the regulation of production. In: Gosling, E. (ed.), *The Mussel Mytilus: Ecology, Physiology, Genetics and Culture*. Elsevier, Amsterdam. pp.171-222.
- Hawkins, A.J.S., Smith, R.F.M., Bayne, B.L., and Héral, M. 1996. Novel observations underlying the fast growth of suspension-feeding shellfish in turbid environments: *Mytilus edulis*. Marine Ecology Progress Series 131: 179-190.
- Hawkins, A.J.S., Smith, R.F.M., Bougrier, S., Bayne, B.L. and Héral, M. 1997. Manipulation of dietary conditions for maximal growth in mussels, *Mytilus edulis*, from the Marennes-Oléron Bay, France. Aquatic Living Resources 10: 13-22.
- Hawkins, A.J.S., Bayne, B.L., Bougrier, S., Héral, M., Iglesias, J.I.P., Navarro, E., Smith, R.F.M. and Urrutia, M.B. 1998. Some general relationships in comparing the feeding physiology of suspension-feeding bivalve molluscs. Journal of Experimental Marine Biology and Ecology 219: 87-103.
- Hawkins, A.J.S., James, M.R., Hickman, R.W., Hatton, S., and Weatherhead, M. 1999. Modelling of suspension-feeding and growth in the green-lipped mussel *Perna canaliculus* exposed to natural and experimental variations of seston availability in the Marlborough Sounds, New Zealand. Marine Ecology Progress Series 191: 217-232.
- Hay and Co. 2003. Baynes Sound carrying capacity study field data report. BC Ministry of Agriculture, Food and Fisheries. MAFF.001.



- Henderson, A., Gamito, S., Karakassis, I., Pederson, P., and Smaal, A. 2001. Use of hydrodynamic and benthic models for managing environmental impacts of marine aquaculture. *Journal of Applied Ichthyology* 17: 163-172.
- Hendricks, T.J. and Eganhouse, R. 1992. Modification and verification of sediment deposition models. Prepared for California State Water Resources Control Board, Sacramento, CA. 331p.
- Hildreth, D.I. and Crisp, D.J. 1976. A corrected formula for calculation of filtration rate of bivalve molluscs in an experimental flowing system. *Journal Marine Biology, Association of the United Kingdom* 56: 111-120.
- ICES, 2004. Report of the Working Group on Marine Shellfish Culture. Portland, Maine, International Council for the Exploration of the Seas May 13-15, 2004. ICES CM 2004/F:02. Ref. G, ACME.
- ICES 2005. Report of the ICES Working Group on Marine Shellfish Culture. La Rochelle, France. May 13-15, 2005. ICES CM 2005/F:04. Ref I, ACME.
- Iglesias, J. 1981. Spatial and temporal changes in the demersal fish community of the Ria de Arosa (NW Spain). *Marine Biology, Berlin, Heidelberg* 65(2): 199-208.
- Iglesias, J.I.P, Navarro, E., Alvarez Jorna, P., and Armentia, I. 1992. Feeding, particle selection and absorption in cockles *Cerastoderma edule* (L.) exposed to variable conditions of food concentration and quality. *Journal of Experimental Biology and Ecology* 162: 177-198.
- Iglesias, J.I.P., Urrutia, M.B., Navarro, E., and Ibarrola, I. 1998. Measuring feeding and absorption in suspension-feeding bivalves: an appraisal of the biodeposition method. *Journal of Experimental Marine Biology and Ecology* 219(1-2): 71-86.
- Incze, L.S., Lutz, R.A., and Watling, L. 1980. Relationships between effects of environmental temperature and seston on growth and mortality of *Mytilus edulis* in a temperate northern estuary. *Marine Biology* 57: 147-156.
- Inglis, G.J. and Gust, N. 2003. Potential indirect effects of shellfish culture on the reproductive success of benthic predators. *Journal of Applied Ecology* 40(6): 1077-1089.
- Ito, S. and Imai, T. 1955. Ecology of oyster bed . I. On the decline of productivity due to repeated culture. *Tohoku Journal of Agricultural Research* 5: 251-268.
- James, M.R., Weatherhead, M.A., and Ross, A.H. 2001. Size-specific clearance, excretion, and respiration rates, and phytoplankton selectivity for the mussel *Perna canaliculus* at low levels of natural foods. *New Zealand Journal of Marine and Freshwater Research* 35: 73-86.
- Jaramillo, E., Bertran, C., and Bravo, A. 1992. Mussel biodeposition in an estuary in southern Chile. *Marine Ecology Progress Series* 82: 85-94.
