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TEMPORAL PERSPECTIVES ON FOOD ACQUISITION BY SUSPENSION-FEEDING BIVALVES:

PLACOPECTEN MAGELLANICUS AND *MYTILUS EDULIS*

by

Peter James Cranford

Submitted in partial fulfilment of the requirements
for the degree of Doctor of Philosophy

at

Dalhousie University
Halifax, Nova Scotia
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ABSTRACT

The primary hypothesis addressed is that food acquisition by bivalve filter feeders is driven not only by physical and morphological constraints on feeding, but also by a complex interplay between different time-scales of variation in oceanographic variables, the time-dependence of compensation capabilities and temporal variations in nutritional demands. A novel approach for monitoring food utilization by bivalve filter feeders was developed that permits time-series measurements to be obtained autonomously under natural conditions. Measurements obtained with this method are shown to exhibit high precision and accuracy. To provide empirical data to help understand and predict fluctuations in feeding/digestion behaviour, food utilization by sea scallop (*Placopecten magellanicus*) and blue mussel (*Mytilus edulis*) cohorts was measured in several coastal regions of Nova Scotia in conjunction with extensive environmental monitoring. Studies were conducted to document responses of scallops to tide- and storm-induced and seasonal changes in oceanographic conditions. The potential for interspecific differences in feeding strategy was addressed by comparing seasonal responses of sea scallop and mussel cohorts. A laboratory study was also conducted to document the time-course and magnitude of digestive compensation responses to changes in food supplies.

The previous hypothesis that food utilization by bivalve filter feeders is a highly automated and unregulated process is not supported by the observations. Scallop and mussel ingestion rates varied over different time-scales in a manner that cannot be explained by assuming continuous feeding. Average clearance rate estimates for scallops and mussels in nature were between 3.2 and 6.6 times lower than predicted assuming maximal clearance rate. Periodic feeding activity was shown to account for a high proportion of daily and seasonal food intake rates. These observations dictate a re-evaluation of current theories on the role of bivalve filter-feeders in controlling seston dynamics, phytoplankton biomass, and trophic structure in many shallow coastal regions.

Short- and long-term ingestion rates were not closely coupled to temperature, the quantity and composition of the seston, or to horizontal and vertical particle flux, but sea scallop clearance rates were directly related to current speed. Observed seasonal variations in feeding behaviour by both species appear to have resulted from the combination of relatively low food availability at the study site and the high energy demands of reproduction. An important mechanism for controlling food intake in both species is the regulation of absorption efficiency (AE). AE was found to be closely related to the quality of the food supply and was shown to be dependant on past feeding history. Absorptive compensation was confirmed for both species in laboratory and field studies and appears to be optimized in a time-averaged manner that minimizes the need for continuous adjustments.

ABBREVIATIONS AND SYMBOLS

$a1$	maximum absorption efficiency
$a2$	rate of increase in absorption efficiency with increasing diet quality
$a3$	diet quality at which absorption efficiency is zero
AE	net absorption efficiency
AE_{POM}	net absorption efficiency of particulate organic matter
AE_{POC}	net absorption efficiency of particulate organic carbon
AE_{PN}	net absorption efficiency of particulate nitrogen
ANOVA	analysis of variance
A	absorption rate
BIOTRAP	common name for a sequentially sampling sediment trap
C or C_{T}	clearance rate of total particulate matter
C:Chl	ratio of concentrations of particulate organic carbon to chlorophyll *a*
C:N	ratio of particulate organic carbon to particulate nitrogen concentrations
d_1	smallest diameter particle retained by filter
d_2	largest diameter organic particle in the seston
d_3	largest diameter particle in the seston
d_r	minimum diameter particle effectively retained by bivalve
Q	diet quality
Q_{10}	metabolic ratio over 10°C
E_{ash}	proportion of inorganic matter in faeces

E_{absorbed}	proportion of absorbed substrate (POM, POC or PN) in faeces
E	egestion or biodeposition rate
F_{ash}	proportion of ash in food
F_{absorbed}	proportion of absorbed substrate (POM, POC or PN) in food
GPT	put passage time
I_a	actual ingestion rate
I_c or I_{T}	calculated ingestion rate of total particulate matter
I_{ash}	calculated ash ingestion rate
I_{S}	calculated ingestion rate at standard body weight and temperature
L	shell length
PIM	particulate inorganic matter (ash)
POC	particulate organic carbon
POM	particulate organic matter
PN	particulate nitrogen
RE	retention efficiency
R	respiration rate
SD	standard deviation
SE	standard error
T	water temperature
TPM	total particulate matter
W	dry tissue weight

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This thesis would not have been completed without the support and dedication of my parents and family. I share this accomplishment with them and hope it will encourage my children, Ellen, Sean and Andrew, to treat difficult tasks simply as stepping stones leading to their goals and to strive for a vocation as enjoyable as science.

Newton described science as "... a cumulative enterprise in which people stand on others' shoulders 'to see farther'". I stand on many shoulders, but it is a particular privilege to add this thesis to the solid foundation of research built by professor Brian Bayne on the physiological ecology of bivalve filter feeders.

CHAPTER ONE

GENERAL INTRODUCTION

1.1 BACKGROUND AND THESIS OBJECTIVES

The major objectives of research on the physiological ecology of suspension-feeding bivalve molluscs are (1) to provide predictive relationships for the growth of bivalves under different oceanographic conditions, (2) to quantify their role in the particle flux, nutrient dynamics and phytoplankton production in aquatic ecosystems, and (3) to indicate the degree of stress exerted on marine animals by a wide array of natural and anthropogenic conditions. Each of these goals require an understanding of the physiological processes of food capture and utilization.

The influence of environmental conditions on the growth of suspension-feeding bivalves has been extensively studied, particularly in relation to fisheries management and the culture of various bivalve species. While it is clear that external forcing functions mediate growth (Bayne and Widdows 1978, Dickie et al. 1984, Mallet et al. 1987, MacDonald and Thompson 1986, Page and Hubbard 1987, Mallet and Carver 1989, Rice and Pechenik 1992, Mallet and Carver 1993, Emerson et al. 1994), relationships between environmental conditions (e.g. temperature, food abundance and composition) and growth are often poorly understood (Grant 1996). Although food and temperature are the two primary environmental factors affecting growth in nature, collinearity between these variables can make it difficult to assign causality for observed growth changes. This lack of causality has also been attributed to growth being the sum total of several energy budget terms that respond differently, and sometimes non-linearly, to environmental changes (Grant 1996). An understanding of the complex interplay that exists between the physiological processes controlling food utilization and potential exogenous and endogenous forcing functions is fundamental to the prediction of bivalve growth (Grant 1996).

Considerable research has been conducted on the physiological responses of bivalves to environmental change (reviews by Bayne and Newell 1983, Griffiths and Griffiths 1987, Hawkins and Bayne 1992, Bayne 1998). However, controversies and uncertainties still exist and several difficult issues remain to be addressed. A review of the extensive literature on bivalve ecophysiology reveals that the majority of researchers support the view that bivalve filter feeders regulate food capture and utilization according to nutritional needs (Hawkins and Bayne 1984 and 1992, Bayne et al. 1988, Bayne 1993 and 1998). A diverse and flexible suite of pre- and post-ingestive mechanisms have been identified by which bivalve filter feeders actively compensate for a variable food supply. These include the regulation of water processing rate, the selective retention and rejection of particles, selective particle absorption and variable absorption efficiency. However, in two critical reviews of the literature on bivalve filter feeding, Jørgensen (1990 and 1996) concluded that no convincing evidence was found supporting theories of physiological control of water pumping, filtration efficiency or sorting of suspended particles according to nutritional needs. Instead, Jørgensen views bivalve filter feeding as an automatized process with food uptake being solely determined by the physical properties of the filter-pump and ambient food concentration. While this view is not widely supported (see Bayne 1998), many recent concepts in bivalve ecology, such as speculations on the capacity of some bivalve communities to control phytoplankton abundance (e.g. Cloern 1982, Officer et al. 1982, Nichols 1985, Hily 1991, Dame 1993 and 1996), are based on simple filtration (clearance) rate models that conform with this view. Resolution of this controvery is required before the role of bivalves in controlling coastal ecosystem structure and function can be more clearly defined.

Studies into the natural food available to suspension-feeding bivalves in coastal waters reveal marked short- and long-term variations in the concentration, composition and nutritional value of seston (Vahl 1980, Cadée 1982, Chanut and Poulet 1982, Rhoads et al. 1984, Fréchette and Bourget 1985, Seiderer and Newell 1985, Hawkins and Bayne 1985, Berg and Newell 1986, Langdon and Newell 1990, Fegley et al. 1992, Emerson et al. 1994). Long-term changes in seston abundance and composition in temperate waters arise primarily from the seasonal cycle of primary production. Variability on a scale of days to weeks can result from algal blooms, horizontal phytoplankton patchiness, storm-induced resuspension of bottom deposits or the spring/neap tidal cycle (Fréchette and Bourget 1987; Bayne 1993). In many coastal systems, fine-scale fluctuations in the seston are superimposed on these longer-term trends and result largely from tide-induced resuspension and deposition of bottom deposits and associated organic and inorganic constituents

(Rhoads et al. 1984, Berg and Newell 1986, Fegley et al. 1992, Muschenheim 1987). The increase in the proportion of inorganic particles in the water column during resuspension events has a 'dilution' effect on food quality (Foster-Smith 1975, Widdows et al. 1979, Newell and Jordan 1983), which is generally defined in terms of the organic and/or elemental content of 'bulk' seston.

The supply of food to filter-feeders is not solely dependent on the concentration and quality of suspended particulate matter but is also a function of flow velocity (Muschenheim 1987, Cahalan *et al.* 1989). Owing primarily to tidal variations in flow, particle flux to bivalves varies significantly over a single tidal cycle. Although suspension-feeding bivalves actively pump water over the sieving structure, the feeding process may be facilitated by the local flow regime. Flow velocity has previously been shown to directly affect feeding behaviour and/or growth rate in the mussel *Mytilus edulis* (Wildish and Kristmanson 1985, Wildish and Miyares 1990), the American oyster *Crassostrea virginica* (Grizzle et al. 1992, Lenihan et al. 1996) and in the scallops *Placopecten magellanicus* (Wildish et al. 1987, Wildish and Kristmanson 1988, Wildish and Saulnier 1993) and *Argopecten irradians concentricus* (Kirby-Smith 1972, Eckman et al. 1989) and may be a major determinant of growth rate (Kirby-Smith 1972).

The ability to predict bivalve growth responses to the different time-scales of environmental change requires information on the time required for physiological processes, which are inherently time-dependant (Bayne 1993), to adapt to the change. The time-constant for regulation of ingestion rate by altering filtration and rejection processes appears to be sufficiently short to allow the animal to respond to even fine-scale temporal variations in environmental conditions (Fréchette and Bourget 1987, Bayne 1993, Navarro and Iglesias 1993, Hawkins et al. 1996). However, while the time-course of digestive regulation has not been documented, Bayne (1993) suggested that it is longer than required to compensate for daily or tidal fluctuations in the seston. The absorption of nutrients during passage of particles through the gut has been identified as the most important regulatory process in the optimization of energy gain in *M. edulis* (Bayne et al. 1993) and further studies are required to understand the strategy by which bivalves regulate this process in responses to the different time-scales of external and internal forcing.

We know little about the importance of fine-scale changes in food acquisition to the daily food intake and long-term growth of bivalves. It has been suggested that at least some bivalves do not attempt to regulate food utilization over the short term, but utilize time-averaged optimization behaviour (Hawkins *et al.* 1985). For example, if food availability fluctuates rapidly over short-time scales, the animal may waste valuable internal resources responding to every change (i.e. making digestive enzyme adjustments). Incorporating some elements of environmentally-induced physiological regulation into bivalve growth models has proven difficult as it is impractical for predictive models to deal with large fine-scale temporal variations in seston (Grant 1996). If it is shown that various bivalve species in nature utilize a time-averaged food utilization startegy, predictive feeding behaviour models would not have to deal with the difficult task of simulating fine-scale temporal variations in seston.

Predicting growth responses over longer time-scales requires information on another difficult issue. Little is known of the dependence of bivalve feeding/digestion processes on the seasonally changing energy costs and nutrient demands of gametogenesis. While short-term deficiencies in energy intake may be met by catabolizing internal energy reserves (Hawkins et al. 1985), seasonal variations in nutritional requirements are more likely to cause shifts in food acquisition. Kreeger (1993) measured the *in vivo* ingestion, digestion and assimilation of dietary protein in mussels *M. trossulus* at four different times of year and concluded that variations in protein uptake were not simply responses to changing seston composition, but were more closely coupled to the high energy and biosynthesis requirements of reproductive activity. Seasonal variations in the utilization of protein and carbon by *M. edulis* also appear to be governed by changing anabolic demands (Kreeger et al. 1995). Few studies have been conducted of the seasonal patterns of food utilization by bivalve suspension feeders and have been limited to monthly or seasonal sampling owing largely to logistical constraints imposed by traditional methodologies (Bayne and Widdows 1978, Widdows et al. 1979, MacDonald and Thompson 1986, Kreeger 1993, Prins et al. 1994, 1995, Kreeger et al. 1995, Smaal et al. 1997, and Smaal and Vonck 1997).

The primary hypothesis addressed in this thesis is that food acquisition by bivalve filter feeders in their natural environment is driven not only by physical constraints on feeding, but also by a complex interplay between the different time-scales of variation in oceanographic variables, the time-dependence of acclimation capabilities and temporal variations in nutritional demands. While the majority of bivalve feeding studies have been concerned primarily with determining instantaneous responses to environmental change, the role of past feeding history and time-dependent physiological processes in defining present food acquisition has only recently begun to be addressed (Bayne, 1993). The component studies of this thesis were designed to provide empirical data that can be used (1) to determine the constraints on food acquisition imposed by time-dependent features of feeding behaviour, and (2) to construct predictive relationships between food utilization behaviour and environmental variables. The former objective addresses the time-scale required for physiological processes to respond to environmental change, the persistence of this response in the face of further change (the influence of past feeding history on present behaviour), and the role of long-term variations in internal energy demands in defining short-term feeding behaviour.

1.2 SPECIES SELECTION.

The sea scallop *Placopecten magellanicus* (Gmelin) and the blue mussel *Mytilus edulis* (L.) have been selected as the key species for these studies. The sea scallop is the most important commercial bivalve species in Canada and the production of a high-value cultured product is currently in an early stage of expansion. Given the socio-economic importance of this fishery and the potential for mariculture, there is an increased demand for basic information on the influence of environmental variables on scallop growth and survival. The majority of mussel landings are supplied by commercial culture, which is well established and is currently experiencing a growth phase in Atlantic Canada. Presently, most mussel farm sites in Nova Scotia are not fully exploited and the potential exists for up to a ten-fold increase in annual production (Lavoie et al. 1993).

Models of the feeding physiology of suspension-feeding bivalves are primarily based on the extensive data available on the feeding and digestive processes of *M. edulis* (Lehman 1976, Jørgenson et al. 1988, Willows 1992). However, interspecific differences in bivalve morphology may result in different feeding/digestion strategies under similar dietary conditions. For example, the capacity to selectively reject non-nutritious particles prior to ingestion varies dramatically among bivalves (Kiørboe and Møhlenberg 1981) and siphonate and non-siphonate taxa exhibit different feeding and growth responses to similar flow regimes (Grizzle *et al.* 1992). Different bivalve species also appear to adopt different strategies for energy acquisition to obtain a competitive advantage in their preferred habitat (Cranford and Gordon 1992, Navarro and Iglesias 1993, Cranford 1994). It therefore appears necessary to conduct studies with each bivalve species so that major physiological differences and generalities can be established across species lines. Considering the relatively vast literature available on *M. edulis* physiological ecology, the emphasis of this thesis was on *P. magellanicus*. However, a direct comparison of seasonal fluctuations in the feeding/digestion behaviour of sea scallops and mussels was conducted.

1.3 PERSPECTIVES ON METHODOLOGY

Much of the information on bivalve physiological responses to environmental variables has been obtained in the laboratory under unnatural conditions of food and tidal regime (reviewes by Winter 1978, Bayne and Newell 1983, Griffiths and Griffiths 1987, Hawkins and Bayne 1992, Bayne 1998). An important question is whether or not bivalves in nature actually feed at the optimal rates observed in the laboratory with bivalves held in static or constant flow chambers and fed cultured algal diets. Several studies indicate that the ambient particle field influences bivalve feeding behaviour to a greater extent than is indicated by studies based solely on algal monoculture diets (Doering and Oviatt 1986, Riemann et al. 1988, Cranford and Gordon 1992, Iglesias et al. 1992, Navarro et al. 1992, Prins et al. 1994, Hawkins et al. 1996). Further, flow variability is also known to affect bivalve feeding (Wildish et al. 1987, Eckman et al. 1989, Wildish and Miyares 1990, Cole et al. 1992, Grizzle et al. 1992), but must be removed to allow traditional laboratory and field methods to measure particle depletion. These studies demonstrate the importance of conducting studies on the functional responses of bivalves under ecologically relevant environmental conditions.

Much of the controversy in the literature over the ability of bivalve filter feeders to physiologically control food intake stems from the argument that the observed changes in clearance rates actually result from the neglect of negative effects of experimental conditions on the 'filter-pump' and not from active regulation (Jørgensen 1990, 1996). For this controversy to be fully resolved, not only must it be proven that variations in food intake are not determined solely by physical constraints on filtration capacity and food concentration, but also that the experimental conditions did not influence the results.

Traditional methods are limited in their ability to provide information on ingestion and absorption rates of undisturbed bivalve filter feeders under natural conditions of flow and particle flux. Therefore, a new approach is required to monitor food utilization *in situ*. Ideally, the method should be autonomous and provide a more continuous record of feeding responses than is provided by traditional methods that require spot sampling and particle-counting instrumentation. The considerable interindividual variability in the physiological status of bivalves (Hawkins and Bayne 1992) may also be avoided if the integrated response of a cohort of animals was measured. In addition to providing ingestion rates, the method should provide simultaneous information on the proportion of organic seston digested (absorption efficiency) as this measurement is required to calculate the total food uptake (absorption rate).

Most studies on resource acquisition in bivalves have been conducted solely in terms of energy (reviewed by Bayne and Newell 1983) or carbon (Gilfillan et al. 1976, Kiϕrboe et al. 1980, Gallager et al. 1981, Seiderer et al. 1982) despite the distinct possibility that nitrogen resources may limit production in coastal waters (Mann 1982). More recent studies have emphasized studying energy, carbon, and nitrogen uptake and utilization, an approach that has increased our understanding of the causes of temporal fluctuations in bivalve productivity in coastal waters (Hawkins and Bayne 1985; Fielding and Davis 1989, Grant and Cranford 1991). To this end, the utilization by bivalves of available organic matter, organic carbon and nitrogen was studied when possible.

1.4 ORGANIZATION OF THESIS

This thesis represents a collection of individual studies that share the hypothesis that bivalve filter feeders regulate food acquisition on different temporal scales in response to changes in endogenous and exogenous forcing. A new *in situ* approach to monitoring food utilization responses of bivalves is described and used to follow sea scallop feeding behaviour during short-term (tidal cycle) variations in oceanographic variables (Chapter 2).

This approach was then used in subsequent *in situ* studies of bivalve feeding/digestion responses during a storm-induced resuspension event (Chapter 4) and during seasonal changes in environmental conditions and the changing demands of the annual reproductive cycle (Chapter 5). A follow-up study designed to determine the precision of feeding/digestion measurements obtained with the *in situ* approach is reported in Chapter 6. As the environmental conditions experienced by animals held in the field cannot be controlled, it was necessary to conduct a laboratory study to determine the time-course and magnitude of digestive acclimation in response to different time-scales of variation in food supplies (Chapter 3). The results of this laboratory experiment were used to help interpret field observations in later chapters. The major results and conclusions of the thesis are presented in Chapter 7 along with a brief description of additional applications of the technologies developed.

The five separate studies reported in this thesis (Chapter 2-6) are presented in the style in which they were, or are intended to be published. Chapters 2 and 6 are presented as research notes and the only sections are the *Abstract* and the main body of the text. Chapters 2 to 5 also contain an *Abstract*, but include separate sections containing *Materials and Methods, Results* and *Discussion*. Some repetition was necessary between methods sections to allow each chapter to stand as an independant article. References from each chapter are combined and presented at the end of the thesis.

CHAPTER TWO

IN SITU TIME-SERIES MEASUREMENT OF INGESTION AND ABSORPTION RATES OF SUSPENSION-FEEDING BIVALVES: *PLACOPECTEN MAGELLANICUS* (GMELIN).

2.1 ABSTRACT.

An adaptation of available methods is described for quantifying the ingestion and absorption rates of suspension-feeding bivalve molluscs exposed *in situ* to natural food sources and flow conditions. This new approach was used to follow the feeding response of the sea scallop *Placopecten magellanicus* (Gmelin) to short-term tidal cycle effects on current speed and seston quality in Lunenburg Bay, Nova Scotia. Unlike traditional methods, sampling is continuous and measurements of food uptake and utilization are averaged over selected time intervals (minutes to days). Scallop feeding activity varied markedly over a tidal cycle and periodic feeding activity accounted for a large proportion of food intake. Ingestion rates were not closely coupled with seston quantity, horizontal particle flux or nutritional value as inferred from pigments, total organic and organic carbon and nitrogen content. The scallops did not alter absorption efficiency in order to adapt to short-term variations in diet quality.

2.2 *IN SITU* TIME-SERIES MEASUREMENT OF INGESTION AND ABSORPTION RATES OF SUSPENSION-FEEDING BIVALVES: *PLACOPECTEN MAGELLANICUS* (GMELIN).

Validation of present hypotheses on the role of suspension-feeding bivalve molluscs in coastal ecosystem dynamics (e.g. Dame 1996; Cloern 1982; Asmus and Asmus 1991) requires accurate quantification of feeding and biodeposition rates. Traditional methods for measuring filtration and ingestion rates of suspension-feeding bivalves involve monitoring the removal of suspended particles by animals enclosed in either closed or constant flow-through systems. Variations on the latter flow-through method include the use of small chambers designed to hold individual animals (Walne 1972), laboratory-based recirculating flumes in which an assemblage of organisms can be placed on natural substrate (Cole et al. 1992) and *in situ* tunnel and open flume systems that canalize tidal water over natural beds of suspension feeders and monitor differences in particle concentrations in inflow and outflow water (Asmus and Asmus 1991; Dame et al. 1992).

The simpler static and flow through chamber methods eliminate natural conditions of flow variability that have been shown to affect bivalve feeding and growth (e.g. Eckman et al. 1989; Wildish and Miyares 1990; Grizzle et al., 1992). Such a response to flow is reasonable considering that the food supply to suspension feeders is a function of both concentration and flow velocity (Muschenheim 1987; Cahalan et al. 1989). Recirculating flumes enable variable flow conditions to be reproduced in the laboratory (Cole et al. 1992) but are limited by the logistic constraints of providing large quantities of natural diets. The feeding response of bivalves to natural suspensions of particulate matter appears to markedly differ from that observed when algal monoculture diets are presented (Bayne and Newell 1983, Doering and Oviatt 1986, Cranford and Gordon 1992). Changing tidal currents and winds cause large short-term variations in the quantity and quality of seston in coastal waters that can also influence feeding behaviour (e.g. Fegley et al. 1992). The supply of natural sources of food is not a concern in *in situ* flume and tunnel methods, however, elimination of lateral advection is required to constrain the flow regime in order to quantify bivalve-induced particle depletion. *In situ* flumes and tunnels can only be used in shallow tidal systems, they tend to suppress natural turbulence, cannot be used when the wind drives currents perpendicular to the tunnel, and are of limited use during periods of low, high, or variable current velocities (Asmus and Asmus 1991).

A new approach is described here for quantifying bivalve suspension-feeding and absorption rates. The principal improvement over traditional methods is that the bivalves are exposed *in situ* to natural particle fluxes and less restrictive flow conditions. The method is well suited to use in the field owing to automation and the elimination of particle-counting instrumentation. Measurements obtained with this method provide a more continuous record of bivalve feeding than that obtained using previous methods requiring periodic sampling. In addition, information on the proportion of particulate organic matter digested (absorption efficiency) is obtained simultaneously with feeding rate data. This measure of food utilization is required for constructing energy and elemental budgets.

Ingestion and absorption rates are calculated from measurements of bivalve biodeposition rate and the proportion of absorbed and non-absorbed components in food (seston) and feces. Biodeposition rates are determined with a sediment trap technique similar in principal to that described by Kautsky and Evans (1987), except in my study a sequential sampling collector was used. The method was applied in a study of the feeding response of the sea scallop *Placopecten magellanicus* to short-term tidal cycle effects on water flow and seston flux in Lunenburg Bay, Nova Scotia, Canada. The site has a maximum water depth of 5.5 m (1.3 m tidal range), is located near the mouth of South Cove (44°21' N, 64°18' W), and has been sampled extensively during a research program designed to model bivalve growth and site carrying capacity.

On 6 October 1992, a sequential sampling trap, similar in basic design to a multi-sample sediment trap described by Zeitschel et al. (1978), was anchored on the seabed. The 1.5 m high, 0.11 m^2 trap, constructed at the Bedford Institute of Oceanography, collects particles in 14 cups programmed to rotate under the collecting funnel at selected time intervals (Fig. 2.1). Particles settling into sample cups are preserved in $HgCl_2$ (0.1% wt/vol) in a brine solution (35 ‰ NaCl). Five scallops (mean shell height = 95 mm, SD = 10) were placed over the open mouth of the trap on a coarse mesh (2 cm) which allowed

Figure 2.1

The BIOTRAP is a 1.5 m high, sequentially sampling sediment trap that can collect up to 14 separate samples in cups that rotate into position under the collecting funnel. The configuration illustrated is drawn to scale and is the same as that deployed in Lunenburg Bay. Five scallops sit on a monofilament mesh (2 cm pores) in the mouth of the trap and are confined to individual cages constructed from flexible nylon tubing (3 mm OD). The total open area in the mouth of the funnel around scallops was 715 cm^2.

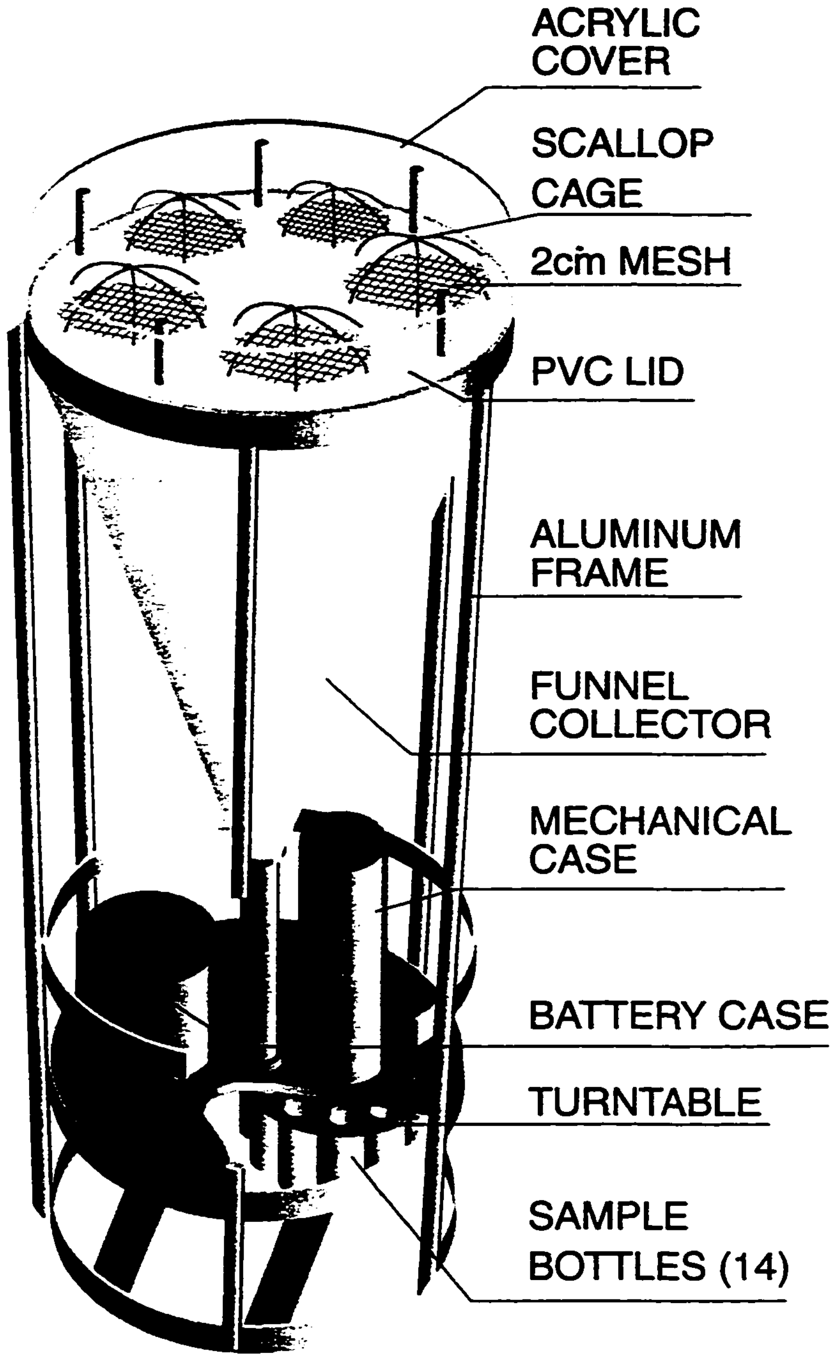
ACRYLIC COVER
SCALLOP CAGE
2cm MESH
PVC LID
ALUMINUM FRAME
FUNNEL COLLECTOR
MECHANICAL CASE
BATTERY CASE
TURNTABLE
SAMPLE BOTTLES (14)

Figure 2.1

feces to fall into the sample cups. In order to reduce seston sedimentation into the trap, the effective area for sedimentation through the mouth was restricted to a region surrounding each animal (Fig. 2.1). In addition, a transparent acrylic cover was positioned 5 cm above the top of the funnel. Because scallops are mobile, they were confined using coarse mesh cages. Since the scallops were cultured at the study site by the ear-hanging method, the ear hole was also used to tie the animal in place in the center of the feeding zone. Prior to deployment, the trap was programmed for hourly cup rotation with an initial one hour delay to allow the scallops to resume normal feeding after placement of the trap. Sampling started at 1045 hours on 6 October and continued to 0045 hours the next day. The scallops used is this study had been at the site for approximately 1 yr.

Current speed and direction were logged at 2-min intervals over a 3-d period with an EGandG Ocean Products acoustic current meter, moored at the same depth and within 20 m of the trap, starting at 1600 hours on 6 October. Hourly water-column profiles were made with calibrated salinity, temperature and oxygen probes between 0900 and 1800 hours on 6 October. Hourly water samples were also collected during this period, which was out of phase with the feces collections (started earlier) because of the lag time required for food particles to pass through the animals and deposit in the sample cups. Water was pumped from 2 m above the seabed and processed as follows. Total suspended particulate matter (TPM; mg dry weight liter^{-1}), ash and organic content

(POM; %) were determined in triplicate for particles collected on prewashed (distilled water) and precombusted (450°C for 6 h) 25-mm Whatman GF/F filters. Salt was expelled by rinsing each filter under vacuum with isotonic ammonium formate. Filters were dried at 60°C for 24 h and weighed to give TPM. The weight of ash remaining after combustion at 450°C for 6 h was determined and POM calculated from the weight loss upon ignition. The organic carbon (POC) and nitrogen (PN) content of seston collected on precombusted GF/F filters was determined with a Perkin-Elmer model 2400 CHN elemental analyzer after fuming the filters over concentrated HCl for 1 h in a closed container to remove inorganic carbon. The chlorophyll *a* and pheophytin content of particles collected in duplicate on Millipore HA filters (0.45-μm porosity) was determined by the fluorometric technique of Holm-Hansen et al. (1965).

After the last sample cup was rotated from under the funnel, the trap was retrieved and the sample cups were removed and refrigerated for transport back to the laboratory. Visual inspection of the samples revealed that only large fecal particles were collected. Pseuodofeces, which are readily distinguishable from feces, were not present. Particles in each cup were subsampled and analyzed as above for total dry weight, POM, POC, PN, chlorophyll *a*, and pheophytin. Weight specific biodeposition rates (mg g^{-1} dry tissue h^{-1}) were calculated for each hourly sampling interval by dividing the total dry weight of egested fecal particles in each cup by the total shell-free dry weight of the five scallops (42.7 g). Seston sedimentation at the study site was measured simultaneously with scallop biodeposition using similar sediment traps (Hargrave et al. 1994) and could have accounted for about 15% of the total mass of particles collected in the cups. However, due to the precautions taken to prevent seston from sedimenting into the trap (see above), no correction was made for seston sedimentation around the scallops.

Water temperature and salinity showed no temporal or depth variation during the study and averaged 9.7°C (SD = 0.6) and 31.1‰. Oxygen levels were consistently above saturation. Current speeds measured 1.5 m above the seabed varied markedly over the tidal cycle, with maximum velocities of 15 cm sec^{-1} occurring during mid-flood tide (Fig. 2.2). Speeds were lowest at mid-ebb and late-flood tide. The high frequency oscillations (approximately 1 h) in current speed are caused by a semi-permanent seiche within Lunenburg Bay (Hargrave et al. 1994). Although current speed measurements were not recorded during the first 5 h of the trap deployment, current speed followed similar patterns over several consecutive tidal cycles (Hargrave et al. 1994), and Figure 2.2 is considered representative of tidal variations in current speed. Hourly water samples were collected over a tidal cycle and seston quantity and quality data are plotted in Fig. 2.3. Total particulates (TPM) averaged 1.5 mg $liter^{-1}$ (SD = 0.4) with peaks observed at late-ebb (1130 hours) and late-flood tide (1600 hours) (Fig. 2.3a). Food quality on both occasions, as indicated by chlorophyll *a*, POM, POC and PN content and the ratio of carbon to chlorophyll *a*, was reduced by an increased proportion of inorganic material

Figure 2.2

Current speed (10-min means of readings at 2-min intervals) at the study site during a tidal cycle. Water depth (broken curve) is estimated from tide tables.

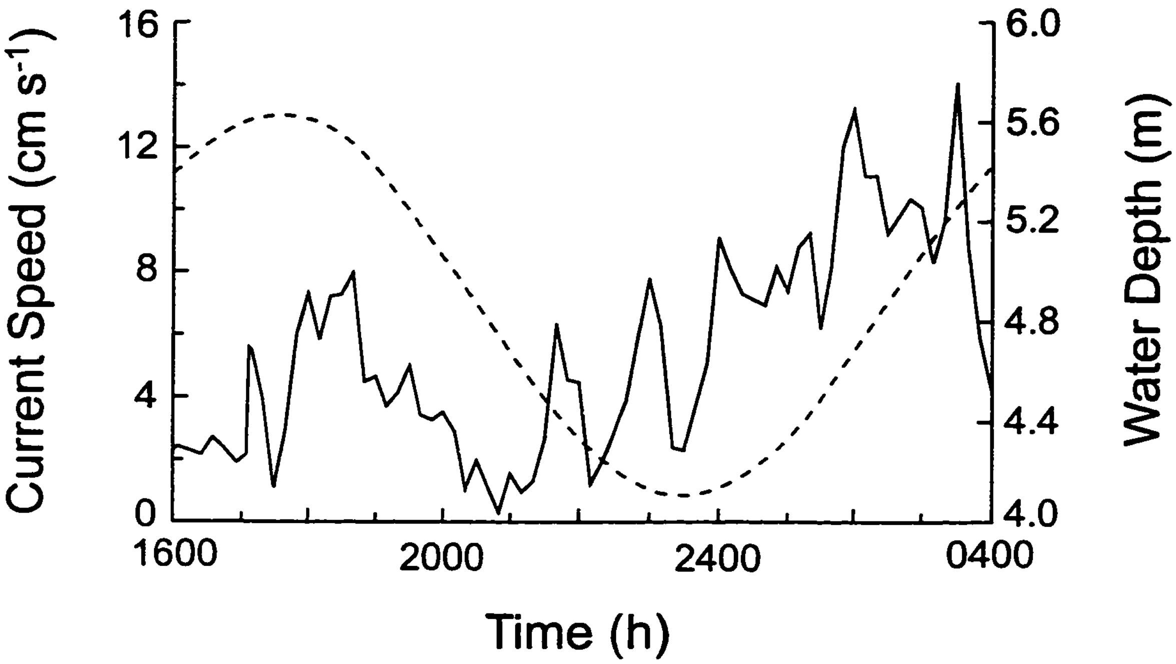
16
12
8
4
0
Current Speed (cm s^{-1})
6.0
5.6
5.2
4.8
4.4
4.0
Water Depth (m)
1600
2000
2400
0400
Time (h)

Figure 2.2

Figure 2.3

Characteristics of seston at the study site. Water samples were collected by pump from 2 m above the seabed. Left axis variables are marked by circles and solid lines and right axis variables are the triangles and broken lines. (a) Mean (±1 SD, n = 3) seston concentration (TPM) and percentage organic matter (POM). (b) Mean (± max:min, n = 2) chlorophyll *a* values expressed volumetrically (left) and as a proportion of total seston dry weight (right). (c) Percentages of organic carbon (POC) and nitrogen (PN) (n = 1). (d) Ratios of carbon to nitrogen and carbon to chlorophyll *a*. The broken curve represents water depth (tidal cycle) during the sampling period.

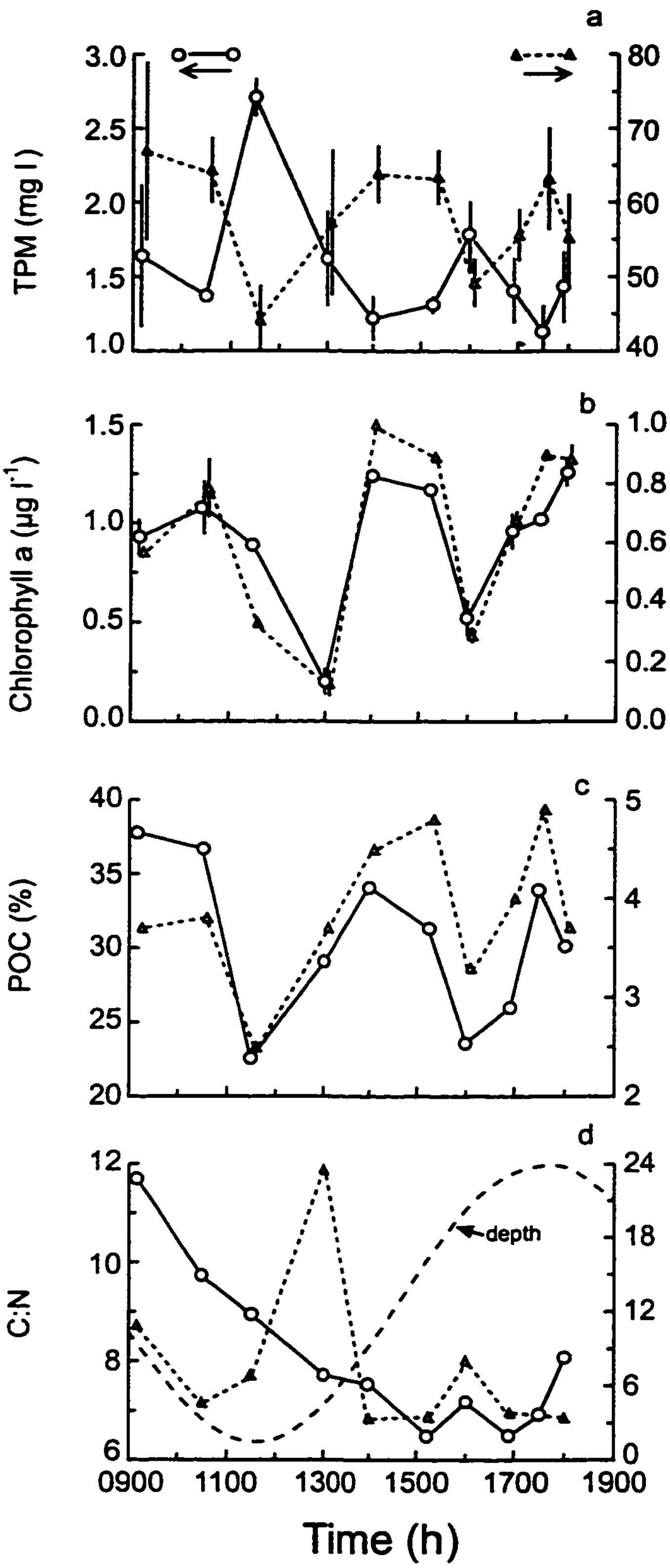
a
b
c
d
TPM (mg l)
POM (%)
3.0
2.5
2.0
1.5
1.0
80
70
60
50
40
Chlorophyll a (µg l⁻¹)
Chlorophyll a (mg g⁻¹)
1.5
1.0
0.5
0.0
0.8
0.6
0.4
0.2
POC (%)
PN (%)
40
35
30
25
20
5
4
3
2
C:N
C:Chl (x100)
12
10
8
6
24
18
12
6
0
depth
0900
1100
1300
1500
1700
1900
Time (h)

Figure 2.3

(Fig. 2.3). The C:N ratio did not follow this trend, but gradually declined during the sampling period (Fig. 2.3d).

Weight-specific scallop biodeposition, as determined from the total weight of particles deposited in sample cups by the five scallops over hourly intervals, is plotted in Fig. 2.4a. Ingestion rates were calculated from these biodeposition data using the inorganic (ash) content of seston and feces as a conservative tracer. Cranford and Grant (1990) confirmed that ash is a suitable inert tracer in digestive studies with *P. magellanicus* and other suspension-feeding bivalves. Since ash is not absorbed during digestion, the rates of ash ingestion (I_{ash}) and egestion (E_{ash}) are equal (changes in gut volume can cause some variation in these two rates on short time-scales, however, this 'noise' would likely be lost in the hourly composite feces samples). Measurements of the proportion of ash in the food (F_{ash}) can then be used to calculate total ingestion rates (I_T; mg dry particles g^{-1} dry tissue h^{-1}) according to the equation:

$$I_T = E_{ash} / F_{ash}. \tag{2.1}$$

Average seston organic and ash contents are suitable for ingestion calculations if variability is low over the feeding period. If variations are large, as seen in this study (Fig. 2.3a), a complication arises in determining which seston sample (food) corresponds to the fecal material collected in the cups. The appropriate feeding period can be determined from either gut passage time measurements or by the detection of distinct pulses of biologically inert natural or synthetic particles in seston and feces samples. As

Figure 2.4

Weight-standardized *Placopecten magellanicus* biodeposition (a) and ingestion rates (b) measured hourly (horizontal bars) at the study site. The broken curve plotted along with biodeposition data represents water depth (tidal cycle) during the sampling period. Ingestion rates were calculated as outlined in the text. Values connected with the solid line were calculated using the mean organic content of seston (58%). The area between the broken lines represents the possible range of error and was calculated using the maximum (67%) and minimum (44%) observed seston organic contents (Fig. 2.3a).

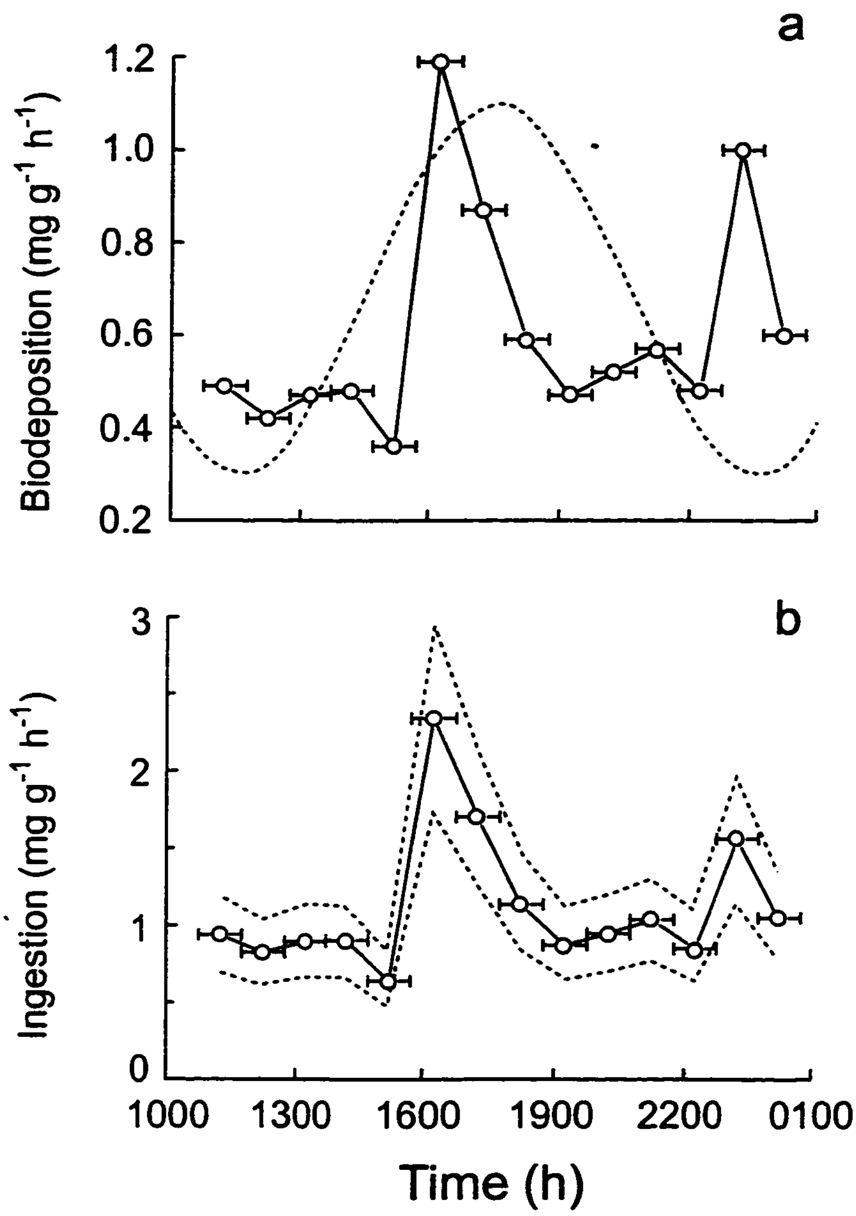
a
Biodeposition (mg g^{-1} h^{-1})
1.2
1.0
0.8
0.6
0.4
0.2
b
Ingestion (mg g^{-1} h^{-1})
3
2
1
0
1000
1300
1600
1900
2200
0100
Time (h)

Figure 2.4

these measurements were not conducted in the present study, ingestion rates were estimated (Fig. 2.4b) with the mean seston ash content (42%) and the total range of error was calculated with the maximum (33%) and minimum (56%) seston ash contents observed over the tidal cycle. This range is assumed to be representative of the food consumed by the scallops during this study. Preingestive particle selection can alter the organic content of ingested particles relative to seston. However, selection requires the production of pseudofeces, which were not present in biodeposits. Even though the large tidal variations in seston organic content cause some uncertainty in ingestion rate estimates, the range of error for each hourly sampling interval was small relative to tidal cycle variations (Fig. 2.4b). Ingestion rates remained relatively constant at about 1 mg g^{-1} h^{-1} during the study period with the exception of marked increases during late-flood (1545-1745 hours) and low tide (2245-2345 hours) (Fig. 2.4b). These periods of high feeding rates accounted for 36% of the total food ingested during the study.

Ingestion rates for *P. magellanicus* measured with the sediment trap method were compared to estimates obtained with allometric relationships between clearance rate and tissue dry weight determined by MacDonald and Thompson (1986) for individuals fed natural seston in flow-through feeding chambers. Ingestion rates predicted for five scallops of similar size as used in the present study were comparable with the lower range of measurements we observed (Table 2.1). Lower rates obtained using traditional methods may be a consequence of replicate averaging of clearance rate measurements.

Table 2.1

Comparison of predicted and observed ingestion rates for *Placopecten magellanicus*. The parameters of the allometric relationships between clearance rate and tissue dry weight (W; g) reported by MacDonald and Thompson (1986) for a population residing at 10 m were used to calculate total clearance (C_T) and ingestion rates ($I_T = C_T \times 1.5$ mg liter^{-1}) for five scallops of similar size as used in this study. Weight and temperature (10°C) standardized ingestion (I_S) was calculated by dividing I_T by total tissue dry weight (42.7 g) and using a Q_{10} of 2.0 (Grant and Cranford 1991).

	Predicted				Observed	
	July	Sept.	Nov.	Mean	Range	Mean
Temp (C)	5.5-8.5	10-12	8-10	-	9.1-10.3	9.7
C_T (liters h^{-1})	15.6	23.7	18.2	-	-	-
I_T (mg h^{-1})	23.4	35.5	27.3	-	29.9-106.8	47.9
I_S (mg g^{-1} h^{-1})	0.68	0.83	0.73	0.75	0.7-2.5	1.1

Averaging greatly reduces the importance of high feeding rate events in feeding rate models because of their lower frequency of occurrence. Considering the importance of these periodic events to total food uptake, they should be better represented in feeding rate models.

Powell et al. (1992) noted that suspension-feeding bivalves in general exhibit two distinct rates of feeding, with the difference being a factor of about three. Similarly, Cranford and Gordon (1992) observed that the same individual sea scallops filtered algal cells (*Tetraselmis suecica*) three times faster than natural seston particles. These observations indicate a capacity of sea scallops to alter feeding rate in response to fluctuations in diet properties. The present study shows that sea scallops generally feed at a lower level, but have the capacity to increase food uptake periodically in response to changes in the food available. Identification of the physical mechanism responsible for this regulation of food intake is beyond the scope of this study, however, the results indicate that feeding is physiologically regulated and not simply determined by the physical properties of the bivalve pump (Jørgensen 1990).