- Jordan, S.J. 1987. Sedimentation and remineralization associated with biodeposition by the American oyster *Crassostrea virginica* (Gmelin). Doctoral dissertation, University of Maryland, College Park, MD, USA. 200p.



- Jordan, T.E. and Valiela, I. 1982. A nitrogen budget of the ribbed mussel, *Geukensia demissa*, and its significance in nitrogen flow in a New England salt marsh. *Limnology and Oceanography* 27: 75-90.
- Jørgensen, C.B. 1966. Biology of Suspension Feeding. Pergamon Press, London. 357p.
- Jørgensen, C.B. 1976. Growth efficiencies and factors controlling size in some mytilid bivalves, especially *Mytilus edulis* L.: Review and interpretation. *Ophelia* 15: 175-192.
- Jørgensen, C.B., Famme, P., Saustrup Kristensen, H., Larsen, P.S., Møhlenberg, F., and Riisgård, H.U. 1986. The bivalve pump. *Marine Ecology Progress Series* 34: 69-77.
- Jørgensen, C.B., Larsen, P.S., Møhlenberg, F., and Riisgård, H.U. 1988. The mussel pump: properties and modelling. *Marine Ecology Progress Series* 45: 205-216.
- Jørgensen, C.B. 1996. Bivalve filter feeding revisited. *Marine Ecology Progress Series* 142: 287-302.
- Jørgensen S.E., Costanza, R., and Xu, F.-L. 2005. Ecological indicators for assessment of ecosystem health. CRC Press, Boca Raton.
- Kaspar, H.F., Gillespie, P.A., Boyer, I.C., and MacKenzie, A.L. 1985. Effects of mussel aquaculture on the nitrogen cycle and benthic communities in Kenepura Sound, Marlborough Sounds, New Zealand. *Marine Biology* 85: 127-136.
- Kautsky, N. and Evans, S. 1987. Role of biodeposition by *Mytilus edulis* in the circulation of matter and nutrients in a Baltic coastal ecosystem. *Marine Ecology Progress Series* 38: 201-2112.
- Kjørboe, T., Møhlenberg, F., and Nøhr, O. 1980. Feeding, particle selection and carbon absorption in *Mytilus edulis* in different mixtures of algae and resuspended bottom material. *Ophelia* 19: 193-205.
- Kjørboe, T. and Møhlenberg, F. 1981. Particle selection in suspension feeding bivalves. *Marine Ecology Progress Series* 5: 291-296.
- Kjørboe, T., Møhlenberg, F., and Nøhr, O. 1981. Effect of suspended bottom material on growth and energetics in *Mytilus edulis*. *Marine Biology* 61: 282-288.
- La Rosa, T., Mirto, S., Favaloro, E., Savona, B., Sara, G., Danovaro, R., and Mazzola, A. 2002. Impact on the water column biogeochemistry of a Mediterranean mussel and fish farm. *Water Research* 36(3): 713-721.
- Labarta, U., Fernandez-Reiriz, M.J., and Babarro, J.M.F. 1997. Differences in physiological energetics between intertidal and raft cultivated mussels *Mytilus galloprovincialis*. *Marine Ecology Progress Series* 152: 167-173.
- Landry, T. 2002. The potential role of bivalve shellfish in mitigating negative impacts of land use on estuaries. *Canadian Technical Report of Fisheries and Aquatic Sciences* pp.155-157.
- Lefebvre, S., Barillé, L., and Clerc, M. 2000. Pacific oyster (*Crassostrea gigas*) feeding responses to a fish-farm effluent. *Aquaculture* 187(1-2): 185-198.



- Leon, I, Mendez,G., and Rubio, B. 2004. Geochemical phases of Fe and degree of pyritization in sediments from Rio de Pontevedra (NW Spain): Implications of mussel raft culture. *Ciencias Marinas* 30(4): 585-602.
- Leonard, M. 2004. Evaluation et caractérisation de la chute de moules dans la lagune de Havre-aux-Maisons aux Iles-de-la-Madeleine, Québec. Thesis (BSc), ENITA Clermiont-Ferrand, 63p.
- Levinton, J.S., Ward, J.E., Shumway, S.E., and Baker, S.M. 2001. Feeding processes of bivalves: connecting the gut to the ecosystem. *In*: Aller, J.Y., Woodin, S.A., and Aller, R.C. (eds.), Organisms-Sediment Interactions. The Belle W. Baruch Library in Marine Science, Number 21, University of South Carolina Press, pp.385-400.
- Levinton, J.S., Ward, J.E., and Shumway,S.E. 2002. Feeding responses in the bivalves *Crassostrea gigas* and *Mytilus trossulus* to chemical composition of fresh and aged kelp detritus. *Marine Biology* 141: 367-376.