Absorption efficiency (AE) was calculated from the content of absorbed (POM, POC, and PN) and inert (ash) indicators in seston (F) and feces (E) according to the equation:

$$AE = [1 - ((F_{ash}:F_{absorbed})/(E_{ash}:E_{absorbed}))] \times 100 \qquad (2.2)$$

(Cranford and Grant 1990). All indicators are expressed as a proportion of seston or feces dry weight. As with the above calculation of ingestion rate, gut passage time should be known in order to select diet samples that correspond with the appropriate feces samples. However, since there was little variation in feces organic and elemental content over the study period (22.4% POM, SD = 4.5; 8.7% POC, SD = 1.5; 1.1% PN, SD = 0.3), accurate AE estimates can be calculated for each seston sample using these averages. AE was calculated in this manner and, as observed by Cranford and Grant (1990), POC and PN were absorbed with slightly higher efficiencies (averaged 83.8%, SD = 5.6, and 83.7%, SD = 6.0, respectively) than POM (78.6%; SD = 6.8) (Fig. 2.5a). The lowest AE values were observed at low and late-flood tide (Fig. 2.5a).

Because AE varied in direct proportion to tidal variations in the organic and elemental content of seston (Fig. 2.3), sea scallops do not appear to control AE (i.e.: attempt to maintain a constant value) to compensate for short-term variations in food quality. The capacity to alter AE may require a longer period of acclimation. *Mytilus edulis* has been shown to alter AE in response to longer term (days to weeks) changes in dietary composition (e.g. Bayne et al., 1987).

The rates of POM, POC, and PN absorption by scallops were calculated for each food sample with data on ingestion rate (Fig. 2.4b), AE (Fig. 2.5a) and diet organic and elemental content (Fig. 2.3a and c). These calculations assume that ingestion rate is constant over the hourly interval that includes the time of water sampling. Despite

Figure 2.5

(a) The efficiency of particulate organic matter (POM), organic carbon (POC) and nitrogen (PN) absorption by *Placopecten magellanicus*. Absorption efficiency (AE) was calculated from water column data (food) and the mean organic and elemental content of feces as outlined in the text. Lack of water column data after 1800 hours limits calculation to the time period indicated. (b) Absorption rate estimates calculated from hourly ingestion rates, the organic and elemental content of seston and absorption efficiency. No ingestion data are available prior to 1045 hours. The broken curve represents water depth (tidal cycle) during the sampling period.

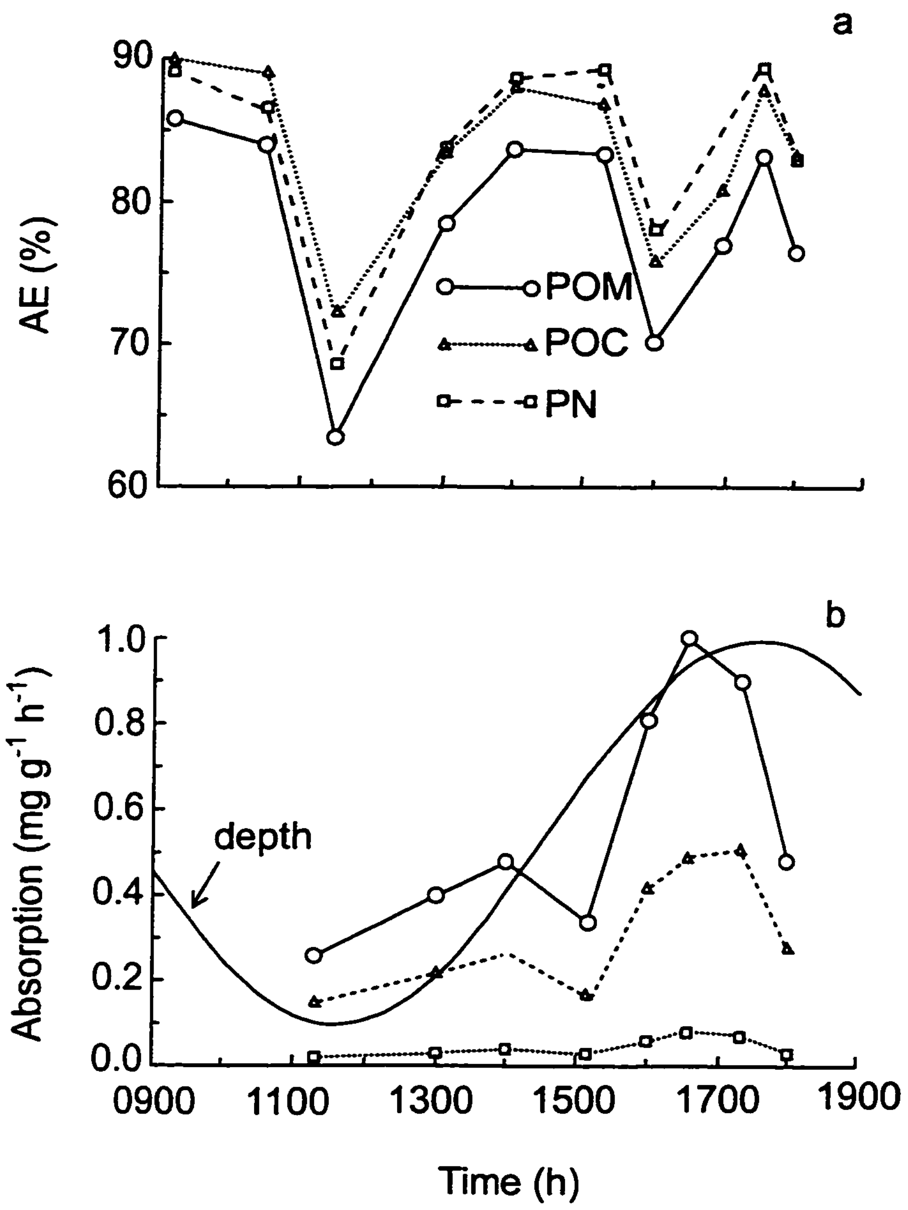
a
90
80
70
60
AE (%)
POM
POC
PN
b
1.0
0.8
0.6
0.4
0.2
0.0
Absorption (mg g-1 h-1)
depth
0900
1100
1300
1500
1700
1900
Time (h)

Figure 2.5

reduced seston quality and AE during late-flood tide (1600 hours), absorption rates (Fig. 2.5b) were high owing to the high ingestion rate at this time. As with the total food ingested, periodic feeding events appear to account for a large proportion of the POM, POC and PN absorbed by the scallops during the study period (Fig. 2.5b).

Results of several studies employing more traditional methods for measuring feeding rates indicate that spatial and temporal variations in seston characteristics (quantity and quality) would likely have marked and predictable impacts on suspension-feeding behaviour and growth rate (e.g. Bayne and Newell 1983, Bayne et al. 1989, Grant and Cranford 1991). Previous laboratory experiments show that *P. magellanicus* feeding rates increase with increasing food quality (Cranford and Grant 1990, Cranford and Gordon 1992). Although seston characteristics such as POM, chlorophyll *a*, POC, and PN content are considered to be indicators of the nutritional value of seston, no clear relation between feeding rate and tidal-induced variations in any of these parameters was observed (Figs. 2.3 and 2.4b). The high ingestion and absorption rates observed during late-flood tide occurred when seston quality appears to be low.

Bulk seston properties (quantity or quality) may be poor predictors of feeding behaviour. The stimulus for increased ingestion may be more dependent on specific properties of the ambient particle field, such as the nature of food particles (e.g. algal species composition or particle size) or the presence of biochemical stimulants (Ward et al. 1992). Alternatively, direct comparison between measures of ingestion at hourly intervals (Fig. 2.4b) with seston quality sampled at discrete times (Fig. 2.3) may not be appropriate considering the possibility of higher frequency variations in seston properties. Further feeding studies are required under similar field conditions of short-term variations in food quality in which seston properties are measured more frequently or continuously in order to provide more insight into bivalve responses to the food environment.

Current speed is believed to be a major determinant of feeding and growth rates in suspension-feeding bivalves owing to its role in supplying food to stationary organisms and conceivably by facilitation of the feeding process (e.g. Wildish et al. 1987, Eckman et al. 1989, Grizzle et al. 1992). The mean horizontal flux of seston (mg dry wt m^{-2} s^{-1}) past the scallops was calculated for each of the hourly intervals that ingestion rates were measured by multiplying the mean TPM concentration (1.5 mg $liter^{-1}$) by mean hourly current speed. Because currents were only measured during the latter half of the study period (1600 - 0045 hours), data on tidal cycle variations in current speed, contained in Fig. 2.2, were used to estimate mean hourly speeds for the period between 1045 - 1600 hours. Horizontal particle flux was also calculated to correspond to times when water samples were collected using observed SPM concentrations and mean current speed measurements (Fig. 2.3a). Seston flux was greatest at mid-flood tide (1245-1545 hours) and lowest at late-flood (1545-1745 hours) and late-ebb tide (1945-2145 hours)(Fig. 2.6). Contrary to current hypotheses, temporal variations in ingestion rates were poorly correlated with seston flux ($r = 0.43$), and ingestion rates were highest during the period

Figure 2.6

Tidal cycle variations in the mean horizontal flux of particulate matter (dry weight) 1.5 m above the sea bed at the study site. The open circles are the mean flux calculated over hourly intervals (horizontal bars) from data on mean current speed and SPM. The closed circles are estimates of particle flux calculated for the times of water sampling. The broken curve represents water depth (tidal cycle) during the sampling period.

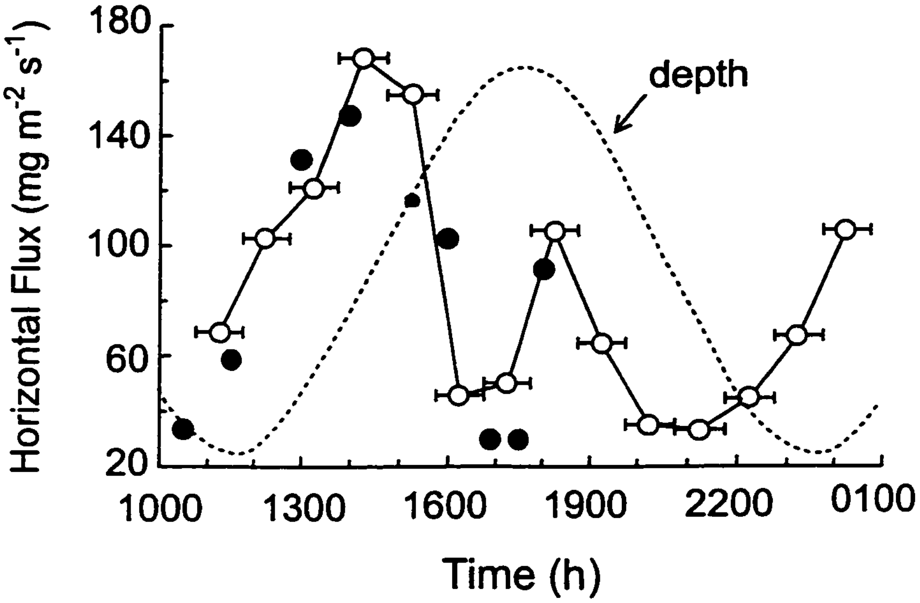
Horizontal Flux (mg m^{-2} s^{-1})
180
140
100
60
20
depth
1000
1300
1600
1900
2200
0100
Time (h)

Figure 2.6

of low particle flux at late-flood tide (Figs. 2.4b and 2.6). The high inorganic content of seston at this time (Fig. 2.3) further reduced the flux of OM, POC, and PN (not shown).

The methods described in this paper facilitate quantification of bivalve feeding processes *in situ* under less restrictive conditions of food supply and water flow and without the limitations and assumptions of previous methods (see above). This study demonstrates the versatility of the sequential sampling trap method and its potential for testing hypotheses, based on laboratory measurements, on the perceived role of suspension-feeding bivalves in coastal ecosystem dynamics. However, the method is not without assumptions or limitations. The effect of the time-series trap apparatus on particle flux to the scallops is assumed to be minimal. This assumption is supported by the similarity of current speed and direction measurements obtained with current meters moored adjacent to and within the mouth of the traps (Hargrave et al. 1994). Although the acrylic cover may cause turbulence across the trap mouth, similar feeding responses have been observed using traps with and without the acrylic cover (Cranford and Hargrave, unpublished. data). Removal of the cover necessitates the use of a second trap without animals to control for sedimenting particles.

Precautions must be taken to ensure that these methods are used under suitable environmental conditions. High current speeds could cause fecal pellets to be swept away rather than being deposited in the trap. Observations indicate that this did not occur at the speeds (<15 cm s^{-1}) observed in this study, however, the method would not be appropriate for high energy environments without modifications. The method would also be inappropriate at higher TPM concentrations. Pseudofeces production under these conditions would alter the organic content of trapped particles and also invalidate calculations of ingestion rate and absorption efficiency. Cranford and Gordon (1992) observed that *P. magellanicus* fed mixed suspensions of seston and clay particles produced pseudofeces at a threshold concentration of 2.0 mg liter^{-1}. MacDonald and Thompson (1986) reported that *P. magellanicus* did not produce pseudofeces when fed natural seston at levels up to 10 mg liter^{-1}. Seston concentrations were below this value during our study (Fig. 2.3a) and visual inspection of biodeposits confirmed the absence of pseudofeces in sample cups.

Owing to the 1.5 m height of the trap, the present configuration does not allow placement of animals within the benthic boundary layer where flow and dietary conditions often differ from those a meter above the seabed (Muschenheim 1987). The method is clearly best suited to studies related to the suspended culture of bivalves. On the other hand, many filtration rate models developed from laboratory data are unable to accurately predict the utilization of particles and growth of bivalves in the field (Doering and Oviatt 1986, Powell et al. 1992). It may be more appropriate to develop predictive relations between environmental factors and benthic bivalve responses with empirical data collected at 1.5 m above the seabed than to attempt to develop these relations by simulating the complexities and variability of nature in the laboratory. Attempts at modelling bivalve growth in coastal waters from the external forcing of biological fluxes have been hampered by an incapacity to incorporate the observed high-frequency fluctuations in bivalve food and temperature (Grant et al. 1993). The *in situ* time-series method measures average feeding and digestion rates, allowing researchers to focus on the effects of longer-term environmental fluctuations.

CHAPTER 3

RELATIONSHIPS BETWEEN FOOD QUANTITY AND QUALITY AND ABSORPTION EFFICIENCY IN SEA SCALLOPS *PLACOPECTEN MAGELLANICUS* (GMELIN).

3.1 ABSTRACT

Laboratory experiments, in which adult sea scallops (*Placopecten magellanicus* Gmelin) were fed rations of varying concentration and organic and elemental composition for periods of 15 and 56 days, were conducted to provide predictive relationships between the quantity and quality of the food supply and the efficiency and rate of absorption of dietary constituents. The absorption efficiency of particulate organic matter (AE_{POM}), organic carbon (AE_{POC}) and nitrogen (AE_{PN}) decreased exponentially with a progressive increase in dietary inorganic content. Regression models indicated that between 74 and 84% of the variation in average AE values was attributed to differences in dietary quality, which was expressed as the POM, POC or PN content per unit dry weight of particulate matter. Changes in absorption efficiency were rapid after a change in seston quality and acclimation was complete within six days. During this time, the AE_{POM} of the lowest quality seston ration (39% organic content) was increased by a factor of 1.8 and AE_{POC} and AE_{PN} progressively increased from negative values to about 60%. Scallops fed a seston diet that alternated between low and high quality (39% and 84% POM, respectively) at 12 hour intervals acclimated to the lower quality diet. These results show that sea scallops respond to low-frequency reductions in food quality by rapidly maximizing the absorption of available resources. By maintaining this adapted state for some period greater than 12 hours, the scallops are able to maintain a relatively high AE despite high-frequency, tidally forced variations in the food supply.

3.2 INTRODUCTION

Studies on the abundance, composition and nutritional value of seston available to suspension-feeding bivalve molluscs residing in coastal and shelf waters reveal large variations over time-scales ranging from minutes to years (see reviews by Bayne 1993, Navarro and Iglesias 1993). In many areas, this natural discontinuity of the food supply is augmented by anthropogenic inputs. Exploratory and production drilling for oil and gas, ocean dumping, marine construction and agriculture activities contribute fine inorganic particles to the near-bed region while trawling and dredging for fish and shellfish and aggregate extraction expose underlying poorly sorted sediments and enhance the mobilization of finer sediments (Messieh et al. 1991).

Functional constraints on particle acquisition and digestive capacity limit the quantity of food assimilated by bivalve filter-feeders per unit time (Kirby-Smith and Barber 1974, Grant et al. 1993). However, a diverse suite of pre- and post-ingestive compensatory mechanisms are available to bivalves for enhancing the quality of captured particles and maintaining an optimal balance between energy acquisition and expenditure (see reviews by Hawkins and Bayne 1992, Bayne 1993, Navarro and Iglesias 1993). The absorption of nutrients during passage of particles through the gut has been identified as the most important regulatory process in the optimization of energy gain by the filter-feeding bivalve *Mytilus edulis* (Bayne et al. 1993). Under conditions of variable food quantity and quality, the optimal feeding model developed for *M. edulis* by Willows (1992) predicts that a high degree of flexibility in the amount of energy invested in digestive processes is required to maximize the rate of energy gain from the diet. While the mechanisms responsible for this digestive flexibility are uncertain, studies have confirmed that absorption efficiency is correlated with food quality in *Mytilus* species (Bayne et al. 1987, Navarro et al. 1991, but see Bayne et al. 1993), the cockle *Cerastoderma edule* (Iglesias et al. 1992, Navarro et al. 1992, Navarro and Iglesias 1993) and the Iceland scallop *Chlamys islandica* (Vahl, 1980). *M. edulis* have been observed to actively regulate absorption efficiency between 2 and 12 days after a change in the food supply (Bayne et al. 1987, Bayne et al. 1993). No such acclimation ability was observed in *C. edule* between 2 and 10 days (Navarro et al. 1992, Navarro and Iglesias 1993).

Comparative studies generally reveal substantial variance in the capacity of different bivalve species to regulate resource acquisition (Hawkins et al. 1990, Navarro and Iglesias 1993), making it necessary to conduct species-specific studies. The sea scallop *Placopecten magellanicus* (Gmelin) was selected as the test species in the present study because: (1) it is the most important commercial shellfish species in Canada; (2) the production of a high-value cultured product is in an expansion phase; and (3) the quantity and quality of the food supply of the highly productive scallop beds on Georges Bank, which straddle the US-Canadian east-coast border, may be altered by the disposal of particulate drilling wastes from proposed oil and gas drilling activities (Gordon et al., 1992).

This laboratory study has two primary objectives: (1) to ascertain the functional relationships between the quantity and quality of food particles and the absorption of dietary constituents by the sea scallop; and (2) to document the time-course and magnitude of absorptive acclimation in response to long- and short-term changes in food quantity and quality. The latter is required in any attempt to predict scallop growth in coastal and shelf waters owing to the different time-scales of variance in the food supply. Resource acquisition in bivalves has generally been studied and modelled solely in terms of energy or carbon (Kiørboe et al. 1980, Seiderer et al. 1982, Willows 1992, Herman 1993). However, nitrogen resources may limit secondary production in coastal waters (Mann, 1988) and filter-feeding bivalves absorb dietary carbon and nitrogen with significantly different efficiencies (Hawkins and Bayne 1985, Cranford and Grant 1990, Bayne et al. 1993). In this study, the absorption of dietary organic matter, carbon and nitrogen were measured simultaneously.

3.3 MATERIALS AND METHODS

3.3.1 Collection and Maintenance.

Sea scallops were collected by commercial dragger from Sable Island Bank and Georges Bank off Nova Scotia. Animals were held on ship in flowing seawater (< 10°C). Individuals not displaying collection injuries were transported to a holding tank at the Bedford Institute of Oceanography and supplied with flowing unfiltered seawater pumped from 5 m depth in Bedford Basin. After a one month period, scallops ranging from 98 to 102 mm shell height (averaged 6.9 g dry tissue) were randomly selected for measurement of absorption rate and efficiency. This study was conducted in conjunction with measurements of the other physiological components of growth (ingestion, respiration and excretion), some of which are reported in Cranford and Gordon (1992). Only relevant data from that part of this study are included here.

Six experimental rations differing in concentration (quantity) and organic and elemental composition (quality) were maintained in recirculating raceway tanks designed to retain diet particles in suspension around filter-feeding bivalves over extended periods (Cranford and Gordon 1992). The rations consisted of pure and mixed suspensions of three particle types: (1) the dried microalga *Tetraselmis suecica* (Algal 161, Celsys, UK); (2) ambient seston in unfiltered seawater pumped from 5 m depth in Bedford Basin; and (3) bentonite (a montmorillonite clay). Bentonite clay was chosen as the biologically inert particle source as it tends to remain in suspension and influence food quality for extended periods and is a major component of solid wastes produced during petroleum drilling activities. Three algal cell and three seston-based rations were prepared by mixing each base diet with different concentrations of bentonite. The algal cell rations contained 1 mg l^{-1} *Tetraselmis* cells combined with either 0, 2 or 10 mg l^{-1} bentonite, and are designated ALG0, ALG2 and ALG10, respectively. Ambient seston in unfiltered seawater was combined with 0, 1 and 5 mg l^{-1} bentonite and are referred to as SES0, SES1 and SES5, respectively. Algal cells and bentonite were delivered to the 290 liter raceway tanks from concentrated stock tanks with a peristaltic pump at 21 ml min^{-1}. The desired concentrations were obtained in the raceways by adjusting stock concentrations. Filtered (5 µm, algal rations) or unfiltered seawater (seston rations) entered each raceway at 10 l min^{-1} giving a residence time of 29 minutes for water and food particles in each tank.

Ten randomly selected scallops were transferred from the holding tank to each of three raceway tanks to measure digestive responses to the ALG0, ALG2 and ALG10 diets. The raceways were initially supplied with filtered seawater (5µm) to allow the animals to clear their guts of previously ingested seston. After four days starvation, all faeces were siphoned from the tanks and each group was supplied with one of the algal rations. At the end of a 12-day feeding period, the input of bentonite was terminated and each tank received the ALG0 ration for an additional three days. Diet and faeces samples were collected at 12-h intervals during the latter 15-day period (May 20 to June 3, 1991). Water samples were siphoned from the raceways at the same depth as the scallops and particles were collected on filters for diet analysis (see below). Composite faeces samples were collected by pipette and stored frozen. Composite sampling was necessary as the flow in the raceways mixed faeces from individuals. Care was taken to exclude pseudofaeces, which are readily distinguishable from faeces in shape, texture and colour. After each sampling, any remaining faeces and pseudofaeces were removed from the tanks by siphoning.

A separate experiment was conducted in which scallops were fed the SES0, SES1 and SES5 rations. This experiment was designed to more closely represent natural processes than is the case with a continuous exposure to cultured microalgal rations. In addition to providing ambient seston as opposed to a microalgal diet, timers were programmed to add the clay to the raceways in the desired concentrations for a period of 12 hours each day for a total of 56 days (June 17 to August 12, 1992). For the remaining 12-hour period each day, the SES1 and SES5 treatments received the SES0 ration. This was done to monitor scallop absorptive responses to frequent fluctuations in diet quality. Composite faeces samples were collected from 30 scallops per ration treatment. Water and faeces sampling were conducted daily for the first six days of the experiment and then at approximately weekly intervals. Sampling was only conducted after the animals were exposed to the test ration for at least 10 hours of the 12-hour cycle. No sampling was conducted during the 12-hour period when all treatments received the SES0 ration. Accumulated faeces and settled diet particles were siphoned from the raceways four hours before faeces samples were collected so that only 'fresh' faeces were sampled.

3.3.2 Diet and Faeces Analysis.

For each diet sample, total suspended particulate matter (TPM: mg dry weight liter^{-1}), ash (% of dry weight) and organic content (POM: % of dry weight) were determined in triplicate by collecting particles on prewashed (distilled water) and precombusted (450°C for 6 h) 25-mm Whatman GF/F filters. Salt was expelled from samples by rinsing each filter under vacuum with isotonic ammonium formate. Filters were then dried at 60°C for 24 h and weighed to give TPM. The weight of ash remaining after combustion at 450°C for 6 h was determined and POM calculated from the weight loss upon ignition. The organic carbon (POC) and nitrogen (PN) contents of particles collected on single precombusted GF/F filters were determined with a Perkin-Elmer model 2400 CHN elemental analyzer after fuming the filters over concentrated HCl for 1 h in a closed container to remove inorganic carbon. The size-distribution of particles in water samples was determined with a Coulter Counter model TaII fitted with a 100 µm aperture. Thawed composite faeces samples were homogenized with a vortex mixer, subsampled onto GF/F filters and analyzed as above for ash, POM, POC, and PN content.

3.3.3 Calculations and Analysis.

The percentage of ingested POM, POC and PN absorbed by the digestive system (net absorption efficiency) was estimated from the proportions of inert (ash) and absorbed (POM, POC and PN) indicators in food (*F*) and faeces (*E*) according to the equation:

$$AE = [1 - (F_{ash}/F_{absorbed})/(E_{ash}/E_{absorbed})] \times 100 \qquad (3.1)$$

(Cranford and Hargrave 1994). Cranford and Grant (1990) compared AE estimates based on calculations with different inert tracers and found ash to be suitable for digestion studies with *P. magellanicus*. Considering that faeces samples represented material ingested over some period prior to sampling, average diet composition data calculated for the duration of each experiment were used to calculate AE rather than data obtained at the time of sampling. As faeces composition was determined from composite samples from 10 (algal rations) or 30 (seston rations) scallops, AE estimates represent population values.

The composition of suspended particles in the raceways can be considerably different from that ingested by the scallops. This stems from the animal's inability to effectively capture approximately 40% of the bentonite owing to its small size (median diameter of 2 µm), and the selective retention and ingestion of particles based on size and composition (Cranford and Gordon 1992, MacDonald and Ward 1994). This enhancement of diet quality was accounted for in AE calculations by estimating the ash, POM, POC and PN content of ingested particles using data on the composition and size spectra of the diets (Fig. 3.1 and 3.2) and particle retention and selection efficiency data (Cranford and Gordon 1992). Examples of these estimates for a wide range of algal cell and seston rations are given in Cranford and Gordon (1992). The absorption rate of POM, POC and PN for each experimental diet was determined as the product of AE (this study) and ingestion rate (Cranford and Gordon 1992).

Curve fitting and regression analysis were performed with SlideWrite Plus Version 5 (Advanced Graphics Software, Inc., Carlsbad, CA.). The data were screened for non-normality and heteroscedasticity by examining normal probability and residual plots, respectively (Wilkinson 1992). No transformations were conducted as the data did not violate the assumptions of regression analysis. Analysis of variance (ANOVA) were performed with SYSTAT Version 5.0 (SYSTAT, Inc., Evanston, Illinois).

3.4 RESULTS

3.4.1 Diets

Water temperature during the 15 day exposure to the *Tetraselmis* cell rations remained between 8.5 and 9.5° C. Temperature was more variable during the 56-day exposure to the seston-based diets and increased rapidly from 10°C on Day 20 to 18°C on

Figure 3.1

Time-series of water temperature (a) and the concentration (b) and quality (c) of particulate matter during the 56-day feeding experiment in which *P. magellanicus* were fed ambient Bedford Basin seston from 5 m depth. The SES1 (triangles) and SES5 (squares) rations contained ambient seston mixed with 1 and 5 mg l^{-1} bentonite, respectively. No bentonite was added to the SES0 (circles) ration, which served as the control.

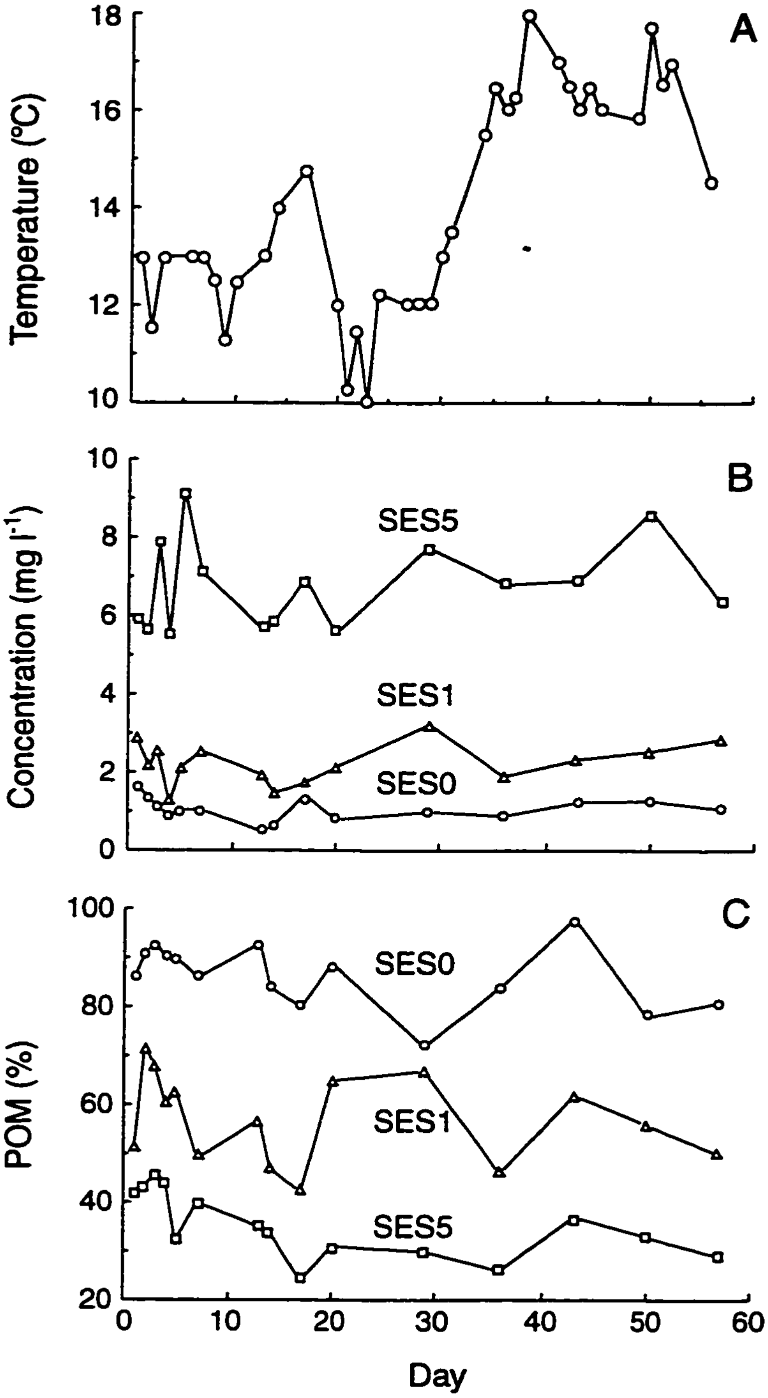
A
Temperature (°C)
18
16
14
12
10
B
Concentration (mg l^{-1})
10
8
6
4
2
0
SES5
SES1
SES0
C
POM (%)
100
80
60
40
20
SES0
SES1
SES5
0
10
20
30
40
50
60
Day

Figure 3.1

Figure 3.2

Characteristic particle size distributions of the six experimental rations. Particle concentrations were determined with a Coulter Counter fitted with a 100 µm aperture. Rations containing different mixtures of *Tetraselmis* cells and bentonite are shown on the bottom graph and rations containing Bedford Basin seston mixed with different levels of bentonite are shown on the top graph.

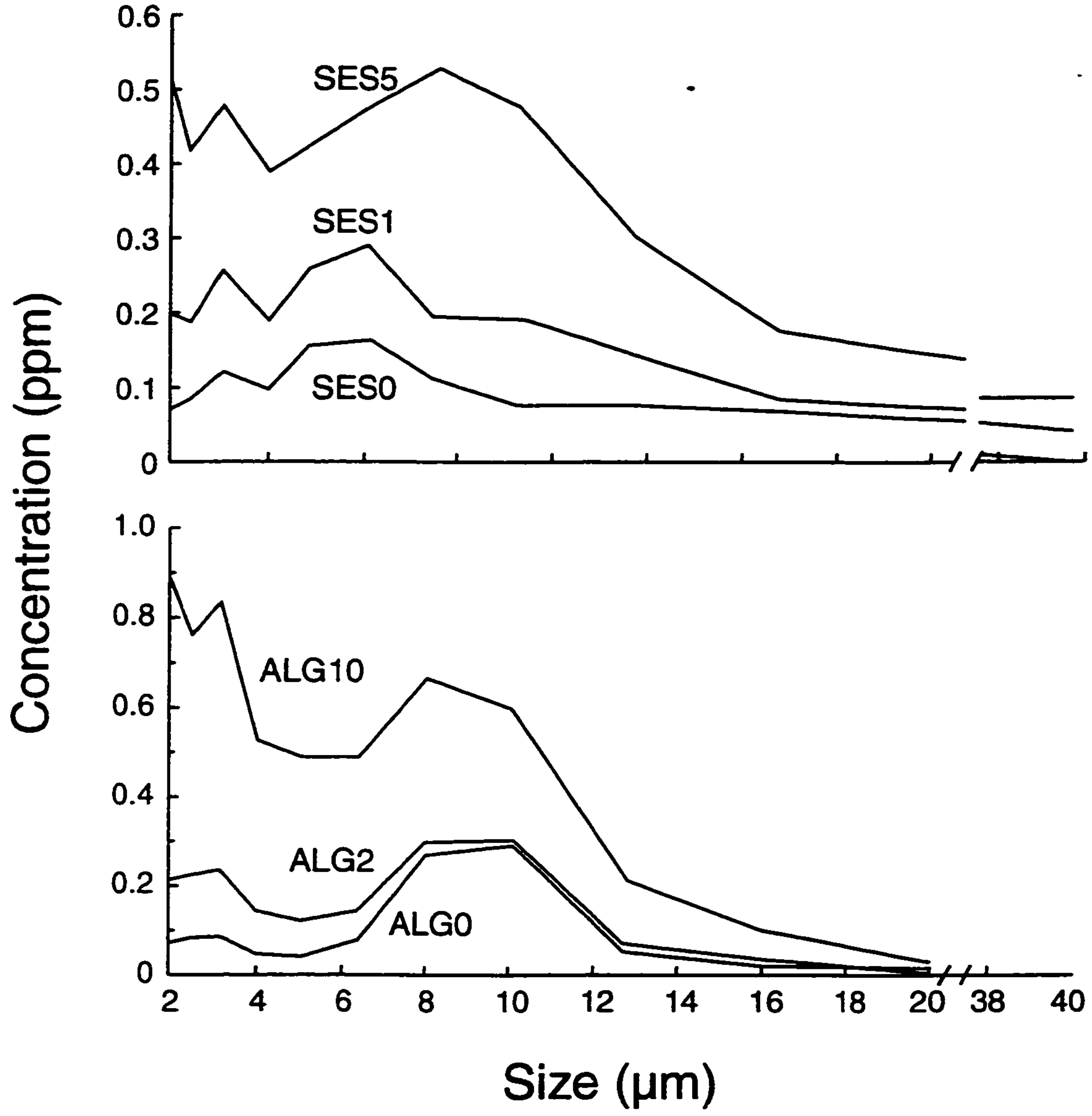
0.6
0.5
0.4
0.3
0.2
0.1
0
SES5
SES1
SES0
1.0
0.8
0.6
0.4
0.2
0
ALG10
ALG2
ALG0
Concentration (ppm)
2
4
6
8
10
12
14
16
18
20
38
40
Size (µm)

Figure 3.2

Day 40 (Fig. 3.1a). Salinity during both experiments was relatively constant at 29-30 ‰. Variables for ration concentration and quality, which is defined here in terms of the POM, POC and PN content of ingested particles, are summarized in Table 3.1. Bedford Basin seston (SES0) was similar in concentration to the *Tetraselmis* (ALG0) ration and appeared to be of high dietary quality. ALG0 had the highest organic content of the experimental rations, but SES0 had higher POC and PN contents (Table 3.1). The relatively high nitrogen content of Bedford Basin seston is shown by the low C:N ratio (Table 3.1). Bedford Basin seston rations remained fairly constant in concentration (Fig. 3.1b) and organic content (Fig. 3.1c) over the 56 day feeding experiment. The addition of bentonite clay to the algal cell and seston diets resulted in a proportional decrease in all indices of diet quality (Table 3.1 and Fig. 3.1). The added clay appears to have adsorbed dissolved organic matter from seawater, resulting in increased levels of POM (mg l^{-1}) in the raceways (data not shown). Characteristic particle size distributions for each diet are shown in Figure 3.2. The *Tetraselmis* cells produced as a peak in size spectra between 6 and 12 µm. Addition of bentonite primarily increased particle concentrations in the lower end of the observed size spectrum, but contained particles as large as 20 µm diameter (Fig. 3.2). A peak within the 4 to 12 µm size range was observed in seston from Bedford Basin but no attempt was made to identify these particles, which were of high nutritional value (Table 3.1).

Table 3.1

Average concentration and composition of diets (± SD) fed to *Placopecten magellanicus* in laboratory experiments. The proportions of algal cells, seston and bentonite particles in each ration are given in the text.

Ration	TPM (mg l^{-1})	POM (%)	POC (%)	PN (%)	C:N
ALG0	0.85 (0.45)	94 (1)	22.3 (4.8)	1.1 (0.3)	21.2 (7.4)
ALG2	2.29 (0.80)	59 (7)	8.7 (1.9)	0.4 (0.1)	21.8 (7.6)
ALG10	9.07 (1.23)	26 (7)	2.2 (0.5)	0.1 (0.0)	19.9 (6.9)
SES0	1.12 (0.37)	84 (10)	26.0 (7.8)	4.0 (1.3)	6.5 (0.6)
SES1	2.49 (1.05)	59 (13)	16.7 (6.0)	2.5 (0.9)	6.7 (0.7)
SES5	6.57 (1.79)	39 (15)	10.8 (2.4)	1.3 (0.4)	8.9 (1.1)

3.4.2 Absorption Efficiency

Time-series of scallop absorptive responses to different concentrations of bentonite added to constant levels of *Tetraselmis* cells are shown in Figure 3.3. Scallops fed the ALG0 ration over 15 days (control algal cell treatment) digested variable proportions of algal POM (AE averaged 78%, SD=11, n=26), POC (84%, 10, 14) and PN (85%, 8, 14) (Fig. 3.3). Animals fed the ALG2 ration absorbed a lower percentage of POM (60%, SD=9, n=22), POC (79%, 9, 11) and PN (56%, 9, 10) than the controls (Fig. 3.3). The AE of ALG2 substrates rapidly decreased over the first four days as it did for the controls, but values remained relatively low or gradually deceased until the bentonite was removed from the diet after 12 days. Scallops exposed to the ALG10 ration had the lowest and least variable AE's of the three groups. The AE of POM (41%, SD=6, n=22), POC (55%, 5, 11) and PN (21%, 7, 11) remained constant during the exposure, except for an initial increase in nitrogen AE during the first three days (Fig. 3.3).

Upon removal of bentonite from the algal cell rations after the 12 day exposure, the scallops fed the ALG2 and ALG10 rations increased AE within a 12 h period to levels comparable with maximum values observed for the ALG0 group (Fig. 3.3). Maximum AE in all three groups was observed immediately after starvation or after removal of bentonite and was always followed by a gradual decrease in AE. The time-series of

Figure 3.3

Time-series of the absorption efficiency of ingested organic matter (AE_{POM}), organic carbon (AE_{POC}) and nitrogen (AE_{PN}) by *P. magellanicus* fed three different rations containing *Tetraselmis suecica* cells mixed with different concentrations of bentonite in 5 µm filtered seawater. See the text and Table 3.1 for the composition of each diet. After 12 days (vertical line) continuous exposure to each diet, all three groups received the ALG0 ration (no bentonite).

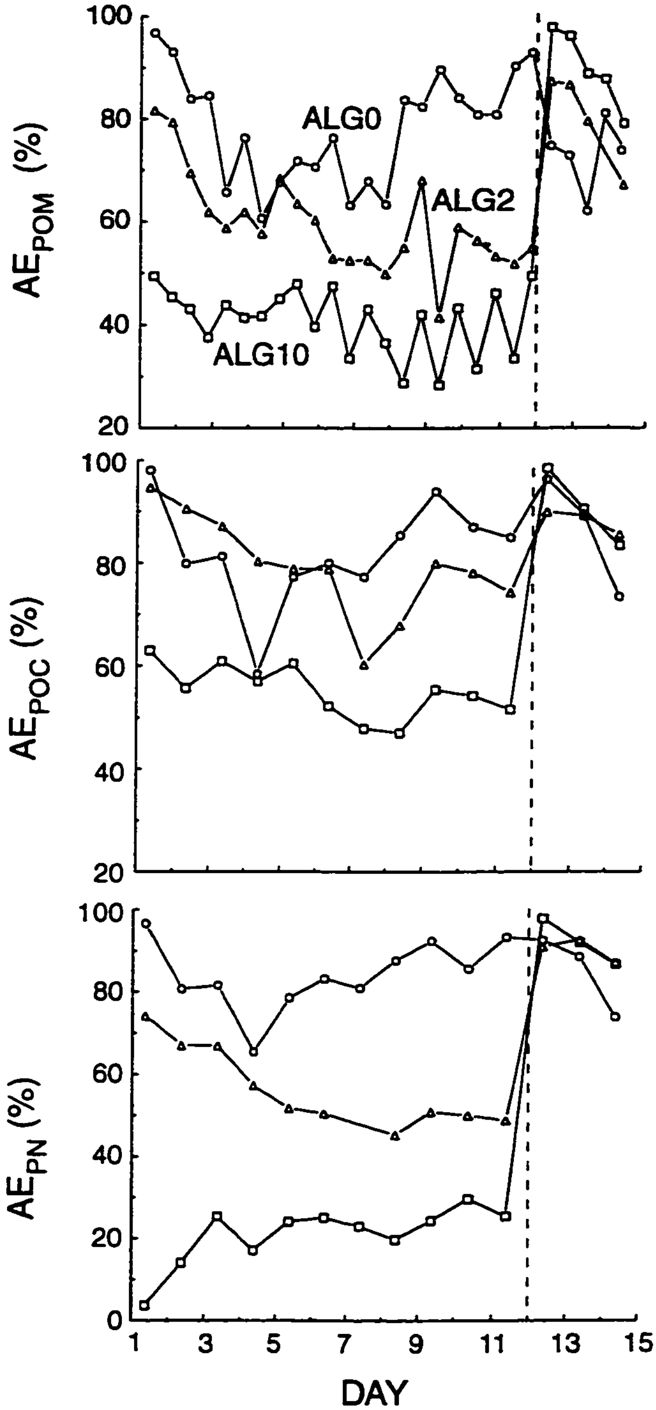
AE$_{POM}$ (%)
100
80
60
40
20
ALG0
ALG2
ALG10
AE$_{POC}$ (%)
100
80
60
40
20
AE$_{PN}$ (%)
100
80
60
40
20
0
1
3
5
7
9
11
13
15
DAY

Figure 3.3

scallop absorption efficiencies during exposure to different concentrations of bentonite added to ambient Bedford Basin seston are shown in Figure 3.4. Note that these measurements were made only during the 12 hour daily period when different concentrations of clay was added to the seston diet. As with the algal cell diets, the addition of bentonite to seston caused a general reduction in the AE of dietary POM, POC and PN. All three groups displayed a progressive increase in AE over the first three to six days of the experiment (Fig. 3.4). The control animals (SES0 treatment) increased AE from about 70% on Day 1 to between 80 and 90% on Day 3. This increase was not associated with a change in water temperature, seston concentration or quality (Fig. 3.1), and appears to indicate digestive acclimation to the altered diet. The SES1 and SES5 groups displayed an even greater initial increase in AE than the controls (Fig. 3.4). Animals fed the SES1 ration increased AE from a Day 1 low of between 30 to 40 % to between 60 and 75% by Day 6. Scallops fed the SES5 ration increased AE from between negative values and 40% on Day 1 to between 60 and 75% on Day 6. Digestive acclimation to the SES5 ration increased the AE of POC and PN to a greater degree than for POM (Fig. 3.4). Despite the initial increase in the AE of the SES1 and SES5 rations, maximum AE values measured for both groups were below those obtained for scallops fed SES0 (Fig. 3.4).

After the initial acclimation period to the seston-based rations, the AE of all three seston groups remained relatively constant until between Day 29 and Day 37 when the AE of POM, POC and PN began to decline in the SES1 and SES5 treatments (Fig. 3.4).

Figure 3.4

Time-series of the absorption efficiency of ingested organic matter (AE_{POM}), organic carbon (AE_{POC}) and nitrogen (AE_{PN}) by *P. magellanicus* fed three different rations containing ambient Bedford Basin seston mixed with different concentrations of bentonite. See the text and Table 3.1 for the composition of each diet. The rations were supplied for 12 hours each day. During the remaining 12 hours, all scallops received 'pure' seston (SES0).

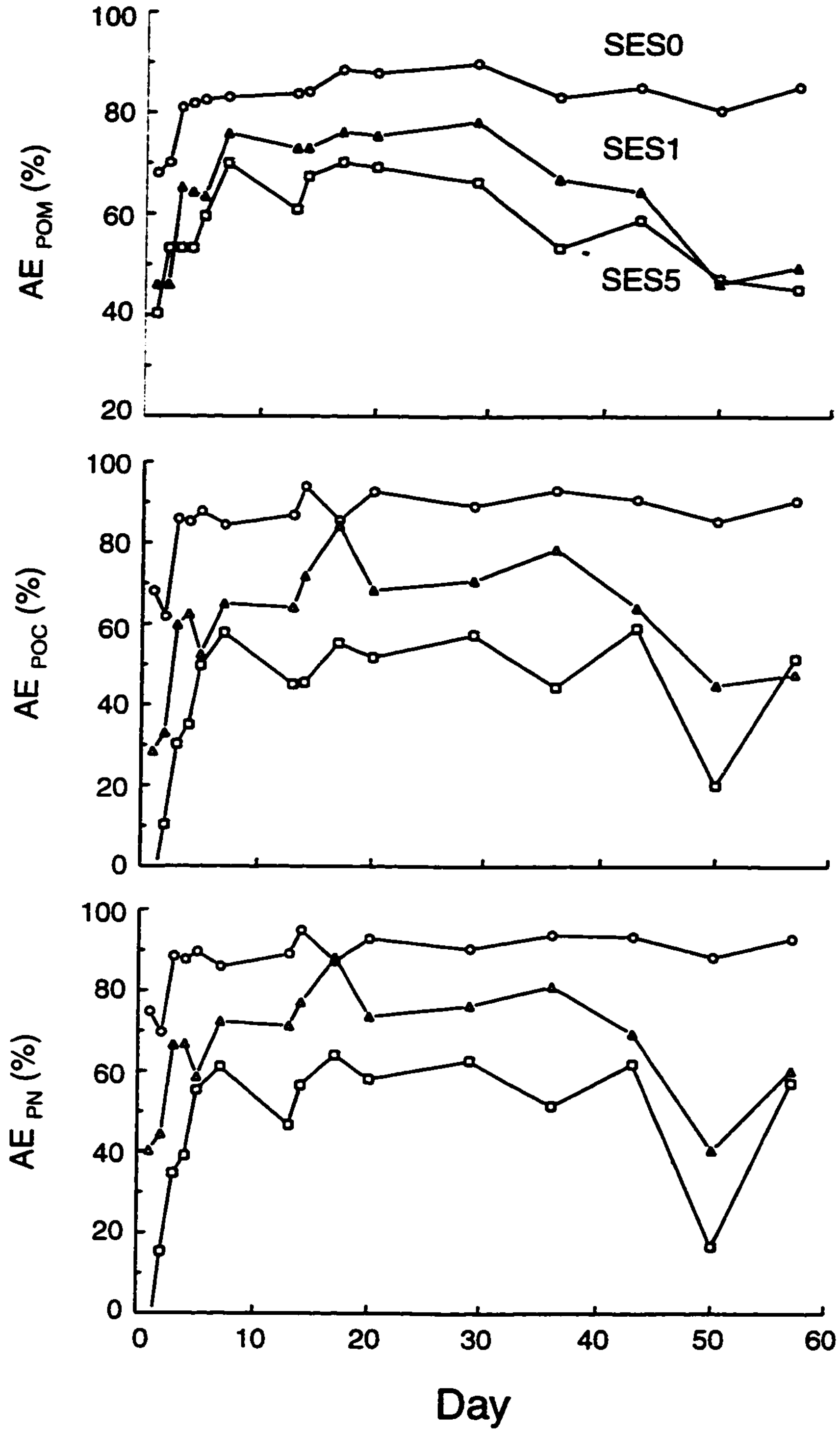
SES0
SES1
SES5
AE POM (%)
AE POC (%)
AE PN (%)
20
40
60
80
100
0
20
40
60
80
100
0
20
40
60
80
100
0
10
20
30
40
50
60
Day

Figure 3.4

This decline during the latter part of the experiment does not appear to be related to measured variations in water temperature or ration quantity and quality (Fig. 3.1). The SES0 group continued to display high AE values to the end of the experiment, despite the 8°C increase in water temperature between Days 20 and 40 (Fig. 3.1)

To test the null hypothesis that the mean AE of algal cells and seston are equal, a two-way factorial analysis of variance (ANOVA) was employed. The fixed factors are ration (ALG0 and SES0) and substrate (POM, POC and PN). The hypothesis was accepted as no significant difference was found in the efficiency by which the scallops absorbed the two diets (Table 3.2). However, the three substrates within the two diets were absorbed with significantly different efficiencies ($p = 0.011$). Owing to the similarity of AE measurements for the pure algal cell and seston rations, any differences in substrate absorption between the six experimental rations must be attributed solely to the concentration of added bentonite. A second two-way factorial ANOVA was employed to determine the effect of bentonite concentration on AE by testing the null hypothesis that mean AE values for the six rations are equal. This hypothesis was rejected as significant differences in AE between rations and substrates were observed (Table 3.2). The significant ration by substrate interaction (Table 3.2) shows the effect of bentonite concentration on AE differs for each substrate. The relationship between bentonite concentration and AE is shown in Figure 3.5. Regression analysis provided the best curve fit to the data, which was a logarithmic decline in AE with increasing levels of

Table 3.2

Summary of ANOVAs for testing significance of differences in *P. magellanicus* absorption efficiencies. "Ration" refers to the experimental diets (Table 3.1) and diet "substrate" is either POM, POC or PN.