- Loosanoff, V.L. and Engle, J.B. 1947. Effects of different concentrations of micro-organisms on the feeding of oysters (*O. virginica*). *Fishery Bulletin of Fish and Wildlife Service, United States*. 51: 31-57.
- Lund, E.J. 1957. A quantitative study of clearance of a turbid medium and feeding by the oyster. *Publications of the Institute of Marine Science, University of Texas*. 4: 296-312.
- Macdonald, B.A. and Ward, J. E. 1994. Variations in food quality and particle selectivity in the sea scallop *Placopecten magellanicus* (Mollusca: Bivalvia). *Marine Ecology Progress Series* 108: 251-264.
- MacDonald, B.A., Bacon, G.S., and Ward, J.E. 1998. Physiological responses of infaunal (*Mya arenaria*) and epifaunal (*Placopecten magellanicus*) bivalves to variations in the concentration and quality of suspended particles. II. Absorption efficiency and scope for growth. *Journal of Experimental Marine Biology and Ecology* 219: 127-141.
- Maestrini, S.Y. and Spano, A.M. 1986. Physiological adaptation and interspecific competition among microalgae in relation to nutrients. *Nova Thalassia, Trieste* 8(3).
- Marsden, I.D. and Weatherhead, M.A. 1999. Shore-level induced variations in condition and feeding of the mussel *Perna canaliculus* from the east coast of the South Island, New Zealand. *New Zealand Journal of Marine and Freshwater Research* 33: 611-622.
- Mattson, J. and Lindén, O., 1983. Benthic macrofauna succession under mussels, *Mytilus edulis* L. (Bivalvia) cultured on hanging longlines. *Sarsia* 68: 97-102.
- Mazouni, N., Gaertner, J.C., and Deslous-Paoli, J.M. 1998. Influence of oyster culture on water column characteristics in a coastal lagoon (Thau, France). *Hydrobiologia*373/374: 149-156.
- Mazouni, N. 2004. Influence of suspended oyster culture on nitrogen regeneration in a coastal lagoon (Thau, France). *Marine Ecology Progress Series* 276: 103-113.



- Mazzola, A. and Sarà, G. 2001. The effect of fish farming organic waste on food availability for bivalve molluscs (Gaeta Gulf, Central Tyrrhenian, MED): stable carbon isotopic analysis. *Aquaculture* 192: 361–379.
- McKindsey, C.W., Anderson, M.R., Barnes, P., Courtenay, S., Landry, T., and Skinner, M. 2006. Effects of shellfish aquaculture on fish habitat. DFO Canadian Scientific Advisory Secretariat Research Document, 2006/011.
- McKinnon, L.J., Parry, G.D., Leparti, S.C., Heislors, S., Werner, G.F., Gason, A.S.H., Fabris, G., and O'Mahony, N. 2003. The environmental effects of blue mussel (*Mytilus edulis*) aquaculture in Port Phillip Bay 1, The State of Victoria, Victoria.
- Meeuwig, J.J., Rasmussen, J.B., and Peters, R.H. 1998. Turbid waters and clarifying mussels: their moderation of empirical chl:nutrient relations in estuaries in Prince Edward Island, Canada. *Marine Ecology Progress Series* 171: 139-50.
- Meyhöfer, E. 1985. Comparative pumping rates in suspension-feeding bivalves. *Marine Biology* 85: 137-142.
- Milke, L.M. and Ward, J.E. 2003. Influence of diet on pre-ingestive particle processing in bivalves. II. Residence time in the pallial cavity and handling time on the labial palps. *Journal of Experimental Marine Biology and Ecology* 293(2): 151-172.
- Miller, D.C., Norkko, A., and Pilditch, C.A. 2002. Influence of diet on dispersal of horse mussel *Atrina zelandica* biodeposits. *Marine Ecology Progress Series* 242: 153-167.
- Miron, G., Audet, D., Landry, T., Moriyasu, and Miki. 2005. Predation potential of the invasive green crab (*Carcinus maenas*) and other common predators on commercial bivalve species found on Prince Edward Island. *Journal of Shellfish Research* 24(2): 579-586.
- Mirto, S., La Rosa, T., Danovaro, R., and Mazzola, A. 2000. Microbial and meiofaunal response to intensive mussel-farm biodeposition in coastal sediments of the western Mediterranean. *Marine Pollution Bulletin* 40(3): 244-252.
- Møhlenberg, F. and Riisgård, H.U. 1978. Efficiency of particle retention in 13 species of suspension feeding bivalves. *Ophelia* 17: 239-246.
- Moore, H.B. 1931. The specific identification of faecal pellets. *Journal of Marine Biology, Association of United Kingdom* 17: 359-365.