Source of variation	df	Sum of squares	Mean squares	F	*p*
(1) ALG0 and SES0 rations only:					
Ration	1	222	222	2.77	0.100
Substrate	2	766	383	4.78	0.011
Interaction	2	39	20	0.25	0.784
Error	92	7375	80		
(2) All six rations:					
Ration	5	72951	14590	108.66	0.000
Substrate	2	1970	985	7.34	0.001
Interaction	10	12481	1248	9.30	0.000
Error	256	34375	134		

bentonite. The absorption of algal nitrogen was particularly sensitive to elevated bentonite levels. Scallops fed the ALG10 ration, which contained the highest concentration of bentonite, absorbed PN at efficiencies that were considerably lower than for either POC or POM (Fig. 3.5). Conversely, absorption of POC in algae and seston does not appear to be correlated with bentonite concentrations between 1 and 10 mg l^{-1} (Fig. 3.5).

The functional relationships between net AE and diet quality (the POM, POC or PN content per unit dry weight of diet particles), were described after Bayne et al. (1987) by the exponential equation;

$$\mathrm{AE} = a1(1 - e^{-a2(Q - a3)}) \qquad (3.2)$$

where Q is dietary quality, and $a1$, $a2$ and $a3$ are parameters describing, respectively, the maximum value of AE, the rate of increase of AE with increasing Q, and the quality where AE is zero. The model was fitted to mean AE data obtained from this study and previously published and unpublished studies conducted by the author using similar techniques (Fig. 3.6; see figure legend for data sources). The correlation coefficients and parameters of the fitted models are given in Table 3.3. The POM, POC and PN content of the diet explained 74, 82 and 84% of the variance in AE, respectively. The regression models predict maximum AE in excess of 90% for all substrates and zero AE at POM, POC and PN contents of 14.1, 4.6 and 0.0%, respectively (Table 3.3). The range of error

Figure 3.5

Effect of bentonite concentration on the absorption efficiency of organic matter (POM), organic carbon (POC) and nitrogen (PN) by *P. magellanicus*. Points are averages (± 1 SD) for time-series data shown in Figures 3.3 and 3.4. See the legend for the base diet and substrate represented by each data point. The best-fit curve shown for the relationship between AE (all rations and substrates) and bentonite concentration (*C*) is described by the equation: $AE = \sqrt{(4567 - 1253 (\ln C))}$, $r = 0.865$, $p = 0.0004$.

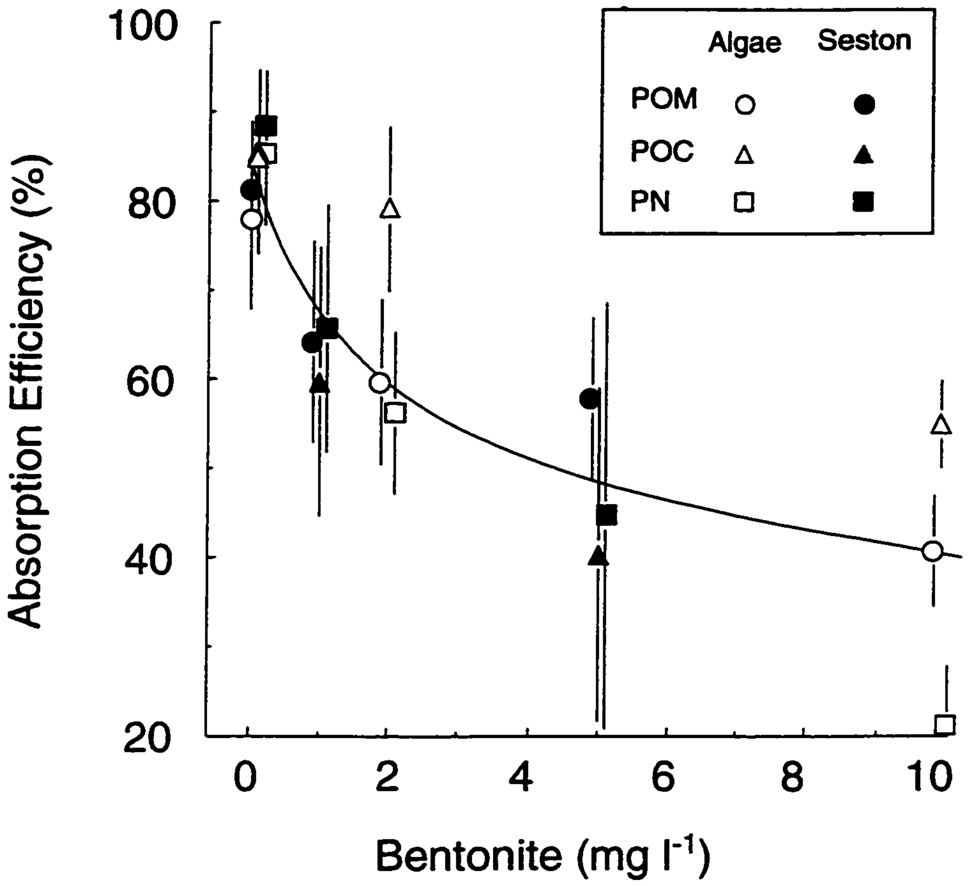
Algae
Seston
POM ○ ●
POC △ ▲
PN □ ■
Absorption Efficiency (%)
100
80
60
40
20
0
2
4
6
8
10
Bentonite (mg l^{-1})

Figure 3.5

Figure 3.6

Relationships between the absorption efficiency (mean ± 1 SD) of particulate organic matter (AE_{POM}), organic carbon (AE_{POC}) and nitrogen (AE_{PN}) by *P. magellanicus* and diet quality, which is expressed as the percentage POM, POC and PN content per unit dry weight of particulate matter. Data: 1- pure and mixed suspensions of *Tetraselmis* cells and bentonite for 12 days (this study, n=11 to 27 determinations); 2 - Bedford Basin seston/bentonite rations for 57 days (this study, n= 15); 3 - phytoplankton and detritus rations for 56 days (Cranford and Grant 1990, n= 8); 4 - Bedford Basin seston, July 12-26, 1991 (Cranford unpublished data, n= 3); 5 - Lunenburg Bay seston, October 6, 1992 (Cranford and Hargrave 1994, n=10); 6 - Bedford Basin seston, August 26-28, 1992 (Cranford unpublished data, n=5). Parameters of the fitted exponential models are given in Table 3.3.

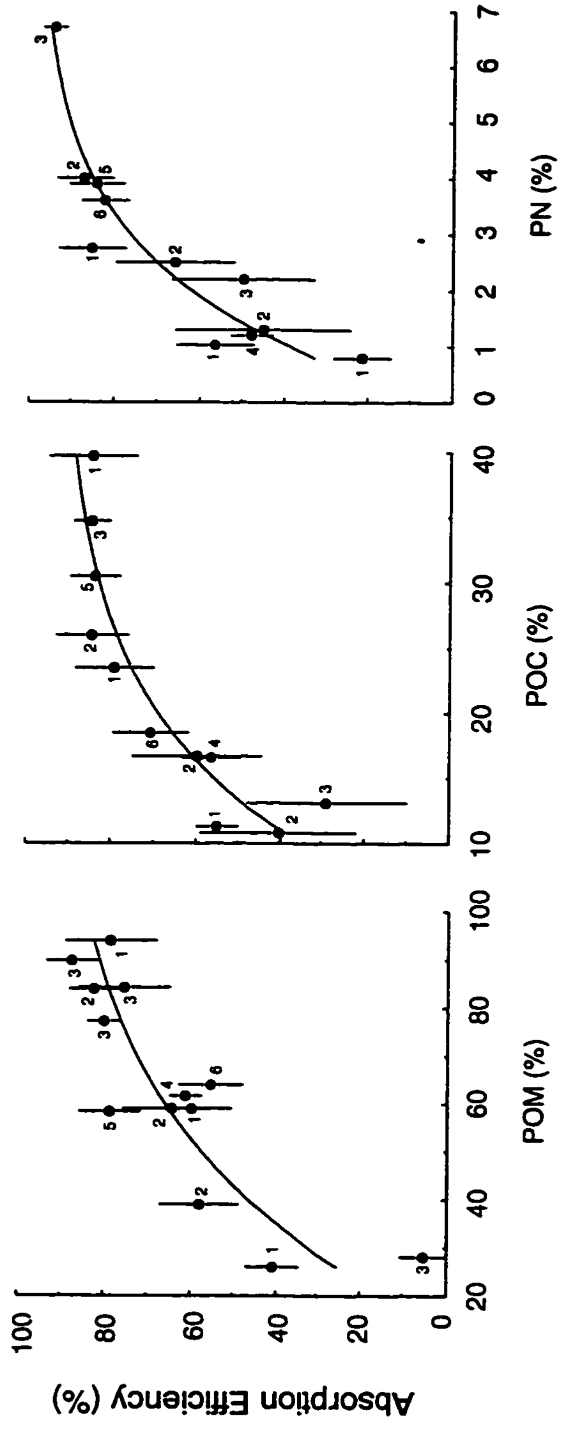
Absorption Efficiency (%)
100
80
60
40
20
0
POM (%)
20
40
60
80
100
POC (%)
10
20
30
40
PN (%)
0
1
2
3
4
5
6
7

Figure 3.6

Table 3.3

Parameters of regression equations (±SE) relating the absorption efficiency (AE) of particulate organic matter (POM), organic carbon (POC) and nitrogen (PN) to diet quality (% POM, POC and PN content per unit weight of particulate matter, respectively). The parameters $a1$, $a2$ and $a3$ of the exponential model (Eqn. 2) are defined in the text and the fitted curves are shown in Figure 3.6.

AE (%)	$a1$ (SE)	$a2$ (SE)	$a3$ (SE)	r	F	p
POM	93.5 (25.7)	0.026 (0.021)	14.1 (9.7)	0.862	14.43	0.005
POC	92.6 (12.8)	0.088 (0.053)	4.6 (3.7)	0.903	17.73	0.005
PN	99.5 (15.2)	0.476 (0.254)	0.0 (0.5)	0.918	21.45	0.003

in estimates of each parameter are given in Table 3.3. A comparison of the equation slopes ($a2$) for each substrate was conducted after recalculating the regression equation for normalized POM, POC and PN data. Judging from the considerable overlap in the 95% confidence intervals calculated for $a2$, the slopes were not significantly different.

3.4.3 Absorption Rate

Sea scallop absorption rates declined rapidly as the amount of bentonite in the diet increased (Fig. 3.7) owing to reductions in both AE (Fig. 3.5) and ingestion rates of organic matter (Cranford and Gordon 1992). Low bentonite concentrations (< 2 mg l^{-1}) caused a greater reduction in seston absorption rates than was calculated for algal cells (Fig. 3.7) as a result of the greater effect of low clay concentrations on seston ingestion rates compared with the algal cell ration (Cranford and Gordon 1992). At clay concentrations in excess of about 5 mg l^{-1}, absorption rates were only 10% of rates calculated for the 'pure' seston and algal cell rations (Fig. 3.7).

Absorption rates were highly correlated and linearly related to the different measures of diet quality (Fig. 3.8). Assuming the relationship remains linear below the range of observations, the models predict zero absorption rates at POM, POC and PN contents of 23%, 6.5% and 0.8%, respectively. The linear relationships observed between diet quality and absorption rate appear to be in conflict with the observed non-linear relation between AE and diet quality (Fig. 3.6). The non-linearity was removed

Figure 3.7

Influence of bentonite concentration on the absorption rate of dietary constituents by *P. magellanicus*. Data were calculated from average absorption efficiency (Fig. 3.5) and ingestion rate (Cranford and Gordon, 1992) data for scallops (average 100 mm shell height and 6.9 g tissue dry weight) fed the six experimental diets described in the text.

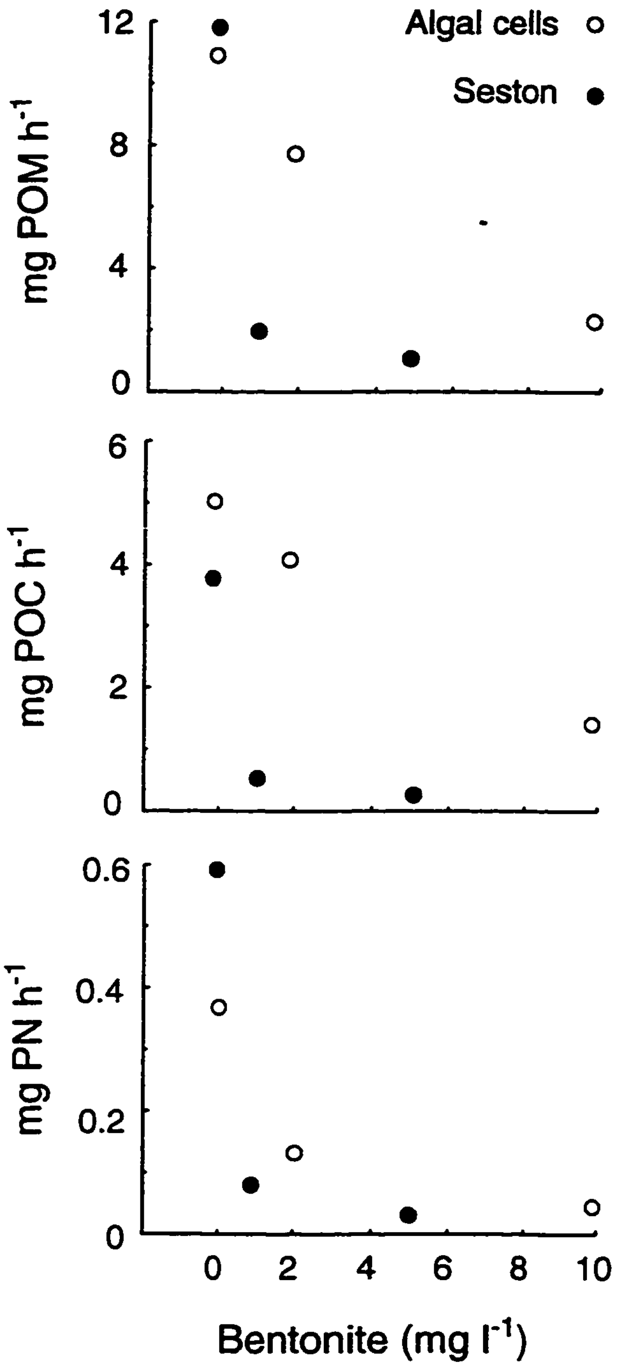
Algal cells ○
Seston ●
mg POM h^{-1}
12
8
4
0
mg POC h^{-1}
6
4
2
0
mg PN h^{-1}
0.6
0.4
0.2
0
0
2
4
6
8
10
Bentonite (mg l^{-1})

Figure 3.7

Figure 3.8

Relationships between different measures of diet quality and the absorption rate (mg scallop^{-1} h^{-1}) of organic matter (POM), organic carbon (POC) and nitrogen (PN) by *P. magellanicus*. The closed circles are the *Tetraselmis* rations and the open circles are the Bedford Basin seston rations. The lines were fit by linear regression and the equations are: AE_{POM}= 0.162(POM)-3.769, r = 0.932, p = 0.025; AE_{POC} = 0.169(POC)-1.100, r = 0.947, p = 0.015; AE_{PN} = 0.158(PN)-0.123, r = 0.936, p = 0.022.

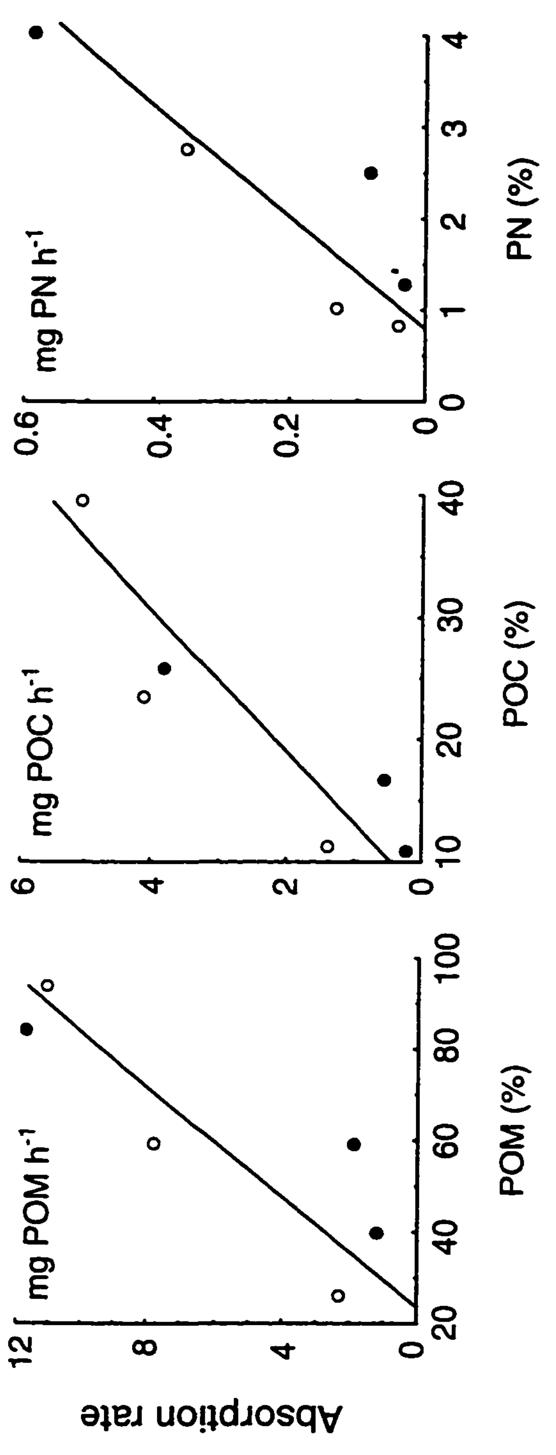
Absorption rate
mg POM h⁻¹
12
8
4
0
20
40
60
80
100
POM (%)
mg POC h⁻¹
6
4
2
0
10
20
30
40
POC (%)
mg PN h⁻¹
0.6
0.4
0.2
0
0
1
2
3
4
PN (%)

Figure 3.8

when AE was multiplied by the ingestion rate of each substrate, which increased exponentially with increasing diet quality (Cranford and Gordon 1992).

3.4 DISCUSSION

Iglesias et al. (1992) pointed out the difficulties of precisely distinguishing the effects of food quantity and quality on physiological process when both are altered simultaneously by adding different levels of inorganic matter to fixed concentrations of organic matter. This method was employed in the present study to simulate natural conditions and, as stated by Iglesias et al. (1992), is more environmentally realistic than an experiment in which a wide range of diet quantities and qualities are produced by varying both organic and inorganic matter concentrations. Separation of effects caused by simultaneous changes in food quantity and quality is somewhat simplified when examining digestion, as opposed to pre-ingestive processes. *P. magellanicus* maintains total ingestion rates (not to be confused with organic matter ingestion rate) constant at diet concentrations in excess of about 1 mg l^{-1} by reducing filtration rate and increasing pseudofaeces production rate (Cranford and Gordon 1992). Because total ingestion rate remains constant over a wide range of diet quantities, any changes in absorption efficiency resulting from elevated inorganic concentrations must be attributed to a reduction in the quality of particles ingested. The observed relationships between bentonite concentration and AE (Fig. 3.5) and absorption rate (Fig. 3.7) are largely artifacts of quantity/quality covariation, and the quality of ingested matter is a better predictor of dietary absorption (Figs. 3.6 and 3.8).

Diet quality, expressed as the POM, POC or PN content per unit weight of particulate matter, explained between 74 and 84% of the variance in sea scallop AE measurements (Table 3.3). Previous studies with the Iceland scallop *Chlamys islandica*, the mussels *Mytilus edulis* and *M. galloprovincialis* and the cockle *Cerastoderma edule* (Vahl 1980, Bayne et al. 1987, Navarro et al., 1991, Iglesias et al. 1992, Navarro et al. 1992, Navarro and Iglesias 1993) have reported similar relationships between AE and diet quality. However, most of these studies have shown a preference for a volumetric description of diet quality (organic weight per unit particle volume) over the gravimetric approach (organic weight per unit particle weight). This preference stems from the results and theoretical arguments of Bayne et al. (1987), who reported that *M. edulis* AE was poorly correlated with dietary POM content. Navarro et al. (1992), however, reported similar correlation coefficients when the AE of *C. edule* was related to both measures of diet quality ($r = 0.84$ for % POM and 0.87 for mg POM mm^{-3}). Considering that AE estimates are based on diet and faeces organic contents (Eqn. 3.1), a relationship between AE and the proportion of POM in the diet is mandatory except when faeces organic content is highly variable and unrelated to diet quality. In sea scallops, faeces POM was highly correlated with food POM ($r = 0.841$, $F = 26.4$, $p = 0.001$) and increased exponentially from a minimum value of 17% for the low quality SES10 diet to >50% for algal cell diets (data not shown). Notwithstanding the theoretical arguments favouring the use of a volumetric indicator of diet quality (Bayne et al. 1987), it has not consistently been related to AE under conditions of widely different diet qualities (Bayne et al. 1993) and is not as easily measured as the organic content.

Interspecific differences in the functional relationship between diet quality and AE have been noted and hypothesized to represent evolutionary adaptations to different habitats (Navarro and Iglesias 1993). These authors have suggested that the diet quality at which AE reaches zero (parameter *a*3 in Eqn. 3.2) can be used as an index of the animals capacity to survive in regions characterized by poor-quality diets. Considering the geographic distribution of sea scallops (limited to open coastal and shelf waters with relatively low suspended matter concentrations), *a*3 should be high compared with mytilid or infaunal species which are widely distributed in environments that experience frequent changes in food quality. Zero AE for *P. magellanicus* is predicted at a POM content of 14% (Table 3.3). Zero AE for *M. edulis* is predicted at 0.07 mg POM mm^{-3} (Bayne et al. 1987), which is equivalent to a POM content of about 7% (calculated from data in Bayne et al. 1987). The lower limit for positive net AE in the infaunal species *C. edule* is 10% (calculated from data in Navarro et al. 1992). These results tend to confirm the value of the *a*3 parameter as a habitat suitability index, but given the wide range of error in estimates of *a*3 (Table 3.3; Bayne et al., 1987), any judgements based solely on this index are not conclusive.

Different components within each diet were absorbed with significantly different efficiencies (Table 3.2). Differential absorption of carbon and nitrogen may result from changes in the balance of biochemical components in the diet or may be related to specific endogenous biochemical demands (Hawkins and Bayne 1985, Bayne et al. 1993). Since the addition of inorganic matter to the phytoplankton diet would not change the balance between biochemical components, the relatively low nitrogen absorption from the low quality ALG10 diet (Fig. 3.5) may indicate that a greater proportion of available carbohydrates and lipids were being absorbed as opposed to protein. Alternatively, the relatively low AE_{PN} may indicate an inability to absorb available protein from low quality diets, even when nitrogen is relatively abundant (e.g. a low C:N ratio). Growth in sea scallops has previously been shown to be limited by the availability of nitrogen (Grant and Cranford 1991), but may be further restricted by reduced nitrogen absorption efficiency during periods of low diet quality. Conversely, *M. edulis* nutrition was limited by the availability and absorption efficiency of carbon (Hawkins and Bayne 1985, but see Bayne et al. 1993). These results underscore the necessity of studying both carbon and nitrogen acquisition in bivalve filter feeders.

A primary objective of this study was to determine the time-course of absorptive acclimation in *P. magellanicus* so that their ability to compensate for the different time-scales of fluctuations in the food supply can be assessed. Owing to the sampling regime (composite faeces sampling), it was not possible to calculate the error (within population variance) in mean AE measurements for each sampling date. This prevented a statistical analysis of the significance of observed changes in AE with time. However, a high degree of confidence in the observed trends was obtained by comparing the magnitude of changes in AE over time with published data on the variance in AE measurements for *P. magellanicus* and other filter-feeding bivalve populations. MacDonald and Thompson (1986) reported a relative dispersion in mean AE values (95% CI/mean) for sea scallops of 15%. The 95% CI for mean AE measurements on other bivalve species (measured using similar techniques as reported in this study) averaged 20% of the mean (Bayne et al. 1987, Navarro et al. 1992, Bayne et al. 1989, 1993).

The initial increase in nitrogen AE during the first three days exposure to the ALG10 ration (Fig. 3.3) was the only indication of any capacity of *P. magellanicus* to adapt digestive processes (increase substrate absorption) to compensate for the negative effect of bentonite on the digestion of algal cells. The observation that maximum AE for the microalgal rations occurred after starvation and immediately after an increase in diet quality (Fig. 3.3) shows that sea scallops enhance absorptive capabilities during periods of low dietary quality. This allows the animal to immediately take advantage of the onset of improved dietary conditions.

Bivalve digestive studies have traditionally been conducted with artificial diets consisting of intertidal sediments and cultured microalgae (i.e.; Bayne et al. 1987, Iglesias et al. 1992, Navarro et al. 1992, Bayne et al. 1993). The organic content of the sediment is meant to represent the detrital component of seston, but it is uncertain to what extent seston is actually represented by the mixtures. In this study, scallops were exposed to natural seston particles and clay was added to vary the inorganic content, an approach that may be more environmentally representative. The importance of utilizing representative diets for predicting bivalve responses is illustrated by the differences observed in sea scallop AE responses to the algal cell and seston rations. While sea scallops did not require an acclimation period to absorb algal cell organic matter with maximum efficiency (Fig. 3.3), an initial period of digestive acclimation was observed in all three seston-based treatments (Fig. 3.4).

The time-scale of absorptive acclimation was rapid enough to help compensate for alterations in the food supply occurring over several days. This would include the effects of storm-induced resuspension of bottom deposits and the onset and decline of algal blooms. These data appear to indicate that absorptive acclimation is of limited value in compensating for high-frequency, tidally forced variations in the food supply. However, it is important to note that the scallops maintained acclimated conditions for several weeks (Fig. 3.4), despite the fact that the seston ration alternated between low (SES1 or SES5) and high quality (SES0) over 12 hour intervals. The animals acclimated to the lower quality diet and maintained acclimated conditions for some period greater than 12 hours. The maintenance of absorptive acclimation enables sea scallops to maximize energy gain from material ingested over the short-term without the need for continually adjusting digestive processes in response to frequent dietary fluctuations. This example of time-averaged optimization behaviour, in which *P. magellanicus* appears to maximize absorption in the short-term based on past feeding conditions, is in contrast to that of Hawkins et al. (1985) who suggested that *M. edulis* regulate absorption over the long-term, rather than making "...wasteful metabolic (enzyme) adjustments to short-term fluctuations in either the quality or quantity of the nutrient supply..."

The time-course of absorptive acclimation has not been measured for any other bivalve species. If other bivalves respond on a similar time scale as observed for *P. magellanicus*, the rapidity of acclimation (up to 50% complete within two days) may explain why it was not observed in *C. edule*. AE measurements for this species only began after two days exposure to reduced quality diets (Navarro et al., 1992; Navarro and Iglesias, 1993). Absorptive acclimation capabilities may also have been underestimated in studies on *M. edulis*, in which AE was first measured on the second day of exposure (Bayne et al. 1987, Bayne et al. 1993). Despite possibly understating its importance, these authors concluded that "the primary mechanism that effects acclimation of the rate of absorption of organics appears to be an enhanced absorption efficiency."

The mechanism(s) by which bivalves regulate AE in response to changes in diet quality is uncertain. Bayne et al. (1987) noted that AE was related to gut passage time, which is dependent on ingestion rate. A negative linear relationship between absorption efficiency and ingestion rate appears to be a common trait among bivalve filter-feeders (Hawkins and Bayne 1992, Navarro and Iglesias 1993). The observed time-scale of absorptive acclimation suggests that the regulation of gut passage time is not the sole compensatory mechanism. Sea scallops immediately alter ingestion rates in response to reduced diet quality (Cranford and Gordon 1992), while absorptive acclimation required several days (Fig. 3.4). Increased gut residence time may have contributed to the initial rapid increase in AE, however, adjustments to the quantity and specific activity of digestive enzymes (Hawkins and Bayne 1992) appear responsible for increases in AE observed over the remaining acclimation period.

The benefit of enhanced absorption efficiency and rate to the energy and elemental balance of sea scallops would likely change with seasonal variations in seston characteristics and endogenous energy demands. The decline in the AE of the seston/clay rations, which started at about Day 30, to levels similar to those measured in unacclimated animals at Day 1 (Fig. 3.4) may reflect such changes. As the diet was consistent in quantity and quality throughout the experiment (Fig. 3.1), the more likely explanation for the decline in AE is a change in endogenous energy demands. Kreeger

(1993) suggested that seasonal changes in protein assimilation rates were more related to changes in reproductive condition of mussels than diet composition. However, changing reproductive energy demands should not be a factor in the present study as it was conducted during the active period of gametogenesis and energy demands should be high throughout the exposure period. AE may have been affected by some other forcing function besides food quality. Water temperature varied substantially during the experiment (Fig. 3.1a), but did not alter AE in the control population and is probably not the causative agent. Another possibility is that chronic exposure to low quality diets or bentonite stresses or damages the animals so that their ability to maintain a high degree of absorptive acclimation is impaired. This was also rejected as there was no significant difference in the growth rate of somatic or reproductive tissues during exposure to the three seston treatments (Cranford, unpublished data). Some other physiological process that requires a long acclimation period may have reduced the need to maximize absorption. Evaluation of this possibility requires analysis of time-series measurements of the other physiological components of growth and is beyond the scope of this paper. An integrated physiological approach may also explain why the three treatments exhibited similar growth despite the fact that absorption rates were substantially lower in the reduced quality treatments (Figs. 3.7 and 3.8).

CHAPTER FOUR

IN SITU FEEDING AND ABSORPTION RESPONSES OF SEA SCALLOPS *PLACOPECTEN MAGELLANICUS* (GMELIN) TO STORM-INDUCED CHANGES IN THE QUANTITY AND COMPOSITION OF THE SESTON.

4.1 ABSTRACT

Time-series of hourly clearance, ingestion and absorption rates and absorption efficiency were measured over 48 h for adult sea scallops (*Placopecten magellanicus*) held *in situ* in a coastal embayment in Nova Scotia, Canada, during a wind-induced resuspension event. Temporal variations in oceanographic variables, and seston quantity and composition (organic matter, organic carbon, nitrogen, chlorophyll *a*, and inorganic particle size spectra) were monitored during the study with moored instruments and hourly water sampling. Resuspension of bottom materials during the storm resulted in large changes in the amount (1 to 30 mg l^{-1} total particulate matter) and nutritional quality (25 to 50% organic content) of seston. High sedimentation rates after the storm were accelerated by flocculation, resulting in the rapid settling of resuspended particles and an increase in seston quality. Observed short-term (hourly) fluctuations in clearance rate were not related to storm- or tide-induced changes in seston characteristics but were directly related to flow velocity. Significantly lower clearance rates were observed at relatively low (< 4 cm s^{-1}) and high (> 9 cm s^{-1}) flow speeds. The overall reduction in ingestion rates after the storm resulted from decreased food availability. Hourly absorption efficiency (AE) measurements were closely related to seston quality (total organic, organic C and N content) and AE declined exponentially with decreasing seston quality. Reductions in AE during the resuspension event were offset by the increased ingestion rate, resulting in no significant

changes in absorption rates for organic matter, C, or N over the sampling period. As the low food quality of the resuspended matter was balanced by increased availability, any physiological regulation of food acquisition (i.e. clearance rate regulation) would have been irrelevant to maintaining food intake constant.

4.2 INTRODUCTION

The sea scallop (*Placopecten magellanicus* Gmelin) supports an important fishery in Canada and the production of a high-value cultured product is currently in an early stage of expansion. A truly predictive model of the physiology and growth of sea scallops would be a valuable tool for the management of wild and cultured scallop fisheries and would demonstrate a fundamental understanding of the complex interplay that exists between the physiological components of growth and exogenous and endogenous forcing functions. Providing accurate predictions of feeding and absorption responses of bivalve filter feeders to environmental change is a formidable task as these must account for the exogenous influences of the different time-scales of variation in the abundance, composition and nutritional value of seston and temperature (reviews by Hawkins and Bayne 1992, Bayne 1993), as well as large short-term fluctuations in flow (Lenihan et al. 1996 and references cited therein) and particle flux (Cahalan et al. 1989, but see Lenihan et al. 1996).

Predicting food acquisition must also account for endogenous forcing by seasonal changes in energy and nutritional demands related to reproductive condition and the status of nutritional reserves, short-term rhythmicity in feeding behaviour, and genotypic differences in physiological performance (reviewed by Hawkins and Bayne 1992). Additional complications arise from the need to account for constraints on the time required for each of a diverse suite of physiological compensation mechanisms to respond to environmental change (Bayne 1993, Cranford 1995), the inhibition of physiological adjustments under certain conditions (Hawkins and Bayne 1985), and the potential for synergistic or antagonistic interactions between the various forcing functions.

The influence of environmental conditions on the physiology and growth of bivalve filter feeders has been extensively studied and it is clear that food and temperature are the two primary environmental factors affecting growth in nature (reviews by Bayne and Newell 1983, Hawkins and Bayne 1992). Notwithstanding observations of a high degree of correlation between mean annual growth and mean annual water temperature (Jones et al. 1989, Emerson et al. 1994), growth appears to be more dependent on food availability than on temperature (Bayne and Newell 1983), and it has been suggested that sea scallop growth may be virtually independent of temperature if sufficient food is available (MacDonald and Thompson 1986).

Studies on the food available to bivalve filter feeders in coastal waters reveal marked temporal variations in particulate matter concentration, composition and nutritional value (Berg and Newell 1986, Fegley et al. 1992, Bayne 1993). Long-term changes in seston abundance and composition in temperate waters arise primarily from the seasonal cycle of primary production. Variability on a scale of days to weeks can result from algal blooms, horizontal phytoplankton patchiness, storm-induced resuspension of bottom deposits or the spring/neap tidal cycle (Fréchette and Bourget 1987, Bayne 1993).

Superimposed on these longer-term trends in seston characteristics are large high-frequency fluctuations that result from tide-induced resuspension and deposition of bottom deposits and associated organic and inorganic constituents during the semi-diurnal tidal cycle (Berg and Newell, 1986; Fegley et al., 1992). The increase in the proportion of inorganic particles in the water column caused by resuspension has a dilution effect on food quality (Foster-Smith 1975, Widdows et al. 1979), which is generally defined in terms of the organic and/or elemental (carbon and nitrogen) content of seston.

Much of our knowledge on bivalve physiological responses to changes in the abundance and composition of the seston has been obtained from experiments where these variables were manipulated and studied in isolation (reviews by Winter 1978, Bayne and Newell 1983, Hawkins and Bayne 1992). These laboratory experiments have generally been conducted under static or constant flow conditions using diets containing some fraction of an algal cell monoculture. It has been established, however, that these algae-enriched diets evoke a feeding behaviour that differs markedly from responses to natural particle suspensions (Doering and Oviatt 1986, Cranford and Gordon 1992, Iglesias et al. 1992, Navarro et al. 1992, Prins et al. 1994, Cranford and Hargrave 1994, Hawkins et al. 1996) and that flow conditions can affect feeding behaviour and growth responses (see above). Consequently, feeding behaviour models and hypotheses on the role of bivalve filter feeders in coastal ecosystem dynamics (Dame 1993), that have been based primarily on laboratory observations, need to be tested under ecologically relevant conditions.

Considering the difficulties of replicating the complexities of nature in the laboratory, the knowledge required to accurately predict temporal variations in bivalve food acquisition must come, at least in part, from *in situ* studies of bivalve feeding behaviour. The approach of Cranford and Hargrave (1994) for autonomously and continuously monitoring bivalve feeding and digestion processes was developed for this purpose and has been used to measure sea scallop responses to the different time-scales of environmental change (hourly to seasonal) in several coastal regions of Nova Scotia, Canada. Studies at all sites were conducted using extensive environmental monitoring programs and *in situ* measurements of sea scallop feeding and digestion behaviour. It was somewhat fortuitous that a storm occurred during one such study in Lunenburg Bay, as the resulting resuspension of bottom deposits provided an opportunity to monitor the functional response of scallops to large changes in seston quantity and quality. The results of this study are used to provide predictive relations of the feeding and digestion responses of *P. magellanicus* to naturally occurring short-term variations in the seston and are compared with laboratory observations of sea scallop responses to natural and artificial rations.

4.3 MATERIALS AND METHODS

The study site in Lunenburg Bay is located on the south-east coast of Nova Scotia, Canada (44°21'N, 64°18'W) and has a maximum water depth of 6.5 m and a tidal range of

1.3 m. The site is the same as that used by Cranford and Hargrave (1994) and has been extensively studied during a research program designed to evaluate and model the oceanographic processes controlling the growth of the sea scallop *Placopecten magellanicus* (Gmelin). Studies of particle transport and vertical flux conducted concurrently with this study will be reported elsewhere.

4.3.1 Environmental Monitoring

Environmental variables were monitored at 1.5 m above the seabed at the site using moored instrument packages and a water sampling program conducted from a vessel anchored at the study site. Water samples were collected using a pump system consisting of a Masterflex® I/P peristaltic pump containing Norprene® food-grade pump tubing. PVC transfer tubing (12.7 mm ID) connected the pump tubing to an intake (a 25 mm ID PVC 'T' connector) located 1.5 m above the seabed on a bottom-mounted frame. Water was continuously pumped at 5 l min^{-1} giving a flow rate at the intake of 8 cm sec^{-1}, which was approximately equal to average current speeds at the site (Cranford and Hargrave 1994). Water samples were collected at hourly intervals between 0830h October 13 and 0730h October 15, 1993 and were immediately filtered. Particles retained on 1.2 µm pore size glass-fibre filters (25-mm diameter Whatman GF/C) were analysed for concentrations of total particulate matter (TPM), inorganic matter (PIM), organic matter (POM), organic carbon (POC), nitrogen (PN) and chlorophyll *a* according to the filter preparation and analytical procedures of Cranford and Hargrave (1994). TPM, PIM and POM were analysed in triplicate and single determinations were performed for POC, PN and chlorophyll *a*. POC and PN analysis were also performed on particles retained on 5.0 µm pore size silver membrane filters (25 mm diameter, Poretics Corp.). The disaggregated inorganic grain size distribution of suspended particulate matter retained on preweighed Millipore SCWP filters was obtained using the low-temperature ashing and Coulter counter techniques described by Milligan and Krank (1991).

A second water sampling program was conducted in which water pumped as above from 1.5 m above bottom was continuously passed through two 25-mm diameter in-line filter holders containing Whatman GF/C and silver membrane (5.0 µm pore size) filters. Water was drawn at 20 ml min^{-1} through each filter by peristaltic pumps and collected in bottles. At hourly intervals between 1400 h October 13 to 0820 h October 15, each filter was replaced and the volume collected (filtered) was determined. Particles retained on filters were analysed as above for POC and PN.

An EGandG Ocean Products acoustic current meter moored 1.5 m above bottom provided speed and direction data at 2-min intervals between 1316 h October 12 to 0800 h October 19. An instrument array containing a SeaTech fluorometer and transmissometer (10 cm path length), a thermister and a data logger was also moored 1.5 m above bottom and sampled every 1 min between 1343h, October 12 and 1647 h, October 15. An identical instrument package programmed with a 15-sec sampling frequency was lowered from the vessel at 30-min intervals to profile the water column. Fluorometer and transmissometer voltage data were converted to chlorophyll *a* and TPM concentrations, respectively, using regression equations describing the relation between each instruments' voltage output and concentrations measured from water samples collected hourly during this study. Wind speed data were obtained from Environment Canada from a weather station located at Western Head, which is approximately 50 km southwest of the sampling site.

4.3.2 Measurement of Sea Scallop Feeding and Digestion Responses

Two sequential sampling sediment traps were used to measure sea scallop biodeposition rates over hourly intervals between 0420h October 13 and 2300h October 15. The traps were identical to those described in Cranford and Hargrave (1994) except that the acrylic shield positioned above the trap mouth was excluded from this study. The sample cups used to collect the biodeposits contained a dense preservative solution (0.1% wt/vol. $HgCl_2$ in 35‰ NaCl) to prevent microbial alteration of settled particles. Sea scallops used in the study were from a single cohort produced in 1989 that was transferred to the study site in 1990 for use in growth experiments. Ten scallops were randomly collected by divers from a bottom mounted frame on which the animals were ear-hung. The shells were cleaned of fouling organisms and five animals were tied in place on the mesh lid of each trap using ear-holes that were drilled in 1990. The two traps were initially anchored to the seabed on October 12 at 1220 h such that the attached scallops were located 1.5 m above the seabed. Both traps had been programmed so that each of the sample cups would rotate under the collecting funnel for 1-h periods. The first trap was programmed with a.16 h delayed start to allow the animals to recover from any disturbance prior to the initiation of sampling. The second trap was programmed with a 30-h delay so that it would start sampling after the first trap had finished collecting its 14 samples.

The two traps were sequentially deployed for a total of five trap deployments to provide hourly measurements of particle deposition rates under the scallops over a total of 70 hours. To minimise disturbance to the animals during retrieval and redeployment of the traps, the trap lids containing the scallops were removed by divers and held underwater until the trap was returned to the seabed. The scallops were then given at least 1 h to recover from this disturbance before the first sample cup rotated under the collecting funnel. Previous studies at the site used paired trap deployments to compare particle fluxes into traps with and without scallops to control for seston sedimentation into the scallop trap (Cranford and Hargrave 1994). This was not done in the present study as both available traps were required for the sequential deployments and because the previous study showed that sedimentation accounted for a small fraction of material deposited under scallops.

At the end of the experiment, the two groups of five scallops were collected and stored frozen. After thawing, each scallop was measured (shell ht. ± 0.01 mm) and the dry weight of soft-tissue was determined by drying at 80°C until constant weight (± 0.01 g). Subsamples of deposits taken from each trap sample cup were prepared and analysed for total dry weight, POM, PIM, POC, and PN concentrations according to techniques described by Cranford and Hargrave (1994). Subsamples were also filtered onto preweighed Millipore SCWP filters and analysed for inorganic grain size using the Coulter counter technique of Milligan and Krank (1991).

Weight-specific egestion rate (mg dry weight $\cdot$ g^{-1} dry tissue $\cdot$ h^{-1}) was determined from the total weight of particles deposited in sample cups by the five scallops over each hourly interval. Total ingestion rate (I_T; mg dry weight $\cdot$ g^{-1} dry tissue $\cdot$ h^{-1}) was calculated according to Cranford and Hargrave (1994). Ingestion rates for POM, POC and PN were calculated as the product of I_T and the proportions of each constituent in seston. Clearance rate (C; l $\cdot$ g^{-1} $\cdot$ h^{-1}) was calculated by dividing I_T by average TPM, calculated from transmissometer data collected over each hourly sampling period. Absorption efficiency (*AE*) was calculated from the proportions of absorbed (POM, POC and PN) and inert (PIM) indicators in seston and faeces according to Cranford and Grant (1990). Absorption rates (mg POM, POC and PN $\cdot$ g^{-1} $\cdot$ h^{-1}) were calculated for each hourly sampling interval as the product of POM, POC and PN ingestion rates and the *AE* of each substrate.

Seston measurements collected during specific feeding periods were used to characterise the diet in the above calculations of scallop feeding rates and digestion efficiencies. The feeding period corresponding with each faeces sample was determined from *in situ* measurements of particle gut passage time (GPT). During the final sediment trap deployment, which started at 0900h on October 15, 1 g of fluorescent polymer (polystyrene divinylbenzene) microspheres (Duke Scientific Corp.) was dispersed in 10 l of seawater in a carboy and pumped down to the mouth of the sediment trap such that the beads were briefly available to the scallops for ingestion (~15 min). Six and 10 µm diameter microspheres were presented to the animals at 1000 h and 1200 h, respectively, on October 15. Both particle sizes are effectively retained by *P. magellanicus* (Cranford and Grant 1990) and were used to replicate the GPT experiment during a single trap deployment. Subsamples from each of the hourly faeces samples were analysed by flow cytometry to determine the number of each type of microsphere in each sample. Peak luminescence of the fluorescent polymer microspheres was detected at excitation and emission wavelengths of 468 and 508 nm, respectively. The total number of beads ingested during each 15 min exposure period was calculated by summing all bead counts over the 12-hour period after the time of ingestion. The feeding period associated with each hourly faeces sample was determined from the frequency distribution of egested microspheres over time and is defined here as the time interval in which 90% of the ingested particles were egested.

4.3.3 Statistical Analysis

Prior to statistical comparisons, data were screened for non-normality and heteroscedasticity by examining normal probability and residual plots, respectively (Wilkinson et al. 1996). No data transformations were necessary as the normality and homoscadasticity assumptions were not violated. The assumption of independent data may be violated for the feeding rate and absorption efficiency estimates as they are calculated from time-series measurements of faeces collected from the same group of animals and observations at any given time may be dependant on previous observations. Comparisons of average feeding and digestion responses during different sampling periods were conducted using paired (dependent) *t*-tests. This test is based on a repeated measures design and the null hypothesis was that the mean values were equal. For regression analysis of time-series data, the independence assumption was tested by examining regression residuals for significant autocorrelations (Wilkinson et al. 1996). The linearity assumption of regression analysis was tested by plotting and examining relationships between variables. When necessary, linearity was achieved using appropriate data transformations. All statistical tests were performed with SYSTAT Version 5.0 (SPSS, Inc., Chicago, Illinois) except for curve fitting, which was conducted with SlideWrite Plus Version 5 (Advanced Graphics Software, Inc., Carlsbad, CA). A significance level of $\alpha = 0.05$ was used, and this value was divided by the number of tests in multiple *t*-test comparisons.

4.4 RESULTS

4.4.1 Storm-Induced Changes in Seston Quantity and Quality

Wind speeds in Lunenburg Bay increased steadily during the latter half of October 12 and continued to rise to a maximum of 50 km h^{-1} by 0300 h on October 13 (Fig. 4.1). Swells generated during the storm entered Lunenburg Bay and impinged on the seabed causing the mobilisation of bottom deposits between 1900h October 12 and 0200 h on October 13. This resuspension event was detected by the moored transmissometer as a rapid increase in TPM concentration from 1 mg l^{-1} to over 20 mg l^{-1} (Fig. 4.1). A comparison of the results of TPM analyses performed on pumped water samples with transmissometer voltage data showed the two estimates to be highly correlated ($r^2 = 0.926$, $n = 46$, $p = 0.000$)(Fig. 4.1). Fluorometer voltage output was not as well correlated with chlorophyll concentrations in water samples ($r^2 = 0.346$, $n= 42$, $p = 0.000$), but temporal patterns were generally similar (Fig. 4.1) and average chlorophyll estimates obtained using both techniques differed by only 10%. During the resuspension event, chlorophyll concentrations increased from 2 to 4 µg l^{-1} (Fig. 4.1). Maximum current velocities of 15-20 cm s^{-1} occurred during flood tide (Fig. 4.1) when currents were flowing to the W (240-300°). Ebb tide currents were generally slower and to the SE (90-135°).

TPM and chlorophyll concentrations near the seabed remained elevated during the

Figure 4.1

Time-series of environmental data from the weather station at Western Head (hourly wind speeds) and from *in situ* probes moored 1.5 m above bottom at the study site in Lunenburg Bay. Current speeds shown are 30-min running means of readings at 2-min intervals by an EGandG Ocean Products acoustic current meter. Transmissometer and fluorometer voltage data collected at 1-min intervals were transformed into total particulate matter (TPM) and chlorophyll *a* concentrations using calibrations based on the analysis of water samples collected from the same depth at the instruments (circles). TPM data after the storm period are shown using an expanded vertical scale. Temperature, TPM and chlorophyll data are illustrated with a 5-min running mean. The lines and numerals above wind speed data indicate the sampling periods of the five sediment trap deployments.

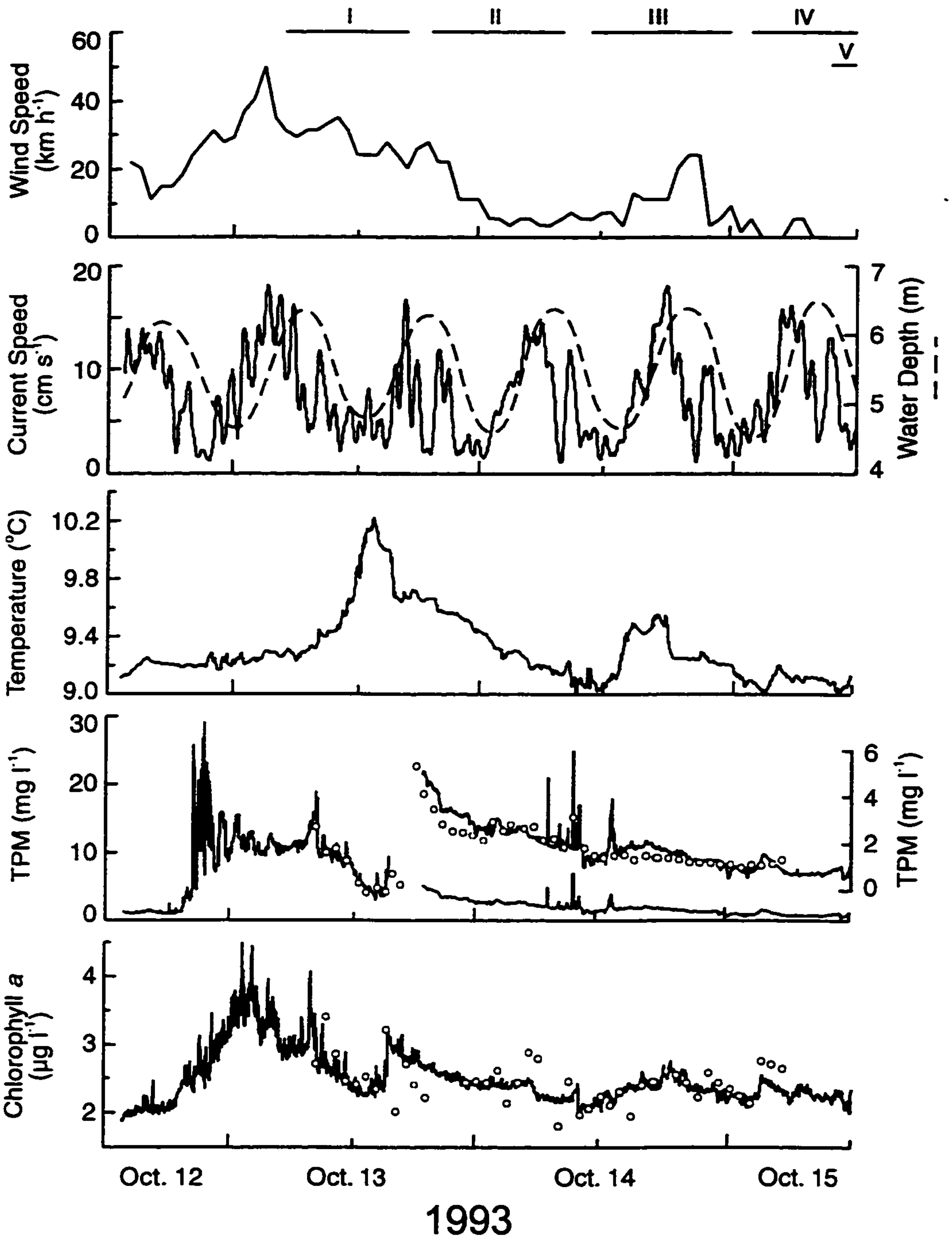
I
II
III
IV
V
Wind Speed (km h⁻¹)
60
40
20
0
Current Speed (cm s⁻¹)
20
10
0
Water Depth (m)
7
6
5
4
Temperature (°C)
10.2
9.8
9.4
9.0
TPM (mg l⁻¹)
30
20
10
0
TPM (mg l⁻¹)
6
4
2
0
Chlorophyll a (µg l⁻¹)
4
3
2
Oct. 12
Oct. 13
Oct. 14
Oct. 15
1993

Figure 4.1

storm until the start of ebb tide at 0640 h on October 13, when warmer (+1°C), clearer waters were advected into the study site (Fig. 4.1). The cooler, more turbid water once again entered the site on the next flood tide (Fig. 4.1), but water column profile data showed this turbidity increase was limited to the bottom 2-m (data not shown). As strong winds and wave action dissipated by the end of October 13, TPM and chlorophyll concentrations rapidly declined to near pre-storm levels, albeit, with some short-term increases in TPM on October 14 caused by SCUBA divers working on the seabed (Fig. 4.1). The inorganic size spectra of suspended particles showed an overall decrease in particle concentration and a gradual fall off at the coarse end of the size distributions during October 13 (Fig. 4.2), but was of constant shape after the start of October 14.

POC and PN concentrations 1.5 m above bottom at the study site were highly correlated with TPM ($r^2 = 0.81$ and 0.78, respectively, $n = 47$, $p < 0.000$) and POM concentrations ($r^2 = 0.81$ and 0.77, respectively, $n = 47$, $p < 0.000$) and declined after the storm (Fig. 4.3). POC and PN concentrations in water samples collected hourly (discrete sampling) and over hourly intervals (continuous sampling) were generally similar (Fig. 4.3). Independent *t*-tests showed significant differences ($p < 0.015$) in POC and PN concentrations retained by the two types of filters (Fig. 4.3). The 5.0-µm filters retained an average of 31% less POC and 25% less PN than was retained by 1.2 µm filters and the difference increased as TPM concentrations decreased after the storm (Fig. 4.3).

The organic content of seston (POM/TPM) during the storm was low due to the

Figure 4.2

Grain size distributions obtained by Coulter counter analysis of inorganic disaggregated seston collected by pump from 1.5 m above bottom at the Lunenburg Bay study site. For clarity, only selected data are shown (every fourth sample starting with the first).

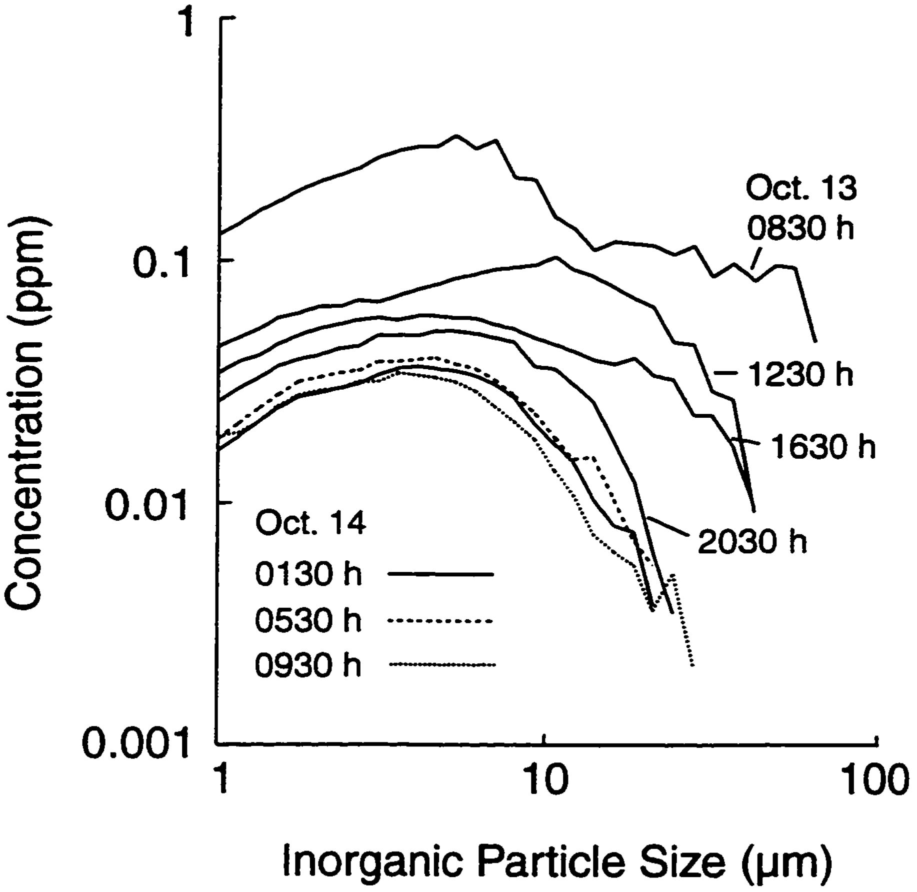
Concentration (ppm)
1
0.1
0.01
0.001
1
10
100
Inorganic Particle Size (µm)
Oct. 13
0830 h
1230 h
1630 h
2030 h
Oct. 14
0130 h
0530 h
0930 h

Figure 4.2

Figure 4.3

Particulate organic carbon (POC) and particulate nitrogen (PN) concentrations in water samples collected hourly (left) and over hourly intervals (right) from 1.5 m above bottom at the study site in Lunenburg Bay. The solid lines show concentrations retained on 1.2 µm pore size filters and the broken lines are concentrations obtained using 5.0 µm filters. Continuous data are plotted at the mid-point of each sample collection interval. The *p*-values shown are from independent *t*-tests comparing concentrations retained by the two types of filters.

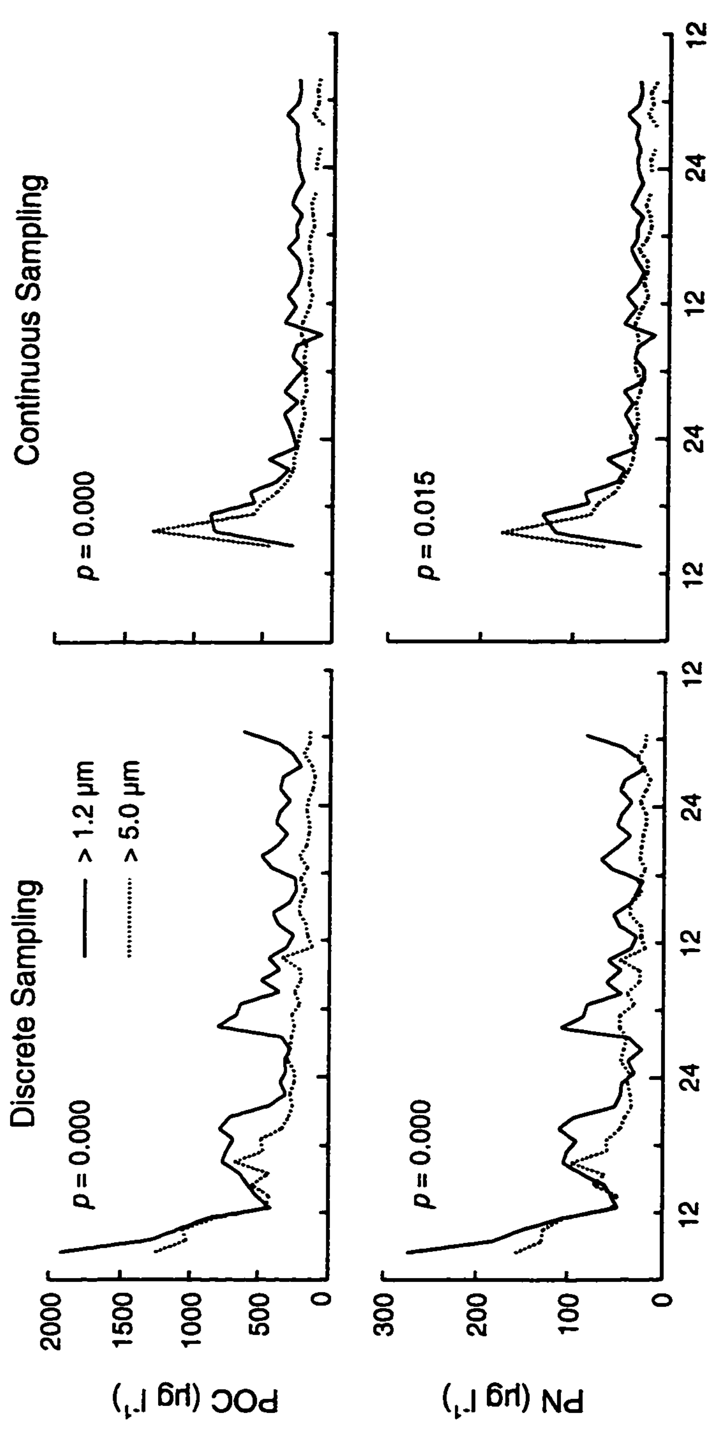
Discrete Sampling
Continuous Sampling
p = 0.000
p = 0.000
p = 0.000
p = 0.015
> 1.2 µm
> 5.0 µm
POC (µg l-1)
2000
1500
1000
500
0
PN (µg l-1)
300
200
100
0
12
24
12
24
12
Oct. 13
Oct. 14
Oct. 15

Figure 4.3

resuspension of inorganic bottom material, but rapidly increased as the bulk of this material settled out of suspension (Fig. 4.4). The anomolously low organic content observed at 1030 h on October 14 (Fig. 4.4) coincided with one of several short-term increases in TPM caused by divers working on the seabed (Fig. 4.1). The close negative relation between TPM (mg l^{-1}) and POM content (%) was best described by the equation:

$$\log \text{POM} = 3.875 - 0.273\ (\log \text{TPM}), \qquad (1)$$

$r^2 = 0.929$, df = 43 and $p = 0.000$. The POC and PN content of seston retained on 1.2 µm filters showed a tendency to increase primarily during flood tide (Fig. 4.4). The C:N ratio of seston retained on the 1.2-µm and 5-µm filters averaged 8.3 (SD = 1.1) and 7.2 (SD = 0.9), respectively, and was highest at the start of flood tide (Fig. 4). The ratio of POC to chlorophyll *a* (C:CHL) declined from a peak value of 480 during the storm to stabilise at approximately 140 by October 15 (Fig. 4.4).

4.4.2 Deposition Rate and Composition of Settled Particles

Scallops held on the sediment traps had an average shell height of 103.1 mm (SD = 4.2) and dry tissue weight of 9.5 g (SD = 1.2). Gonad mass was less than 5% of total dry tissue weight for all animals. Particle deposition rate varied considerably over the course of

Figure 4.4

Estimates of seston quality from hourly samples of water pumped from 1.5 m above bottom at the study site in Lunenburg Bay. Particulate organic matter (POM, mean ± SD, n= 3), organic carbon (POC) and nitrogen (PN) contents and the ratio of carbon to chlorophyll *a* (C:CHL) are calculated from data shown in Figures 1 and 3 and are for seston retained on 1.2 μm pore size filters. The broken line plotted along with PN data indicates relative water depth. The C:N ratio is shown for particles retained on 1.2 μm (solid line) and 5.0 μm (dotted line) pore size filters. The lines and numerals at the top of the figure indicate the sampling periods of the five sediment trap deployments.

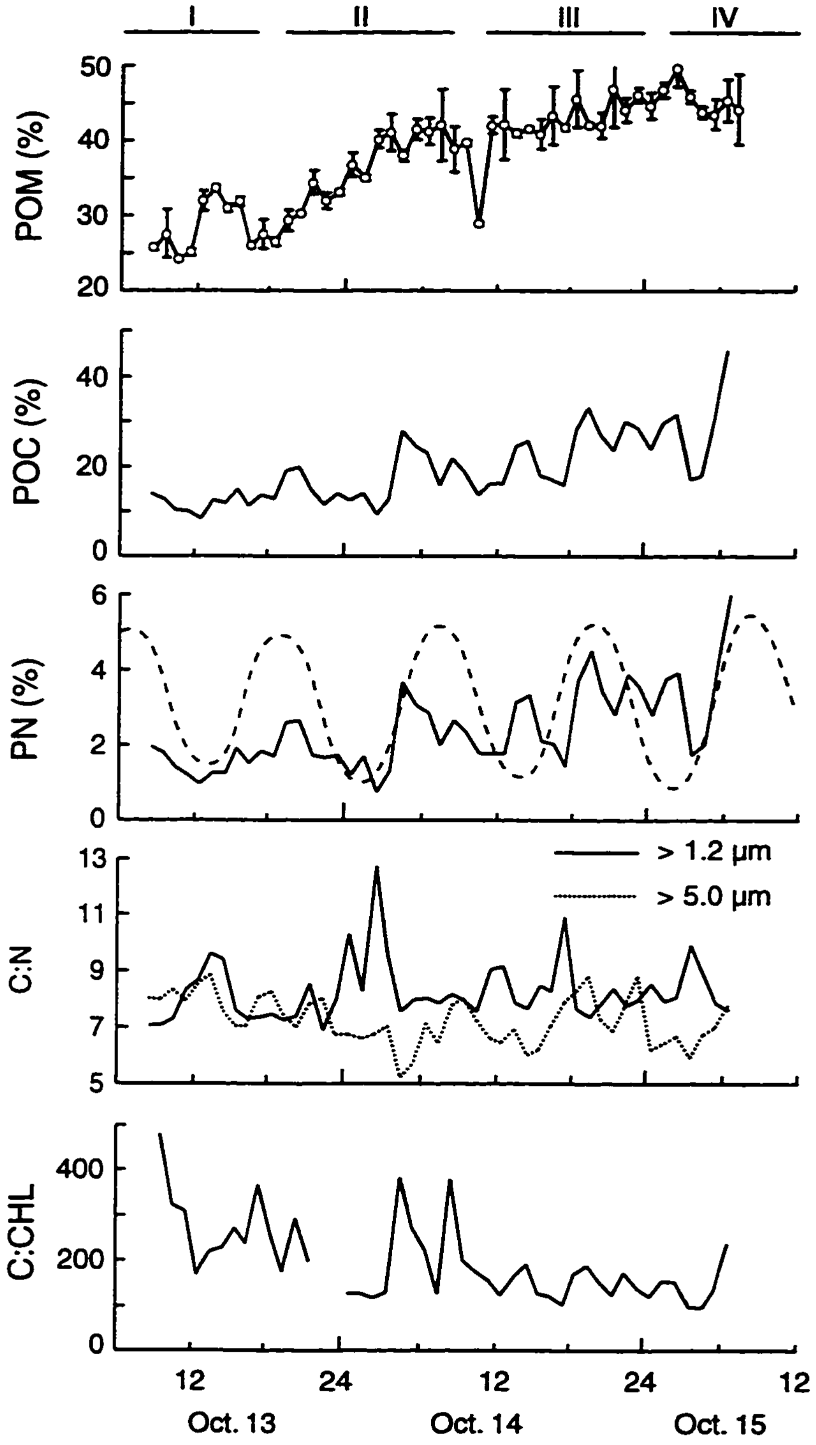
I
II
III
IV
POM (%)
50
40
30
20
POC (%)
40
20
0
PN (%)
6
4
2
0
C:N
13
11
9
7
5
> 1.2 µm
> 5.0 µm
C:CHL
400
200
0
12
24
12
24
12
Oct. 13
Oct. 14
Oct. 15

Figure 4.4

this study (Fig. 4.5) and linear regression analysis on log transformed data showed a close exponential relationship between hourly deposition rate and TPM concentrations averaged over similar hourly intervals ($r^2 = 0.81$, $n = 64$, $p = 0.000$). This relation was not as close when October 13 (storm) data are excluded ($r^2 = 0.39$, $n = 45$, $p = 0.000$). Visual analysis of deposit samples collected during October 13 showed a high proportion of unconsolidated material along with faecal pellets. This observation indicates that the high deposition rates observed during October 13 resulted largely from the rapid sedimentation of high suspended particle loads as opposed to the egestion of faeces by scallops. The high vertical particle flux during October 13 was also indicated by; (1) the rapid decrease in suspended TPM, POC and PN concentrations immediately after the storm (Figs. 4.1 and 4.3), (2) the decrease in the coarse silt and sand (> 20 µm) content of suspended (Fig. 4.2) and settled (Fig. 4.5) particles as larger particles rapidly fell out of suspension, and (3) the increase in the POM, POC and PN content of suspended and settled particles prior to the start of October 14 as the low quality resuspended sediment settled back to the seabed (Figs. 4.4 and 4.5). Visual observation of deposit samples collected after October 13 found that non-faecal material constituted a small fraction of the total particles present.

The low POM, POC and PN contents of several samples collected during October 14 at the start of the Trap III collection period (Fig. 4.5) coincided with the presence of a high proportion of sand particles (110 to 150 µm diameter) in deposit samples. Trap

Figure 4.5

Deposition rate and composition of settled particles collected by sediment traps containing sea scallops, *Placopecten magellanicus*, at the study site in Lunenburg Bay. Each of the five trap deployments are identified by the numerals shown at the top of the graph and data are plotted at the mid-point of hourly sample collection intervals. The percentage of total inorganic particle volume greater than 20 µm diameter (coarse silt and sand) and greater than 50 µm (sand) was calculated from grain-size distributions obtained by Coulter counter analysis of ashed material. The organic matter (POM), organic carbon (POC) and nitrogen (PN) content of deposited material are expressed as a percentage of the total dry weight of particles collected in each sample cup. The POM content of settled material collected during Trap III is shown before (solid line) and after (broken line) sieving to remove particles greater than 90 µm.

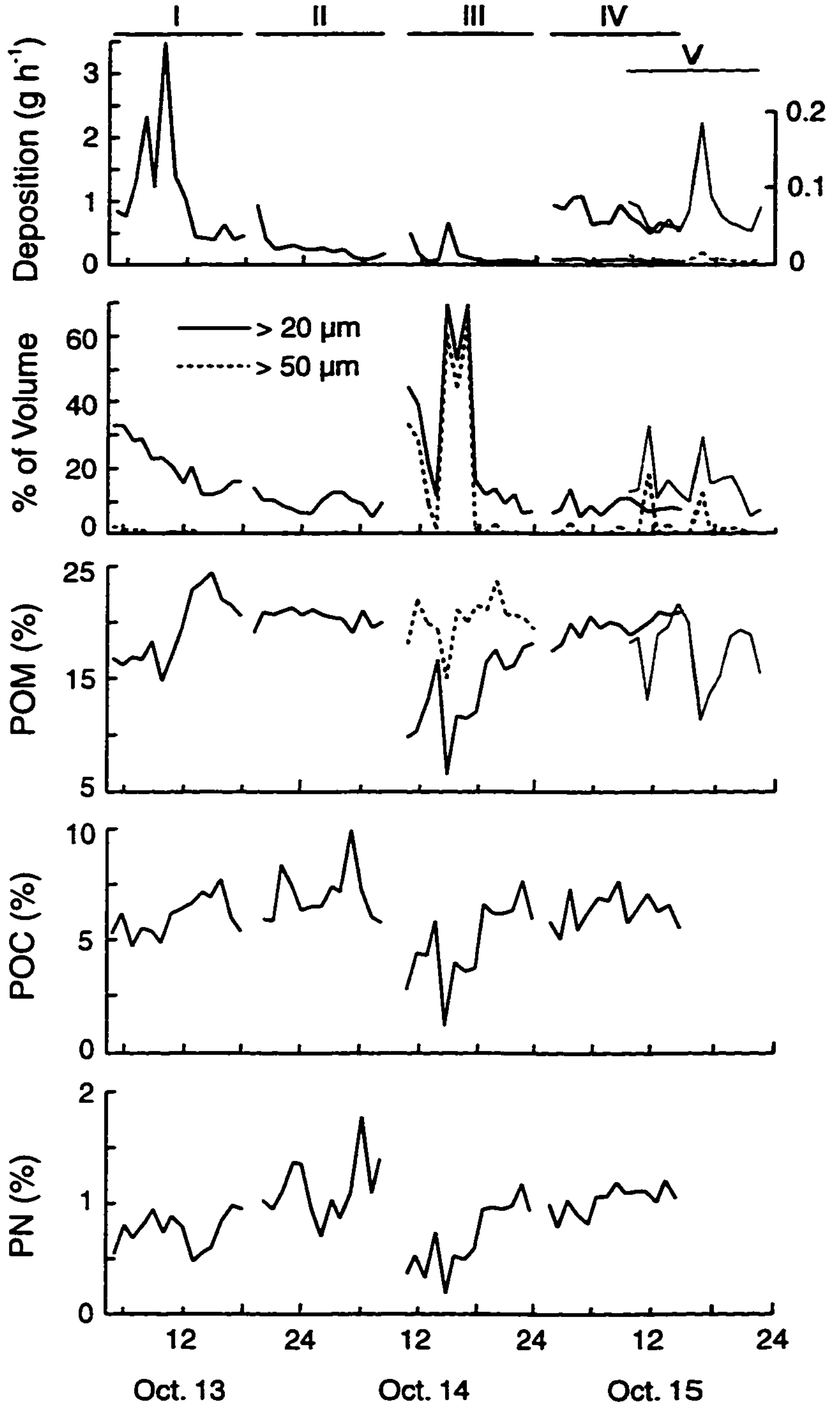
I
II
III
IV
V
Deposition (g h-1)
3
2
1
0
0.2
0.1
0
% of Volume
60
40
20
0
> 20 µm
> 50 µm
POM (%)
25
15
5
POC (%)
10
5
0
PN (%)
2
1
0
12
24
12
24
12
24
Oct. 13
Oct. 14
Oct. 15

Figure 4.5

samples containing a high sand content were often associated with peaks in particle deposition rate (Fig. 4.5). As no sand particles were found in the inorganic size spectra of pumped water samples, the pumping technique was apparently biased against large, dense particles. Settled material collected during the Trap III collection period were reanalysed for POM content after screening through a 90 µm Nytex mesh to remove the sand. The samples were washed through the mesh with isotonic ammonium formate and collected on GF/C filters for analysis as above. Insufficient material remained for a reanalysis of POC and PN contents. Removal of the sand fraction increased POM contents in Trap III samples (averaged 20.4% , SD = 2.0) to values comparable with those obtained during the Trap II (20.5% ± 0.7) and Trap IV (19.8% ± 1.0) sampling periods (Fig. 4.5). Samples of deposits containing a high sand content were excluded from feeding rate calculations and the sieved POM values were used in POM absorption efficiency calculations. Settled particles collected after October 13 that did not contain a high proportion of sand were relatively constant in POM (mean = 20.1%, SD = 1.43, n = 37), POC (6.7%, 0.91, 29) and PN (1.06%, 0.20, 29) content (Fig. 4.5) and had an average C:N ratio of 6.5 (SD = 1.2).

Deposition rates and the POM content of settled material measured during the six hour period during October 15 in which the Trap IV and V sampling periods overlapped were generally similar (Fig. 4.5). A high sand content and concomitant low POM content was noted in one of the samples collected in Trap V that was not observed in the comparable Trap IV sample (Fig. 4.5). No carbon or nitrogen analysis was conducted on

Trap V samples as the polymer microspheres used in the gut passage time experiment would have affected the results.

4.4.3 Gut Passage Time

The five scallops held over the sediment trap consumed a total of 5.7 million 6 µm diameter beads and 25.6 million 10 µm diameter beads during the two 15-min exposure periods. Only 2% of the 6 µm beads recovered and 4% of the 10 µm beads recovered were recovered within an hour after exposure, indicating a low rate of pseudofaeces production (Fig. 4.6). This is consistent with visual observations of deposit samples, which showed that pseudofaeces were not present. An initial pulse of egested microspheres was observed in faeces samples collected between three and five hours after ingestion (Fig. 4.6). While 70% of the recovered 10-µm beads were egested within five hours, the recovered 6-µm beads were retained longer and a similar percentage was not egested until seven hours after ingestion. Within ten hours after ingestion, over 90% of the recovered beads were egested. Average GPT for the 6-µm beads was 5.8 h (SD = 2.7) and 4.4 h (SD = 2.2) for the 10 µm beads. Combining the results of the two experiments gave a slightly skewed frequency distribution with a GPT of 5.2 ± 2.7 h (mean ± SD).

Calculations of feeding rates and absorption efficiencies from biodeposition rate and faeces composition data also require an estimate of the quality (POM, POC or PN content) of ingested particles (Cranford and Hargrave 1994). The GPT experiment indicated; (1)

Figure 4.6

Frequency distribution of 6- and 10-µm diameter fluorescent microspheres in sea scallop (*P. magellanicus*) faeces samples collected over consecutive hourly intervals (horizontal bars) after the time of addition. The 6 and 10 µm diameter microspheres were presented to the animals at 1000 h and 1200 h, respectively, on October 15. (Flow cytometry data provided by W. Li.)

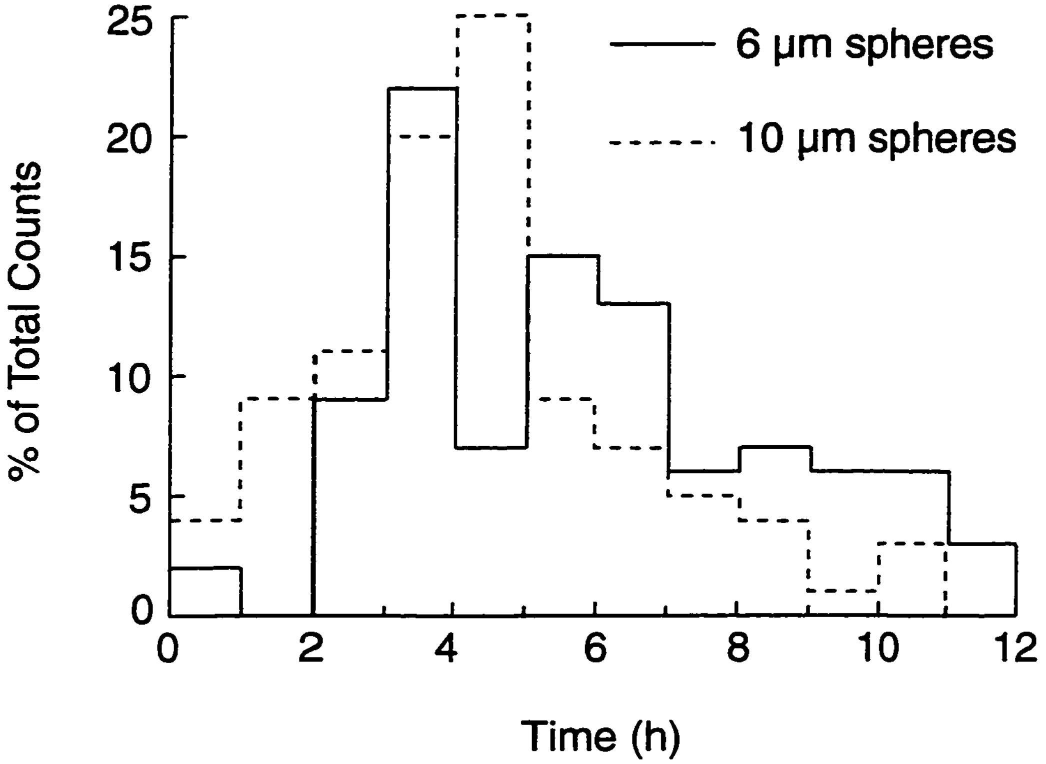
% of Total Counts
0
5
10
15
20
25
0
2
4
6
8
10
12
Time (h)
6 μm spheres
10 μm spheres

Figure 4.6

that hourly faeces samples contained material ingested mainly between two and 10 hours prior to egestion (accounted for 90% of egested microspheres) and (2) the relative contribution to a faeces sample of particles ingested at different times during this feeding period varied (Fig. 4.6). Therefore, seston quality values measured between two and 10 hours prior to the faeces collection period were used to characterise the diet. Prior to calculating the average POM, POC and PN content for each feeding period, each hourly seston quality measurement was weighted according to its contribution to the faeces sample. Frequency weights were based on the average distribution of microsphere counts in faeces over time (Fig. 4.6). For example, material ingested between three and four hours prior to egestion comprised the largest fraction of each faeces sample and was given a frequency weight of 21%, while particles ingested between nine and ten hours before egestion contributed less to the faeces sample and were given the lower frequency weight of 5%. These calculations assume that GPT remained constant during the study period. In addition to calculating the average feeding and digestion response for each hourly sampling interval by using these weighted mean diet quality estimates, the total range of error in each estimate was determined by repeating the calculations using the maximum and minimum seston quality values observed during each feeding period.

4.4.4 Sea Scallop Functional Response to Storm-induced Changes in Seston

Calculations of *in situ* feeding and digestion responses were confined to the post-storm period owing to the high vertical flux of resuspended sediments during the storm, which contaminated faecal deposits. In addition, faeces samples containing a high proportion of sand (Fig. 4.5), or collected three hours after termination of water sampling on October 15 were excluded. Total ingestion rates were highest at the start of October 14 (Fig. 4.7) when seston quantity (TPM concentration) was relatively high (Fig. 4.1) and quality (POM, POC and PN content) low (Fig. 4.4). Clearance rates (*C*) averaged 1.8 l g^{-1} h^{-1} (SD = 0.6; n = 29) or 17.1 l h^{-1} (SD = 5.5) for individuals during the post-storm study period (Fig. 4.7). Hourly clearance and ingestion rate estimates obtained using the maximum and minimum seston ash contents observed over each feeding period were similar to estimates based on average diet quality (Fig. 4.7), indicating that these calculations are not as sensitive to diet quality fluctuations as they are to changes in egestion rate.

A comparison of the same animals held on Trap II and Trap IV found no significant difference in average *C* (paired *t*-test, d.f. = 8, $p = 0.174$). Short periods of low clearance activity (Fig. 4.7) coincided with peak current speeds during flood tide (Fig. 4.1). Median current speeds (the mean was not used as it is influenced to a greater degree by extreme values) were calculated over the same hourly periods as for the feeding rate estimates. Paired *t*-tests, used to compare average *C* at low (< 4 cm s^{-1}), medium (4-9 cm s^{-1}) and high (>9 cm s^{-1}) current speeds found significantly higher *C* at medium current speeds than at either low (d.f. = 6, $p = 0.025$) or high (d.f. = 8, $p = 0.025$) speeds.

Figure 4.7

Time-series of the clearance (l g^{-1} h^{-1}) and ingestion rate (mg dry weight (DW) g^{-1} h^{-1}) of particulate matter by sea scallops, *Placopecten magellanicus*, (103 mm mean shell height, SD = 4.2, n= 10) held on sediment traps in Lunenburg Bay during the indicated period. The solid lines indicate average responses calculated using weighted mean seston diet quality measurements (see text for details). The area between the broken lines represents the possible range of error in each variable and was calculated using the maximum and minimum diet quality observed during the 10 hour period prior to each faeces sample collection. Data points are plotted at the mid-point of hourly sample collection intervals by the three sediment traps identified by the numerals at the top of the graph. Faeces samples from Trap III containing a high sand content (Fig. 4.5) were excluded from the calculations. The smooth broken line plotted along with clearance data indicates relative water depth.

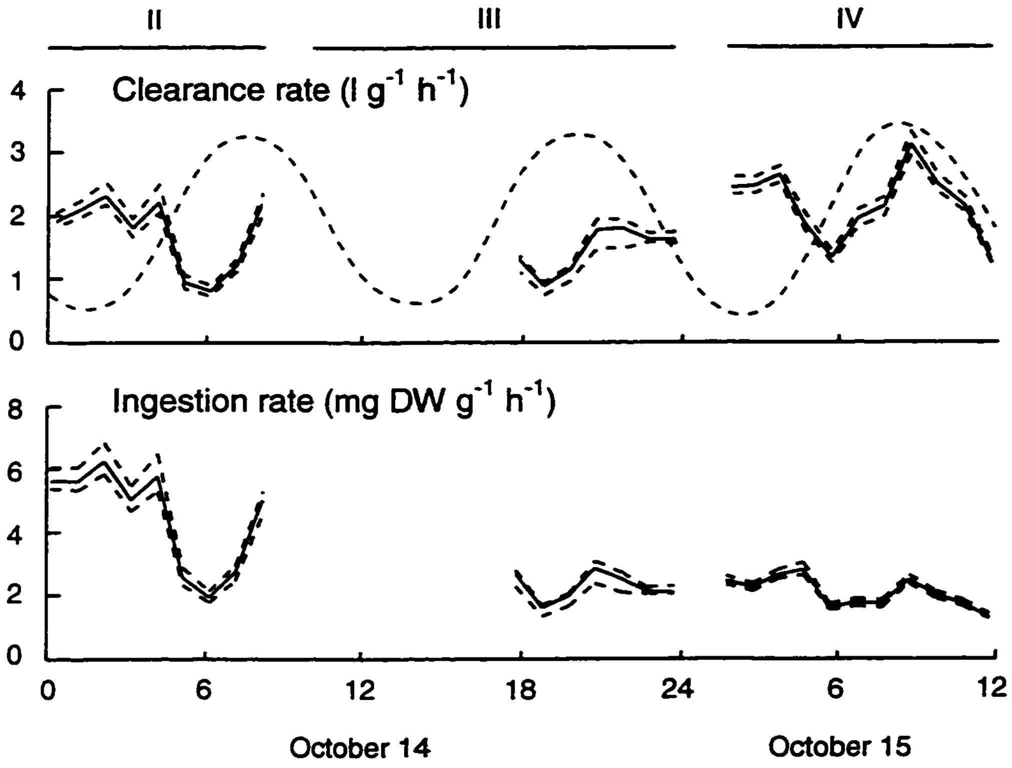
II
III
IV
Clearance rate (l g^{-1} h^{-1})
4
3
2
1
0
Ingestion rate (mg DW g^{-1} h^{-1})
8
6
4
2
0
0
6
12
18
24
6
12
October 14
October 15

Figure 4.7

Temperature fluctuations during the period of feeding measurements were less than 0.6°C (Fig. 4.1) and do not appear to be related to short-term changes in C (Fig. 4.7).

Ingestion rates of POM, POC and PN were highest at the start of October 14 and declined to a constant rate for the remainder of the study (Fig. 4.8). Large short-term fluctuations in the POC and PN content of seston (Fig. 4.4) resulted in a larger potential range of error in POC and PN ingestion rate calculations compared with that estimated for POM ingestion rate (Fig. 4.8). The absorption efficiency of POM (AE_{POM}) gradually increased during October 14 from approximately 40% to stabilise at 71% (SD = 1.3) during October 15. The low minimum AE_{POM} values observed during October 14 (Fig. 4.8) resulted from the influence of the low POM content of seston at 1030 h on October 14 that coincided with a short-term increase in TPM (Fig. 4.1). POC and PN absorption efficiency (AE_{POC} and AE_{PN})were also relatively low at the start of October 14 (Fig. 4.8), but were highly variable at this time owing to short-term fluctuations in both food and faeces POC and PN content (Figs. 4.4 and 4.5). By October 15, AE_{POC} increased to 84% (SD = 1.9) and AE_{PN} to 79% (SD = 3.0) (averages are for October 15 data). The inverse relation between AE and ingestion rate (Figs. 4.7 and 4.8) resulted in absorption rates for all dietary substrates that were relatively constant throughout the study period (Fig. 4.8). Paired *t*-tests of the same population held on Trap II and IV revealed no significant difference (d.f. = 8 , $p > 0.1$) in average absorption rates of POM, POC or PN.

Figure 4.8

Time-series of weight-specific ingestion and absorption rates and absorption efficiency of particulate organic matter (POM), organic carbon (POC) and nitrogen (PN) by sea scallops, *Placopecten magellanicus*, in Lunenburg Bay during the indicated study period. The presentation of data is the same as described in Figure 4.7.

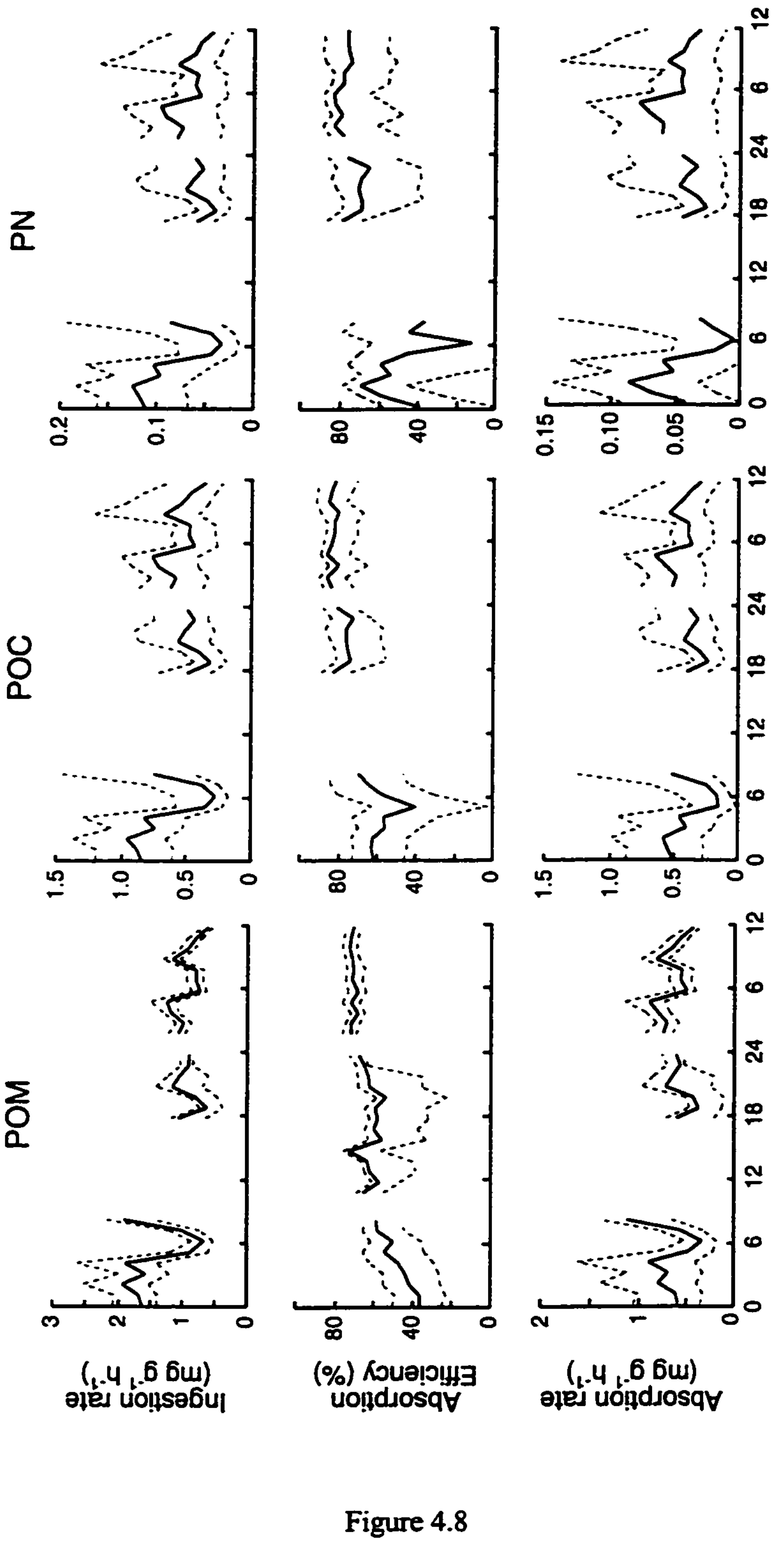
POM
POC
PN
Ingestion rate (mg g-1 h-1)
Absorption Efficiency (%)
Absorption rate (mg g-1 h-1)
3
2
1
0
80
40
0
2
1
0
1.5
1.0
0.5
0
80
40
0
1.5
1.0
0.5
0
0.2
0.1
0
80
40
0
0.15
0.10
0.05
0
0
6
12
18
24
6
12
October 14
October 15

Figure 4.8

Functional relations between absorption efficiency and diet quality were described after Bayne et al. (1987) by fitting AE_{POM}, AE_{POC} and AE_{PN} data to the exponential equation;

$$AE = a1(1-e^{(-a2(Q-a3)}), \tag{2}$$

where Q is the weighted mean diet quality (POM, POC or PN content of seston averaged over each eight hour feeding period) and $a1$, $a2$ and $a3$ are parameters describing, respectively, the maximum asymptotic AE, rate of AE increase with increasing Q, and the Q at which AE is zero. The equation parameters, and statistics for the fitted models are given in Table 4.1. Autocorrelation plots of the residuals from regression analysis of time-series AE data showed non-significant autocorrelations at all time lags. This indicates that the AE estimates were independent and did not violate this assumption of regression analysis. The POM, POC and PN content of the diet were highly correlated with AE (Table 4.1). The Q's corresponding with zero AE were predicted with a high degree of confidence from observed data and averaged 21% for POM, 9.5% for POC and 1.2% for PN (Table 4.1). The maximum asymptotic AE_{POM} of 92% was higher than that estimated for POC or PN (83 and 85%, respectively). However, the former estimate was extrapolated well beyond the maximum observed AE_{POM} of 73% (Fig. 4.9). AE_{POC} and AE_{PN} estimates were generally higher than for AE_{POM} and, unlike AE_{POM}, asymptotic values were reached within

Table 4.1

Parameters of exponential models describing the relation between the absorption efficiency of particulate organic matter (AE_{POM}), organic carbon (AE_{POC}) and nitrogen (AE_{PN}) and different measures of diet quality (% POM, POC and PN content per mass of seston).. The model (Eqn. 2) and parameters are defined in the text and the fitted curves are shown in Fig. 4.9.

AE (%)	*a*1 ± SE	*a*2 ± SE	*a*3 ± SE	r^2	SE	*F*	*p*
AE_{POM}	92.0 ± 13.8	0.058 ± 0.024	20.6 ± 2.4	0.899	3.5	136.4	0.000
AE_{POC}	84.6 ± 2.4	0.238 ± 0.074	9.5 ± 1.4	0.845	4.9	65.6	0.000
AE_{PN}	82.9 ± 5.5	1.555 ± 0.570	1.2 ± 0.2	0.754	9.0	36.8	0.000

Figure 4.9

Absorption efficiency of total particulate organic matter (POM), particulate organic carbon (POC) and nitrogen (PN) as a function of diet quality, which is expressed as the percentage POM, POC and PN content per unit dry weight of particulate matter. Diet quality estimates are weighted means that are calculated as described in the text. The solid curves were fitted to these data and the equations are given in Table 4.1. The broken curves were fitted to results from previous field and laboratory studies with *P. magellanicus* (Chapter 3).

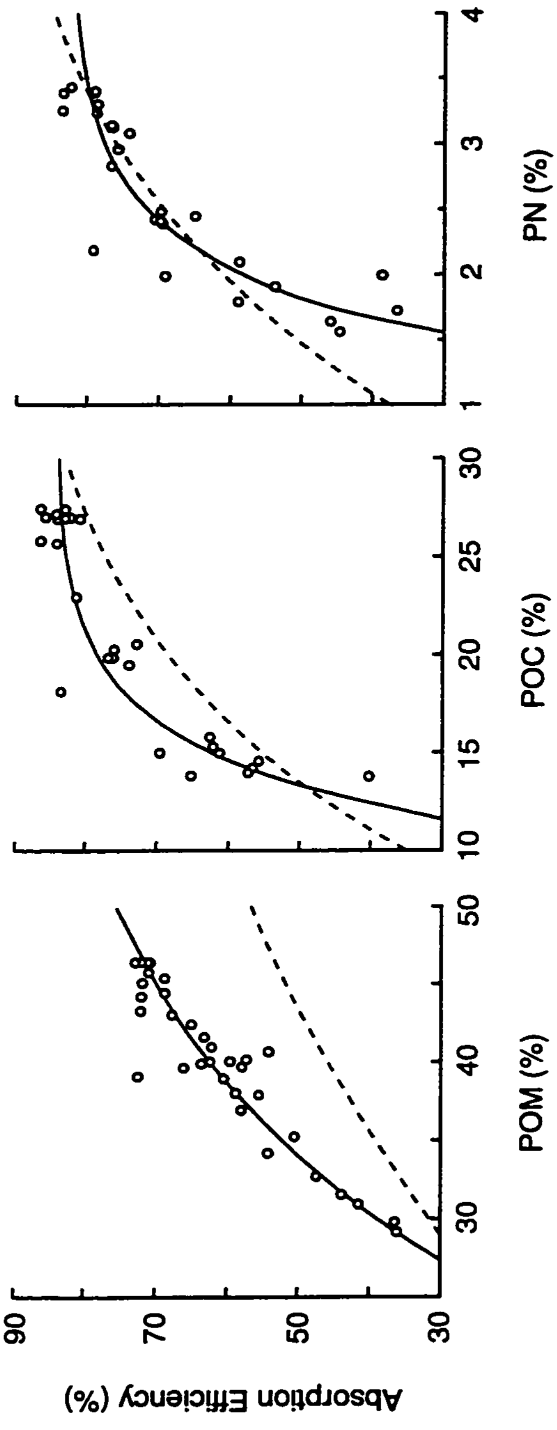
Absorption Efficiency (%)
90
70
50
30
30
40
50
POM (%)
10
15
20
25
30
POC (%)
1
2
3
4
PN (%)

Figure 4.9

the range of diet qualities observed (Fig. 4.9). A comparison of the equation slopes (parameter *a2*) found no significant difference for the different dietary substrates (95% confidence intervals calculated for normalised *a2* estimates overlapped). However, at the lower range of Q's observed, AE_{POC} and AE_{PN} declined much more rapidly with decreasing Q than was observed for AE_{POM} (Fig. 4.9).

4.5 DISCUSSION

4.5.1 Functional Response of Scallops to Storm-induced Environmental Change

The resuspension of bottom material during the storm greatly increased the abundance of POM, chlorophyll *a*, POC and PN in suspension near the seabed (Figs. 4.1 and 4.3). The benefit of this increased food availability to bivalve filter-feeders is believed to depend on their capacity to compensate for the concomitant decrease in the overall quality of seston (Fig. 4.4) that results from the resuspension of inorganic grains and detrital materials (Figs. 4.2 and 4.4) (Bayne et al. 1993, and references cited therein). Insignificant differences in average clearance rates (*C*) during the Trap II and IV sampling periods (Fig. 4.7) indicate that observed changes in ingestion rate were not an active feeding response to changes in diet quantity and quality, but were simply the result of different particle concentrations in the volume of water cleared.

The uniformity of average *C* estimates between sampling periods is consistent with laboratory observations for *P. magellanicus* that have shown *C* to be independent of seston concentrations within the observed TPM range (1 to 6 mg l^{-1})(MacDonald and Ward 1994). However, the lack of any apparent regulation of *C* by food quality (Fig.. 4.4) appears to contradict laboratory data showing a positive relationship between *C* and POM content (Cranford and Gordon 1992) and chlorophyll *a* concentration (MacDonald and Ward, 1994). The relationships observed in the laboratory may be attributed to the use of artificial diets (seston supplemented with algal cells to vary diet quality). When diets containing cultured algal cells are excluded from the analysis of feeding behaviour, the relationship between *C* and diet quality is no longer apparent. The anomalous feeding responses of sea scallops to rations containing algal cells was demonstrated in paired experiments in which the same individuals were observed to clear algal cells three times faster than seston of similar concentration and POM content (Cranford and Gordon 1992).