- Muschenheim, D.K. 1987. The dynamics of near-bed seston flux and suspension-feeding benthos. *Journal of Marine Research* 45: 473-496.
- Navarro, E., Iglesias, J.I.P., and Ortega, M.M. 1992. Natural sediment as a food source for the cockle *Cerastoderma edule* (L.): effect of variable particle concentration on feeding, digestion, and scope for growth. *Journal of Experimental Marine Biology and Ecology* 156: 69-87.
- Navarro, E. and Thompson, R.J. 1997. Biodeposition by the horse mussel *Modiolus modiolus* (Dillwyn) during the spring diatom bloom. *Journal of Experimental Marine Biology and Ecology* 209: 1-13.



- Navarro, J. M. and Winter, J.E. 1982. Ingestion rate, assimilation efficiency and energy balance in *Mytilus chilensis* in relation to body size and different algal concentrations. *Marine Biology* 67: 255-266.
- Navarro, J.M. and Thompson, R.J. 1994. Comparison and evaluation of different techniques for measuring absorption efficiency in suspension feeders. *Limnology and Oceanography* 39(1): 159-164.
- Newell, C.R. 1979. Biology of intertidal animals. Marine Ecological Surveys Ltd. Faversham, U.K. 781p.
- Newell, C.R. and Shumway, S.E. 1993. Grazing of natural particulates by bivalve molluscs: a spatial and temporal perspective. *In: Dame, R.F. (ed.), Bivalve Filter Feeders in Estuarine and Coastal Ecosystem Processes*. Springer-Verlag, Berlin. pp.85-148.
- Newell, C.R., Campbell, D.E., and Gallagher, S.M. 1998. Development of the mussel aquaculture lease site model MUSMODÓ: a field program to calibrate model formulations. *Journal of Experimental Marine Biology and Ecology* 219: 143-169.
- Newell, C.R. 1999. The effects of current speed and particle concentration on mussel (*Mytilus edulis*) filtration rates: A recirculating flume study. *Journal of Shellfish Research* 18(1): 300.
- Newell, C.R. 2004. Ecosystem influences of natural and cultivated populations of suspension-feeding bivalve molluscs: a review. *Journal of Shellfish Research* 23: 51-61.
- Newell, R.I.E. and Langdon, C.J. 1996. Mechanisms and physiology of larval and adult feeding. *In: Kennedy, V.S., Newell, R.I.E., and Eble, A.F. (eds.), The Eastern Oyster Crassostrea virginica*. Maryland Sea Grant, College Park, MD. pp.185– 229.
- Newell, R.I.E., Cornwell, J.C., and Owens, M.S. 2002. Influence of simulated bivalve biodeposition and microphytobenthos on sediment nitrogen dynamics: A laboratory study. *Limnology and Oceanography* 47(5): 1367-1379.
- Newell, R.I.E., Fisher, T.R., Holyoke, R.R., and Cornwell, J.C. 2005. Influence of Eastern oysters on nitrogen and phosphorus regeneration in Chesapeake Bay, USA. *In: Dame, R. and Olenin, S. (eds.), The Comparative Roles of Suspension Feeders in Ecosystems*. Volume 47, NATO Science Series: IV - Earth and Environmental Sciences. Springer, Netherlands. pp.93-120.
- Ogilvie, S., Ross, A.H., James, M.R., and Schiel, D.R. 2003. *In situ* enclosure experiments on the influence of cultured mussels (*Perna canaliculus*) on phytoplankton at times of high and low ambient nitrogen. *Journal of Experimental Marine Biology and Ecology* 295: 23-39.
- Olaso, T. 1979. Biología de los equinodermos de la Ria de Arosa. *Boletín del Instituto Español de Oceanografía* 5: 81-127.
- Olaso, T. 1982. Ecología de los equinodermos de la Ria de Arosa. *Boletín del Instituto Español de Oceanografía* 7: 4-29.
- Pearson, T.H. and Rosenberg, R. 1978. Macrobenthic succession in relation to organic enrichment and pollution in the marine environment. *Oceanography and Marine Biology: An Annual Review* 16: 229-231.



- Petersen, J.K. 2004. Methods for measurement of bivalve clearance rate - a hope for common understanding. *Marine Ecology Progress Series* 276: 309-310.
- Petersen, J.K., Bougrier, S., Smaal, A.C., Garen, P., Robert, S., Larsen, J.E.N., and Brummelhuis, E. 2004. Intercalibration of mussel *Mytilus edulis* clearance rate measurements. *Marine Ecology Progress Series* 267: 187-194.