Although *C* estimates averaged over different sampling periods were similar, large short-term (hourly) fluctuations were observed that appear to be related to the semi-diurnal tidal cycle (Fig. 4.7). The apparent inhibition of feeding activity at relatively low (< 4 cm s^{-1}) and high flows (> 9 cm s^{-1}) generally support the findings of numerous laboratory studies. Flow velocity has previously been shown to directly affect feeding behaviour and/or growth rate in the mussel *Mytilus edulis* (Wildish and Kristmanson 1985, Wildish and Miyares 1990), the American oyster *Crassostrea virginica* (Grizzle et al. 1992, Lenihan et al. 1996) and in the scallops *P. magellanicus* (Wildish et al. 1987, Wildish and Kristmanson 1988, Wildish and Saulnier 1993) and *Argopecten irradians concentricus* (Kirby-Smith 1972, Eckman et al. 1989). Feeding behaviour may have been indirectly influenced by tidal flow through the resuspension of bottom materials or the influx of higher quality seston during flood tide. Resuspension is an unlikely cause of *C* variations as peak tidal flows had little impact on seston concentration (Fig. 4.1). *C* was probably not influenced by the higher POC and PN content of seston during flood tide (Fig. 4.4) as this would suggest an inverse relationship with diet quality, which is inconsistent with previous observations (Cranford and Gordon 1992, MacDonald and Ward 1994).

Another potential explanation for short-term variations in clearance and ingestion activity is rhythmicity in physiological processes. Rhythmic periodicity in feeding behaviour is a common phenomenon in suspension-feeding bivalves that may be related to endogenous influences (review by Morton 1983). *M. edulis* have been shown to exhibit pronounced temporal fluctuations in deposition and excretion rates and faeces composition that do not appear to be related to exogenous influences (Hawkins et al. 1983). These authors hypothesised that the rhythmicity of physiological processes resulted from the co-ordination of feeding behaviour with alternating cycles of extracellular and intracellular digestion. Temporal variations in the POM, POC or PN content of sea scallop faeces (Fig. 4.5) were relatively small and therefore do not indicate a cyclic release of glandular and intestinal faeces. The short-term rhythmicity of feeding behaviour in *P. magellanicus* appears to have been influenced to a greater extent by tidal currents than by endogenous influences.

The most important compensatory response of bivalve filter feeders to variable diets for the optimisation of net energy gain is the regulation of digestive processes (Bayne et al. 1987, 1993). It was not possible to directly assess the importance of absorptive acclimation in compensating for storm-induced changes in seston because the increase in absorption efficiency (AE) after the storm (Fig. 4.8) may also be attributed to an increase in diet quality (Fig. 4.9). Given that the time required for complete absorptive acclimation in sea scallops is approximately six days (Cranford 1995), and that the storm altered the food supply for little more than one day, it appears that digestive acclimation did not play much of a compensatory role. Sea scallops, however, maintain a high state of digestive acclimation under conditions of variable diets (Cranford 1995). This may explain why scallops fed resuspended bottom material (28% POM content) in the laboratory absorbed only 10% of available POM (Cranford and Grant 1990), while the *in situ* AE response to a similar diet quality was over three times higher (Fig. 4.9). In fact, the *in situ* AE was generally higher than that predicted using the equations of Cranford (1995), which are based largely on the results of laboratory experiments (Fig. 4.9). Past feeding history has only recently been identified as an important source of variation in present bivalve feeding behaviour (Bayne et al. 1987, Bayne 1993) and warrants further study so that it may be more adequately understood and modelled.

The high accuracy of the AE predictor functions based on diet quality was indicated by the low standard error (SE) of estimate values (Table 4.1). The maximum asymptotic AE_{POC} and AE_{PN} values of 83-85% are lower than predicted by Cranford (1995), but are similar to values reported for pure algal cell rations (Cranford and Grant 1990). The POC to chlorophyll *a* ratio of seston during the time of maximal AE averaged 140, indicating that seston at these times was composed largely of living phytoplankton. There was no indication of an enhanced AE of nitrogen relative to carbon (Fig. 4.9), as has been observed in the laboratory for *P. magellanicus* (Cranford and Grant 1990, Cranford 1995), *C. edule* (Prins and Smaal 1989, Iglesias et al. 1996, Urrutia et al. 1996), and *M. edulis* (Prins and Smaal 1989). However, POC and PN were absorbed more readily than bulk organic matter and AE_{POM} failed to reach an asymptotic value within the observed range of seston organic content (Fig. 4.9). The relatively low AE_{POM} suggests that some organic component of seston was more refractory than the C and N fractions. The rapid drop-off in AE_{POC} and AE_{PN} that occurred as the phytoplankton dominated diet was 'diluted' with resuspended bottom material (Fig. 4.9) is different than the gradual decline observed when diet quality was reduced by the addition of clay to natural seston and algal cell rations (Cranford 1995). This more rapid decline in AE with the addition of resuspended sediment likely resulted from the presence of refractory organic materials that would reduce AE without markedly changing the C or N content of the diet. AE_{POM} did not decrease as rapidly as AE_{POC} or AE_{PN} as the maximum values were already relatively low.

4.5.2 Assessment of Assumptions in Scallop Food Acquisition Rate Calculations

Estimates of bivalve feeding and digestion behaviour obtained using the biodeposition method depend on the validity of two major assumptions. The first assumption, which also applies to similar estimates obtained using particle depletion methods, is that ingested rations are measured accurately. Characterisation of the food supply must take into account the particle retention properties of the animals feeding apparatus. The proportion of available particles retained by *P. magellanicus* (retention efficiency; RE) varies with particle size and is optimal for particles larger than 5 µm (Cranford and Grant 1990). Below 5 µm, RE declines exponentially such that approximately 50% of 2 µm particles are retained. Unfortunately, characterising the diet of sea scallops is not as simple as collecting seston on a 5 µm pore size filter. Fine particles often exist in marine environments as components of aggregates or flocs of a size that can be effectively retained. As these flocs are easily disrupted when sampled, a fine mesh filter may be more suitable for collecting and analysing natural diets.

Inorganic grain size spectra of seston collected as the storm subsided showed a progressive decrease in the proportion of coarser grains in suspension as well an overall decrease in the concentration of all particle sizes (Fig. 4.2). The former observation indicates some differential settlement according to grain size while the later indicates that the settling velocity of fine particles was greatly accelerated by their incorporation into flocs. The shape of the inorganic particle size distributions, and particularly the initial slope of the distribution, is consistent with observations of flocculated suspensions analysed as disaggregated material (Kranck and Milligan 1992). Visual inspection of *in situ* photographs of particulate matter present throughout the water column during this study, taken with a Benthos 373 plankton silhouette camera, failed to detect the presence of large flocs (Milligan, unpublished data). However, frequent resuspension and deposition of bottom material in shallow coastal waters may limit the maximum size of flocs (Eisma and Kalf 1987), such that these microflocs would be smaller than the resolution of the camera (~50 µm). The capacity of bivalve filter-feeders to effectively retain fine particles contained in flocs depends on whether or not feeding processes disrupt the flocs into component particles prior to their capture. A comparison of the inorganic particle size spectra of seston and faeces samples collected during the post-storm period showed a rapid drop-off in concentration of particles less than 6 µm in faeces despite the fact that peak seston concentrations occurred at 2 µm (data not shown). The enrichment in faeces of particles larger than 5 µm is consistent with laboratory measurements of the retention efficiency of disaggregated particles by *P. magellanicus* (Cranford and Grant 1990) and indicates that fine particles were 'lost' after disruption of flocs by feeding processes. It may therefore be concluded that a filter with a pore-size of approximately 5 µm is the appropriate choice for characterising sea scallop diets, at least in the present study.

The comparison of POC and PN concentrations retained by 1.2 µm (GF/C) and 5.0 µm (Poretics) pore-size filters (Fig. 4.3) showed that the former overestimated the quantity of food available to scallops, particularly when TPM was low. An inverse relation between particle size and diet quality was indicted by the increase in the POM, POC and PN content of seston (Fig. 4.4) as larger particles settled out of suspension (Fig. 4.2). Such a relationship between diet quality and particle size may be explained by differences in the surface area available for the adsorption of nutritious materials relative to the volume of different sized particles. By retaining fine particles that are not effectively retained by scallops, GF/C filters appear to overestimate both the quantity and quality of scallop rations. This problem of accurately characterising natural diets using standard filtration techniques can be extended to most bivalve filter feeders as only a few species have particle retention properties comparable with the GF/C and GF/F filters that are traditionally used. This problem is compounded by observations that several species, including *P. magellanicus*, exhibit control over the minimum size of particles effectively retained (Palmer and Williams 1980, Bayne and Newell 1983, Cranford and Gordon 1992, Stenton-Dozey and Brown 1992, Barillé et al. 1993, MacDonald and Ward 1994).

The primary purpose for measuring gut passage time in this study was to identify the feeding period associated with faeces samples, so diets could be identified and used along with biodeposition data to calculate feeding rates and efficiencies. To my knowledge, the reported estimates of GPT for *P. magellanicus* are the first for this species and the first to be based on *in situ* measurements for any bivalve species. The pulse-chase experiments, in which inert beads were briefly presented to scallops for ingestion and then collected in faeces over time, showed that particles ingested at a given time can have markedly different residence times in the gut (Fig. 4.6). Previous definitions of GPT have been based on the time required for 90% or 95% of ingested tracer particles to be egested (Bayne et al. 1989, Hawkins et al. 1990, Navarro et al. 1992) and approximate the gut evacuation time. The gut evacuation time for the scallops in the present study was approximately 10 hours (Fig. 4.6). It would be inappropriate to use this measurement to determine the time of particle ingestion for each faeces sample as only 5 or 10% of the material contained in faeces samples was ingested 10 hours earlier (Fig. 4.6). If diets are changing rapidly, this would result in large errors in feeding behaviour calculations. As the majority of ingested particles are egested prior to the gut evacuation time (Fig. 4.6), a mean or median GPT would be a somewhat better choice for identifying diets, but these estimates also incorrectly assume that all material in the faeces was ingested instantaneously, when in fact it was ingested over a much longer feeding period. In an attempt to solve this problem, ingested rations were characterised by averaging seston quality measurements over an eight hour feeding periods (2-10 hours prior to egestion) after applying frequency weights to hourly seston data to account for changes in their relative contribution to each faeces sample (Fig. 4.6; see Section 4.4.3).

The previous discussion has documented the difficulties of accurately quantifying both the quantity and quality of materials ingested by bivalve-filter feeders, even without significant pre-ingestive particle selection taking place. Fortunately, ingestion and absorption rates calculated using the biodeposition method (Iglesias et al. 1992, Cranford and Hargrave 1994) do not require estimates of food abundance, and are generally more sensitive to changes in egestion rate than to changes in diet quality (Figs. 4.7 and 4.8). In contrast, ingestion and absorption rates based on bivalve-induced particle depletion, using static and flow-through feeding chambers or *in situ* tunnel and flume systems, are more dependant on accurate estimates of food abundance. On the other hand, clearance rate estimates based on measurement of the depletion of particles retained with 100% efficiency should be more accurate that those obtained with the biodeposition method, which would be underestimated if food quantity measurements included particles not retained by the animal. It is important to note, however, that both methods have produced similar clearance and ingestion rate estimates for natural diets (Cranford and Hargrave 1994, Urrutia et al. 1996).

The second major assumption of food acquisition rate calculations is that egestion rates are measured accurately. The *in situ* biodeposition method of monitoring the feeding and absorption behaviour of bivalve filter feeders assumes that particles that settle into the sediment trap are from faeces (Cranford and Hargrave 1994). The calculations would be invalid if settled seston altered the quantity and quality of the biodeposits. Owing to a lack of suitable measurements to control for high seston sedimentation rates into sediment traps containing scallops, deposition-rate data collected during the storm could not be used to calculate scallop feeding rates. However, visual observations of trap samples showed that virtually all of the particles collected after October 13 were faecal pellets. Previous measurements of the flux of seston and biodeposits into sediment traps containing scallops at the study site at the same time of year showed that settled seston could have accounted for 15% of the mass of particles collected (Cranford and Hargrave 1994). Suspended TPM, POC, PN and chlorophyll *a* concentrations measured during that study were similar to post-storm levels reported here, and a similarly low contribution of seston to biodeposits is expected. While the present sampling design prevents determination of the effect on scallops of high seston concentrations observed during the storm, I was able to determine feeding and digestion responses to food concentrations that are most commonly experienced by sea scallops (<10 mg l^{-1}) and to large changes in seston quality. The lack of a control sediment trap (no scallops) in the present study could, however, result in feeding rates being overestimated by as much as 15%.

Feeding and absorption calculations based on *in situ* biodeposition measurements also assume that egestion rates are not overestimated as a result of the deposition of pseudofaeces. In addition, pre-ingestive particle selection, which requires pseudofaeces production, would affect ingested diet quantity and quality and further reduce the accuracy of feeding calculations. Observations of *P. magellanicus* fed diets of resuspended bottom material and mixtures of seston and coarse silt have shown that pseudofaeces production increases markedly after rations exceed 10 mg l^{-1} (Grant et al., 1997). The addition of clay to seston reduced this pseudofaeces threshold to 2 mg l^{-1} (Cranford and Gordon 1992). Sea scallops fed natural seston have been observed to produce pseudofaeces at food concentrations as low as 2 mg l^{-1} (MacDonald and Ward 1994). However, the authors concluded that because the amounts produced were less than 1% of particles cleared, the impact on the quality of ingested diets was very low and the behaviour of questionable biological significance. Visual observations of material collected in sample cups and the lack of any rapid deposition of inert tracer particles during GPT experiments (Fig. 4.6) confirmed the absence of detectable amounts of pseudofaeces.

4.5.3 Conclusions

An understanding of the influence of seston quantity and quality on the ingestion and absorption of food particles is fundamental to the prediction of bivalve growth and for the management of aquaculture (Grant 1996). However, bivalve feeding responses to changes in the seston can appear erratic and inconsistent (Fréchette and Bourget 1987). This impression could be perpetuated by the observation that sea scallops maintained a relatively fixed average clearance rate during periods when empirical data predict that the large change in diet quality warranted a change in clearance rate (Cranford and Grant 1990, Cranford and Gordon 1992, MacDonald and Ward 1994). Although these observations appear contradictory, they need to be compared in the context of the impact of experimental conditions on the animals net energy balance. It was not necessary for the scallops to regulate clearance rate to maintain a constant absorption rate because the storm-induced reductions in AE resulting from reduced food quality (Fig. 4.9) were counteracted by increased ingestion rates caused by the greater abundance of food (Figs. 4.1 and 4.3). While these opposing effects of food quantity and quality variations resulted in relatively stable absorption rates during the present study (Fig. 4.8), absorption rates may have varied between dietary treatments in the laboratory studies, resulting in a net energy imbalance and the need for compensatory changes in clearance rate.

It is reasonable to expect that bivalve populations that experience frequent resuspension events will adopt a feeding/digestion strategy that minimises the energy costs of compensating for a variable food supply. The strategy of sea scallops for dealing with resuspended particles at concentrations where abundant populations are found (less than 10 mg l^{-1}) appears to be to maintain a state of absorptive acclimation sufficient to balance absorbed energy losses from reduced food quality (Fig. 4.9) with ingested energy gains from increased food quantity (Fig. 4.8). This allows the animals to maintain a constant absorption rate during resuspension events without additional compensatory interventions. Such a strategy reduces the need for predictive feeding behaviour models to deal with the very difficult task of simulating scallop functional responses to fine-scale temporal variations in seston.

CHAPTER FIVE

SEASONAL VARIATION IN FOOD UTILIZATION BY THE SUSPENSION FEEDING BIVALVE MOLLUSCS *MYTILUS EDULIS* AND *PLACOPECTEN MAGELLANICUS*.

5.1 ABSTRACT

Seston utilization by adult *Mytilus edulis* and *Placopecten magellanicus* cohorts was measured using an *in situ* method over a total period of 139 days during the spring, summer and fall of 1995 in Bedford Basin and Mahone Bay, Nova Scotia, Canada. Daily seston utilization measurements were combined with extensive water sampling to construct predictive empirical models of bivalve ingestion based on environmental variables. Particle concentrations were highest in May in Bedford Basin (~5 mg l^{-1}) and remained below 2 mg l^{-1} in Mahone Bay. Seston quality varied between 30 (summer) and 90% (spring) organic content during the study. Large seasonal changes in the rates and efficiencies of feeding and absorption were observed, but only 28% of the variance in daily ingestion rates of both species could be explained by a wide range of potential environmental influences (temperature, seston abundance and composition and vertical particle flux). Ingestion and absorption rates of scallops and mussels were highest during the spring, when diet quantity and quality were high, and during late-autumn, when quantity and quality were low. These data indicate that seston utilization and related growth was not caused solely by seasonal food and temperature fluctuations, but imply physiological regulation of feeding and digestion. Both species displayed a large capacity for controlling clearance and digestion rates. Clearance rates during October and November were at least twice as high as observed at other times of the year, and absorption efficiency gradually decreased at high diet quality and increased when quality

was low. Temporal variations in food utilization by both species may be explained by the combined constraints on maximizing net energy gain of relatively low food availability and the seasonally changing energy demands of reproduction. The accuracy of various bivalve clearance (filtration) rate models was assessed by comparing predicted responses with average *in situ* clearance rate estimates. Only those models based on natural seston rations provided adequate predictions of clearance behaviour. Clearance rate predictions based on algal cell rations overestimated *in situ* clearance at all times of the year and do not appear to apply to animals in nature.

5.2 INTRODUCTION

Two goals of physiological research on suspension feeding bivalve molluscs are to provide predictive relationships for growth under different environmental conditions and to quantify the role of bivalves in the particle flux, nutrient dynamics and phytoplankton production in coastal ecosystems. The development of bioenergetic simulation models for estimating the carrying capacity of coastal waters for bivalve culture represents an integration of these goals as this requires an understanding of both the physiological ecology of individuals and the consequences of their activities for their trophic resources (Grant 1996, Bayne 1998). Speculations on the capacity of dense bivalve communities to control phytoplankton and seston at the coastal ecosystem scale (reviews by Dame 1993, 1996) are based largely on a much simpler modelling approach that conforms to the theory advanced by Jϕrgensen (1990, 1996) that water processing by bivalve fliter-feeders is a highly automatized and unregulated process, and that maximal clearance rates measured *in vitro* using optimal concentrations of cultured microalgae apply to animals in nature. These assumptions are controversial considering the extensive literature supporting the view that food acquisition rates and efficiencies are physiologically regulated according to nutritional needs (reviews by Bayne and Newell 1983, Griffiths and Griffiths 1987, Hawkins and Bayne 1992, Bayne 1998) and observations that natural seston is generally cleared at much lower rates than pure algal cell suspensions (Doering and Oviatt 1986, Riemann et al. 1988, Cranford and Gordon 1992, Iglesias et al. 1992, Navarro et al. 1992, Prins et al. 1994, Cranford and Hargrave 1994, Hawkins et al. 1996). Jϕrgensen, however, in a recent review (1996) maintains that clearance values below maximal are attributed to negative effects of experimental conditions, including methodical problems and the use of improper food regimes to which the animals are not adapted (also see Riisgård and Larsen 1995, Clausen and Riisgård 1996).

Confidence in feeding-behaviour and growth models, whether developed for aquaculture management or for more fundamental purposes, requires resolution of this controversy and continued progress on other difficult issues. An important question is the dependence of bivalve feeding/digestion processes on the seasonally changing energy costs and nutrient demands of gametogenesis. While short-term deficiencies in energy intake may be met by catabolizing internal energy reserves (Hawkins et al. 1985), seasonal variations in nutritional requirements are more likely to cause shifts in food acquisition strategy. Kreeger (1993) measured the *in vivo* ingestion, digestion and assimilation of dietary protein in mussels *Mytilus trossulus* at four different times of year and concluded that variations in protein uptake were not simply responses to changing seston composition, but were more closely coupled to the high energy and biosynthesis requirements of reproductive activity. Seasonal variations in the utilization of protein and carbon by *M. edulis* also appear to be governed by changing anabolic demands (Kreeger et al. 1995). In contrast, Smaal et al. (1997) and Smaal and Vonck (1997) did not detect a relationship between clearance rate and reproductive condition in *M. edulis*.

Few studies have been conducted of the seasonal patterns of food utilization by bivalve suspension feeders, and none has been performed on animals held *in situ* under natural conditions of food supplies and horizontal and vertical particle flux. Previous studies have also been limited to monthly or seasonal sampling owing largely to logistical constraints imposed by traditional methodologies (Bayne and Widdows 1978, Widdows et al. 1979, MacDonald and Thompson 1986, Kreeger 1993, Prins *et al.* 1994, 1995, Kreeger et al. 1995, Smaal et al. 1997, and Smaal and Vonck 1997). The present study utilizes the *in situ* biodeposition approach of Cranford and Hargrave (1994) for autonomously and continuously monitoring feeding and digestion processes in bivalve filter feeders. The method provides clearance, ingestion, absorption and egestion rates and absorption efficiency estimates that are integrated over pre-defined sampling periods (minutes to days). Daily measurements of food utilization by *M. edulis* and sea scallop *Placopecten magellanicus* cohorts were obtained during the present study. In addition to permitting measurements on undisturbed animals held *in situ*, this approach is well suited to seasonal studies because the daily faeces collection periods tend to average out large short-term variations in feeding/digestion responses that may be attributed to endogenous rhythms, high-frequency changes in exogenous influences, and interindividual variability (Hawkins and Bayne 1992, Cranford and Hargrave 1994, Cranford et al. 1998).

The primary objective of the present study was to quantify feeding and digestion responses of suspension-feeding bivalves to the potential exogenous influences of temperature and seston quantity and quality and to the endogenous demands of reproduction. The responses of sea scallops and mussels were monitored simultaneously to provide insight into interspecific differences in seasonal feeding strategies. Further to this, I compared *in situ* clearance rate estimates for each species with potential clearance rates calculated using *in vivo* clearance rate models to explore the hypothesis of Jϕrgensen (1990, 1996) and others that bivalve filter feeders exploit the full capacity of the 'filter-pump' in nature.

5.3 MATERIALS AND METHODS

5.3.1 Experimental conditions

Time-series of scallop and mussel feeding and digestion responses were obtained over a total period of 139 days during the spring, summer and fall of 1995. Daily estimates of clearance, ingestion and absorption rate and absorption efficiency were determined according to the sequentially sampling biodeposition method described in Cranford and Hargrave (1994) and Cranford et al. (1998). A new type of sediment trap was designed and constructed specifically for this study (Fig. 5.1). Improvements over the trap described in Cranford and Hargrave (1994) include; an increase in the number of sample cups from 14 to 39, a weight reduction from 68 to 30 kg to allow deployment from small vessels, a height reduction from 1.5 to 1 m to bring the animals closer to the

Figure 5.1

Schematic illustration of the sediment trap used to collect sequential samples of faeces produced by a cohort of bivalves. The trap is 1.0 m high with an aperture area of 0.29 m^2 and a capacity to collect 39 faeces samples in 50 ml cups containing a dense preservative (0.1% wt/vol. HgCl in 35‰ NaCl). The animals under study are held in a 50 cm diameter cage that is 7 cm high and constructed of 2 cm mesh polyethylene. The funnel walls are inclined 28° from vertical.

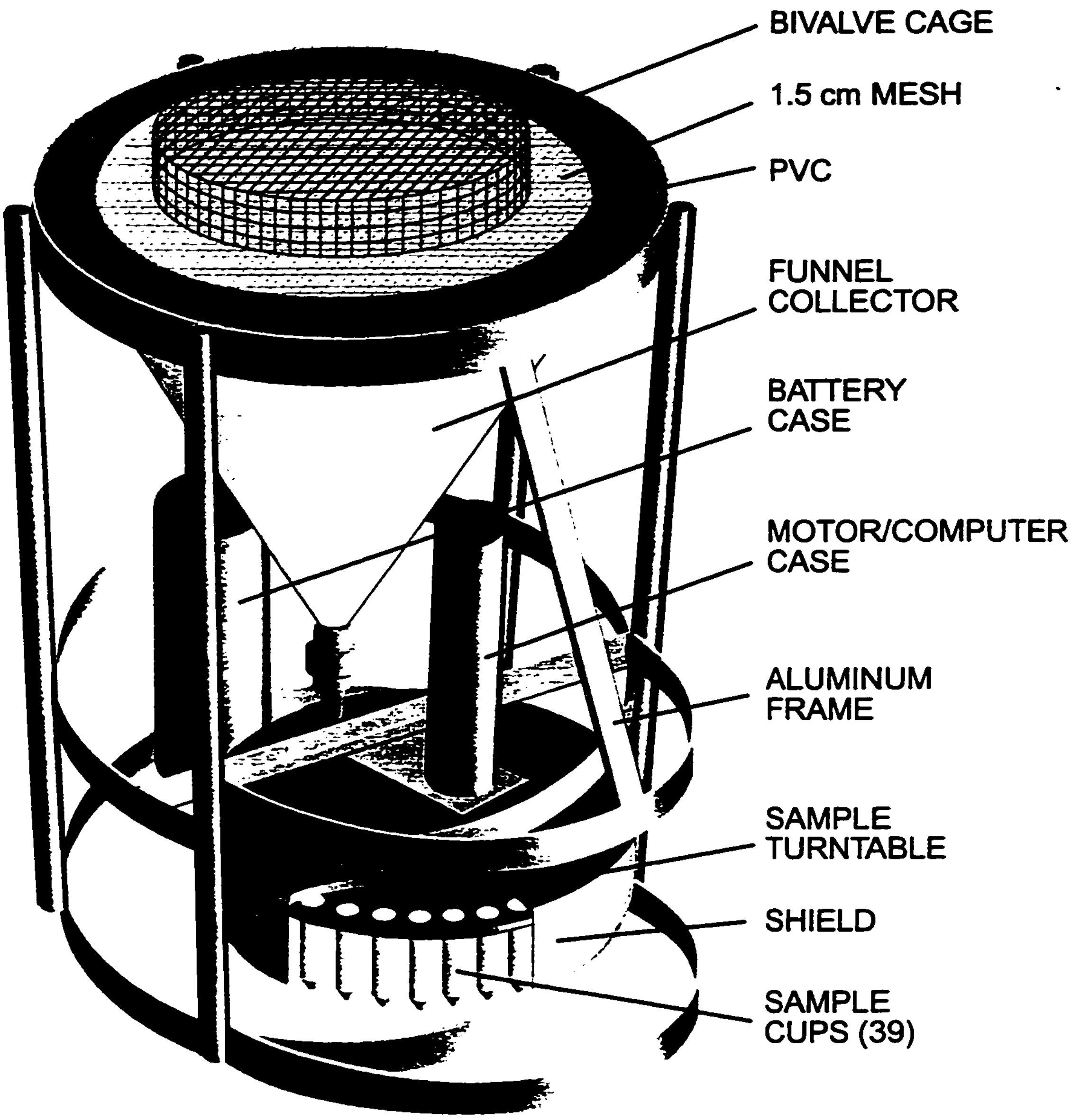
BIVALVE CAGE
1.5 cm MESH
PVC
FUNNEL COLLECTOR
BATTERY CASE
MOTOR/COMPUTER CASE
ALUMINUM FRAME
SAMPLE TURNTABLE
SHIELD
SAMPLE CUPS (39)

Figure 5.1

seabed, and an increase in mouth area from 0.11 to 0.29 m^2 to increase the number of individuals that can be accommodated on the trap. The animal cage was also modified (Fig. 5.1) to remove the need to tie the animals in place (see Fig. 2.1, Chapter 2). Three identical traps were constructed so that two could be used to monitor bivalve biodeposition (one for each species) while a third trap controls for natural particle sedimentation (no animals).

The three traps were deployed for 40-day periods on four separate occasions (Table 5.1). The first deployment was intended primarily to test the instruments, which were moored at 5 m depth in Bedford Basin adjacent to the Bedford Institute of Oceanography (44°41'N, 63°39'W: total depth of 44 m). Subsequent studies were conducted at Graves Shoal in Mahone Bay (44°33'N, 64°12'W: total depth of 13.7 m) where the traps were anchored to the seabed (animals at 12.7 m depth). All trap deployments were programmed for daily sampling after an initial one-day delayed start, which was provided to allow the animals an opportunity to recover from any handling stress.

5.3.2 Animals

Sea scallops *Placopecten magellanicus* and blue mussels *Mytilus edulis* for the Bedford Basin study were obtained from a commercial grower in Mahone Bay, Nova

Table 5.1. Timing of environmental sensor and sediment trap deployments at the two study sites in 1995 and details on the number, shell size and total dry weight of scallops (*Placopecten magellanicus*) and mussels (*Mytilus edulis*) held on each sediment trap. Numbers in parenthesis are ± 1 SD.

	Bedford Basin	Mahone Bay		
	BB	MB1	MB2	MB3
Duration:	Apr.21- May 30	June 14- July 21	Sept. 15 - Oct. 24	Oct. 27- Dec. 4
Start/end time:	1200 h	1200 h	1200 h	1200 h
Individuals on trap:				
scallop	7	7	11	11
mussel	25	26	23	23
Mean size (mm):				
scallop (height)	90.9 (1.9)	96.7 (3.9)	94.2 (4.3)	93.9 (6.0)
mussel (length)	76.9 (1.1)	76.9 (4.1)	78.5 (5.1)	82.1 (5.3)
Mean dry body weight (g):				
scallop start	6.1 (1.7)	8.8 (0.8)	6.3 (1.4)	-
scallop finish	7.6 (0.9)	9.3 (1.8)	-	8.4 (1.6)
mussel start	2.8 (0.5)	3.2 (0.5)	1.8 (0.6)	-
mussel finish	3.0 (0.5)	2.3 (0.4)	-	2.7 (0.4)

Scotia, and held in pearl nets at the study site for approximately one month prior to being transferred to the sediment trap cages. The Graves Shoal, Mahone Bay site is adjacent to a sea scallop culture site where both species are available for collection by divers from the seabed and are already adapted to local conditions. The animals were graded to a narrow size range and cleaned of epiphytes before being placed in the cage over the mouth of the sediment trap. At the start of each sampling period, between 7 and 11 scallops and 23 to 25 mussels were placed on each trap and a subsample of 12 scallops and 25 mussels was returned to the laboratory for biomass determinations. The dry tissue weight of individuals was determined after drying at 80°C until constant weight (±0.01g) was obtained. Scallop gonad was dissected and weighed separately from the remaining tissue. After the traps were recovered, the final dry-tissue weight of experimental animals was determined as above. Information on sampling dates and the size, weight, and number of animals used in each experiment are given Table 5.1. The same cohort of animals was used during the final two sampling periods (September to December).

5.3.3 Seston analysis

During each trap deployment, water temperature, salinity and current speed and direction were recorded with an Aanderra RCM8 current meter at 10 min. intervals at the same depth as the animals. Total suspended particulate matter (TPM, mg l^{-1}) and chlorophyll *a* (µg l^{-1}) concentrations were monitored hourly with an instrument package containing a SeaTech® fluorometer and transmissometer (10 cm path length) and data logger. During weekly visits to the site, stored data were downloaded, the battery was replaced and optical surfaces were cleaned. Each sensor's voltage output was calibrated with seston concentration data from weekly water samples. To obtain water samples at the depth of the experimental animals in Mahone Bay, two 1.7 l Niskin bottles were attached to a PVC frame containing a bottom triggering device that closed the bottles when they reached 1 m above the seabed. TPM, particulate organic matter (POM), inorganic matter (PIM), chlorophyll *a*, organic carbon (POC) and nitrogen (PN) concentrations were determined for seston filtered onto 1.2µm filters (Whatman GF/C) according to Cranford and Hargrave (1994). Single determinations were made for all seston variables except TPM, POM, and PIM, which were measured in triplicate. Similar analyses were performed on subsamples of seston particles deposited in sample cups under the control trap using methods described in Cranford and Hargrave (1994). In addition, the disaggregated grain size distribution of sedimented particles was obtained using a Coulter Multisizer fitted with a 140 µm aperture tube. Each control trap sample was disaggregated for two minutes prior to size analysis using an ultrasonic sapphire-tipped probe (Misonix®).

5.3.4 Physiological rates and efficiencies

Daily weight-specific egestion rate (mg dry weight · g dry tissue^{-1} · d^{-1}) for each species was determined by subtracting the total dry weight of particles deposited in sample cups under the control trap from the dry weight of particles collected in corresponding cups under the experimental traps. Daily cohort responses were divided by the dry tissue weight of animals on each trap, which was calculated for each day assuming linear growth between the initial and final biomass measurements. Total ingestion rate (I_T: mg dry weight · g dry tissue^{-1} · d^{-1}) was calculated according to Cranford and Hargrave (1994) as:

$$I_T = E_{ash}/F_{ash}, \tag{5.1}$$

where E_{ash} is the egestion rate of ash and F_{ash} is the proportion of ash in the food (PIM). POM ingestion rates were estimated as the product of I_T and the POM content of the seston. Given that gut passage times reported for *M. edulis* and *P. magellanicus* are shorter than the daily sampling periods (Hawkins et al. 1990, Cranford et al. 1998), no correction was made to I_T calculations for the time-lag between food ingestion and egestion (see Cranford et al. 1998). Clearance rate (C: l · g^{-1} · h^{-1}) was calculated by dividing I_T by average daily TPM, calculated from transmissometer data collected over each daily sampling period, and then scaling this daily rate to an average hourly value. The absorption efficiency of POM (AE_{POM}) was calculated from the proportions of absorbed (POM) and inert (PIM) tracers in seston and faeces samples according Cranford and Hargrave (1994). Absorption rates (mg POM · g^{-1} · d^{-1}) were estimated as the product of daily POM ingestion rate and AE_{POM}.

5.3.5 Potential clearance rates

Clearance rate (*C*) estimates of scallops and mussels held *in situ* during this study were compared with potential *C* values calculated for animals of similar size using available clearance (filtration) rate models. Potential *C* estimates were divided into two categories (Table 5.2). The first category includes models derived from observations of bivalves fed optimal concentrations of cultured microalgae in the laboratory. These 'optimal' condition models have frequently been applied in the calculation of population clearance rates (Cloern 1982, Officer et al. 1982, Cohen et al. 1984, Nichols 1985, Fréchette et al. 1989, Hily 1991). For *M. edulis*, allometric equation parameters reported in Table 5.2 are based on Riisgård and Mϕhlenberg (1979), which were confirmed by Riisgård (1991). As no direct observations are available for *P. magellanicus* fed optimal diets, potential *C* was calculated using a generic equation (Table 5.2) that represents the average response of five species of bivalve filter-feeders (Mϕhlenberg and Riisgård 1979). Note that these authors observed scallop (*Pecten furtivus* and *P. opercularis*) *C* to be about twice the rate predicted using this model. Jϕrgenson *et al.* (1990) and Riisgård (1991) report that bivalves fed optimal algal cell diets in the laboratory respond

Table 5.2. Average weight-specific clearance rate (C, l · g dry weight^{-1} · h^{-1}) of sea scallops *Placopecten magellanicus* (*P. m*) and mussels *Mytilus edulis* (*M. e*) calculated over the different sampling periods for animals of similar size as used in the present study (Table 1). C estimates from *in situ* measurements conducted during the present study are presented for comparison with various clearance rate model predictions. All equation predictions, which are in units of l · ind.$^{-1}$ · h^{-1}, were divided by the average tissue mass of individuals held *in situ* (Table 2.1). Daily model predictions for both species were averaged over the total 139 day sampling period. W is dry tissue weight (g), L is shell length (mm), and T is temperature (°C).

Category and Source	Species	Sampling Site and Period				Mean (n=139)
		BB April-May	MB1 June-July	MB2 Aug.-Oct.	MB3 Oct.-Dec.	
1. ***In situ*:**						
This study	*P. m*	0.276	0.063	0.496	1.047	0.451
	M. e	0.291	0.446	0.124	2.111	0.750
2. 'Optimal' Condition:						
Möhlenberg and Riisgård (1979); $6.96W^{0.67}$, $Q_{10} = 2$						
	P. m	2.411	2.292	4.418	3.187	2.973
	M. e	3.152	3.463	6.474	4.662	4.276
Riisgård and Möhlenberg (1979)[*]; $0.85(W \times 10^{3})^{0.72} \times 0.06$, $Q_{10} = 2$						
	M. e	3.521	3.856	7.124	5.167	4.741
Powell et al. (1992); $-1.199+0.121(L)+8.165\times10^{-5}(L^{2})$						
	P. m	1.616	1.184	1.599	1.391	1.439
	M. e	2.980	3.179	4.105	3.757	3.451
3. 'Natural' Condition:						
MacDonald and Thompson (1986); $0.94W^{0.67}$						
	P. m	0.507	0.446	0.498	0.476	0.481
Smaal et al. (1997); $1.52W^{0.51}$						
	M. e	0.903	0.931	1.043	0.974	0.956
Doering and Oviatt (1986)[*]; $\{[((L/10)^{0.96})(T^{0.95})]/2.95\} \times 0.06$						
	P. m	0.102	0.098	0.338	0.202	0.173
	M. e	0.197	0.271	0.904	0.564	0.449
Powell et al. (1992); $-0.074+0.013(L)+1.796\times10^{-4}(L^{2})$						
	P. m	0.403	0.303	0.405	0.351	0.363
	M. e	0.696	0.742	0.957	0.899	0.813

[*] The 0.06 factor converts model output in units of ml ind.$^{-1}$ min^{-1} to l ind.$^{-1}$ h^{-1}.

to temperature changes and a Q_{10} of 2 was employed (Jϕrgenson *et al.*, 1990) to correct potential *C* measured at 10-15 °C to ambient temperatures observed in the present study.

The second category of potential *C* estimates, referred to here as 'natural' condition predictions, are based on the average allometric equations of MacDonald and Thompson (1986) for *P. magellanicus* and Smaal et al. (1997) for *M. edulis* (Table 5.2). Model parameters reported by Smaal et al. (1997) are similar to the average values suggested for suspension feeding bivalves by Bayne and Newell (1983). In these studies, bivalves were presented natural seston diets at temperatures between 0 and 20 °C. No temperature corrections were made to model predictions as both species have been observed to be independent of temperature when acclimated to natural diets (Bruce MacDonald, personal communication, Widdows and Bayne 1971, Bayne and Newell, 1983, Smaal et. al. 1997). The *C* equation of Doering and Oviatt (1986) was employed as a generic bivalve model for predicting *C* responses to natural diets. This equation accounts for both the effects of body size and temperature on clearance rate. While this model was developed specifically for the hard clam *Mercenaria mercenaria*, it has been used to model growth in other bivalve species (Powell et al. 1992). These authors reviewed the literature that relate bivalve size to *C* and fitted two curves to data from a wide range of bivalve filter-feeders. These generic equations are given in Table 5.2, with the 'high gear' and 'low gear' models presented in the 'optimal' and 'natural' condition categories, respectively.

5.3.6 Statistical analysis

All statistical tests were performed at $\alpha = 0.05$ with SYSTAT Version 6.1 (SPSS, Inc., Chicago, Illinois). Prior to performing any analysis, each variable was screened for normality and homoscadasticity by examining normal probability and residual plots, respectively (Wilkinson et al., 1996). The linearity assumption of regression analysis was tested by plotting and visually examining relationships between variables. Appropriate data transformations were employed when an assumption was violated. As the physiological rates and efficiencies are based on repeated measures of the same animals, the assumption of independent data was tested by examining regression residuals for significant autocorrelations (Wilkinson et al., 1996).

Environmental variables significantly related to scallop and mussel ingestion rates were identified from a Pearson correlation matrix using Bonferroni-adjusted probabilities. It was necessary to normalise ingestion rates of both species with a log transformation. Those variables found to be significantly related to ingestion rate and that were not strongly collinear ($r^2 > 0.25$) were used in stepwise multiple regressions. Separate regression models were calculated using environmental data averaged over the daily trap sampling intervals from *in situ* instruments (fluorometer, transmissometer and control sediment trap) and data collected at approximately weekly intervals using Niskin bottles. Daily ingestion rate data were used in both models, but were selected to correspond with weekly water sampling for the latter analysis.

5.4 RESULTS

5.4.1 Environmental conditions

The experimental animals held in Bedford Basin and Mahone Bay were exposed to sea-water temperatures ranging from 2 to 16°C. Owing to failure of the thermistor during the summer Mahone Bay study (MB1), temperature data from 10 m depth in Mahone Bay were obtained from a site near Indian Point, approximately 10 km SW of Graves Shoal. A comparison of simultaneous data collected at these two Mahone Bay sites during the MB2 and MB3 sampling periods showed a similar time-series of temperature changes (Fig. 5.2). Salinity at 5 m depth in Bedford Basin was between 28.0 and 30.5 psu and current speeds averaged 3.8 cm sec^{-1} (SD = 4.1 cm sec^{-1}). Salinity at the Graves Shoal, Mahone Bay site was higher (30.5 ± 0.13 psu) than at the Bedford Basin site and current speeds were lower (2.4 ± 0.9 cm sec^{-1}).

Hourly *in situ* fluorometer and transmissometer data from both sites were converted to chlorophyll *a* and TPM concentrations, respectively, using regression

Figure 5.2

Time-series of environmental data from *in situ* instruments in Bedford Basin (BB; 5 m depth) and Graves Shoal, Mahone Bay (MB; 12.7 m depth). Horizontal lines at the top of the figure identify the sites and timing of the four instrument deployment periods listed in Table 5.1. Seawater temperatures shown are 30 min running means of readings at 10 min intervals. Temperature data for the MB1 sampling period were not collected at Graves Shoal, but were from a site in Mahone Bay (10 m depth) that displayed similar temperature patterns (data collected at both sites during the fall are plotted for comparison). Total particulate matter (TPM) and chlorophyll *a* concentrations were measured at 1 h intervals with moored instruments. Results from the analysis of water samples (circles) were used for instrument calibration. Note the different vertical scales used for displaying TPM and chlorophyll data from Bedford Basin (left scale) and Mahone Bay (right).

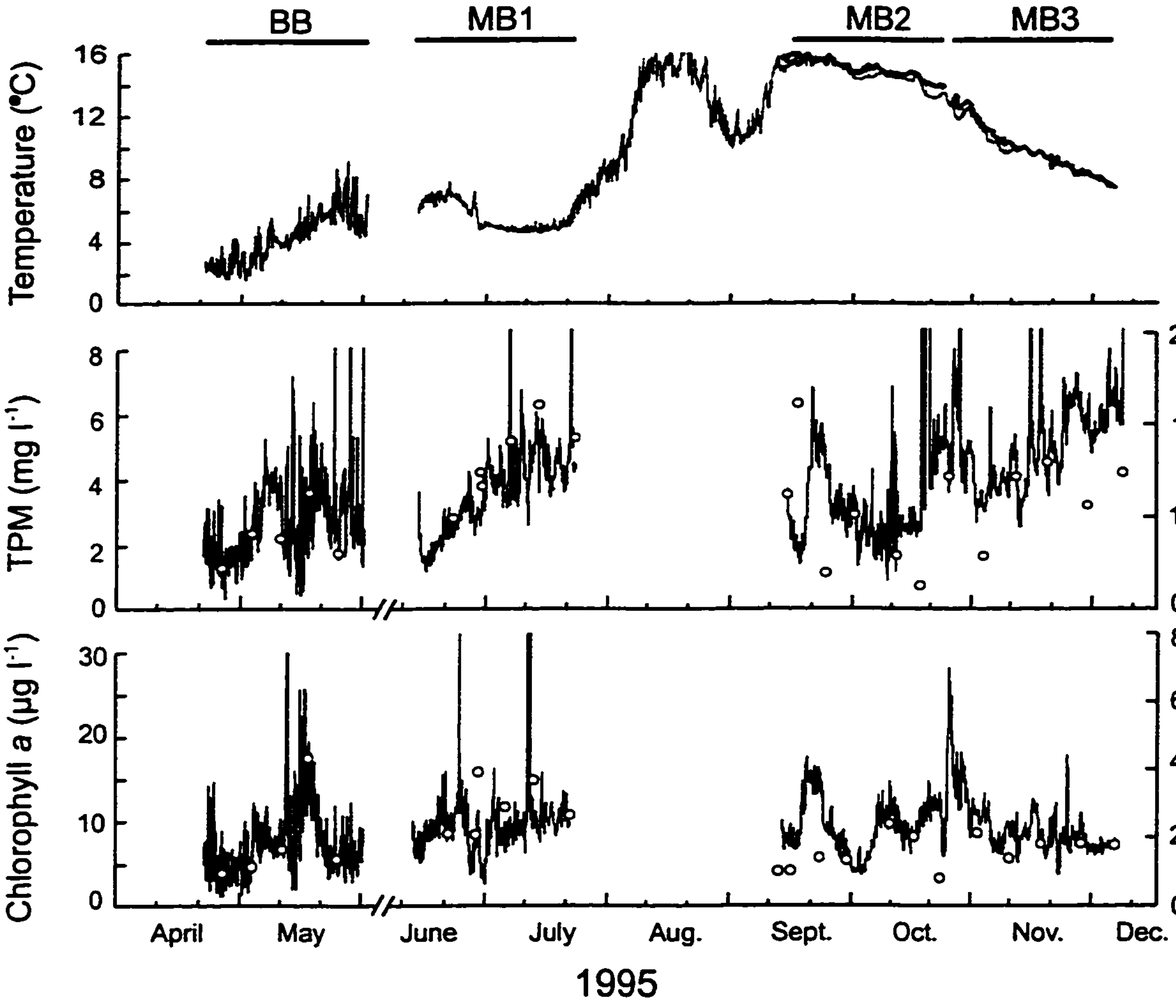
BB
MB1
MB2
MB3
Temperature (°C)
16
12
8
4
0
TPM (mg l-1)
8
6
4
2
0
2.0
1.5
1.0
0.5
Chlorophyll a (µg l-1)
30
20
10
0
8
6
4
2
0
April
May
June
July
Aug.
Sept.
Oct.
Nov.
Dec.
1995

Figure 5.2

equations describing the relationship between instrument voltage output and data on chlorophyll *a* ($r^2 = 0.770$, $p < 0.001$) and TPM ($r^2 = 0.745$, $p < 0.001$) concentrations in water samples collected weekly with Niskin bottles. A phytoplankton bloom was observed in Bedford Basin between May 10 and 20 when chlorophyll *a* levels reached 30 $\mu g\ l^{-1}$ (Fig. 5.2). Chlorophyll concentrations at the Mahone Bay site were lower than in Bedford Basin (note the different vertical scales used in Figure 5.2 to display Bedford Basin and Mahone Bay data) and the only sign of a fall bloom was a short-term peak in chlorophyll of ~7 $\mu g\ l^{-1}$ in late October (Fig. 5.2). Seston concentration (TPM) during the study averaged 2.6 mg l^{-1} (SD = 0.9) for Bedford Basin and 1.3 mg l^{-1} (SD = 1.4) for Mahone Bay. TPM and chlorophyll *a* concentrations were not correlated ($r^2 = 0.04$). POC and PN concentrations were highest during the spring bloom in Bedford Basin but were relatively constant during the Mahone Bay phase of the study (Fig. 5.3).

Several estimates of seston quality were calculated to assess the nutritive value of the seston to experimental animals. Large variations in the POM, POC, and PN content of seston were observed both within and between the two sites (Fig. 5.3). Bedford Basin seston was generally high in organic content during the spring with the POC and PN content increasing after the spring bloom to 62 and 11%, respectively. The C:N and C:chlorophyll *a* (C:Chl) ratios of Bedford Basin seston were less variable and averaged 6.1 (SD = 0.3), and 129 (39), respectively. The POM/POC ratio of seston during the study averaged 0.55 (SD = 0.17). The POM content of Mahone Bay seston was relatively low throughout the summer with quality gradually declining from 57% in June to 33% in

Figure 5.3

The composition of seston collected at approximately weekly intervals from 5 m depth in Bedford Basin (BB) and 12.7 m depth in Mahone Bay (MB). Horizontal lines at the top of the figure designate the periods sampled during each instrument deployment. POM, particulate organic matter (mean ± SD); POC, particulate organic carbon; PN, particulate nitrogen; C:CHL, ratio of carbon to chlorophyll *a*; and C:N, ratio of POC to chlorophyll *a*. Percent of total seston was calculated from total particulate matter (TPM) data shown in Fig. 5.2.