- Phillippart, C.J.M., Cadée, G.C., van Raaphorst, W., and Riegman, R. 2000. Long-term phytoplankton-nutrient interactions in a shallow coastal sea: Algal community structure, nutrient budgets and denitrification potential. *Limnology and Oceanography* 45(1): 131-144.
- Pietros, J.M. and Rice, M.A. 2003. The impacts of aquacultured oysters, *Crassostrea virginica* (Gmelin, 1791) on water column nitrogen and sedimentation: results of a mesocosm study. *Aquaculture* 222(1-4): 407-422.
- Pilditch, C.A., Grant, J., and Bryan, K.R. 2001. Seston supply to sea scallops (*Placopecten magellanicus*) in suspended culture. *Canadian Journal of Fisheries and Aquatic Sciences* 58: 241-253.
- Pillay, T.V.R. 2004. *Aquaculture and the environment*. Blackwell Publishing, Oxford. 196p.
- Plew, D.R., Stevens, C.L., Sigel, R.H., and Hartstein, N.D. 2005. Hydrodynamic implications of large offshore mussel farms. *IEEE Journal of Oceanic Engineering* 30(1).
- Pouvreau, S., Jonquères, G., and Buestel, D. 1999. Filtration by the pearl oyster *Pinctada margaritifera*, under conditions of low seston load and small particle size in a tropical lagoon habitat. *Aquaculture* 176: 295-314.
- Powell, A.W.B. 1979. *New Zealand Mollusca. Marine, land and freshwater shells*. William Collins, Auckland.
- Powell, E.N., Hofmann, E.E., Klinck, J.M., and Ray, S.M. 1992. Modelling oyster populations. I. A commentary on filtration rate. Is faster always better? *Journal of Shellfish Research* 11: 387-398.
- Pregnall, M.M. 1993. Regrowth and recruitment of eelgrass, *Zostera marina*, and recovery of benthic community structure in areas disturbed by commercial oyster culture in the South Slough National Estuarine Research Reserve, Oregon. A thesis: Bard College, Ammandale-On-Hudson, N.Y.
- Prins, T.C. and Smaal, A.C. 1994. The role of the blue mussel *Mytilus edulis* in the cycling of nutrients in the Oosterschelde estuary (The Netherlands). *Hydrobiologia* 282/283: 413-426.
- Rao, R.D. 1953. Rate of water propulsion in *Mytilus californianus* as a function of latitude. *Biological Bulletin, Marine Biological Laboratory, Woods Hole*. 104: 171-181.
- Ricciardi, A. and Bourget, E. 1999. Global patterns of macroinvertebrate biomass in marine intertidal communities. *Marine Ecology Progress Series* 185: 21-35.
- Riisgård, H.U. and Randlov, A. 1981. Energy budgets, growth and filtration rates in *Mytilus edulis* at different algal concentrations. *Marine Biology* 61: 227-234.
- Riisgård, H.U. 2001a. The stony road to reliable filtration rate measurements in bivalves: a reply. *Marine Ecology Progress Series* 215: 307-310.



- Riisgård, H.U. 2001b. On measurement of filtration rates in bivalves - the stony road to reliable data: review and interpretation. *Marine Ecology Progress Series* 211: 275-291.
- Riisgård, H.U. 2001c. Inaccurate bivalve clearance rate measurements: a reply. *Marine Ecology Progress Series* 221: 307-309.
- Riisgård, H.U., Kittner, C., and Seerup, D.F. 2003. Regulation and opening state and filtration rate in filter-feeding bivalves (*Cardium edule*, *Mytilus edulis*, *Mya arenaria*) in response to low algal concentrations. *Journal of Experimental Marine Biology and Ecology* 184(1-2): 105-127.
- Riisgård, H.U. 2004. Intercalibration of methods for measurement of bivalve filtration rates - a turning point. *Marine Ecology Progress Series* 276: 307-308.
- Roberts, D. 1976. Mussels and pollution. In: Bayne, B.L. (ed.) *Marine mussels ecology and physiology*. International Biological Programme. Cambridge University Press, New York.
- Robinson, S., Lander, T., MacDonald, B., Barrington, K., Chopin, T., Martin, J.D., Bastarache, S., Belyea, E., Haya, K., Sephton, F., Page, J.L., Martin, J.L., Eddy, S., Steward, I., and Fitzgerald, P. 2003. Development of integrates aquaculture of three trophic levels (finfish, seaweed and shellfish): the AquaNet project in the Bay of Fundy, Canada. The production dynamics of mussels as filter-feeder utilizing enhanced seston fields within a salmon aquaculture site. In: *Beyond Monoculture, Abstracts of Aquaculture Europe Symposium 2003*: 65-66.
- Robinson, W.E. and Langton, R.W. 1980. Digestion in a subtidal population of *Mercenaria mercenaria* (Bivalvia). *Marine Biolog* 58: 173-179.
- Romero, P., Gonzalez-Gurriaran, E., and Penas, E. 1982. Influence of mussel rafts on spatial and seasonal abundance of crabs in the Ria de Arouosa, North-West Spain. *Marine Biology*. Berlin, Heidelberg 72(2): 201-210.
- Rosenberg, R. 2001. Marine benthic faunal successional stages and related sedimentary activity. *Scientia Marina* (Barcelona) 65(2): 107-119.
- Ruppert, E.E. and Barnes, R.D. 1994. Invertebrate Zoology, 6th Edition. Saunders College Publishing, Harcourt Brace College Publishers, Orlando, FL. 1056 pp.
- Saranchova, O.L. and Kulakovskii, E.E. 1982. Effect of environmental salinity on different developmental stages of sea stars *Asterias rubens* and mussels *Mytilus edulis*. *Soviet Journal of Marine Biology* 8(1): 32-36.
- Schlieper, E., Kowalski, R., and Erman P. 1958. Beitrag zur ökologisch-zellphysiologischen Charakterisierung des borealen Lamellibranchier *Modiolus modiolus* L. *Kieler Meeresforsch* 14: 3-10.
- Segal, E., Rao, K.K., and James, T.W. 1953. Rate of activity as a function of intertidal height within populations of some littoral molluscs. *Nature* 172: 1108-1109.
- Shaw, K.R. 1998. PEI benthic survey. Technical Report of Environmental Science, 4. Department of Environment and Department of Fisheries and Environment, 75 p.



- Shumway, S.E., Cucci, T.L., Newell, R.C., and Yentsch, C.M. 1985. Particle selection, ingestion and absorption in filter-feeding bivalves. *Journal of Experimental Marine Biology and Ecology* 91: 77-92.
- Silvert, W. and Cromey, C.J. 2000. Modelling impacts. *In: Black, K.D. (ed.), Environmental Impacts of Aquaculture*. Sheffield Academic Press, pp.154-181. ISBN 0-8493-0501-2.
- Smaal, A.C. and Prins, T.C. 1993. The uptake of organic matter and the release of inorganic nutrients by suspension feeding bivalve beds. *In: Dame, R.F. (ed.), Bivalve Filter Feeders in Estuarine and Coastal Ecosystem Processes*. Springer-Verlag, Berlin, pp. 273-298.
- Smith, J. and Shackley, S.E. 2004. Effects of a commercial mussel *Mytilus edulis* lay on a sublittoral, soft sediment benthic community. *Marine Ecology Progress Series* 282: 185-191.
- Souchu, P., Vaquer, A., Collos, Y., Landrein, S., Deslous-Paoli, J.M., and Bibent, B. 2001. Influence of shellfish farming activities on the biogeochemical composition of the water column in Thau lagoon. *Marine Ecology Progress Series* 218: 141-152.
- Stehlik, L.L. and Meise, C.J. 2000. Diet of winter flounder in a New Jersey estuary: Ontogenetic change and spatial variation. *Estuaries* 23(3): 81-391.
- Stenton-Dozey, J.M.E., Jackson, L.F., and Busby, A.J. 1999. Impact of mussel culture on macrobenthic community structure in Saldanha Bay, South Africa. *Marine Pollution Bulletin* 39(1-12): 357-366.
- Stenton-Dozey, J., Probyn, T., and Busby, A. 2001. Impact of mussel (*Mytilus galloprovincialis*) raft-culture on benthic macrofauna, in situ oxygen uptake, and nutrient fluxes in Saldanha Bay, South Africa. *Canadian Journal of Fisheries and Aquatic Sciences* 58: 1021-1031.
- Strain, P.M. 2002. Nutrient Dynamics in Ship Harbour, Nova Scotia. *Atmosphere-Ocean* 40(1): 45-58.
- Strang, T.J. 2003. Nutrient generation under mussel farms: the environmental effects of mussel aquaculture in coastal bays. Thesis (MSc), Memorial University of Newfoundland, St. John's, Newfoundland, Canada.
- Sundbäck, K. and Graneli, W. 1988. Influence of microphytobenthos on the nutrient flux between sediment and water: A laboratory study. *Marine Ecology Progress Series* 43(1-2): 63-69.
- Sundbäck, K., Miles, A., and Goransson, E. 2000. Nitrogen fluxes, denitrification and the role of microphytobenthos in microbial shallow-water sediments: An annual study. *Marine Ecology Progress Series* 200: 59-76.
- Taghon, G.L., Nowell, A.R.M., and Jumars, P.A. 1984. Transport and breakdown of fecal pellets: biological and sedimentological consequences. *Limnology and Oceanography* 29: 64-72.