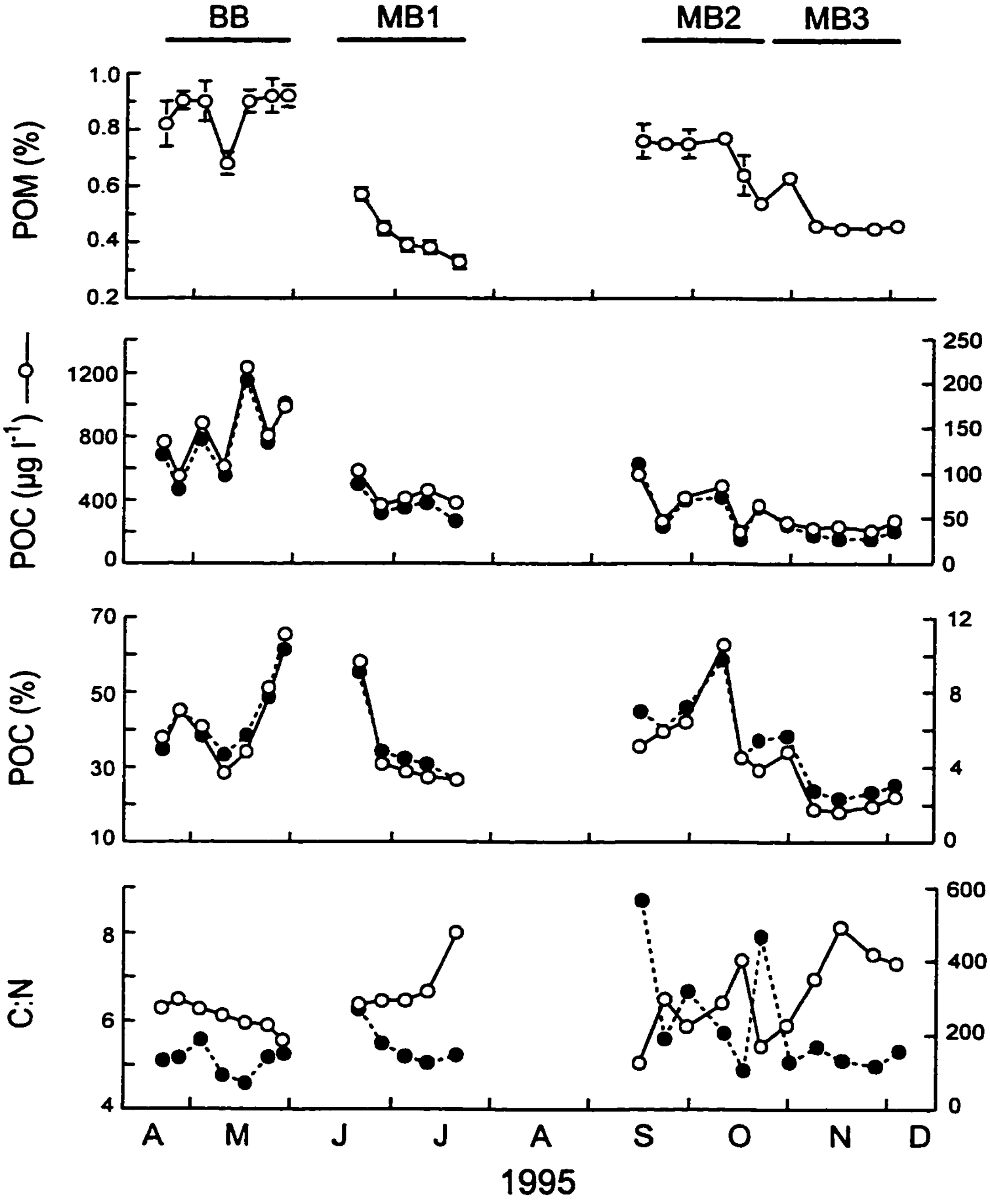
BB
MB1
MB2
MB3
POM (%)
1.0
0.8
0.6
0.4
0.2
POC (µg l^{-1})
1200
800
400
0
PN (µg l^{-1})
250
200
150
100
50
0
POC (%)
70
50
30
10
PN (%)
12
8
4
0
C:N
8
6
4
C:CHL
600
400
200
0
A
M
J
J
A
S
O
N
D
1995

Figure 5.3

July. Similar declines in POC and PN content were observed during this period. The POM, POC and PN content of seston was relatively high in September and October, but all declined to low values in November. C:N ratios for Mahone Bay seston were between 5 and 8 and C:Chl values averaged 226 (SD = 142).

Daily vertical particle flux and settled particle composition data, shown in Figure 4, were obtained from analysis of particulate matter deposited in the control sediment trap (no animals). Total periods sampled during the MB2 and MB3 deployments were reduced when the control trap stopped operating after 29 and 34 days, respectively. Total vertical particle flux was highly variable at the study sites, with large short-term fluctuations occurring during all study periods except September and October (MB2), when particle flux was consistently low. Two extended periods of high particle flux were observed in Bedford Basin during April and May and both occurred during periods of relatively low TPM concentration (Figs. 5.2 and 5.3). Hourly TPM was averaged over the same daily intervals as sampled by the traps and a comparison with daily particle flux found a significant inverse relationship ($r^2 = 0.23$, $p = 0.002$). An inverse relationship was also observed between the POM content of settled particles and particle flux ($r^2 = 0.538$, $p < 0.001$). Neither relationship was evident in Mahone Bay data, although the highest quality (POM content) particles settled out during September and October when particle flux was low.

Figure 5.4

Daily sedimentation rates of particulate matter (DW, dry weight) and the organic (POM) and chlorophyll *a* (CHL) content of settled material collected at 5 m depth in Bedford Basin (BB) and at 12.7 m depth in Mahone Bay (MB) by the sediment traps described in the text. Data are plotted at the midpoint of each daily sampling interval.

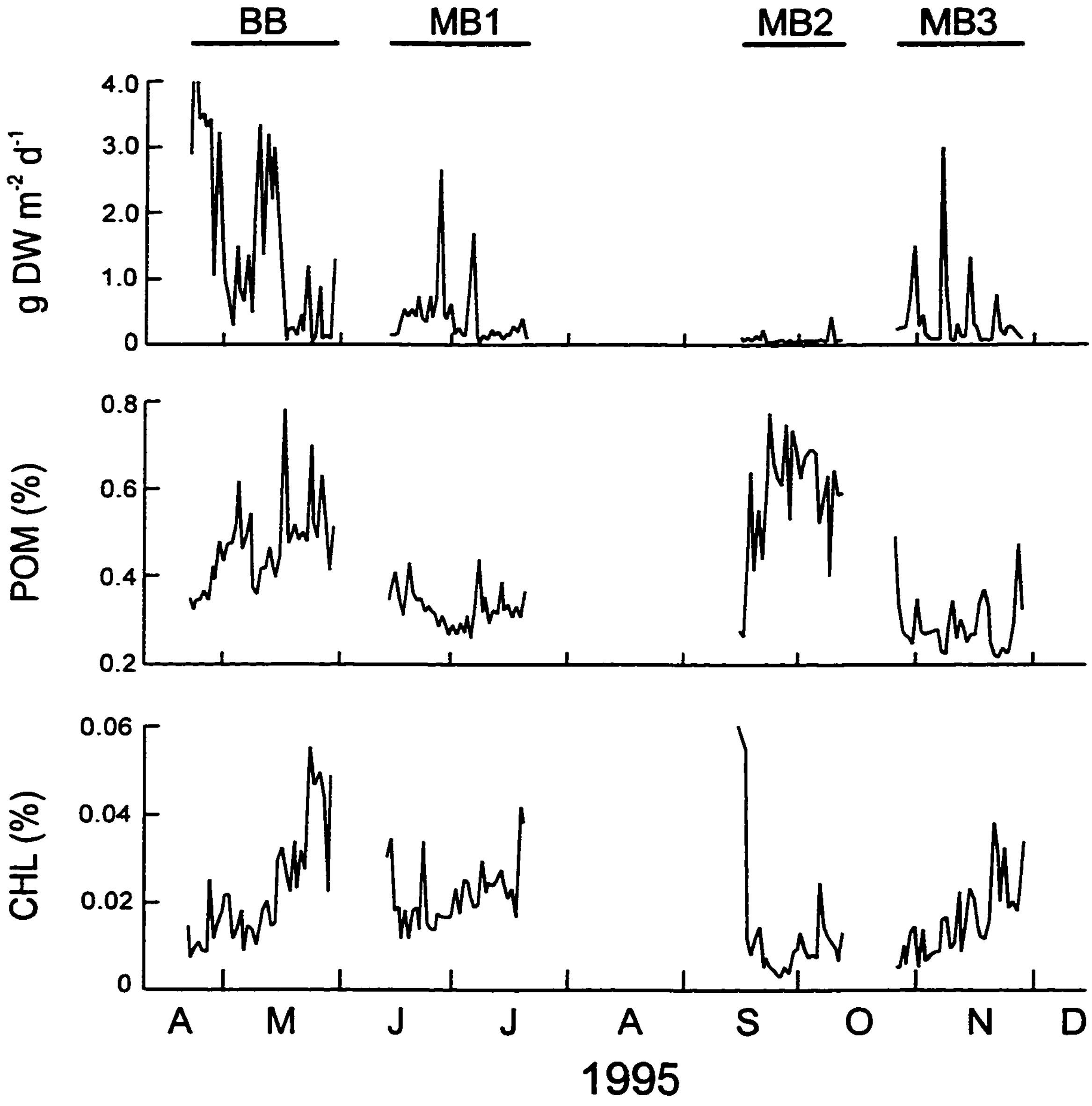
BB
MB1
MB2
MB3
g DW m^{-2} d^{-1}
4.0
3.0
2.0
1.0
0
POM (%)
0.8
0.6
0.4
0.2
CHL (%)
0.06
0.04
0.02
0
A
M
J
J
A
S
O
N
D
1995

Figure 5.4

The chlorophyll *a* content of settled particles increased during the spring bloom and continued to increase after the bloom subsided (Fig. 5.4). Chlorophyll content was relatively low in Mahone Bay during the summer and fall, but increased during November and early December. The highest chlorophyll content was observed in Mahone Bay at the beginning of the September sampling period.

The disaggregated grain size distributions of settled material collected daily in the control sediment trap are summarized in Figure 5.5. Settled particles collected in Bedford Basin in April contained a relatively high proportion of fine particles (<10 µm diameter) compared with all other periods sampled both in Bedford Basin and Mahone Bay. The May phytoplankton bloom in Bedford Basin coincided with a high proportion of particle concentrations in the 9-11 µm size-range. Settled particle size-distributions from Mahone Bay contained a high proportion of 7 and 40 µm particles in June, but the former peak was not evident in July samples. Few particles larger than 15 µm were captured during the fall although a relatively high proportion of particles were in the 8-12 µm range between September and December (Fig. 5.5).

5.4.2 Bivalve growth and physiological responses

Sea scallop biomass increased during all sampling periods (Table 5.1) with gonad development accounting for the majority of total tissue growth (73%) during the spring

Figure 5.5

Grain size distributions obtained by Coulter Multisizer analysis of disaggregated sediment collected by the control (no animals) sediment trap. Particle concentrations, relative to total concentration, are an average (± 1 SE) of all daily samples (sample size given) collected within the indicated monthly period. April and May data are from Bedford Basin and all other data are from Mahone Bay.

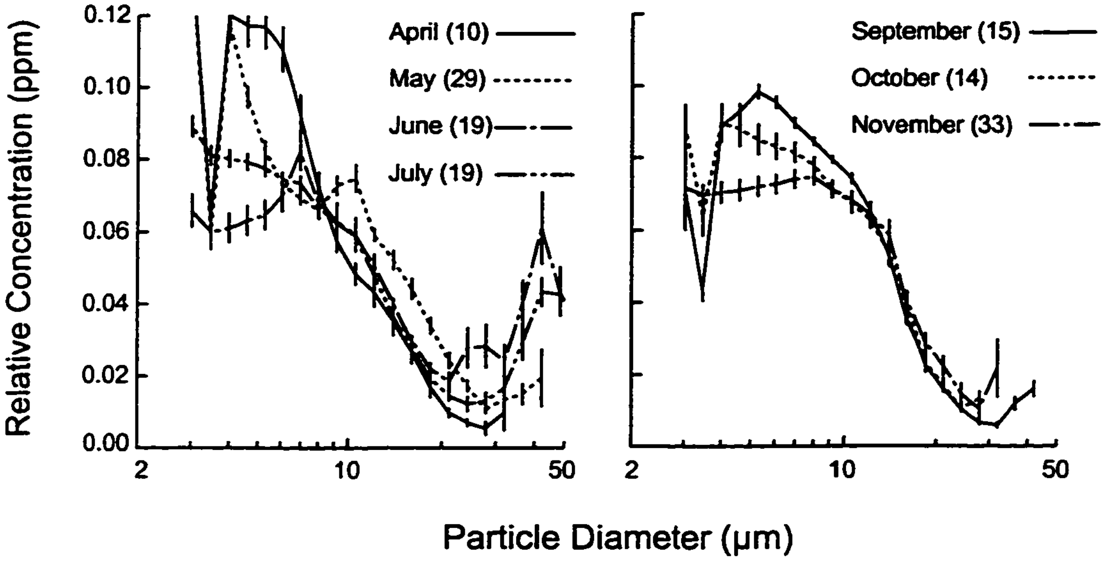
Relative Concentration (ppm)
0.12
0.10
0.08
0.06
0.04
0.02
0.00
2
10
50
2
10
50
Particle Diameter (µm)
April (10)
May (29)
June (19)
July (19)
September (15)
October (14)
November (33)

Figure 5.5

and summer. A 67% decrease in gonad mass was observed between September 15 and December 4. Mussel biomass increased during spring and fall sampling periods, but decreased during June and July (Table 5.1).

Averaged over each instrument deployment period (Table 5.1), sediment traps containing bivalves collected between 1.6 and 22.7 times more particulate material than was deposited into the control trap, with the lowest difference observed in Bedford Basin. The control trap stopped sampling after 29 days during MB2 and after 34 days during MB3 and bivalve physiological responses were calculated only for days when control trap data were available to correct for sedimentation of non-faecal particles.

Daily weight-specific sea scallop and mussel egestion rates were highly variable over both daily and seasonal time-scales and reached peak values during November (Figs. 5.6 and 5.7). Both species egested similar amounts in Bedford Basin during the spring, however, interspecific differences were observed during all sampling periods in Mahone Bay, with scallop egestion being relatively high during October and mussel egestion being relatively high during other periods. The organic content of faeces from both species was highly variable through the year and ranged between 20 to 70% of total dry weight (Figs. 5.6 and 5.7). Mussels and scallops generally produced faeces of similar organic content, except during MB2 when the organic content of mussel faeces was relatively high.

Figure 5.6

Daily weight-standardised egestion (DW, dry weight), ingestion and absorption (POM, particulate organic matter) rates and absorption efficiency (AE) of sea scallops *Placopecten magellanicus* held at 5 m depth in Bedford Basin (BB) and at 12.7 m depth in Mahone Bay (MB). The proportion of organic matter in daily faeces samples is shown as the open circles in the top graph. The possible range of error in calculated feeding/digestion responses is identified as the shaded region between maximum and minimum estimates (see text for a description of calculations). Separate estimates are provided for each day that water samples were collected (closed circles). All data are plotted at the midpoint of daily sampling intervals.

Placopecten magellanicus

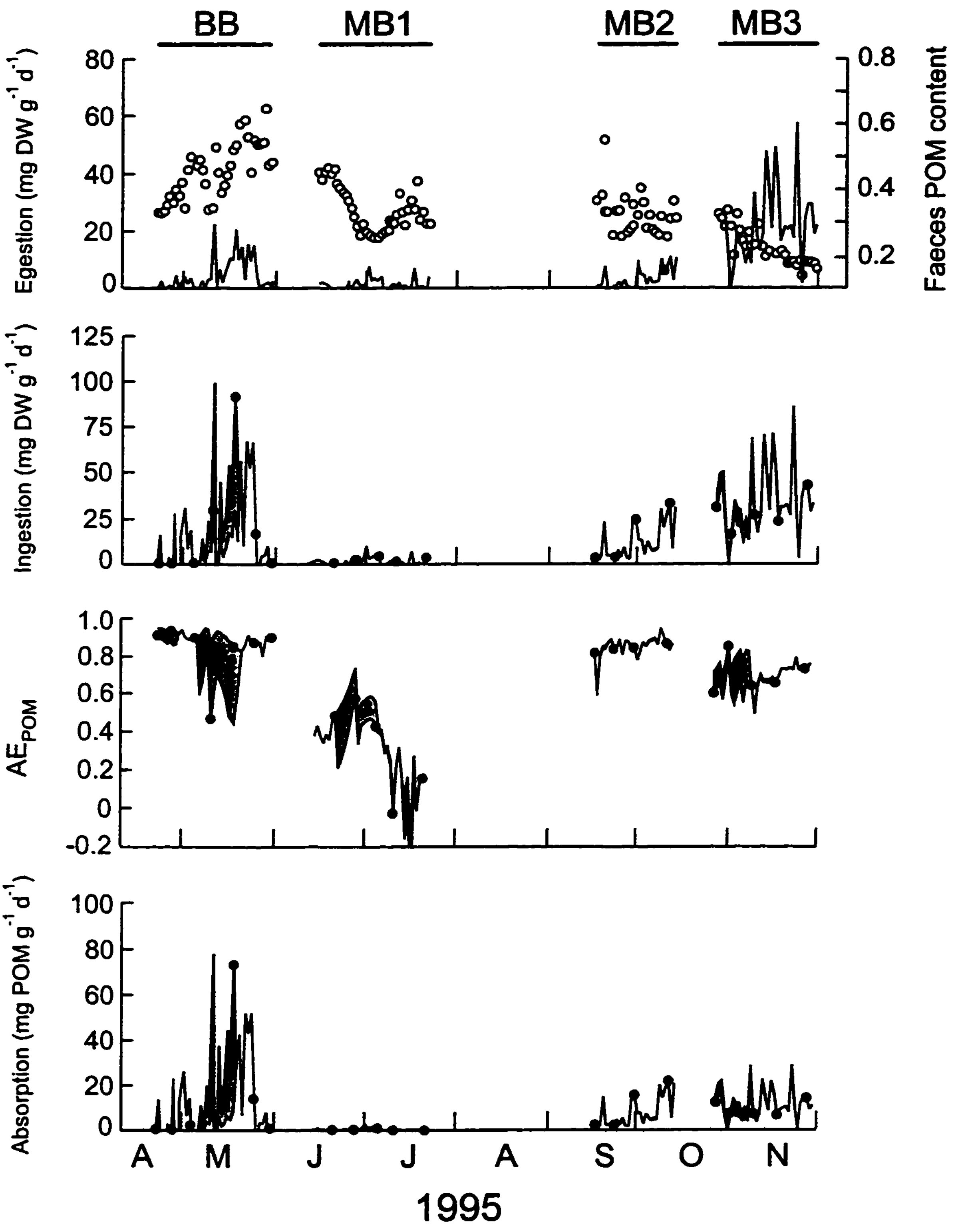

Figure 5.6

Figure 5.7

As in Figure 5, except that data are for blue mussels *Mytilus edulis*.

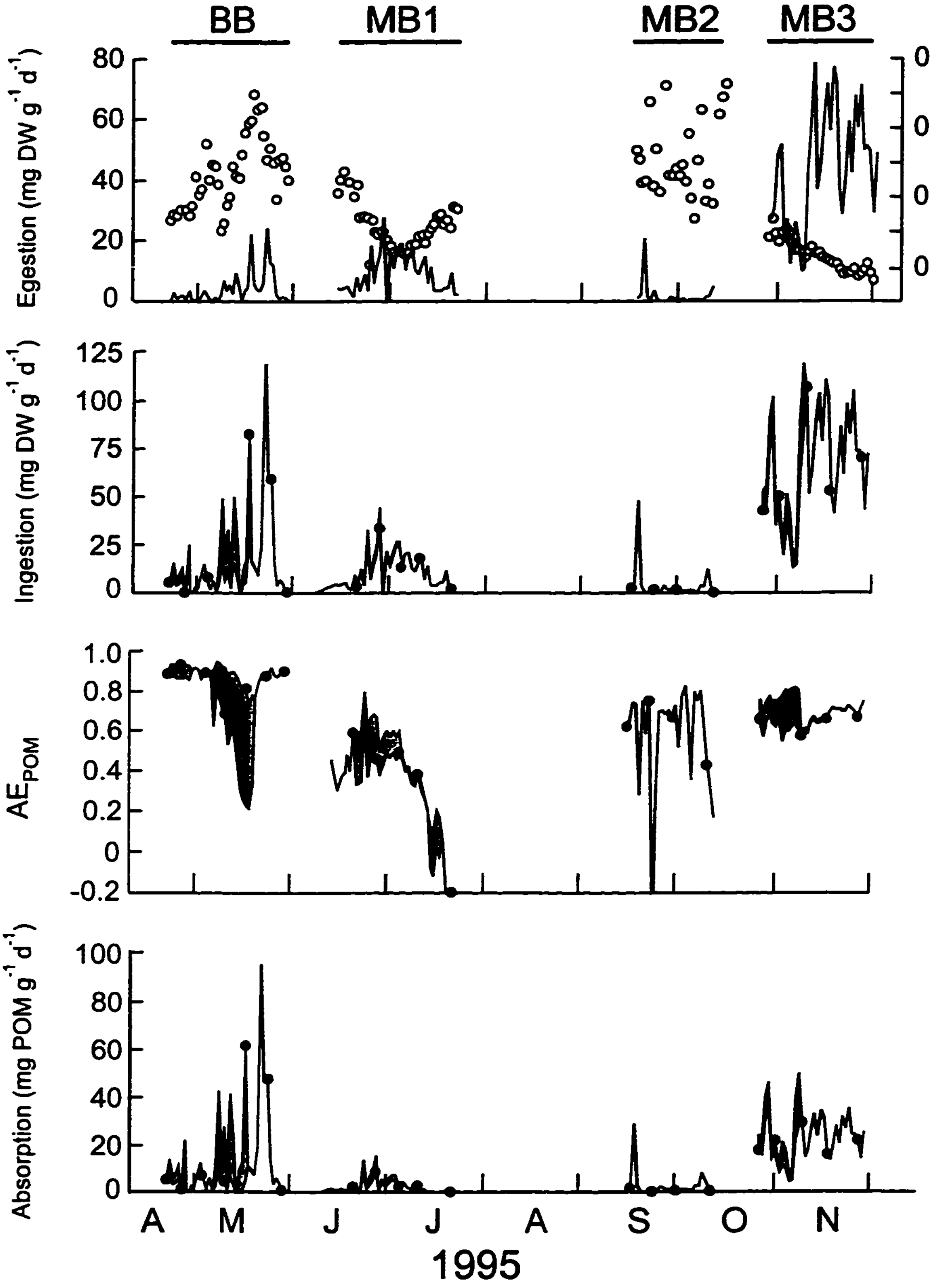
BB
MB1
MB2
MB3
Egestion (mg DW g⁻¹ d⁻¹)
80
60
40
20
0
Faeces POM content
0.8
0.6
0.4
0.2
Ingestion (mg DW g⁻¹ d⁻¹)
125
100
75
50
25
0
AE_POM
1.0
0.8
0.6
0.4
0.2
0
-0.2
Absorption (mg POM g⁻¹ d⁻¹)
100
80
60
40
20
0
A
M
J
J
A
S
O
N
1995

Figure 5.7

Three separate estimates of the total weight of seston ingested daily by scallops and mussels were calculated. First, weight-specific I_T was calculated only for those days when data are available for seston ash (PIM) content. To account for possible errors in extrapolating weekly seston PIM measurements to daily faeces collections, maximum and minimum daily I_T estimates were calculated based on a two week running average of maximum and minimum observations of seston PIM content. Difference in daily maximum and minimum I_T estimates were generally low (Fig. 5.6 and 5.7) owing to the low short-term variability in seston organic content at both sites (Fig. 5.3). Mussel and scallop I_T estimates generally followed similar temporal patterns as with egestion rate (Figs. 5.6 and 5.7) except that the low seston ash content in Bedford Basin during spring resulted in high I_T estimates.

The net absorption efficiency of POM (AE_{POM}) was highest during the spring and lowest during the summer (Figs. 5.6 and 5.7), generally reflecting differences in seston POM content (Fig. 5.3). However, fluctuations in faeces POM content also had a large influence such that AE_{POM} for both species was higher in November than in June during periods when the seston POM content was similar (Fig. 5.8). The relatively low AE of the mussels during MB2, compared to the scallops, also resulted from differences in faeces POM content (Figs. 5.6 and 5.7). Functional relationships between each species net AE and seston quality were described by the exponential equations:

Figure 5.8

Net absorption efficiency of particulate organic matter (AE_{POM}) by *Mytilus edulis* (open symbols, broken line) and *Placopecten magellanicus* (closed symbols, solid line) as a function of the POM content of seston during the four sampling periods defined in Table 5.1. The lines were fitted by least squares and the equations (Eqns. 5.2 and 5.3) and fit statistics are given in the text.

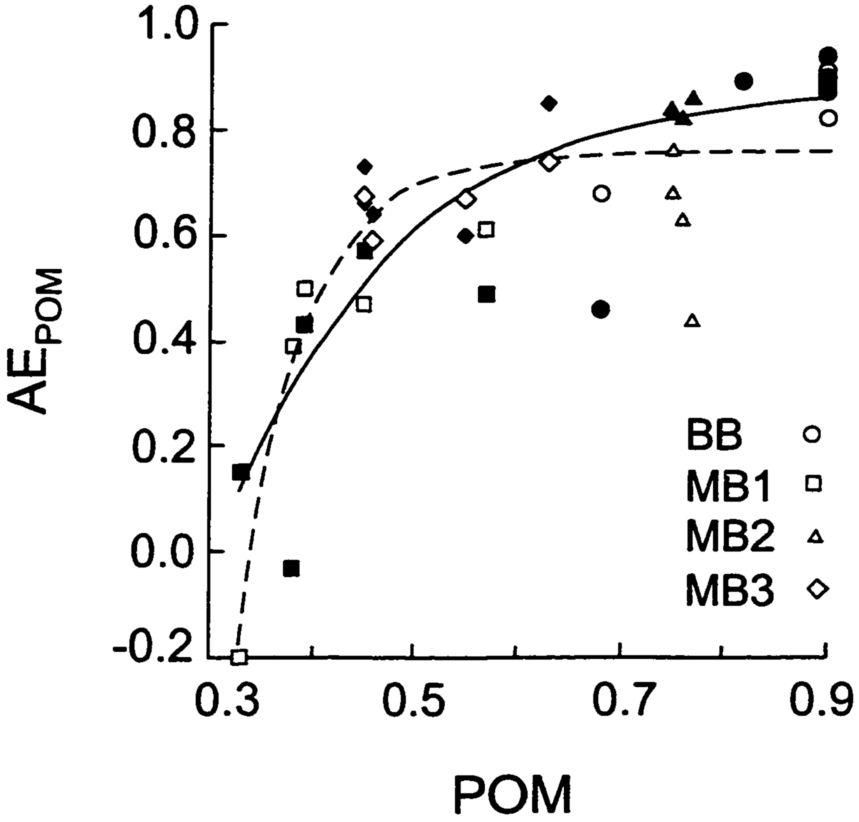

Figure 5.8

$$\text{Scallop } AE_{\mathrm{POM}} = 0.886\ (\pm 0.163) \times (1 - e^{-6.052\ (\pm 5.213)\ [\mathrm{POM}\ -\ 0.307\ (\pm 0.069)]}) \qquad (5.2)$$

$$\text{Mussel } AE_{\mathrm{POM}} = 0.759\ (\pm 0.077) \times (1 - e^{-15.911\ (\pm 8.205)\ [\mathrm{POM}\ -\ 0.342\ (\pm 0.016)]}) \qquad (5.3)$$

where $r^2 = 0.710$ and 0.758, respectively, residual df = 16, $p < 0.05$ and bracketed values indicate 95% confidence limits for each parameter. Despite the significant relations illustrated in Figure 5.8, which show that AE_{POM} increased with increasing seston POM content, the large standard error of estimate values (0.15 and 0.13, respectively) indicate that model predictions have low precision. As a result, no significant interspecific differences in equation parameters were detected (95% confidence limits overlapped).

The relatively high I_{T} of mussels during the summer (MB1), compared to scallops, occurred during a period of low AE_{POM}, resulting in a large reduction in absorption rates. A high proportion of the material ingested by both species during November was also inorganic (Fig. 5.3), however, the very high ingestion rates resulted in elevated absorption rates during this period. Approximately 36% of the POM absorbed by both species during the 139 day sampling period occurred during May and much of this was absorbed in several brief periods during and after the phytoplankton bloom. The second most important feeding period was November, which accounted for approximately 40% and 53% of total scallop and mussel absorption, respectively.

5.4.3 Empirical models of ingestion

Daily weight-specific ingestion rates (ln-transformed I_T) of sea scallop and mussel cohorts were not significantly related to seston quantity variables (daily averaged TPM and chlorophyll *a* concentrations, Pearson's $r < 0.20$, Bonferroni-adjusted $p > 0.9$) and only sea scallop I_T was significantly, albeit poorly, correlated with water temperature ($r = 0.399$, $p < 0.001$). For both species, the best predictors of I_T were variables associated with settled material collected by the control sediment trap (Figs. 4 and 5). Mussel I_T showed a significant negative relationship with the organic content of settled material ($r = -0.528$, $p < 0.001$). Scallop ingestion was related to the concentration of particles between 6 and 14 µm diameter, expressed as a proportion of total settled particle concentrations determined by Coulter analysis ($r = 0.442$, $p < 0.001$), and inversely related to ln-transformed vertical particle flux ($r = -0.306$, $p = 0.017$). However, the latter was strongly collinear with water temperature ($r = -0.621$, $p < 0.001$) and was excluded from regression models. The 6 to 14 µm particle size range was selected for this analysis as it included particles prominent during the spring phytoplankton bloom, and included concentration maxima observed in size-distributions during June and November (Fig. 5.5).

Multiple stepwise regression analysis of the above selected variables identified significant relations between daily averaged environmental variables and ingestion rates that were best described by the following linear equations:

Scallop, $\ln I_T = 0.042\ (\mathrm{SIZE}) + 0.065\ (\mathrm{TEMP}) - 1.882$ (5.4)

Mussel, $\ln I_T = -3.028\ (\mathrm{SEDPOM}) + 2.186$ (5.5)

where $r^2 = 0.279$ and 0.281, respectively, residual df = 132, $p < 0.001$ and TEMP is water temperature, SIZE is the proportion of total settled particle concentrations between 6 and 14 µm diameter and SEDPOM is the organic content (%) of settled particles. The assumption of independence of I_T estimates was not violated as autocorrelations of regression residuals from both analysis were low ($r^2 < 0.12$) over all time lags. Despite extensive sampling of environmental variables during this study, the best empirical models explained only 28% of the variance in sea scallop and mussel ingestion rates.

The Pearson correlation matrix of environmental variables sampled over approximately weekly intervals by Niskin bottles (n = 20, Figs. 5.1 and 5.2) also showed seston quantity variables (TPM and chlorophyll *a*) to be poor predictors of I_T for both species ($r^2 < 0.1$, $p = 1.000$). Seston quality variables (POM, POC and PN content of TPM, ratios of C:N and C:CHL, and SIZE) tended to be more closely related to ingestion rate, however, none of the variables passed the criteria (Bonferroni-adjusted $\alpha < 0.05$) for regression modeling.

5.4.4 In situ and potential clearance rate

Weight-specific clearance rate (*C*) estimates of sea scallops and mussels calculated using *in situ* measurements obtained during this study are presented in Table 5.2. Although ingestion rates of both species were relatively high during the spring in Bedford Basin (Figs. 5.6 and 5.7), this resulted primarily from elevated TPM concentrations as the *C* of both species was relatively low at this time of year. The highest *C* values for both species were observed during November, and the mussels cleared approximately twice the volume of water (per unit mass) as the scallops at this time (Table 5.2). The lowest *C* values were observed during June and July for scallops, and during September and October for mussels.

Average *C* predictions obtained using the 'optimal' *C* models overestimated *in situ C* by a factor of between 3.2 and 6.6 (Table 5.2). Even during November, when *in situ C* was greatest, potential *C* values were on average double the *in situ* estimate. The generic 'high gear' model of Powell et al. (1992), which is a function of shell length, provided similar *C* over-predictions as the biomass-based equations of Mϕhlenberg and Riisgård (1979) and Riisgård and Mϕhlenberg (1979).

The 'natural' condition models were generally much more accurate at predicting the average *in situ C* of both species (Table 5.2), with the exception of the Doering and Oviatt (1986) relation, which underestimated *in situ C* by a factor of 1.7 for mussels and 2.6 for scallops. Potential *C* values provided by the generic 'low gear' model of Powell et al. (1992) were similar to average values provided by species-specific models of MacDonald and Thompson (1986) and Smaal et al. (1997). It is important to note, however, that all these comparisons were based on the 139 day average *C* response. Daily and seasonal *in situ C* estimates often deviated markedly from all predicted values (Table 5.2).

5.5 DISCUSSION

5.5.1 Exogenous and endogenous forcing of food utilization

According to the view of Jørgensen (1990, 1996), food utilization by bivalve filter-feeders is a highly automated and unregulated process, and any temporal variations in ingestion rate must be directly attributed to food supply variations (Hawkins and Bayne 1992). Empirical models of food ingestion by *P. magellanicus* and *M. edulis* were constructed from data collected during this study to determine relationships between food intake and seasonal changes in temperature and food quantity, quality and vertical flux. At best, environmental data were only able to explain 28% of the variation in sea scallop and mussel ingestion rates, and this analysis was based on an extensive water sampling program of numerous environmental variables. Less frequent environmental sampling (approximately weekly) failed to identify any variable that was closely correlated with observed ingestion rates. Although ambient water temperature was found to be significantly correlated with sea scallop ingestion (Pearson's r = 0399, p < 0.001), the apparent relationship was driven by the high leverage exerted by a few observations. High and low ingestion rates were observed at both temperature extremes (Figs. 5.2 and 5.6). The poor relationship between ingestion rate and temperature is consistent with previous observations of thermal acclimation of feeding behaviour by sea scallops and blue mussels (B. MacDonald, personal communication, Widdows and Bayne 1971, Bayne and Newell, 1983, Smaal et. al. 1997, but see Jørgensen et al. 1990 and Riisgård 1991).

The results of multiple regression analysis indicate that sea scallop and mussel food intake was not passively (autonomous view of filter-feeding behaviour) driven by numerous potential exogenous influences. Large short-term fluctuations in food quantity and quality, which are a common phenomenon in many coastal regions including Mahone Bay and Bedford Basin (Fig. 5.2), could have had a greater impact on bivalve feeding behaviour than was indicated by the daily integrated ingestion rate measurements. For example, it is possible that a short period of rapid food intake caused by a short-term increase in food abundance could account for much of the total daily food intake (Cranford and Hargrave, 1994). However, this would not explain observed seasonal variations in ingestion rate, as the magnitude of short-term fluctuations in TPM and chlorophyll *a* remained relatively constant throughout the study period (Fig. 5.2). Riisgård and Møhlenberg (1979) suggested that variable feeding behaviour results from periodic overloading of the feeding system. This is unlikely in the present study as food concentrations at the Bedford Basin and Mahone Bay sites were consistently low (Fig. 5.2). Prins et al. (1994) had similar problems finding a straightforward relation between mussel clearance rate and seston composition variables and suggested this resulted from the inhibitory effect of a *Phaeocystis* bloom on feeding behaviour. The independence of scallop and mussel food intake from observed environmental changes may be related to an overly simplistic characterization of the nature of the particulate food (Grant and Bacher 1998) or to endogenous regulation of physiological processes.

Several specific observations of sea scallop and mussel feeding/digestion behaviour support the view that food utilization at the study sites was constrained not by environmental forcing, but by endogenous factors that varied over time. Large differences in clearance and ingestion rates and absorption efficiency were observed in Mahone Bay during the summer (MB1) and late autumn (MB3) (Figs. 5.6 and 5.7, Table 5.2) when the food supply was similar in abundance and quality (Figs. 5.2 and 5.3). The relatively high scallop and mussel absorption efficiencies observed in November, compared with June and July, partially resulted from the active regulation of absorptive efficiency. The gradual decline in the organic content of faeces during November occurred when seston POM content remained constant (Figs. 5.6 and 5.7), suggesting that the animals were maximizing absorption by reducing metabolic energy losses to faeces. This absorptive acclimation ability has previously been observed in the laboratory for mussels (Bayne et al. 1987, 1993) and sea scallops (Cranford 1995). In response to the generally high organic content of Bedford Basin seston during April and May, the scallops and mussels gradually increased faeces organic content, resulting in decreased absorption efficiency. The continuous availability of a high quality diet in the spring appeared to prompt the animals to reduce absorption efficiency and digestive energy investments. Bivalves fed high-quality diets in the laboratory have also been observed to reduce absorption efficiency (Cranford 1995, Kreeger 1993 and references cited). It is this high flexibility of absorptive responses to seasonally changing rations that resulted in the relatively poor relationships observed between AE and POM (Fig. 5.8), compared with previous observations of AE responses to short-term changes in diet quality (Hawkins et al. 1996, Cranford, 1998). Several examples of interspecific differences in feeding/digestion responses were also observed (Figs. 5.6 and 5.7) that are unlikely to be caused by differential responses to similar environmental forcing.

The feeding strategy of animals, including bivalve filter-feeders, has often been explained or predicted on the basis of maximizing net energy intake (Lehman 1976, Pyke et al. 1977, Taghon, 1981, Willows 1992). An optimal feeding behaviour model for *M. edulis* predicts that feeding rate at low food availability is constrained by the energetic costs of food processing (Willows 1992). POM concentrations in Mahone Bay, which ranged between 0.4 and 1.2 mg l^{-1}, are not much greater than the maintenance ration for *M. edulis* (Bayne and Newell 1983). The major costs of nutrient acquisition are the energy requirements and metabolic losses to faeces associated with digestion/absorption processes (Hawkins and Bayne 1992). The observation that absorption efficiency was reduced during a prolonged period of high food quantity and quality during the spring (Figs. 5.6 and 5.7) is typical of "exploiter" species (Bayne and Newell, 1983) that conserve energy under favourable dietary conditions by reducing digestive energy investment (Willows 1992) to maximize energy gain from the food supply. During prolonged exposure to low quantity and quality diets in June, July and November, metabolic losses to faeces were relatively low, indicating that the animals attempt to maximize energy gain under low food conditions by increasing the energy invested in digestive processes. Although predicted to remain constant (Willows 1992), the metabolic digestive investment appears to vary seasonally in both species.

Optimal foraging models generally predict a positive relationship between ingestion rate and food quality (Taghon 1981) and this prediction has been confirmed empirically for sea scallops and mussels (Bayne et al. 1987, Cranford and Grant 1990). However, no clear relationship between ingestion rate and seston POM, POC or PN content was observed in the present study. Observed seasonal changes in bivalve feeding rates cannot be explained solely by the constraints of food processing costs at low food availability as suggested by Willows (1992). For example, the highest feeding rates were observed in November when food abundance was low and the organic content of the faeces indicated a high digestive investment. An additional constraint on the optimal net energy intake that is known to vary seasonally is the metabolic cost associated with reproductive activity. Although it is difficult to separate the influence of reproduction on metabolic activity from other potential factors, the high energetic requirements of reproduction consistently result in respiration rate maxima coinciding with the reproductive periods of mussels (Bayne and Widdows 1978, Thompson 1984, Grant et al. 1993, Smaal et al. 1997, Hatcher et al. 1997) and sea scallops (MacDonald and Thompson 1986, Shumway et al. 1988). Gametogenesis in *M. edulis* in Nova Scotia is initiated during early winter, is rapid during the spring and spawning starts in May and continues through to the end of June (Freeman 1974, Mallet and Carver 1993). *P. magellanicus* initiate gametogensis during early winter, growth and ripening of the gonad occurs during the spring and summer, and spawning takes place in August to September (Robinson et al. 1981, Barber et al. 1988, MacDonald and Thompson 1986). The decrease in scallop and mussel tissue weight during the fall and summer, respectively, (Table 5.1) are consistent with these patterns.

If the high metabolic requirements of reproduction cannot be met from the food supply or internal reserves, a reduction in feeding activity and related metabolic expenditures is one strategy for optimizing energy intake. This is consistent with empirical observations of bivalve feeding responses to maintenance rations or partial starvation (Bayne and Newell 1983) and the observation that sea scallops and mussels display an energy conservationist strategy (see above). The relatively low feeding activity of the scallops between June and October may therefore have resulted from the cumulative constraints of low food availability and the high energy demands of gametogenesis. In contrast, the relatively high ingestion rate of mussels during June and July may have been permitted by low reproductive energy expenditures during this period of germinal quiescence. Both species also exhibited relatively high clearance and ingestion rates during November, when reproductive demands are known to be low. A high correlation between clearance rate and reproductive condition is not required for gametogenic energy demands to control the optimal food intake. If food is abundant during peak energy demands, as they often are for mussels in the spring, maintaining a relatively low clearance rate may be a better energy conservation strategy. This may explain why no such relationship has been observed (this study, Small and Vonck 1997, Small et al. 1997).

The only results that cannot be explained by the annual cycles and demands of reproduction are the low feeding and absorption rates of mussels during September and

October. Based on the relatively high food quality and low reproductive demand anticipated during this time, optimal foraging theory predicts a higher food intake. Some other factor(s) appear responsible for this uncharacteristic mussel behaviour. For example, this may result from prolonged nutritive stress resulting from the depleted state of energy reserves after spawning in spring (Thompson 1984), the low food availability in the summer and the absence of a fall phytoplankton bloom in Mahone Bay. The scallops were not as nutritionally stressed during this period as the energy reserves they accumulate in the spring are not fully utilized until spawning in the fall (Thompson 1977, Robinson et al. 1981). Summer nutritive stress is one explanation for the high summer mortalities that are a common occurrence in Nova Scotia mussel populations (Mallet and Carver 1993).

5.5.2 Accuracy of potential clearance rate estimates

Species-specific and generic clearance models were highly inaccurate at predicting the short- to medium-term (days to months) feeding behaviour of sea scallop and mussel cohorts held *in situ* (Table 2). Only when clearance behaviour was averaged over a long time-scale (the full 134 day sampling period) did any of the models provide reasonable results. The most accurate predictions of *in situ* clearance were based on feeding experiments employing natural seston rations (Table 5.2). The optimal condition models overestimated *in situ* clearance by 320 to 660%. The fact that the generic 'low gear' model of Powell et al. (1992) provided clearance rates that were at least as accurate those provided by the species-specific allometric clearance relationships (MacDonald and Thompson 1986, Smaal et al. 1997) indicates that, on average, the water processing rate of a wide-spectrum of bivalve filter-feeders is remarkably similar. The accuracy of *in situ* clearance rate estimates is addressed in Chapter 6.

The conclusion of Clausen and Riisgård (1996) that food uptake by *M. edulis* in nature is characterized by the full exploitation of their filtration capacity depends on their assumption that living phytoplankton are the sole trophic resource of bivalve filter feeders. However, a lower clearance rate can explain actual growth if a greater proportion of detrital POM is utilized as a food source. Much of the material characterized as POM consists of organic-mineral aggregates of pytoplankton, protozoans, colloids and detrital organic matter, some of which is adsorbed to mineral particles (reviewed by Grant and Bacher, 1998). The C:Chl ratio of seston provides an index of the relative importance of phytoplankton in available rations. Although C:Chl values for phytoplankton of up to ~ 100 have been observed, recent modeling studies of field diatom populations indicate a ratio between 21 and 47 (Gallegos and Vant 1996). The low C:Chl observed during the spring phytoplankton bloom (~ 70) indicates a dominant phytoplankton signature at this time, but the average value of 205 over the study period (Fig. 3) shows that heterotrophic and detrital carbon are important POM sources at all times of the year at the study sites. The high food quality of these alternative carbon sources is demonstrated by the high absorption efficiencies observed during September and October (AE > 80% in scallops and > 60% in mussels, Figs. 5.6 and 5.7) when seston phytoplankton content was lowest (C:Chl ratio often exceeded 300).

Jϕrgenson (1990, 1996) and Riisgård and Larsen (1995) have speculated that the low clearance rate measurements prevalent in the literature reflect sub-optimal experimental conditions in which the animals were disturbed, were not properly acclimated, or water was refiltered within dense animal aggregates. The *in situ* biodeposition method was designed to eliminate potential laboratory feeding behaviour artifacts (Cranford and Hargrave 1994) and care was taken to use acclimated animals. Animal densities used were also low and incapable of depleting ambient particle concentrations to the degree necessary to account for the relatively low clearance behavior.

The low accuracy of the 'optimal' feeding condition models in predicting mussel and scallop clearance behaviour in nature (Table 5.2) dictates a reevaluation of conclusions based on the wide application of these models. Recent studies in bivalve ecology have emphasized that seston dynamics in many shallow coastal regions are strongly coupled with bivalve filter-feeding activity to the extent that infaunal and epifaunal bivalve communities often play a major role in controlling phytoplankton biomass and trophic structure (Dame 1993, 1996). Cloern (1982) and Officer et al. (1982) used the filtration model of Møhlenberg and Riisgård (1979) to calculate that the bivalve community in South San Francisco Bay cleared a volume of water equivalent to the volume of the Bay at least once daily. Because this clearance time is smaller than the hydrodynamic residence time and the phytoplankton growth constant, the conclusion was reached that grazing by bivalve filter feeders controls phytoplankton production. Nichols (1985) and Hily (1991) used a similar approach and came to the same conclusion for the Northern San Francisco Bay and the Bay of Brest, respectively. The fact that many bivalve feeding studies show much lower clearance rates of natural diets (see above) indicates that the potential clearance time of coastal systems may be up to six times longer than reported, resulting in a time constant for water recycling by bivalves that may no longer support conclusions of a strong influence of bivalve grazing in controlling phytoplankton populations. Further, as the clearance behaviour of the bivalve cohorts varied seasonally (Table 5.2), the time-scale on which bivalve populations feed at a rate sufficient to deplete phytoplankton and allocthonous inputs in these systems is probably extremely variable.

The widespread expansion of bivalve culture operations in estuarine and coastal systems is increasing the potential for bivalve filter feeders to impact regional trophic structure. Simulation models of bivalve bioenergetics and culture sites are being developed to help determine the sustainability of existing and expanded culture operations and to predict impacts on coastal ecosystems (e.g. Grant 1996). Such predictions are highly sensitive to the consumption rate and digestability of seston (Grant and Bacher 1998) and it is therefore essential that bivalve food utilization be more fully comprehended, so it can be more accurately modelled, particularly at low food concentrations (Scholten and Smaal 1998). To this end, the present study has attempted to resolve some difficult and sometimes controversial issues: (1) the assumption that suspension-feeding bivalves fully exploit their clearance capacity in nature; (2) the ability of bivalves to physiologically control food utilization; (3) and food utilization/optimization strategies of different bivalves. It is clear from the results of this study that further advances in bioenergetic/ecosystem modeling will benefit from observations of physiological processes under natural conditions, particularly with respect to identifying important interactions between potential exogenous and endogenous forcing functions.

CHAPTER SIX

PRECISION AND ACCURACY OF *IN SITU* TIME-SERIES MEASUREMENTS OF FOOD ACQUISITION BY SUSPENSION-FEEDING BIVALVES.

6.1 ABSTRACT

The precision of food acquisition measurements obtained for suspension-feeding bivalves using the *in situ* time-series biodeposition method was determined by comparing the feeding/digestion responses of two sea scallop, *Placopecten magellanicus*, cohorts (9 scallops with average shell height of 93.8 mm, SD = 3.5) in Whitehaven Harbour, Nova Scotia over a 78-h period in August, 1995. Both cohorts exhibited similar behaviour with food intake gradually increasing during the experiment. The standard error of clearance, ingestion, absorption and egestion rates and absorption efficiency estimates were less than 3.6% of the mean response of the two cohorts. Absorption efficiency (AE) was the only variable found to be significantly different between cohorts, but the difference in average AE values between cohorts was small (4.2%). The quantitative effect of differential particle retention by bivalves and the GF/C filters used to sample bivalve diets was determined using observed and theoretical particle size distributions and retention efficiencies. Calculated ingestion rates underestimated actual ingestion by up to 30%, with the greatest error occurring for sea scallops, which are less effective at retaining fine particles than mussels, and when the seston is characterized by relatively large particles and/or small inorganic particles. It is concluded that the method is highly precise, relatively accurate and a valuable tool for directly monitoring the food acquisition behaviour of bivalves in their natural environment.

6.2 PRECISION AND ACCURACY OF *IN SITU* TIME-SERIES MEASUREMENTS OF FOOD ACQUISITION BY SUSPENSION-FEEDING BIVALVES.

6.2.1 Precision

A new approach for measuring food intake (clearance, ingestion, and absorption rates) by suspension-feeding bivalves held *in situ* is described in Chapter 2 and used to monitor bivalve feeding and digestion responses to oceanographic variables and endogenous forcing (Chapters 2, 4 and 5). The precision of the *in situ* time-series method has yet to be addressed as all previously reported measurements are based on unreplicated data. Replication was not possible in these studies as all the available sediment traps were required to meet experimental objectives. Although the method was designed to reduce variability in physiological measurements by providing estimates that represent the integrated response of a cohort of animals over a set period, variability may be large owing to considerable interindividual variability in the physiological status of bivalve filter-feeders (Hawkins and Bayne 1992).

As part of a collaborative study designed to assess the carrying capacity of a sea scallop *Placopecten magellanicus* culture site in Whitehead Harbour, Nova Scotia (45° 15.10'N, 61°10.37'W), the precision of the time-series biodeposition method was assessed. Only those data collected that are necessary for quantifying variability in food acquisition data are reported herein and no attempt was made to interpret scallop responses to environmental conditions in Whitehead Harbour. The three sediment traps described in Chapter 5 (Fig. 5.1) were used in this study and the sampling cups were filled with a dense preservative (0.1% HgCl in 35‰ NaCl). The sediment traps were each suspended 10 m above the seabed (total depth was 20 m) between a subsurface float, which was attached by a 5-m long cable to a three-point bridle at the top of the trap, and an anchor that was tethered to a bridle at the trap base. Sea scallops collected from the culture site, which was adjacent to the sampling location, were cleaned of epiphytes and placed over the mouth of two of the traps (nine scallops per trap). The scallops selected were of a narrow size (average shell height = 93.8 mm, SD = 3.5) and weight (average dry tissue weight = 11.3 g, SD = 1.8) range. The third trap, without animals, served to control for particle sedimentation. The traps were deployed between 1700 and 1800 h on August 7, 1995 and the first sample cups were moved into position under the sampling funnel at 2200 h on the same day. Each trap was programmed for two-hour sampling intervals. Sampling ended at 0400 h on August 11, and the traps were retrieved the same day.

While the traps were sampling, the site was visited periodically between 0900 h on August 8 and 1830 h on August 10. A total of 21 separate water samples were collected by Niskin bottle at a depth of 10 m. Water was processed in duplicate for analysis of total particulate matter (TPM) and particulate organic matter (POM). Seston was filtered onto washed and tared 1.2μm filters (Whatman GF/C), rinsed with isotonic ammonium formate to remove salt, dried at 60°C to constant weight and weighed to give TPM. POM was determined as the difference between TPM and the weight of ash remaining on filters after combustion at 450°C for 6 hours. Particulate matter deposited in sample cups was homogenized, subsampled and analyzed as above for TPM and POM.