- Taylor, D.L. 2003. Size-dependent predation on post-settlement winter flounder *Pseudopleuronectes americanus* by sand shrimp *Crangon septemspinosa*. *Marine Ecology Progress Series* 263: 197-215.
- Tenore, K.R. and Dunstan W.M. 1973. Comparison of feeding and biodeposition of three bivalves at different food levels. *Marine Biology* 21: 190-195.



- Tenore, K.R., and Gonzalez, N. 1976. Food chain patterns in the Ria de Arosa, Spain: an area of intense mussel culture. Proceedings 10th EMBS, Ostend, Belgium. 2: 601–619.
- Tenore, K.R., Boyer, L.F., Cal, R.M., Corall, J., Garcia-Fernandez, C., Gonzalez, N., Gonzalez-Gurriaran, E., Hanson, R.B., Iglesias, J., Krom, M., Lopez-Jamar, E., McClain, J., Pamatmat, M.M., Perez, A., Rhoads, D.C., de Santiago, G., Tietjen, J., Westrich, J., and Windom, H.L. 1982. Coastal upwelling in the Rias Bajas, NW Spain: contrast in the Rias de Arosa and the Muros. *Journal of Marine Research* 40: 701-772.
- Theede, H. 1963. Experimentelle Untersuchungen über die filtrations leistung der miesmuschel *Mytilus edulis* L. *Kieler Meeresforschungen* 19: 20-41.
- Thompson, R.J. and Bayne, B.L. 1972. Active metabolism associated with feeding in the mussel *Mytilus edulis*. *Journal of Experimental Marine Biology and Ecology* 9: 111-124.
- Thorne, A.J. 1998. Alterations in the structure of macrobenthic communities related to the culture of oysters (*Crassostrea gigas*). Univeristy of Tasmania, Hobart, Australia. 102 pp.
- Tschuchiya, M. 1980. Biodeposit production by the mussel *Mytilus edulis* L. on rocky shores. *Journal of Experimental Marine Biology and Ecology* 47: 203-22.
- Urrutia, M.B., Iglesias, J.I.P., Navarro, E., and Prou, J. 1996. Feeding and absorption in *Cerastoderma edule* under environmental conditions in the Bay of Marennes-Oléron (western France). *Journal of the Marine Biology, Association of the United Kingdom* 76: 431-450.
- Urrutia, M.B., Navarro, E., Ibarrola, I., and Iglesias, J.I.P. 2001. Preingestive selection processes in the cockle *Cerastoderma edule*: mucus production related to rejection of pseudofeces. *Marine Ecology Progress Series* 209: 177-187.
- Vahl, O. 1972. Efficiency of particle retention in *Mytilus edulis* L. *Ophelia* 10: 17-25.
- Vahl, O. 1973. Efficiency of particle retention in *Chlamys islandica* (O.F. Muller). *Astarte* 6: 21-25.
- Velasco, L.A. and Navarro, J.M. 2002. Feeding physiology of infaunal (*Mulinia edulis*) and epifaunal (*Mytilus chilensis*) bivalves under a wide range of concentrations and qualities of seston. *Marine Ecology Progress Series* 240: 143-155.
- Velasco, L.A. and Navarro, J.M. 2005. Feeding physiology of two bivalves under laboratory and field conditions in response to variable food concentrations. *Marine Ecology Progress Series* 291: 115-124.
- Verwey, J. 1952. On the ecology of distribution of cockle and mussel in the Dutch Waddensea, their role in sedimentation, and the source of their food supply. *Archives Neerlandaises de Zoologie* 10: 171-239.
- Waite, R.P. 1989. The nutritional biology of *Perna canaliculus* with special reference to intensive mariculture systems. PhD Thesis, University of Canterbury, New Zealand.
- Walne, P.R. 1972. The influence of current speed, body size and water temperature on the filtration rate of five species of bivalves. *Journal of the Marine Biology, Association of the United Kingdom* 52: 345-374.



- Walker, T.R., Grant, J., Hill, P.S., Cranford, P., Lintern, G., and B. Scofield. 2005. Measuring particle dynamics in Arctic and mussel aquaculture environments. Proceedings of the 12th Canadian Coastal Conference. Dartmouth, Nova Scotia, November 6-9, 2005.
- Ward, J.E., Cassell, H.K., and MacDonald, B.A. 1992. Chemoreception in the sea scallop *Placopecten magellanicus* (Gmelin): I. Stimulatory effects of phytoplankton metabolites on clearance and ingestion rates. *Journal of Experimental Marine Biology and Ecology* 163: 235–250.