Hourly egestion rates (mg dry weight $\cdot$ individual^{-1} $\cdot$ h^{-1}) during each 2-h sampling period were calculated by subtracting the total dry weight of particles deposited in sample cups under the control trap from the weight of particles collected in corresponding cups under the traps containing scallops and then dividing by two. Total ingestion rate (I_T: mg dry weight $\cdot$ ind.$^{-1}$ $\cdot$ h^{-1}) was calculated according to Equation 2.1 (Chapter 2) using data collected on the egestion rate of ash and the proportion of ash in the seston. Average seston values were used in all calculations as variability in the organic and ash content of seston (ash content = 1 - POM content) was low over the sampling period (average POM = 70.9%, SD = 3.6, n = 21). This relatively constant seston POM content eliminates the need to account for gut passage time in the calculations (see Chapter 4).

Clearance rate (C: l $\cdot$ ind.$^{-1}$ $\cdot$ h^{-1}) was calculated by dividing I_T by the average TPM measured over the sampling period (1.69 mg l^{-1}, SD = 0.28, n = 21). The net absorption efficiency of POM (AE_{POM}) was calculated from the proportions of absorbed (POM) and inert (ash) tracers in seston and faeces samples according to Equation 2.2

(Chapter 2). Absorption rates (mg POM · ind^{-1} · h^{-1}) were estimated as the product of hourly POM ingestion rate and AE_{POM}.

During sampling, water temperature and current speeds at the study site averaged 16.2°C and 4 cm sec^{-1}, respectively and salinity was between 29.8 and 30.0 psu (P. Cranford, unpublished data). Total particle sedimentation into the control trap was 16.3% and 14.0% of the total dry weight of material deposited in the two traps containing scallops. Time-series of clearance, ingestion, absorption and egestion rates and absorption efficiency for each scallop cohort are shown in Figure 6.1. Food intake rates of both cohorts were similar and showed a trend towards increased food utilization during the sampling period. Clearance rates were relatively low for animals of the size used, but were similar to values observed in Minas Basin during the summer of 1995 (Chapter 5).

Between trap variability in the different variables related to food acquisition was extremely low, with the coefficient of variation (SD/mean x 100) observed to be between 1.1 and 4.7% (Table 6.1). The standard error (SE) of the estimate is generally considered to be the best measure of precision and was less than 3.6% of mean values (Table 6.1). Independent sample *t*-tests were used to test the hypothesis that food acquisition was not significantly different ($\alpha = 0.05$) between the two scallop cohorts during the sampling period. Bonferroni probabilities were calculated as protection for multiple tests. All variables were screened for normality and homoscedasticity prior to the analysis and no transformations were necessary. Only absorption efficiency was found to be significantly

Figure 6.1

Time-series of hourly clearance, ingestion, absorption and egestion rates and absorption efficiency of two sea scallop, *Placopecten magellanicus*, cohorts held on two sediment traps in Whitehead Harbour in 1995. The number and size of animals in each cohort is given in the text. Data points are plotted at the mid-point of two-hour sample collection intervals. DW is total dry weight and POM is particulate organic matter.

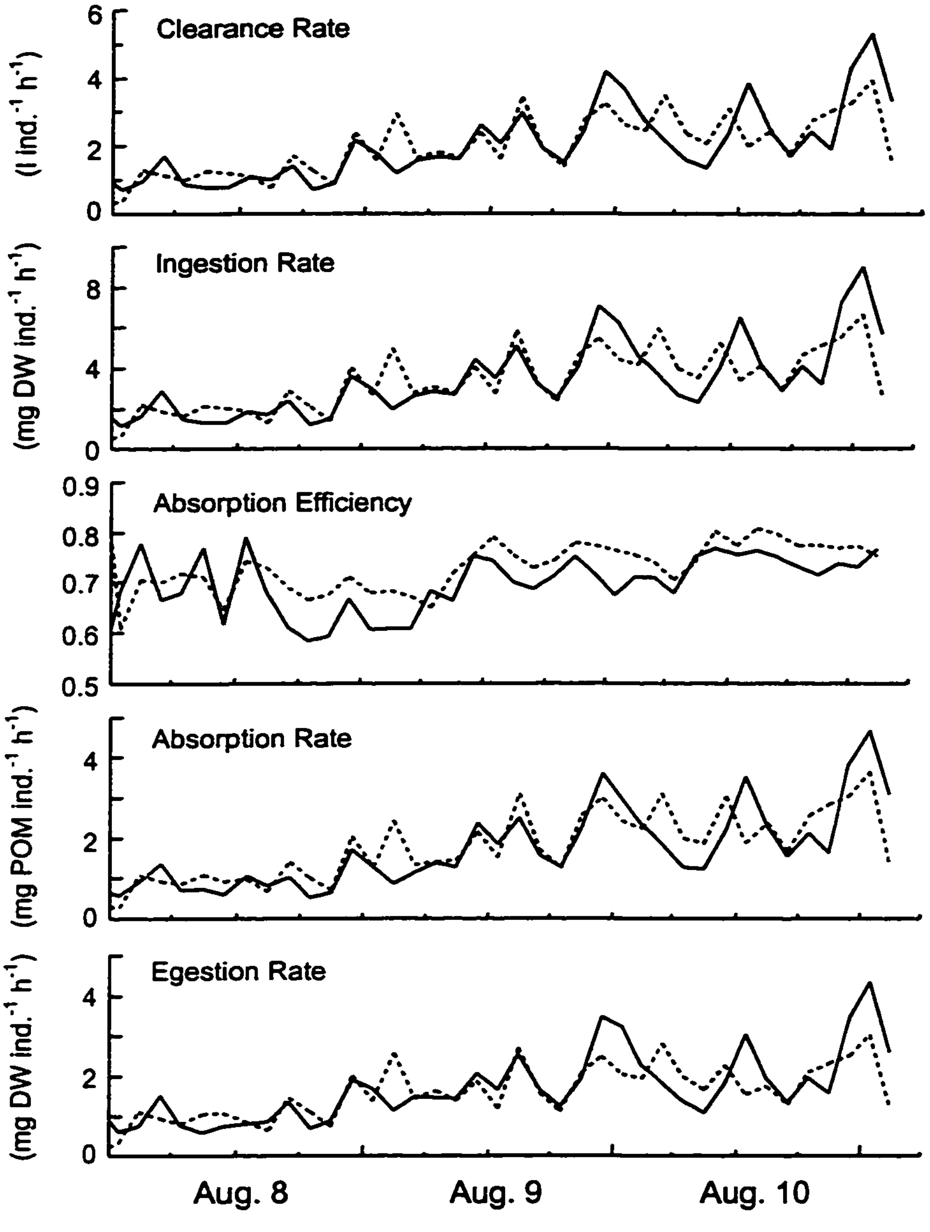
Clearance Rate
(l ind.$^{-1}$ h^{-1})
0
2
4
6
Ingestion Rate
(mg DW ind.$^{-1}$ h^{-1})
0
4
8
Absorption Efficiency
0.5
0.6
0.7
0.8
0.9
Absorption Rate
(mg POM ind.$^{-1}$ h^{-1})
0
2
4
Egestion Rate
(mg DW ind.$^{-1}$ h^{-1})
0
2
4
Aug. 8
Aug. 9
Aug. 10

Figure 6.1

Table 6.1

Average seston clearance (C; l individual^{-1} h^{-1}), ingestion (I_T; mg dry weight ind.$^{-1}$ h^{-1}), absorption (A, mg POM ind.$^{-1}$ h^{-1}) and egestion (E; mg dry weight ind.$^{-1}$ h^{-1}) rates and absorption efficiency (AE) of two cohorts of sea scallops *Placopecten magellanicus* held on sediment traps at 10 m depth in Whitehaven Harbour, Nova Scotia, between August 7-11, 1995. Rate variables are reported for individual animals by dividing cohort values by the number of animals on the traps. Cohort estimates are mean ± SD (n = 39). The results of *t*-test comparisons of each variable between cohorts are shown (d.f. = 16 for shell height and 76 for all other variables) and Bonferroni adjusted *p*-values are given.

	Shell height (mm)	C	I_T	AE	A	E
Cohort 1	94.1±3.8	2.00±0.91	3.38±1.54	0.74±0.06	1.78±0.86	1.60±0.69
Cohort 2	93.8±3.2	2.03±1.11	3.43±1.88	0.70±0.06	1.73±1.01	1.71±0.88
mean	93.9	2.02	3.40	0.72	1.75	1.65
SE	1.2	0.02	0.03	0.02	0.03	0.06
CV(%)	3.7	1.1	1.1	4.2	2.3	4.7
t-value	0.131	-0.135	-0.134	2.915	0.264	-0.613
p	1.000	1.000	1.000	0.023	1.000	1.000

different between cohorts (Table 6.1). However, average *AE* values for each cohort only differed by 4.2%, and absorption rates were not significantly different (Table 6.1).

It is concluded that feeding/digestion responses provided by the time-series biodeposition method exhibit high precision. The large interindividual variability in measurements obtained using bivalves held in static and flow-through chambers (Hawkins and Bayne 1992) is largely eliminated, as intended, by measuring cohort responses over longer sampling periods than has previously been possible.

6.2.2 Accuracy

Absorption rates estimated using the *in situ* method are subject to some error as the calculations assume seston retention efficiency by the bivalve to be equal to that of a 1.2 μm pore-size GF/C filter. In fact, retention is optimal for particles larger than approximately 5 μm for *P. magellanicus* (Cranford and Grant 1990) and 3 μm for *M. edulis* (Riisgård 1988). Ingestion rates obtained using Equation 2.1 ($I_T = E_{\mathrm{ash}}/F_{\mathrm{ash}}$) may be susceptible to significant error as a result of the high proportion of total inorganic seston grains between 1 and 5 μm diameter (Fig. 4.2). The assumption that the fraction of ash retained on filters is equal to that ingested could easily be violated. An analysis of potential error was performed by calculating the retainable fractions of inorganic and total particles using observed particle size distributions and information on particle retention efficiencies for *M. edulis* and *P. magellanicus* (Mohlenberg and Riisgard 1978, Cranford and Gordon 1992). The degree of error in ingestion rate estimates was assessed by calculating the ratio of calculated (I_c) and actual (I_a) particle ingestion. An equation for this ratio was derived by first defining I_a and I_c with the equations

$$I_a = E_{ash}/(F_{ash})_{retained}, \tag{6.1}$$

$$I_c = E_{ash}/(F_{ash})_{filtered}, \tag{6.2}$$

where 'retained' and 'filtered' refer to seston particles captured by the bivalve and the GF/C filter, respectively. The F_{ash} terms are defined as

$$(F_{ash})_{retained} = (PIM)_{retained}/(TPM)_{retained}, \tag{6.3}$$

$$(F_{ash})_{filtered} = (PIM)_{filtered}/(TPM)_{filtered}, \tag{6.4}$$

where *PIM* and *TPM* are mass concentrations of particulate organic matter and total particulate matter, respectively. Equations 6.1 to 6.4 were combined to define the ratio

$$I_c/I_a = (PIM)_{retained}(TPM)_{filtered} \,/\, (PIM)_{filtered}(TPM)_{retained}. \tag{6.5}$$

Using typical inorganic (Fig. 4.2) and total particle size distributions (Fig. 5.5) and concentrations, particle retention by filters and bivalves was summed over particle size intervals to give

$$I_c/I_a = (0.567*2.000)/(0.850*1.829) = 0.730$$

for sea scallops, and

$$I_c/I_a = (0.725*2.000)/(0.850*1.930) = 0.886$$

for mussels. Therefore, actual *in situ* ingestion rates reported for *P. magellanicus* are underestimated by ~27% while *M. edulis* ingestion rates are more accurate, owing their ability to retain finer particles than scallops, and underestimated by ~11%.

The error in ingestion rate calculations will vary depending with changes in particle size distribution. Assuming conventional size distributions for PIM and TPM and using a simple diameter-dependent expression for retention efficiency (e.g. particle retention drops from 1 to 0 at some minimum particle size), Equation 6.5 was rewritten in terms of particle diameters. The equation, as derived by Dr. Paul Hill (Dalhousie University) in Appendix I, becomes

$$I_c/I_a = (\ln d_2/d_r \ln d_3/d_1) \;/\; (\ln d_2/d_1 \ln d_3/d_r), \tag{6.6}$$

where d_r is the minimum diameter effectively retained by the bivalve, d_1 is the smallest particle retained by the filter (1 μm), d_2 is the largest inorganic particle in the seston and d_3 is the largest particle in the seston. The quantitative effect of a variable size-distribution of particles on sea scallop ingestion rate calculations was examined using a wide range of values for d_2 and d_3 and the results are summarized in Figure 6.2. These calculations were performed assuming d_r equals 3 μm to account for particle retention by scallops between 1 and 5 μm. The largest error in I_c estimates occurs when inorganic particles in seston are relatively small and particles are relatively large (Fig. 6.1). Fortunately, the largest inorganic particles observed were ~20 μm diameter (Fig. 4.2) and total particles were smaller than 50μm (Fig. 5.5), resulting in scallops ingestion rates generally being underestimated by only 10-15% (Fig. 6.1).

To assess the accuracy of absorption rate estimates, the actual growth of individual scallops and mussels (Table 5.1) was compared with growth estimates calculated by summing daily absorption rates (C x TPM x AE) and subtracting daily respiration rate (R). This is the same approach as used by Clausen and Riisgård (1996) to compare mussel growth in nature with growth estimates based on the assumption of a maximum clearance rate. For consistency, growth estimates for *M. edulis* were calculated using the same allometric relationship for R (ml O_2 h^{-1} = $0.475W^{0.663}$) and the same energy equivalents for oxygen and dry tissue mass as used by these authors. *P. magellanicus* tissue was assumed to be 24.5 J mg^{-1} (MacDonald and Thompson 1985) and routine oxygen consumption was estimated using an average allometric relationship with dry weight (W, g), where $R = 0.35W^{0.81}$ (Bricelj and Shumway 1991). Seston POM was assumed to average 23.5 J mg^{-1} (Widdows et al., 1979). Growth was estimated for the fall sampling periods for mussels and for the spring period for scallops (Table 5.1) as these periods do not include spawning. The resulting mussel growth estimate of 23.0 kJ over the 99-day period examined was 20% greater than observed (0.9 g tissue growth x 20.5 J mg^{-1} = 18.5 kJ). Sea scallop growth was estimated at 38.4 kJ over the 39-day period, which was only 4% greater than the 36.8 kJ observed. As these discrepancies can be explained by additional energy losses to excretion and the energy costs of growth and reproduction, the similarity of actual and calculated growth provides a high level of confidence in the accuracy of reported *in situ* absorption rates.

Figure 6.2

Quantitative effect of different values for the largest particle (d_3) and inorganic particle (d_2) in the seston on the ratio of calculated (I_c) and actual (I_a) ingestion rates. The ratio was calculated using Equation 6.6 assuming values for the smallest particle on the filter (d_1) was 1 μm (pore size of GF/C filter is 1.2 μm) and the minimum diameter retained by a scallop (d_r) was 3 μm (see text for details).

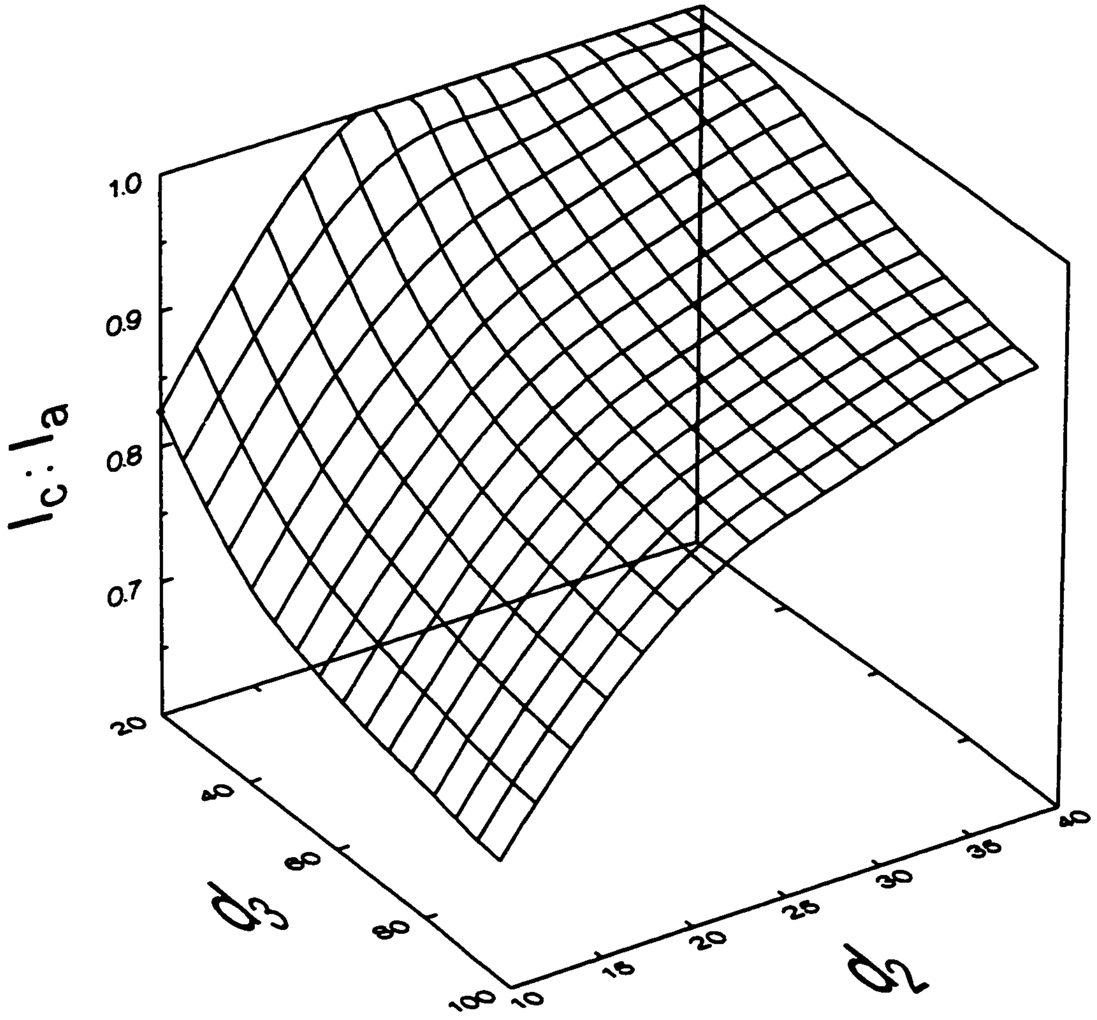

Figure 6.2

The combined advantages of high precision, reasonably high accuracy, and semi-automated sampling under environmentally representative conditions (Chapter 2) makes the *in situ* time-series method ideally suited for a wide range of applications where a measure of interindividual variability is not required.

CHAPTER SEVEN

SUMMARY AND CONCLUSIONS.

7.1 INTRODUCTION.

Recent attempts to predict the growth of bivalve filter feeders under different oceanographic conditions and current concepts of their role in the particle flux, nutrient dynamics and phytoplankton production in aquatic ecosystems depend on an accurate knowledge of food acquisition rates. This includes a thorough understanding of the constraints on food acquisition, the influence and interactive effects of numerous potential exogenous and endogenous and forcing functions, and the interplay between the physiological components of growth (Fig. 7.1). Controversies and uncertainties still exist regarding the regulation of food acquisition processes by bivalve filter feeders (Jørgensen 1996, Bayne 1998) and several difficult issues were addressed in this thesis. The primary hypothesis of the thesis is that food acquisition by bivalve filter feeders in their natural environment is driven by a combination of physical constraints on feeding, environmental forcing over different time-scales, the time-dependence of acclimation capabilities, and temporal variations in energy and nutritional demands related to gametogenesis.

Empirical data provided by a novel *in situ* method for monitoring food acquisition processes by the sea scallop *Placopecten magellanicus* and the blue mussels *Mytilus edulis* were used to quantitatively assess the influence of numerous environmental variables on food acquisition processes. These data were obtained over time-scales relevant to tide, storm and seasonal fluctuations in environmental conditions. Observed seasonal variations in food utilization behaviour were interpreted in the context of

Figure 7.1

Conceptual diagram of the potential exogenous and endogenous influences constraining and modulating behavioural and physiological processes that control food acquisition by bivalve filter feeders.

Constraints and Potential Influences on Food Acquisition

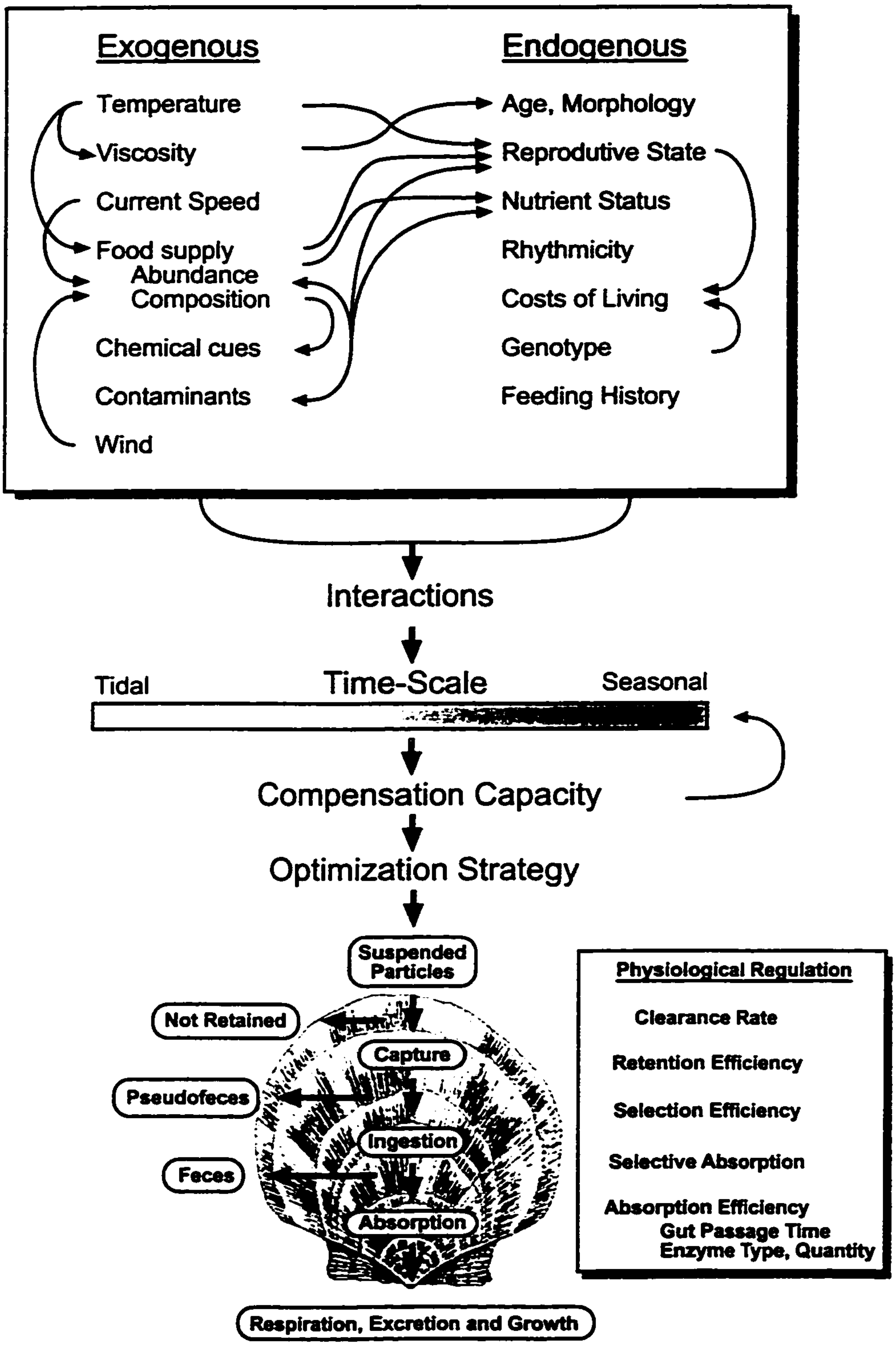

Figure 7.1

simultaneous forcing by oceanographic conditions and the high nutrient and energy demands of gametogenesis. Additional laboratory studies were conducted to document the time-course of physiological acclimation responses to environmental change and the persistence of this response in the face of further change (the influence of feeding history on present behaviour). The major results and conclusions of these studies are summarized in the following sections.

7.2 *IN SITU* TIME-SERIES MEASUREMENT OF FOOD ACQUISITION BY SUSPENSION-FEEDING BIVALVES.

Laboratory experiments have a limited capacity to duplicate natural conditions where suspended particulate matter can vary dramatically in concentration, composition and form (i.e. degree of particle aggregation) over different time-scales (Chapters 2, 4 and 5). As a result, the knowledge required to predict temporal changes in food acquisition by bivalves must also come from *in situ* studies. There is an increasing trend towards conducting studies on the bioenergetics of bivalve filter feeders in the field, but even the most recent methods employed do not allow feeding and absorption to be measured under strict field conditions.

Food ingestion by bivalves has traditionally been measured by determining the rate of particle depletion in static or flow-through enclosures caused by one or more bivalves (reviewed by Smaal and Widdows 1994). These methods have been adapted for field use (Bayne and Widdows 1978, Prins et al. 1994, Asmus and Asmus 1991, Dame et al. 1992), but are labour intensive, require expensive and delicate electronic equipment (i.e. Coulter Counter), and the required enclosure (chamber, tunnel or flume) disrupts aggregated food supplies and alters flow conditions and horizontal and vertical particle flux. Bivalve feeding behaviour has been monitored *in situ* by measuring shell-gape using time-lapse video (e.g. Newell et al. 1998) or high frequency electromagnetic induction systems such as the Musselmonitor® (Baldwin and Kramer 1994). However, these methods do not provide quantitative measurements of food acquisition rates and efficiencies.

An important characteristic of traditional particle depletion methods is that they measure the instantaneous feeding response of the animal. Considerable short-term variation in feeding behaviour results in high variability between individuals and even among replicates. Hawkins and Bayne (1992) suggested that a method that provides an integrated average response by undertaking measurements over longer periods would improve our ability to define a 'normal' physiological state. The approach developed in this thesis (Chapter 2) for monitoring bivalve feeding and absorption *in situ*, addresses this need by providing information on food acquisition responses that are integrated over different time-scales. The *in situ* time-series method is based on the automatic collection of feces at regular and programmed intervals, produced by a cohort of bivalves held over the mouth of a sequentially sampling sediment trap. When quantitative feces collections are conducted with simultaneous sampling of food supplies (using pumps or Niskin bottles to collect water samples, and using electronic sensors to provide higher-frequency data on TPM concentration), clearance, ingestion and absorption rates can be estimated. This high precision in the food acquisition estimates (SE < 4% of the mean response, Chapter 6) results from the ability of the method to 'average out' very high-frequency changes in feeding behaviour as well as interindividual variability. As a result, the method increases our capacity to define the 'normal' physiological state of bivalve populations over selected sampling intervals.

The recent development of the 'biodeposition method' for quantifying feeding and absorption rates (Iglesias et al. 1998) is similar in principal to the method described in this thesis and also provides a continuous measure of feeding behaviour. However, the biodeposition method lacks the automation that would allow extensive long-term studies to be conducted and, as described, cannot be used to collect information under strict field conditions as the animals are not held *in situ*.

The assumptions and limitations of the time-series method are fully outlined and addressed in Chapers 2, 4 and 5 and many of the potential methodical problems are the same as identified and discussed by Iglesias et al. (1998) for their biodeposition method. For the accurate measurement of bivalve feeding and absorption rates, the organic and inorganic content of ingested particles must be quantified without error (Eqns. 2.1 and 2.2). Natural bivalve rations are generally characterized as suspended particulate material retained by GF/C glass fiber filters (nominal pore size of 1.2 µm). However, sea scallops and mussels do not effectively retain particles less than 5- and 3-µm, respectively

(Møhlenberg and Riisgård 1978, Cranford and Gordon, 1992), and many species have been shown to possess the capacity to alter fine particle retention efficiency. The quantitative effect of differential particle retention by bivalves and GF/C filters on ingestion rate calculations was assessed in Chapter 6 and it was found that observed particle size distributions result in reported ingestion rates being underestimated by up to 27% for scallops and 11% for mussels, which are more effective at retaining finer particles. Further analysis using conventional particle size distributions show that the greatest errors will be incurred when seston particles tend to be large and inorganic grains are small (Fig. 6.2). Clearance rate estimates would be underestimated to a similar degree as ingestion rates ($C = I_T$ /TPM). Because the majority of seston mass (TPM) is associated with larger particles, errors in quantifying bioavailable TPM using GF/C filters are small.

Under conditions of highly variable diets, food acquisition calculations based on biodeposition time-series require additional information on the time the food was ingested. This problem was addressed in Chapter 4 with the first *in situ* estimates of bivalve gut passage time. These data showed that particles ingested at any given time can remain in the gut for widely different periods. As a result, the food supply corresponding with hourly feces collections was estimated using a weighted mean of time-series seston data as opposed to using the traditional approach of relying on a single gut transit time.

A comparison of maximum and minimum clearance, ingestion and absorption rate estimates, calculated using a range of diet organic content estimates showed the results to be much more sensitive to changes in egestion rate than to changes in dietary POM content (Figs 2.4, 2.5, 4.7 and 4.8). As a result, it is important that egestion rates are measured accurately. Consequently, all feces produced by the bivalve cohort during each collection period must be retained by the sediment trap and remain unaltered in the sample cup. The latter is solved using standard sediment trap proceedures for preserving settled organic matter (Chapter 2). Any non-fecal particulate matter deposited in the trap would result in overestimation of egestion and food acquisition rates and could change the bulk organic content of settled material. Sedimentation of non-fecal material into the trap during initial studies in Lunenburg Bay (Chapter 2) was reduced by placing a cover above the trap mouth and by reducing the effective area for seston sedimentation around animals (Fig. 2.1). Analysis of settled material collected during simultaneous deployment of an identical control trap (without animals) was used to correct for this problem in latter studies.

An important potential source of feces sample contamination that is not accounted for by the control trap is pseudofeces production. All bivalve filter-feeders reject some proportion of non-nutritional particles as pseudofeces at high particle concentrations. Consequently, the sediment-trap approach is limited to regions where particle concentrations are below the threshold where significant quantities of pseudofeces are produced. Fortunately, the method may be applied to numerous coastal and shelf regions characterized by relatively low particle loads (less than ~10 mg l^{-1}). Many bivalves have been observed to produce pseudofeces even at low particle concentrations (Ward et al.

1993). However, MacDonald and Ward (1994) found the pseudofeces production rate of sea scallops at low particle concentrations to be less than 1% of particle clearance rate. Such a low rate would have an insignificant impact on calculations of feeding and absorption rates.

Egestion rates would also be inaccurate if feces were carried away by currents rather than being deposited in the collecting funnel. The method is therefore limited to lower energy regions where feces will settle into the trap and not be swept away by high currents. Although not mentioned in Chapter 4, an underwater video camera was positioned over the trap mouth to record scallop activity during each deployment period. A white lid was used on the trap mouth in place of the PVC lid previously used (Fig. 2.1) so that any feces not deposited around the animals would be easily visible. Scallops feces were observed to be released as long strings that hung down into the collecting funnel before breaking off. No fecal pellets were observed to be swept away, even when current speeds reached 15 cm s^{-1}. Despite these observations, the new traps described in Chapter 5 (Fig. 5.1) were designed with a different lid design that increased the area for feces sedimentation outside the bivalve cage. This feature was included so that even if the feces was expelled by rapid valve movements, it would settle into the trap before being swept away. For example, a fecal pellet settling at an average speed of 2.5 cm s^{-1} (Cranford, unpublished data) would settle the 2 cm distance required to fall below the baffled lid (a conservative estimate) within 0.8 sec. At a current speed of 15 cm s^{-1}, the pellet would have travel a horizontal distance of 12 cm. Even if the pellet was released at the edge of the bivalve cage, it would be captured before reaching the edge of the trap.

An indication of the overall accuracy of food acquisition estimates provided by the *in situ* time-series method was provided by comparing actual growth rates of scallops and mussels with rates predicted (scope for growth or net energy balance) by subtracting energy expenditures (calculated using available allometric relations for routine respiration rate) from the measured energy absorption rates. As the growth predictions were within 20% of the observed growth (Chapter 5), and much of this discrepancy can be accounted for by additional energy losses, it was concluded that absorption rates provided by the method are reasonably accurate. Therefore, when used under proper conditions, the *in situ* time-series method provides highly precise and reasonably accurate estimates of the clearance, ingestion, and absorption rates of bivalve filter feeders.

7.3 REGULATION OF INGESTION.

A full understanding of the food utilization behaviour of suspension-feeding bivalve requires knowledge of the constraints and influences on feeding and digestion imposed by numerous potential factors (Fig. 7.1). Assuming unlimited food availability, the maximum food acquisition capacity of bivalves is linked to physical constraints on particle capture, morphological limitations on ingestion and digestion rate, and to certain rate-limiting physiological functions (Hawkins and Bayne, 1992). Each of these factors may limit particle retention, selection, ingestion and/or absorption rates and efficiencies.

Important physical constraints on particle retention and the capacity of the bivalve ciliary pump are imposed by the dynamics of fluid flow around particle-collecting structures (Jørgensen 1990, Jørgensen et al. 1990, Shimeta and Jumars 1991). Flow velocity can limit food intake by creating a pressure differential between the internal pressure field in the mantle cavity, created by the ciliary pump, and the external pressure field caused by flow velocity (Wildish and Kristmanson 1997). The effect of flow velocity on bivalve filter-feeding has been demonstrated in numerous laboratory studies (see references cited in Chapter 5), and is confirmed from observations of reduced clearance rates in sea scallops during periods of relatively low (<4 cm s^{-1}) and high (>9 cm s^{-1}) flows in Lunenburg Bay. The reduced clearance rates at low flows are not likely to be directly related to flow, but may result from bivalve-induced particle depletion at low particle flux. Clearance rate inhibition at higher flows does appear to be the direct result of back pressure on the ciliary pump, resulting in reduced pump efficiency and a valve closure response (Jørgensen 1990, Wildish and Saulnier, 1993).

The capacity for food intake is also limited by the morphological constraint of a limited gut volume and the time required to digest food. Both factors impose a major bottleneck on ingestion rate. While the animal must cope with physical limitations, morphological adaptations and the active regulation of physiological performance can help to mitigate this bottleneck. An important and controversial question in the study of bivalve physiological energetics is whether or not the physiological status of bivalves is responsive to numerous potential endogenous and exogenous influences (Fig. 7.3).

The hypothesis of bivalve filter feeding as "automatized", with no capacity for compensation to changes in the food environment (Jørgensen 1990, 1996, Riisgård and Larsen 1995, Clausen and Riisgård 1996), limits any changes in maximal pumping and clearance rate capacity to a few behavioural responses. According to this theory, observed changes in valve gape and the extension and retraction of mantle edges and siphons, which are correlated with pumping rate (Jørgensen et al. 1988), are not mechanisms by which food intake is optimized. Riisgård and Larsen (1995) interpreted these responses as secondary effects of suboptimal conditions that alter the efficiency of the ciliary pump.

Rejection of the "automatized" hypothesis, as implied by Jørgensen (1996), requires two conditions to be proven. It must be shown that the bivalves have a capacity to physiologically control feeding processes, and it must be abundantly clear that the experimental conditions employed do not have a negative effect on the animal's behaviour. Jørgensen (1996) has routinely attributed and dismissed departures from this hypothesis as resulting from flawed experimental conditions. The methods used in this thesis were specifically designed to obtain information on food utilization under oceanographic conditions that closely approximate the animals' natural state. Great care was also taken to use animals that were not stressed, were acclimated to the study site, and to minimize disturbances during each study. The conditions are therefore less likely to be flawed than the laboratory conditions used in the few studies cited to support this hypothesis (Møhlenberg and Riisgård 1979, Riisgård and Møhlenberg 1979, Riisgård 1991).

It appears that *P. magellanicus* and *M. edulis* are able to feed at their theoretical maximal capacity in nature for short periods (from daily clearance data summarized in Table 5.2). However, the studies conducted in Lunenburg Bay (Chapters 2 and 4), Mahone Bay and Bedford Basin (Chapter 5), and Whitehaven Harbour (Chapter 6) provide ample evidence to show that maximal feeding is an extreme and seldom observed condition within a wide and highly flexible range of feeding capabilities of these species. Clearance rates of scallops and mussels measured over daily intervals for a total of 139 days in Bedford Basin and Mahone Bay showed a high degree of seasonal variation and were on average between 3 and 5 times lower than theoretical maximum values (Table 5.2). This large difference in potential and observed clearance rates cannot be attributed to the underestimation of *in situ* ingestion rate estimates (Chapter 6) as actual and calculated ingestion only differed by a maximum of 30% (Fig. 6.2).

Inherent with the hypothesis of continuous water processing at maximal capability is the existence of a high correlation between ingestion rate and TPM (C x TPM = I). However, daily ingestion rates of *P. magellanicus* and *M. edulis* were not significantly related to seston quantity (Pearson's $r < 0.21$, Bonferroni-adjusted $p > 0.9$). Together, these data support the results of numerous laboratory and mesocosm measurements that have reported relatively low clearance rates of natural seston compared with algal cells (Doering and Oviatt 1986, MacDonald and Thompson 1986, Cranford and Grant 1990, Riemann et al. 1988, Cranford and Gordon 1992, Iglesias et al. 1992, Navarro et al. 1992, Prins et al. 1994, Hawkins et al. 1996) and that have been challenged by Jørgensen (1996) as being flawed by methodical errors. The hypothesis of bivalves performing at a constant and maximal rate in nature (Jørgensen 1996) cannot be accepted based on the results of this thesis.

In situ measurements of the food utilization behaviour of scallops and mussels have revealed the importance of relatively short periods of high feeding activity in contributing to longer-term nutrient uptake. Tidal-cycle variations in hourly scallop clearance and ingestion rates were generally small (Figs. 2.4 and 4.7), but occasional periods of elevated feeding activity were shown to account for a high proportion of total organic, organic carbon and nitrogen intake during the study period (Fig. 2.5). Similarly, but over an annual time-scale, high periods of increased absorption during May and November (Figs. 5.6 and 5.7) accounted for approximately 70% of total organic matter absorbed by scallops and mussels (Chapter 5). Relatively short periods of high feeding activity are therefore responsible for a high proportion of daily and annual food intake.

The acute and chronic effects of temperature on particle capture and water processing rates has received considerable attention, but the capacity of bivalves to achieve thermal independence through physiological regulations, remains controversial

(Bayne et al. 1977, Jørgensen et al. 1990, Jørgensen 1990, Hawkins and Bayne, 1992 and references cited). The acute temperature response of suspension-feeders results from a combination of independent biochemical and mechanical effects. Mechanical effects are caused by temperature-induced changes in seawater viscosity that affect particle capture by altering feeding currents and the capture of particles by feeding structures. This change in viscosity has been cited to account for a large proportion of the effects of temperature on feeding performance and is believed to limit the effectiveness of physiological compensation responses (Jørgensen et al. 1990, Podolsky 1994). This would indeed be the case if the animals were feeding at maximal capacity, however, given the observation that bivalves seldom utilize maximal feeding, there appears to be considerable scope for compensatory physiological responses to achieve thermal independence in feeding performance. In fact, the capacity for regulation of feeding behaviour to chronic temperature variations by *P. magellanicus* and *M. edulis* is apparent from the low correlation observed between ingestion rate and seasonal temperature changes (Chapter 5). The biochemical basis for temperature compensation involves the regulation of enzyme reaction rates (reviewed by Hawkins and Bayne 1992). The ability to acclimate feeding processes to relatively low seasonal temperatures appears to be a major reason why winter growth in mussels in Nova Scotia is more limited by food supplies, than by temperature (Mallet et al. 1987).

Bivalve communities in coastal waters must contend with large variations in the abundance and composition of food over time-scales ranging from minutes (Chapters 2 and 4) to seasons (Chapter 5). The observed high degree of flexibility in food acquisition responses over different time-scales may be an indication that bivalves regulate physiological processes to help compensate for dietary imbalances caused by a variable food supply. Regulation of feeding and absorption processes would permit tissue growth trends to be somewhat independent of food fluctuations. Indeed, multiple regression analysis showed daily ingestion rates to be independent of the food supply, but were driven by the combined effects of food availability and large seasonal changes in feeding behaviour. For example, high absorption rates of scallops and mussels in the spring were attributed primarily to high food availability (Figs. 5.2, 5.6 and 5.7), while the high absorption rates in the late-fall resulted from markedly increased clearance rates (Table 5.2). Food supplies in November were of relatively low quality (Fig. 5.3), but average clearance rates during this period were between four (scallops) and seven (mussels) time higher than rates averaged over the remainder of the 139 day study period. These data clearly show that annual food acquisition trends can be independent of the food supply as a result of the large capacity to modulate feeding behaviour. It has previously been assumed that the increase in mussel tissue growth in the fall (Mallet and Carver 1993) was the direct response of increased food availability supplied by the fall phytoplankton bloom. This may be the case in a typical year, but in the absence of a fall bloom, scallops and mussels can maintain high fall growth rates through physiological compensation.

This thesis has attempted to identify predictive relationships between food acquisition responses and environmental variables, including descriptors of food quantity and quality. Although scallop and mussel feeding behaviour appears to be highly responsive to food supplies in laboratory experiments (reviews by Bayne and Newell 1983, Griffiths and Griffiths 1987, Hawkins and Bayne 1992, Bayne 1998, Hawkins et al. 1998), no clear relationships were observed between tidal and seasonal variations in seston variables and clearance rate (Chapters 2, 4 and 5). It is important to note that all the studies conducted during this thesis were performed under conditions of relatively low seston concentrations. The total range in TPM at all study sites and periods was between 0.5 and 6 mg l^{-1}. Observations of significant changes in sea scallop and mussel feeding behaviour to variable seston quantity have been conducted over larger concentration ranges (e.g.; Cranford and Gordon 1992 [1-20 mg l^{-1}], Bacon et al. 1998 [1-15 mg l^{-1}], Hawkins et al. 1996 and 1998 [10-90 mg l^{-1}]). Laboratory experiments with sea scallops and mussels have also found significant differences in clearance rates that are attributed to seston quality (e.g. Cranford and Grant 1990, MacDonald and Ward 1994, Bacon et al. 1998, Hawkins et al. 1998), but the relation is not always clear and both positive (Cranford and Grant 1990, MacDonald and Ward 1994) and negative (Bacon et al. 1998) relationships have been reported for sea scallops. Although a wide range in seston quality was observed in the present studies (25-90% POM), the low correlation with ingestion rate must be interpreted in the context of the relatively low range of food availability. Data presented in Bacon et al. (1998) indicate that sea scallop clearance rate is independent of seston quality at low concentrations.

The general lack of correlation observed between ingestion rate and various descriptors of the food supply may also stem from: (1) the limited ability of the statistical methods to quantify complex interactions between multivariate forcing functions, many of which may cause a non-linear response; (2) the measurement of bulk seston variables that inadequately characterise food quality and the stimulatory/inhibitory properties of seston components on feeding behaviour; (3) the presence of time-averaged behaviour in which present feeding responses are determined by feeding history, (4) a feedback on feeding behaviour imposed by the regulation of digestive processes; and (5) the additional influence on the animal's energy balance, and concomitant compensatory feeding responses, of variable endogenous nutrient demands. Several of these factors are discussed further below.

The observation that bivalves exhibited substantially different feeding behaviour in July and November, despite similarly poor dietary conditions, indicates the presence of another important influence besides food quantity and quality. Bivalves undergo large seasonal variations in metabolic energy and nutrient demands associated with the changing biosynthesis requirements of the reproductive cycle. Biosynthesis is an energydemanding process and will cause large seasonal shifts in the animal's energy balance (Kreeger et al. 1996). Assuming that food acquisition behaviour is regulated to compensate for shifts in energy and/or nutrient gain (Hawkins and Bayne 1992, Bayne 1998), it is reasonable that the observed feeding and absorption responses were not solely controlled by food supplies, but were also influenced by reproductive demands.

7.4 REGULATION OF ABSORPTION.

Absorption efficiency (*AE*) of sea scallops was highly predictable based on short-term variations in diet quality, expressed as the POM, POC or PN content per unit weight of seston (Figs. 3.6, 4.9; Tables 3.3, 4.1). Notwithstanding concerns regarding the classification of complex particle regimes based on a single descriptor like POM (Grant and Bacher 1998), the close relationship between *AE* and POM suggests that this simple measurement is an appropriate descriptor of diet quality (Figs. 3.6, 4.9, Grant 1996). Large interspecific differences in the capacity of bivalve filter feeders to effectively absorb POM are evident from studies with *P. magellanicus* (Figs. 3.6 and 4.9), *M. edulis*, cockles (*Cerastoderma edule*), and oysters (*Crassostrea gigas*) (Bayne et al. 1987, Navarro et al. 1991, Hawkins et al, 1996, 1998, Hawkins et al. 1998). These differences in digestive capacity provide insight into the suitability of different habitats for each species. To illustrate this point, Figure 7.2 shows the theoretical consequence of sediment resuspension on food uptake for each species. The resuspension event observed

Figure 7.2

Theoretical consequences of a resuspension event on the absorption rate (*A*) of four species of bivalve filter feeders (Species: 1 - *Cerastoderma edule*; 2 - *Mytilus edulis*; 3 - *Placopecten magellanicus*; and 4 - *Crassostrea gigas*). To illustrate the effect of interspecific differences in absorption efficiency on food acquisition, clearance rate for standard sized individuals (1 g) was assumed to be constant (an arbitrary value was selected) with diet and between species. Relationships between absorption efficiency (*AE*) and the organic content of seston (POM) for each species are from Table 4.1 and Hawkins et al. (1998).

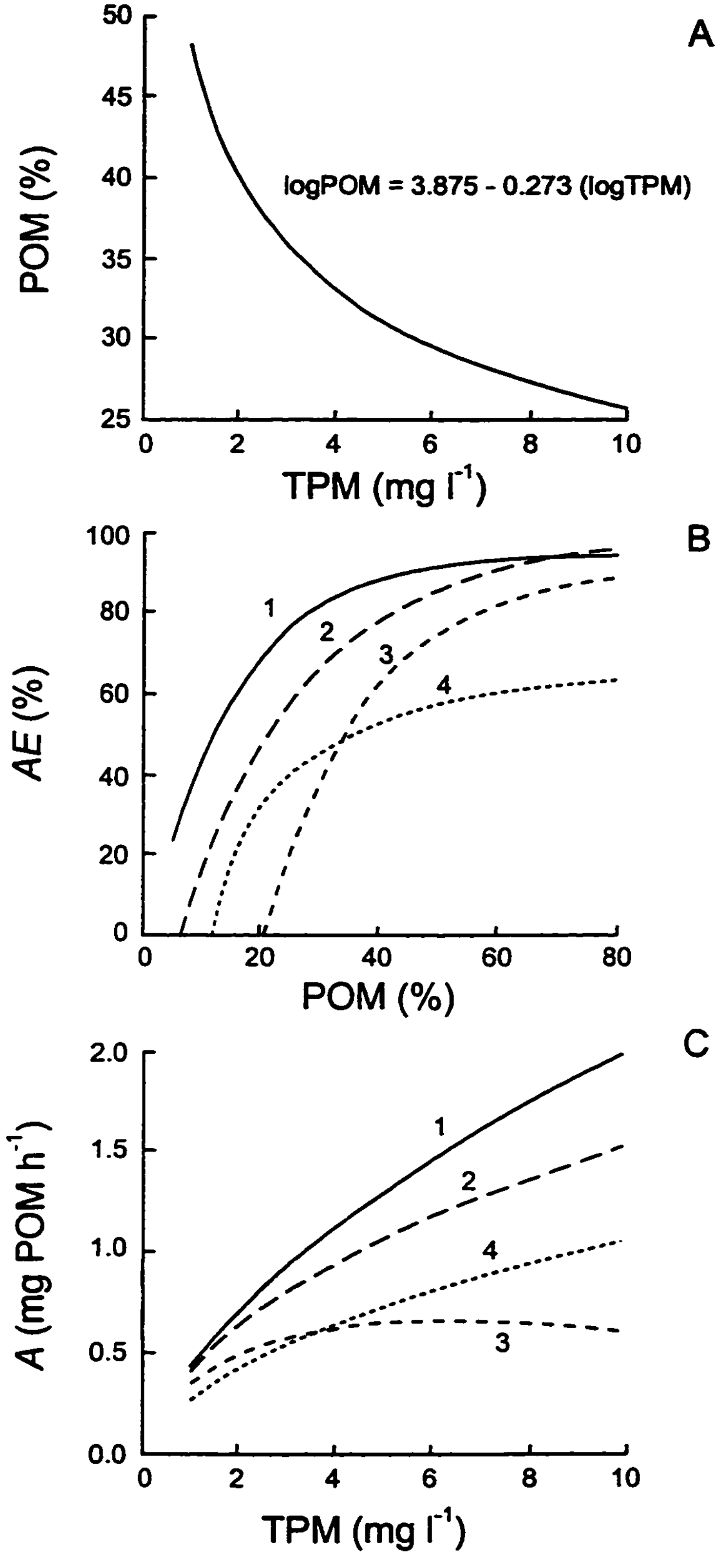
A
POM (%)
50
45
40
35
30
25
logPOM = 3.875 - 0.273 (logTPM)
0
2
4
6
8
10
TPM (mg l-1)
B
AE (%)
100
80
60
40
20
0
1
2
3
4
0
20
40
60
80
POM (%)
C
A (mg POM h-1)
2.0
1.5
1.0
0.5
0.0
1
2
4
3
0
2
4
6
8
10
TPM (mg l-1)

Figure 7.2

in Lunenberg Harbour (Fig 4.1) was used as an example. Equation 4.1 provided POM content estimates for TPM concentrations between 1 and 10 mg l^{-1} (Fig. 7.2A). *AE* at each POM value was then estimated from the relationships shown in Figure 7.2B. Clearance rate (*C*) was assumed to be constant (an arbitrary value of 1 l h^{-1} for 1 g animals was used) over this range of TPM, and for all species so that the effects of variable *AE* on absorption rate can be compared between each species. Absorption rates were calculated by multiplying POM ingestion rate (*C* x POM concentration) by *AE*.