- Ward, J.E., MacDonald, B.A., and Thompson, R.J. 1993. Mechanisms of suspension feeding in bivalves: Resolution of current controversies by means of endoscopy. *Limnology and Oceanography* 38(2): 265-272.
- Ward, J.E., Levinton, J.S., Shumway, S.E., and Cucci, T. 1997. Site of particle selection in a bivalve mollusc. *Nature* 390: 131-132.
- Ward, J.E., Levinton, J.S., Shumway, S.E., and Cucci, T. 1998a. Particle sorting in bivalves: *in vivo* determination of the pallial organs of selection. *Marine Biology* 131: 283–292.
- Ward, J.E., Sanford, L.P., Newell, R.I.E., and MacDonald, B.A. 1998b. A new explanation of particle capture in suspension-feeding bivalve molluscs. *Limnology and Oceanography* 43 (5): 741–752.
- Ward, J.E., Sanford, L.P., Newell, R.I.E., and MacDonald, B.A. 2000. The utility of *in vivo* observations for describing particle capture processes in suspension-feeding bivalve molluscs. *Limnology and Oceanography* 45(5): 1203-1210.
- Ward, J.E., Levinton, J.S., and Shumway, S.E. 2003. Influence of diet on pre-ingestive particle processing in bivalves. I. Transport velocities on the ctenidium. *Journal of Experimental Marine Biology and Ecology* 293(2): 129-149.
- Ward, J.E. and Shumway, S.E. 2004. Separating the grain from the chaff: particle selection in suspension- and deposit-feeding bivalves. *Journal of Experimental Marine Biology and Ecology* 300: 83-130.
- Widdows, J. and Bayne, B.L. 1971. Temperature acclimation of *Mytilus edulis* with reference to its energy budget. *Journal of the Marine Biology, Association of the United Kingdom* 51: 827-843.
- Widdows, J., Fieth, P., and Worrall, C.M. 1979. Relationships between seston, available food and feeding activity in the common mussel, *Mytilus edulis*. *Marine Biology* 50: 195-207.
- Widdows, J. 1985. Physiological procedures. In: Bayne, B.L., Brown, D.A., Burns, K., and Dixon, D.R. and 5 others (eds.) *The effects of stress and pollution on marine animals*. Praeger Scientific Publications, New York: 161-178.
- Widdows, J., Donkin, P., Brinsley, M.D., Evans, S.V., Salkeld, P.N., Franklin, A., Law, R.J., and Waldo, M.J. 1995. Scope for growth and contaminant levels in North Sea mussels *Mytilus edulis*. *Marine Ecology Progress Series* 127: 131-148.



- Widdows, J., Brinsley, M.D., Salkeld, P.N., and Elliott, M. 1998. Use of annular flumes to determine the influence of current velocity and bivalves on material flux at the sediment-water interface. *Estuaries* 21(4A): 552-559.
- Widdows, J. 2001. Bivalve clearance rates: inaccurate measurements or inaccurate reviews and misrepresentation? *Marine Ecology Progress Series* 221: 303-305.
- Williams, L.G. 1982. Mathematical analysis of the effects of particle retention efficiency on determination of filtration rate. *Marine Biology* 66: 171-177.
- Winter, J.E. 1970. Filter feeding and food utilisation in *Arctica islandica* L. and *Modiolus modiolus* L. at different food concentrations. *In: Maine food chains*. Proceedings of a symposium held at the University of Aarhus, Denmark, 1968. Steele, J.H. (ed), pp.196-206.
- Winter, J.E. 1973. The filtration rate of *Mytilus edulis* and its dependence on algal concentration, measured by a continuous automatic recording apparatus. *Marine Biology* 22: 317-328.
- Winter, J.E. 1978. A review on the knowledge of suspension-feeding in lamellibranchiate bivalves, with special reference to artificial aquaculture systems. *Aquaculture* 13: 1-33.
- Wright, R.T., Coffin, R.B., Ersing, C.P. and Pearson, D. 1982. Field and laboratory measurements of bivalve filtration of natural marine bacterioplankton. *Limnology and Oceanography* 27(1): 91-98.
- Wong, W.H., Levinton, J.S., Twining, B.S., Fisher, N.S., Kelaher, B.P., and Alt, A.K. 2003. Assimilation of carbon from a rotifer by mussels *Mytilus edulis* and *Perna viridis*: a potential food-web link. *Marine Ecology Progress Series* 253: 175-182.
- Word, J.Q. 1978. The infaunal trophic index. *In: Annual Report 1978*. Coastal Water Research Project, El Segundo, California, USA. pp.19-39.
- Yokoyama, H. 2003. Environmental quality criteria for fish farms in Japan. *Aquaculture* 226: 45-56.