P. magellanicus absorption rate remained relatively constant as TPM increased and POM content decreased (Fig. 7.2C), similar to the observed trend (Fig. 4.8). Higher concentrations would cause a sharp decline in POM absorption. However, as the other species are more effective at digesting low quality diets (Fig. 7.2B), they derive a benefit from the resuspension of bottom deposits. It should be noted that calculated and measured *A* values are not comparable owing to to the arbitrary and constant *C* values used in the calculations. What Figure 7.2 illustrates is that sea scallops have evolved digestive processes that limit their distribution to regions characterised by relatively high quality diets. The cockle, *C. edule*, is particularly well suited to turbid environments as it can utilize a large proportion of very low quality seston (Fig. 7.2B).

The absorption of nutrients during passage of food through the gut has been identified as the most important process in the regulation of an optimal balance between energy acquisition and expenditure (Bayne et al. 1993). Laboratory experiments described in Chapter 2 were designed to document short- and long-term changes in the magnitude of adaptation of absorptive processes in sea scallops resulting from a change in food quantity and quality. The scallops responded rapidly to the change in diet such that absorption efficiency of organic matter, carbon and nitrogen was maximized within six days (Fig. 3.4). The observed time-course for complete acclimation of digestive processes suggests that the regulation of absorption is of limited value for compensating for high-frequency (tide-induced) variations in the food supply. This conclusion was also reached from an interpretation of AE responses to tidal-cycle fluctuation in seston (Chapter 2). However, experiments in which food quality was varied over 12-h intervals showed that scallops regulated digestive processes to maximize AE to the lower quality diet and maintained this enhanced absorptive state (in terms of the capacity of enzyme systems to maximize absorption of ingested materials) during the periods when food quality improved (Fig. 3.4). Similarly, scallops that were starved or were maintained on a low quality diet for up to 12 days, exhibited a high absorptive state that permitted them to maximize absorption rate when the food supply improved (Fig. 3.3). This strategy of maintaining a high absorptive state when food is scarce, or of highly variable nutritional value, may be less wasteful energetically than a strategy in which the animal attempts to adjust digestive processes to every short-term change in the diet.

Seasonal observations of the change in the organic content of feces and the net AE of scallops and mussels held in Bedford Basin and Mahone Bay provide additional evidence of the high flexibility of absorptive processes (Chapter 5). When diet quality remained high, such as during the spring phytoplankton bloom, a high net AE can be achieved even when metabolic fecal losses are high (Figs. 5.6 and 5.7). Under these conditions, the bivalves exploited the diet by reducing absorption efficiency and the energy costs associated with digestion. This was evidenced by the gradual increase in organic losses to feces (Figs. 5.6 and 5.7). Similar observations of a decrease in AE after exposure to high quality food (microalgae) was observed in the laboratory (Fig. 3.3). When exposed to low food quality for extended periods, such as observed in the summer and late-fall (Fig 5.3), absorption processes are maximized, as indicated by the gradual decrease in feces organic content (Figs. 5.6 and 5.7). The results of this thesis, along with those of previous studies (Bayne et al. 1987, 1993), show that scallops and mussels display a high degree of control over the processes and efficiencies of digestion and absorption.

7.5 SYNOPSIS.

The new automated approach developed for continuously measuring food acquisition by bivalve filter feeders allows feeding and digestion parameters to be monitored with high precision under natural conditions of food supplies and particle flux. Measurements obtained using this *in situ* time-series method showed that periodic feeding events were responsible for a high proportion of daily and seasonal food intake. Observations of the high flexibility of feeding responses in sea scallops and blue mussels are not consistent with the theory of continuous and maximal feeding behaviour by bivalves in nature. The thermal acclimation capabilities of both species provide additional evidence to show that feeding behaviour is not controlled solely by physical constraints on particle capture. Seasonal changes in scallop and mussel food intake were largely independent of available food supplies as a result of variable feeding behaviour. Although current speeds were noted to have a significant effect on hourly clearance rate estimates for scallops, little of the variance in seasonal feeding responses could be explained by observed changes in measured environmental conditions. It appears that the seasonally changing energy and nutritional demands associated with the gametogenic cycle had a large influence on feeding behaviour at the study site. This is consistent with the hypothesis of Bayne (1993, 1998) and others that bivalves control physiological processes to compensate for shifts in net nutrient/energy gain.

Absorption efficiency proved to more predictable than feeding behaviour as it was closely related to short-term changes in the POM, POC and PN content of the seston. Bivalve growth is highly sensitive to small changes in AE (Grant and Bacher 1998) and growth models would benefit by incorporating this increased predictive knowledge. Scallops and mussels both exhibited a capacity for absorptive acclimation, giving the animals a high degree of control over absorption rate. AE in both species was regulated based on an 'exploitive' strategy in which AE was reduced when food quality was high and maximized when exposed to low or variable quality rations.

In conclusion, the combined results of the laboratory and field studies conducted for this thesis support the general hypothesis presented in Chapter 1 that food acquisition by bivalve filter feeders is driven not only by physical and morphological constraints on feeding, but also by a complex interplay between different time-scales of variation in oceanographic variables, the time-dependence of compensation capabilities and temporal variations in nutritional demands. Many current concepts regarding the role of bivalve communities in controlling particle flux and nutrient dynamics in coastal systems are largely based on the hypothesis of maximal and continuous feeding behaviour. These theories need to be revised as they generally do not account for the low clearance rates of natural seston or the seasonal dynamics of food utilization by bivalves. Incorporating observations of temporal variations in *in situ* feeding behaviour into ecosystem models would permit a more accurate assessment of the ecological impact of bivalve communities in coastal systems.

APPENDIX

Derivation of Equation 6.6

Actual and calculated ingestion rates are defined as

$$I_a = \frac{E_{ash}}{(F_{ash})_{retained}}, \tag{1}$$

$$I_c = \frac{E_{ash}}{(F_{ash})_{filtered}}, \tag{2}$$

where I_c and I_a are based on seston collected on membrane filters (GF/C) and retained by the bivalve, respectively. The F_{ash} terms are defined as

$$(F_{ash})_{retained} = \frac{(PIM)_{retained}}{(TPM)_{retained}}, \tag{3}$$

$$(F_{ash})_{filtered} = \frac{(PIM)_{filtered}}{(TPM)_{filtered}}, \tag{4}$$

where *PIM* and *TPM* are mass concentrations of particulate organic matter and total particulate matter, respectively. Equations 1 to 4 were combined to define the ratio

$$\frac{I_c}{I_a} = \frac{(PIM)_{retained}(TPM)_{filtered}}{(PIM)_{filtered}(TPM)_{retained}}. \tag{5}$$

Assume that particle size distributions for *PIM* and *TPM* follow the form

$$n\,(d) = Ad^{-4}, \tag{6}$$

where $n\,(d)$ is the number concentration of particles in the diameter d to $d + dd$, and A is concentration of some reference size. The mass concentration is then

$$m(d) = \frac{(\rho\pi A)}{6}d^{-1}, \tag{7}$$

where ρ is the density of the material in question. The mass in a size interval in the seston is

$$\frac{\rho\pi A}{6}\int_{di}^{dj} d^{-1}\,\mathrm{d}d, \tag{8}$$

which upon integration yields

$$\frac{\rho\pi A}{6}\ln d_j / d_i. \tag{9}$$

The mass in a size interval of ingested particles must account for differential retention of various particle sizes, so mass is given by

$$\frac{\rho\pi A}{6}\int_{di}^{dj} RE(d)d^{-1}\,\mathrm{d}d, \tag{10}$$

where *RE (d)* is the dimensionless retention efficiency. To solve for mass in a size interval in the diet it is assumed that

$$RE\,(d) = 0 \text{ if } d<d_r \text{ and } 1 \text{ otherwise}, \tag{11}$$

where d_r is the minimum diameter effectively retained by the bivalve. With this simple definition of *RE (d)*, mass on an interval in the diet becomes

$$\frac{\rho\pi A}{6}\ln d_j / d_r. \tag{12}$$

By assigning some diameters, Eq. 5 is rewritten in terms of particle diameters. Let

d_1 = smallest particle retained by filter,
d_2 = largest inorganic particle in the seston,
d_3 = largest particle in the seston.

With these definitions, the quantities in Eq. 5 become

$$(PIM)_{retained} = \frac{\rho_{PIM}\pi A_{PIM}}{6}\ln d_2 / d_r, \tag{13}$$

$$(PIM)_{filtered} = \frac{\rho_{PIM}\pi A_{PIM}}{6}\ln d_2 / d_1, \tag{14}$$

$$(TPM)_{retained} = \frac{\rho_{TPM}\pi A_{TPM}}{6}\ln d_3 / d_r, \tag{15}$$

$$(TPM)_{filtered} = \frac{\rho_{TPM}\pi A_{TPM}}{6}\ln d_3 / d_1, \qquad (16)$$

and Eq. 5 becomes

$$\frac{I_c}{I_a} = \frac{\ln d_2 / d_r \ln d_3 / d_1}{\ln d_2 / d_1 \ln d_3 / d_r}. \qquad \text{(Equation 6.6)}$$

REFERENCES

Asmus, R.M., and H. Asmus. 1991. Mussel beds: limiting or promoting phytoplankton. *J. Exp. Mar. Biol. Ecol.*, Vol. 148: 215-232.

Bacon, G.S., B.A. MacDonald, and J.E. Ward, 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. *J. Exp. Mar. Biol. Ecol.*, Vol. 219: 105-125.

Baldwin, I.G., and K.J.M. Kramer, 1994. Biological early warning systems (BEWS). In, *Biomonitoring of coastal waters and estuaries*, edited by K.J.M. Kramer, CRC Press, Inc., Boca Raton, Florida, pp. 1-28.

Barber, B.J., R. Getchell, S. Shumway, and D. Schick, 1988. Reduced fecundity in a deep-water population of the giant scallop *Placopecten magellanicus* in the Gulf of Maine, USA. *Mar. Ecol. Prog. Ser.*, Vol. 42, pp. 207-212.

Barillé, L., J. Prou, M. Héral, and S. Bourgrier, 1993. No influence of food quality, but ration-dependent retention efficiencies in the Japanese oyster *Crassostrea gigas*. *J. Exp. Mar. Biol. Ecol.* Vol. 17, pp. 91-106.

Bayne, B.L., 1993. Feeding physiology of bivalves: time-dependence and compensation for changes in food availability. In, *Bivalve filter feeders and marine ecosystem processes*, edited by R.F. Dame, NATO ASI series, Vol. G 33. Springer-Verlag, Berlin, pp. 1-24.

Bayne, B.L., 1998. The physiology of suspension feeding bivalve molluscs: an introduction to the Plymouth "TROPHEE" workshop. *J. Exp. Mar. Biol. Ecol.*, Vol. 219, pp. 1-19

Bayne, B.L., and J. Widdows, 1978. The physiological ecology of two populations of *Mytilus edulis* L. *Oecologia*, Vol. 37, pp. 137-162.

Bayne, B.L., and R.C. Newell. 1983. Physiological energetics of marine molluscs, p. 407-515. *In* K.M. Wilber and A.S. Saleuddin [eds.], *The Mollusca*, Vol. 4. Academic.

Bayne, B.L., J. Widdows, and C. Worrall, 1977. Some temperature relationships in the physiology of two ecologically distinct bivalve populations, pp. 379-400. *In* F.J.

Vernberg, A. Calabrese, F.P. Thurberg, and W. Vernberg [eds.], *Physiological responses of marine biota to pollutants*, Academic Press, New York.

Bayne, B.L., A.J.S. Hawkins and E. Navarro, 1987. Feeding and digestion by the mussel *Mytilus edulis* L. (Bivalvia:Mollusca) in mixtures of silt and algal cells at low concentrations. *J. Exp. Mar. Biol. Ecol.*, Vol. 111, pp. 1-22.

Bayne, B.L., A.J.S. Hawkins, and E. Navarro. 1988. Feeding and digestion in suspension-feeding bivalve molluscs: the relevance of physiological compensations. *Am. Zool.*, Vol. 28, pp. 147-159.

Bayne, B.L., A.J.S. Hawkins, E. Navarro, and I.P. Iglesias, 1989. Effects of seston concentration on feeding, digestion and growth in the mussel *Mytilus edulis*. *Mar. Ecol. Prog. Ser.*, Vol. 55: 47-54.

Bayne, B.L., J.I.P. Iglesias, A.J.S. Hawkins, E. Navarro, M. Heral, and J.M. Deslous-Paoli, 1993. Feeding behaviour of the mussel, *Mytilus edulis*: responses to variations in quantity and organic content of the seston. *J. mar. biol. Ass. U.K.*, Vol. 73, pp. 813-829.

Berg, J.A., and R.I.E. Newell, 1986. Temporal and spatial variations in the composition of seston available to the suspension feeder *Crassostrea virginica*. *Estuar. Coast. Shelf. Sci.*, Vol. 23, pp. 375-386.

Bricelj, V.M., and S. Shumway, 1991. Physiology: Energy acquisition and utilization. In, *Scallops: Biology, ecology and aquaculture*, edited by S.E. Shumway, Elsevier, Amsterdam, pp. 305-346.

Cadée, G.C. 1982. Tidal and seasonal variation in particulate and dissolved organic carbon in the western Dutch Wadden Sea and Marsdiep tidal inlet. *Neth. J. Sea Res.* Vol. 15, pp. 228-249.

Cahalan, J.A., S.E. Siddall, and M.W. Luckenbach, 1989. Effects of flow velocity, food concentration and particle flux on growth rates of juvenile bay scallops *Argopecten irradians*. *J. Exp. Mar. Biol. Ecol.*, Vol. 129, pp. 45-60.

Chanut, J-P., and S.A. Poulet, 1982. Short-term variability of the size spectra of suspended particles in a rapidly changing environment. *Estuar. Coastal Shelf Sci.*, Vol. 15, pp. 497-573.

Clausen, I., and H.U. Riisgård, 1996. Growth, filtration and respiration in the blue mussel, *Mytilus edulis*: no evidence for physiological regulation of the filter-pump. *Mar. Ecol. Prog. Ser.*, Vol. 141, pp. 34-45.

Cloern, J.E. 1982. Does the benthos control phytoplankton biomass in South San Francisco Bay? *Mar. Ecol. Prog. Ser.*, Vol. 9, pp. 191-202.

Cohen, R.R.H., P.V. Dresler, E.J.P. Phillips, and R.L. Cory, 1984. The effect of the asiatic clam, *Corbiculs fluminea*, on phytoplankton of the Potomac River, Maryland. *Limnol. Oceanogr.*, Vol. 29, pp. 170-180.

Cole, B.E., J.K. Thompson, and J.E. Cloern. 1992. Measurement of filtration rates by infaunal bivalves in a recirculating flume. *Mar. Biol.*, Vol. 113, pp. 219-225.

Cranford, P.J., 1994. Physiological compensation responses of sea scallops (*Placopecten magellanicus*) to fluctuations in the food supply and the presence of suspended inorganic matter. *Can. Tech. Rep. Fish. Aquat. Sci.*, No. 1994, pp. 190-199.

Cranford, P.J., 1995. Relationships between food quantity and quality and absorption efficiency in sea scallops *Placopecten magellanicus* (Gmelin). *J. Exp. Mar. Biol. Ecol.*, Vol. 189, pp. 124-142.

Cranford, P.J., and J. Grant, 1990. Particle clearance and absorption of phytoplankton and detritus by the sea scallop *Placopecten magellanicus* (Gmelin). *J. Exp. Mar. Biol. Ecol.*, Vol. 137, pp. 105-121.

Cranford, P.J., and D.C. Gordon Jr., 1992. The influence of dilute clay suspensions on sea scallop (*Placopecten magellanicus*) feeding activity and tissue growth. *Neth. J. Sea Res.*, Vol. 30, pp. 107-120.

Cranford, P.J, and B.T. Hargrave, 1994. *In situ* time-series measurement of ingestion and absorption rates of suspension-feeding bivalves: *Placopecten magellanicus* (Gmelin). *Limnol. Oceanogr.*, Vol. 39, pp. 730-738.

Cranford, P.J., C. W. Emerson, B.T. Hargrave, and T.G. Milligan, 1998. *In situ* feeding and absorption responses of sea scallops *Placopecten magellanicus* (Gmelin) to storm-induced changes in the quantity and composition of the seston. *J. Exp. Mar. Biol. Ecol.*, Vol. 219, pp. 45-70.

Dame, R.F., 1993. The role of bivalve filter feeder material fluxes in estuarine ecosystems, pp. 371-420. In, *Bivalve Filter Feeders in Estuarine and Coastal Ecosystem Processes*, edited by R.F. Dame, NATO ASI Series, Vol. G 33, Springer-Verlag, Heidelberg.

Dame, R.F. 1996. *Ecology of Marine bivalves: An ecosystem approach.* CRC Press, Boca Raton. pp. 1-579.

Dame, R.F., J.D. Spurrier, and R.G. Zingmark. 1992. In situ metabolism of an oyster reef. *J. Exp. Mar. Biol. Ecol.*, Vol. 164, pp. 147-159.

Dame, R., R. Zingmark, H. Stevenson, and D. Nelson. 1980. Filter feeder coupling between the estuarine water column and benthic subsystems, p. 521-526. *In* V.S. Kennedy [ed.], Estuarine perspectives. Academic.

Dickie, L.M., P.R. Boudreau, and K.R. Freeman. 1984. Influence of stock and site on growth and mortality in the blue mussel (*Mytilus edulis*). *Can. J. Fish. Aquat. Sci.*, Vol. 41, pp. 134-140.

Doering, P.H., and C.A. Oviatt. 1986. Application of filtration rate models to field populations of bivalves: an assessment using experimental mesocosms. *Mar. Ecol. Prog. Ser.* Vol. 31, pp. 265-275.

Eckman, J.E., C.H. Peterson, and J.A. Cahalan. 1989. Effects of flow speed, turbulence and orientation on growth of juvenile bay scallops, *Argopecten irradians concentricus* (Say). *J. Exp. Mar. Biol. Ecol.*, Vol. 132, pp. 123-140.

Eisma, D., and J. Kalf, 1987. Distribution, organic content and particle size of suspended matter in the North Sea. *Neth. J. Sea Res.*, Vol. 21, pp. 265-285.

Emerson, C.W., J. Grant, A. Mallet, and C. Carver, 1994. Growth and survival of sea scallops *Placopecten magellanicus*: effects of culture depth. *Mar. Ecol. Prog. Ser.*, Vol. 108, pp. 119-132.

Fegley, S.R., B.A. MacDonald, and T.R. Jacobsen, 1992. Short-term variation in the quantity and quality of seston available to benthic suspension feeders. *Estuar. Coast. Shelf Sci.*, Vol. 34, pp. 393-412.

Fielding, P.J., and C.L. Davis, 1989. Carbon and nitrogen resources available to kelp bed feeders in an upwelling environment. *Mar. Ecol. Prog. Ser.*, Vol. 55, pp. 181-189.

Foster-Smith, R.L., 1975. The effect of concentration of suspension and inert material on the assimilation of algae by three bivalves. *J. Mar. Biol. Assoc. U.K.*, Vol. 55, pp. 411-418.

Fréchette, M., and E. Bourget, 1985. Energy flow between the pelagic and benthic zones: factors controlling particulate organic matter available to an intertidal mussel bed. *Can. J. Fish. Aquat. Sci.*, Vol. 42, pp. 1158-1165.

Fréchette, M., and E. Bourget, 1987. Significance of small-scale spatio-temporal heterogeneity in phytoplankton abundance for energy flow in *Mytilus edulis*. *Mar. Biol.*, Vol. 94, pp. 231-240.

Fréchette, M., C. A. Butman, and W.R. Geyer, 1989. The importance of boundary-layer flows in supplying phytoplankton to the benthic suspension feeder, *Mytilus edulis* L. *Limnol. Oceanogr.*, Vol. 34, pp. 19-36.

Freeman, K.R., 1974. Growth, mortality and seasonal cycle of *Mytilus edulis* in two Nova Scotian embayments. *Tech. Rept. Fish. Mar. Ser.*, No. 500, 112 p.

Gallager, S.M., R.D. Turner, and C.J. Berg, 1981. Physiological aspects of wood consumption, growth and reproduction in the shipworm *Lyrodus pedicellatus* Quatrefages (Bivalvia:Teredinidae). *J. Exp. Mar. Biol. Ecol.*, Vol. 52, pp. 63-77.

Gallegos, C.l., and W.N. Vant, 1996. An incubation procedure for estimating carbon-to-chlorophyll ratios and growth-irradiance relationships of estuarine phytoplankton. *Mar. Ecol. Prog. Ser.*, Vol. 138, pp. 275-291.

Gilfillan, E.S., D. Mayo, S. Hanson, D. Donovan, and L.C. Jiang. 1976. Reduction to carbon flux in *Mya arenaria* caused by a spill of No. 6 fuel oil. *Mar. Biol.*, Vol. 37, pp. 115-123.

Gordon, D.C., P.J. Cranford, D.K. Muschenheim, J.W. Loder, P.D. Keizer, and K. Krank, 1992. Predicting the environmental impacts of drilling wastes on Georges Bank scallop populations. In, *Managing the environmental impact of offshore oil production*, edited by P.M. Ryan. Proceedings of the 32nd annual meeting of the Canadian Society of Environmental Biologists,St. John's, Newfoundland, Canada, pp. 139-147.

Grant, J., 1996. The relationship of bioenergetics and the environment to the field growth of cultured bivalves. *J. Exp. Mar. Biol. Ecol.*, Vol. 200, pp. 239-256.

Grant, J., and P.J. Cranford, 1991. Carbon and nitrogen scope for growth as a function of diet in the sea scallop *Placopecten magellanicus*. *J. mar. biol. Ass. U.K.*, Vol. 71, pp. 437-450.

Grant, J., and C. Bacher, 1998. Comparative models of mussel bioenergetics and their validation at field culture sites. *J. Exp. Mar. Biol. Ecol.*, Vol. 219, pp. 21-44.

Grant, J., M. Dowd, K. Thompson, C. Emerson and A. Hatcher. 1993. Perspectives on field studies and related biological models of bivalve growth and carrying capacity. In, *Bivalve filter feeders and marine ecosystem processes*, edited by R.F. Dame, NATO ASI series, Vol. G 33, Springer-Verlag, Berlin, pp. 371-420.

Griffiths, C.L., and R.J. Griffiths, 1987. Bivalvia. In, *Animal energetics, Vol. 2: Bivalvia through Reptilia*, edited by T.J. Pandian and F.J. Vernberg, Academic press, New York, pp. 1-88.

Grizzle, R.E., R. Langan, and W.H. Howell, 1992. Growth responses of suspension-feeding bivalve molluscs to changes in water flow: differences between siphonate and nonsiphonate taxa. *J. Exp. Mar. Biol. Ecol.*, Vol. 162, pp. 213-228.

Hargrave, B., G. Siddall, G. Steeves, and G. Awalt, 1994. A current-activated sediment trap. *Limnol. Oceanogr.* Vol. 39, pp.

Hatcher, A., J. Grant, and B. Schofield, 1997. Seasonal changes in the metabolism of cultured mussels (*Mytilus edulis* L.) from a Nova Scotian inlet: the effects of winter ice cover and nutritive stress. *J. Exp. Mar. Biol. Ecol.*, Vol. 217, pp. 63-78.

Hawkins, A.J.S., and B.L. Bayne, 1984. Seasonal variation in the balance between physiological mechanisms of feeding and digestion in *Mytilus edulis* (Bivalvia: Mollusca). *Mar. Biol.*, Vol. 82, pp. 233-240.

Hawkins, A.J.S., and B.L. Bayne, 1985. Seasonal variation in the relative utilization of carbon and nitrogen by the mussel *Mytilus edulis*: budgets, conversion efficiencies and maintenance requirements. *Mar. Ecol. Prog. Ser.*, Vol. 25, pp. 181-188.

Hawkins, A.J.S., and B.L. Bayne, 1992. Physiological interrelations, and the regulation of production, pp. 171-222. In, *The mussel Mytilus: ecology, physiology, genetics and culture,* edited by E. Gosling, Elsevier, Amsterdam.

Hawkins, A.J.S., B.L. Bayne, and K.R. Clarke, 1983. Co-ordinated rhythms of digestion, absorption and excretion in *Mytilus edulis* (Bivalvia: Mollusca). *Mar. Biol.*, Vol. 74, pp. 41-48.

Hawkins, A.J.S., P.N. Salkeld, B.L. Bayne, E. Gnaiger, and D.M. Lowe, 1985. Feeding and resource allocation in the mussel *Mytilus edulis*: evidence for time-averaged optimization. *Mar. Ecol. Prog. Ser.*, Vol. 20, pp. 273-287.

Hawkins, A.J.S., E. Navarro and J.I.P. Iglesias, 1990. Comparative allometries of gut content, gut passage time and metabolic faecal loss in *Mytilus edulis* and *Cerastoderma edule*. *Mar. Biol.*, Vol. 105, pp. 197-204.

Hawkins, A.J.S., R.F.M. Smith, B.L. Bayne and M. Héral, 1996. Novel observations underlying the fast growth of suspension-feeding shellfish in turbid environments: *Mytilus edulis*. *Mar. Ecol. Prog. Ser.*, Vol. 131, pp. 179-190.

Hawkins, A.J.S., B.L. Bayne, S. Bougrier, M. Héral, J.I.P. Iglesias, E. Navarro, R.F.M. Smith, and M.B. Urrutia, 1998. Some general relationships in comparing the feeding physiology of suspension-feeding bivalve molluscs. *J. Mar. Biol. Ecol.*, Vol. 219, pp. 87-103.

Herman, P.M.J., 1993. A set of models to investigate the role of benthic suspension feeders in estuarine ecosystems. In, *Bivalve filter feeders in estuarine and coastal ecosystem processes*, edited by R.F. Dame, NATO ASI series, Vol. G 33, Springer-Verlag, Berlin, pp. 421-454.

Hily, C., 1991. Is the activity of benthic suspension feeders a factor controlling water quality in the Bay of Brest? *Mar. Ecol. Prog. Ser.*, Vol. 69, pp. 179-188.

Holm-Hanson, O., C.J. Lorenzen, R.W. Holmes, and J.D.H. Strickland. 1965. Fluorometric determination of chlorophyll. *J. Cons. Int. Explor. Mer.*, Vol. 30, pp. 3-15.

Iglesias, J.I.P., E. Navarro, P. Alvarez Jorna, and I. Armentia, 1992. Feeding, particle selection and absorption in cockles *Cerastoderma edule* (L.) exposed to variable conditions of food concentration and quality. *J. Exp. Mar. Biol. Ecol.*, Vol. 162, pp. 177-198.

Iglesias, J.I.P., M.B. Urrutia, E. Navarro, P. Alvarez-Jorna, X. Larretxea, S. Bougrier, and M. Heral, 1996. Variability of feeding processes in the cockle *Cerastoderma edule* (L.) in response to changes in seston concentration and composition. *J. Exp. Mar. Biol. Ecol.*, Vol. 197, pp. 121-143.

Iglesias, J.I.P., M.B. Urrutia, E. Navarro, I. Ibarrola, 1998. Measuring feeding and absorption in suspension-feeding bivalves: an appraisal of the biodeposition method. *J. Exp. Mar. Biol. Ecol.*, Vol. 219, pp. 71-86.

Jones, D.S., M.A. Arthur, and D.J. Allard, 1989. Sclerochronological records of temperature and growth from shells of *Merceneria merceneria* from Narragansett Bay, Rhode Island. *Mar. Biol.*, Vol. 102, pp. 225-234.

Jϕrgenson, C.B. 1990. Bivalve filter feeding; hydrodynamics, bioenergetics, physiology and ecology. Olsen and Olsen.

Jørgenson, C.B., 1996. Bivalve filter feeding revisited. *Mar. Ecol. Prog. Ser.*, Vol. 142, pp. 287-302.

Jørgenson, C.B, P.S. Larsen, M. Møhlenberg, and H.U. Riisgård, 1988. The bivalve pump: properties and modelling. *Mar. Ecol. Prog. Ser.*, Vol. 45, pp. 205-216.

Jørgenson, C.B, P.S. Larsen, and H.U. Riisgård, 1990. Effects of temperature on the mussel pump. *Mar. Ecol. Prog. Ser.*, Vol. 64, pp. 89-97.

Kautsky, N., and S. Evans. 1987. Role of biodeposition by *Mytilus edulis* in the circulation of matter and nutrients in a Baltic coastal ecosystem. *Mar. Ecol. Prog. Ser.*, Vol. 38, pp. 201-212.

Kiϕrboe, T., and F. Mϕhlenberg, 1981. Particle selection in suspension-feeding bivalves. *Mar. Ecol. Prog. Ser.*, Vol. 5, pp. 291-296.

Kiϕrboe, T., F. Mϕhlenberg, and O. Nϕhr, 1980. Feeding, particle selection and carbon absorption in *Mytilus edulis* in different mixtures of algae and resuspended bottom material. *Ophelia*, Vol. 19, pp. 193-205.

Kirby-Smith, W.W., 1972. Growth of the bay scallop: The influence of experimental water currents. *J. Exp. Mar. Biol. Ecol.*, Vol. 8, pp. 7-18.

Kirby-Smith, W.W., and R.T. Barber, 1974. Suspension-feeding aquaculture systems: effects of phytoplankton concentration and temperature on growth of the bay scallop. *Aquaculture*, Vol. 3, pp. 135-145.

Kranck, K., and T.G. Milligan, 1992. Characteristics of suspended particles at an 11-hour anchor station in San Francisco Bay, California. *J. Geophysical Res.*, Vol. 97, pp. 11,373-11,382.

Kreeger, D.A., 1993. Seasonal patterns in utilization of dietary protein by the mussel *Mytilus trossulus*. *Mar. Ecol. Prog. Ser.*, Vol. 95, pp. 215-232.

Kreeger, D.A., A.J.S. Hawkins, B.L. Bayne, and D.M. Lowe, 1995. Seasonal variation in the relative utilization of dietary protein for energy and biosynthesis by the mussel *Mytilus edulis*. *Mar. Ecol. Prog. Ser.*, Vol. 126, pp. 177-184.

Langdon, C.J., and R.I.E. Newell, 1990. Utilization of detritus and bacteria as food sources by two bivalve suspension-feeders, the oyster *Crassostrea virginica* and the mussel *Geukensia demissa*. *Mar. Ecol. Prog. Ser.*, Vol. 58, pp. 299-310.

Levoie, R.E., D.J. Scarratt, K. Freeman, and B. Bradford, 1993. Shellfish culture in Nova Scotia, pp. 47-52. In: *The science review of the Bedford Institute of Oceanography, the Halifax Fisheries Research Laboratory and the St. Andrews Biological Station: 1990-91*. Published by the Department of Fisheries and Oceans, Scotia-Fundy Region.

Lehman, J.T., 1976. The filter-feeder as an optimal forager, and the predicted shapes of feeding curves. *Limnol. Oceanogr.*, Vol. 21, pp. 501-516.

Lenihan, H.S., C.H. Peterson, and J.M. Allen, 1996. Does flow speed also have a direct effect on growth of active suspension-feeders: An experimental test of oysters. *Limnol. Oceanogr.*, Vol. 41, pp. 1359-1366.

MacDonald, B.A., and R.J. Thompson, 1986. Influence of temperature and food availability on the ecological energetics of the giant scallop *Placopecten magellanicus*. III. Physiological ecology, the gametogenic cycle and scope for growth. *Mar. Biol.*, Vol. 93, pp. 37-48.

MacDonald, B.A., and J.E. Ward, 1994. Variations in food quality and particle selectivity in the sea scallop *Placopecten magellanicus* (Mollusca: Bivalvia). *Mar. Ecol. Prog. Ser.*, Vol. 108, pp. 251-264.

Mallet, A.L., C.E. Carver, S.S. Coffen, and K.R. Freeman. 1987. Winter growth of the blue mussel *Mytilus edulis* L.: importance of stock and site. *J. Exp. Mar. Biol. Ecol.*, Vol. 108, pp. 217-228.

Mallet, A.L,. and C.E.A. Carver. 1989. Growth, mortality, and secondary production in natural populations of the blue mussel, *Mytilus edulis*. *Can. J. Fish. Aquat. Sci.*, Vol. 46, pp. 1154-1159.

Mallet, A.L., and C.E.A. Carver, 1993. Temporal production patterns in various size groups of the blue mussel. *J. Exp. Mar. Biol. Ecol.*, Vol. 170, pp. 75-89.

Mann, K.H., 1982. Ecology of coastal waters, a systems approach. Blackwell, Oxford.

Mann, K.H., 1988. Production and use of detritus in various freshwater, estuarine, and coastal marine ecosystems. *Limnol. Oceanogr.*, Vol. 33, pp. 910-930.

Messieh, S.N., T.W. Rowell, D.L.Peer, and P.J. Cranford, 1991. The effects of trawling, dredging and ocean dumping on the eastern Canadian continental shelf seabed. *Con. Shelf Res.*, Vol. 11, pp. 1237-1263.

Milligan, T.G. and K. Krank, 1991. Electro-resistance particle size analyzers. In, *Theory, Methods and Applications of Particle Size Analysis*, pp. 109-118, edited by J.P.M. Syvitski, Cambridge University Press, New York.

Møhlenberg, F., and H.U. Riisgård. 1979. Filtration rate, using a new indirect technique, in thirteen species of suspension-feeding bivalves. *Mar. Biol.*, Vol. 54, pp. 143-147.

Morton, B.S., 1983. Feeding and digestion in bivalvia. In, *The Mollusca. Vol. 5, Physiology,* edited by A.S.M. Saleuddin and K.M. Wilbur, Academic Press, New York.

Muschenheim, D.K., 1987. The dynamics of near-bed seston flux and suspension-feeding benthos. J. Mar. Res. 45: 473-496.

Navarro, E., J.I.P. Iglesias, A. Perez Camacho, U. Labarta, and R. Beiras, 1991. The physiological energetics of mussels (*Mytilus galloprovincialis* Lmk) from different cultivation rafts in the Ria de Arosa (Galicia, N.W. Spain). *Aquaculture.*, Vol. 94, pp. 197-212.

Navarro, E., and J.I.P. Iglesias, 1993. Infaunal filter-feeding bivalves and the physiological response to short-term fluctuations in food availability and composition. In, *Bivalve filter feeders in estuarine and coastal ecosystem processes*, pp. 25-56, edited by R.F. Dame, NATO ASI series, Vol. G 33, Springer-Verlag, Berlin.

Navarro, E., J.I.P. Iglesias, and M.M. Ortega, 1992. Natural sediment as a food source for the cockle *Cerastoderma edule* (L.): effect of variable particle concentration on feeding, digestion and the scope for growth. *J. Exp. Mar. Biol. Ecol.*, Vol. 156, pp. 69-87.

Newell, C.R., D.E. Campbell, and S.M. Gallagher, 1998. Development of the mussel aquaculture lease site model MUSMOD©: a field program to calibrate model formulations. *J. Exp. Mar. Biol. Ecol.*, Vol. 219, pp. 143-169.

Newell, R.I.E., and S.J. Jordan, 1983. Preferential ingestion of organic material by the American oyster *Crassostrea virginica*. *Mar. Ecol. Prog. Ser.*, Vol. 13, pp. 47-53.

Nichols, F.H., 1985. Increased benthic grazing: an alternative explanation for low phytoplankton biomass in northern San Francisco Bay during the 1976-1977 drought. *Est., Coast. Shelf Sci.*, Vol. 21, pp. 379-388.

Officer, C.B., T.J. Smayda, and R. Mann, 1982. Benthic filter feeding: a natural eutrophication control. *Mar. Ecol. Prog. Ser.*, Vol. 9, pp. 203-210.

Page, H.M., and D.M. Hubbard, 1987. Temporal and spatial patterns of growth in mussels *Mytilus edulis* on an offshore platform: relationships to water temperature and food availability. *J. Exp. Mar. Biol. Ecol.*, Vol. 111, pp. 159-179.

Palmer, R., and L. Williams, 1980. Effect of particle concentration on filtration efficiency by the bay scallop *Argopecten irradians* and the oyster *Crassostrea virginica*. *Ophelia*, Vol. 19, pp. 163-174.

Podolsky, R.D., 1994. Temperature and water viscosity: physiological versus mechanical effects on suspension feeding. *Science*, Vol. 265, pp. 100-103.

Powell, E.N., E.E. Hofmann, J.M. Klink, and S.M. Ray. 1992. Modelling oyster populations I. A commentary on filtration rate. Is faster always better? *J. Shellfish Res.*, Vol. 11, pp. 387-398.

Prins, T.C., and A.C. Small, 1989. Carbon and nitrogen budgets of the mussel *Mytilus edulis* L. and the cockle *Cerastoderma edule* (L.) in relation to food quality. *Scientia Marina*, Vol. 53, pp. 477-482.

Prins, T.C., N. Dankers, and A.C. Smaal, 1994. Seasonal variation in the filtration rates of a semi-natural mussel bed in relation to seston composition. *J. Exp. Mar. Biol. Ecol.*, Vol. 176, pp. 69-86.

Prins, T.C., V. Escavarage, A.C. Smaal, and J.C.H. Peeters, 1995. Nutrient cycling and phytoplankton dynamics in relation to mussel grazing in a mesocosm experiment. *Ophelia*, Vol. 41, pp. 289-315.

Pyke, G.H., H.R. Pulliam, and E.L. Charnov, 1977. Optimal foraging: a selective review of theory and tests. *Q. Rev. Biol.*, Vol. 52, pp. 137-154.

Rhoads, D.C, L.F. Boyer, B.L. Wesh, and G.R. Hampson, 1984. Seasonal dynamics of detritus in the benthic turbidity zone (BTZ); implications for bottom-rack molluscan mariculture. *Bull. Mar. Sci.*, Vol. 35, pp. 536-549.

Rice, M.A. and J.A. Pechenik. 1992. A review of the factors influencing the growth of the northern quahog, *Mercenaria mercenaria* (Linnaeus, 1758). *J. Shellfish Res.*, Vol. 11, pp. 279-287.

Riemann, B., T.G. Nielsen, S.J. Horsted, P.K. Bjørsen, and J. Pock-Steen, 1988. Regulation of phytoplankton biomass in estuarine enclosures. *Mar. Ecol. Prog. Ser.*, Vol. 48, pp. 205-215.

Riisgård, H.U., 1988. Efficiency of particle retention and filtration rate in 6 species of Northeast American bivalves. *Mar. Ecol. Prog. Ser., Vol.* 45, pp. 217-223.

Riisgård, H.U., 1991. Filtration rate and growth in the blue mussel, *Mytilus edulis* Linnaeus, 1758: Dependence on algal concentration. *J. Shellfish Res.*, Vol. 10, pp. 29-35.

Riisgård, H.U., and F. Møhlenberg, 1979. An improved automatic recording apparatus for determining the filtration rate of *Mytilus edulis* as a function of size and algal concentration. *Mar. Biol.*, Vol. 52, pp. 61-67.

Riigård, H.U., and P.S. Larsen, 1995. Filter-feeding in marine macro-invertebrates: pump characteristics, modelling and energy cost. *Biol. Rev.*, Vol. 70, pp. 67-106.

Robinson, W.E., W.E. Wehling, M.P. Morse and, C. McLeod, 1981. Seasonal changes in soft-body component indices and energy reserves in the Atlantic deep-sea scallop, *Placopecten magellanicus*. *Fish. Bull.*, Vol. 79, pp. 449-458.

Shimeta, J., and P.A. Jumars, 1991. Physical mechanisms and rates of particle capture by suspension-feeders. *Oceanogr. Mar. Biol. Annu. Rev.*, Vol. 29, pp. 191-257.

Scholten, H., and A.C. Smaal, 1998. Responses of *Mytilus edulis* L. to varying food concentrations: testing EMMY, and ecophysiological model. *J. Exp. Mar. Biol. Ecol.*, Vol. 219, pp. 217-239.

Seiderer, L.J., and R.C. Newell, 1985. Relative significance of phytoplankton, bacteria and plant detritus as carbon and nitrogen resources for the kelp bed filter-feeder *Choromytilus meridionalis*. *Mar. Ecol. Prog. Ser.*, Vol. 22, pp. 127-139.

Seiderer, L.J., R.C. Newell and P.A. Cook, 1982. Quantitative significance of style enzymes from two marine mussels (*Choromytilus meridionalis* Krauss and *Perna perna* Linnaeus) in relation to diet. *Mar. Biol. Lett.*, Vol. 3, pp. 257-272.

Shumway, S.E., J. Barter, and J. Stahlnecker, 1988. Seasonal changes in oxygen consumption in the giant scallop, *Placopecten magellanicus* (Gmelin). *J. Shellfish Res.*, Vol. 7, pp. 77-82.

Smaal, A.C., and J. Widdows, 1994. The scope for growth of bivalves as an integrated response parameter in biological monitoring, pp. 247-262. In: Kramer, K.J.M., ed., *Biomonitoring of Coastal Waters and Estuaries*. CRC Press, Inc., Boca Raton, Florida.

Smaal, A.C., and A.P.M.A. Vonck, 1997. Seasonal variation in C, N and P budgets and tissue composition of the mussel *Mytilus edulis*. *Mar. Ecol. Prog. Ser.*, Vol. 153, pp. 167-179.

Smaal, A.C., A.P.M.A. Vonck, and M. Bakker, 1997. Seasonal variation in physiological energetics of *Mytilus edulis* and *Cerastoderma edule* of different size classes. *J. Mar. Biol. Ass. U.K.*, Vol. 77, pp. 817-838.

Stenton-Dozey, J.M.E., and A.C. Brown, 1992. Clearance and retention efficiency of natural suspended particles by the rock-pool bivalve *Venerupis corrugatus* in relation to tidal availability. *Mar. Ecol. Prog. Ser.*, Vol. 82, pp. 175-186.

Taghon, G.L., 1981. Beyond selection: optimal ingestion rate as a function of food value. *Amer. Nat.*, Vol. 118, pp. 202-214.

Thompson, R.J., 1977. Blood chemistry, biochemical composition, and the annual reproductive cycle in the giant scallop, *Placopecten magellanicus*, from Southeast Newfoundland. *J. Fish. Res. Board Can.*, Vol. 34, pp. 2104-2116.

Thompson, R.J., 1984. The reproductive cycle and physiological ecology of the mussel *Mytilus edulis* in a subarctic, non-estuarine environment. *Mar. Biol.*, Vol. 79, pp. 277-288.

Urrutia, M.B., J.I.P. Iglesias, E. Navarro, and J. Prou, 1996. Feeding and absorption in

Cerastoderma edule under environmental conditions in the Bay of Marennes-Oleron (Western France). *J. Mar. Biol. Assoc. U.K.*, Vol. 76, pp. 431-450.

Vahl, O., 1980. Seasonal variations in seston and in the growth rate of the Iceland scallop, *Chlamys islandica* (O.F. Müller) from Bassfjord, 70°N. *J. Exp. Mar. Biol. Ecol.*, Vol. 48, pp. 195-204.

Walne, P.R. 1972. The influence of current speed, body size and water temperature on the filtration rate of five species of bivalve. *J. Mar. Biol. Assoc. UK.* Vol. 52, pp. 345-374.

Ward, J.E., H.K. Cassell, and B.A. MacDonald. 1992. Chemoreception in the sea scallop *Placopecten magellanicus* (Gmelin). I. Stimulatory effects of phytoplankton metabolites on clearance and ingestion rates. *J. Exp. Mar. Biol. Ecol.*, Vol. 163, pp. 235-250.

Ward, J.E., B.A. MacDonald, R.J. Thompson, and P.G. Beninger, 1993. Mechanisms of suspension feeding in bivalves: resolution of current controversies by means of endoscopy. *Limnol. Oceanogr.*, Vol. 38, pp. 265-272.

Widdows, J., and B.L. Bayne, 1971. Temperature acclimation of *Mytilus edulis* with reference to its energy budget. *J. Mar. Biol. Assoc. U.K.*, Vol. 51, pp. 827-843.

Widdows, J., P. Fieth, and C.M. Worrall, 1979. Relationships between seston, available food and feeding activity in the common mussel *Mytilus edulis*. *Mar. Biol.*, Vol. 50, pp. 195-207.

Wildish, D.J. and D.D. Kristmanson, 1985. Control of suspension feeding bivalve production by current speed. *Helgol. Meersunters.*, Vol. 39, pp. 237-243.

Wildish, D.J., and D.D. Kristmanson, 1988. Growth response of giant scallops to periodicity of flow. *Mar. Ecol. Prog. Ser.*, Vol. 42, pp. 163-169.

Wildish, D.J., and D.D. Kristmanson, 1997. Benthic suspension feeders and flow. Cambridge University Press, Cambridge, UK, pp. 1-409.

Wildish, D.J., and Miyares, M.P. 1990. Filtration rate of blue mussels as a function of flow velocity: preliminary experiments. *J. Exp. Mar. Biol. Ecol.*, Vol. 142, pp. 213-219.

Wildish, D.J., and A.M. Saulnier, 1993. Hydrodynamic control of filtration in *Placopecten* *magellanicus*. *J. Exp. Mar. Biol. Ecol.*, Vol. 174, pp. 65-82.

Wildish, D.J., D.D. Kristmanson, R.L. Hoar, A.M. DeCoste, S.D. McCormick, and A.W. White, 1987. Giant scallop feeding and growth responses to flow. *J. Exp. Mar. Biol. Ecol.*, Vol. 113, pp. 207-220.

Wilkinson, L., 1992. SYSTAT for Windows: Statistics, Version 5 Edition. Evanston, IL: SYSTAT, Inc. 750 pp.

Wilkinson, L., G. Blank, and C. Gruber, 1996. *Desktop Data Analysis with SYSTAT.* Prentice Hall, New Jersey, 798 p.

Willows, R.I., 1992. Optimal digestive investment: A model for filter-feeders experiencing variable diets. *Limnol. Oceanogr.*, Vol. 37, pp. 829-847.

Winter, J.E., 1978. A review of knowledge of suspension-feeding in lamellibranchiate bivalves, with special reference to artificial aquaculture systems. *Aquaculture* Vol. 13, pp. 1-33.

Zeitschel, B., P. Diekmann, and A. Uhlmann. 1978. A new multisample sediment trap. *Mar. Biol.*, Vol. 45, pp. 285-288.

IMAGE EVALUATION
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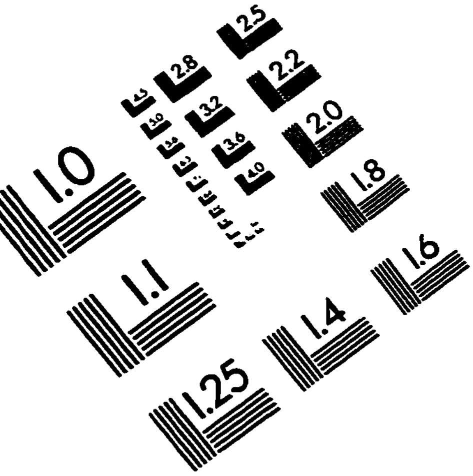

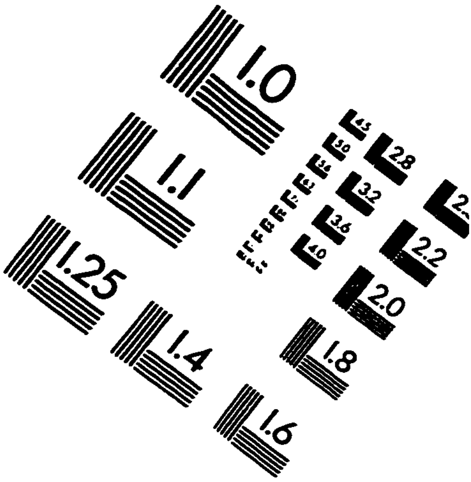

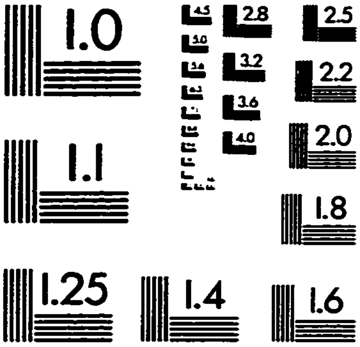

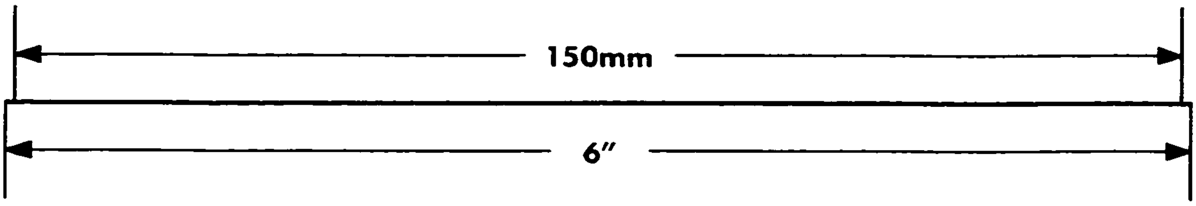

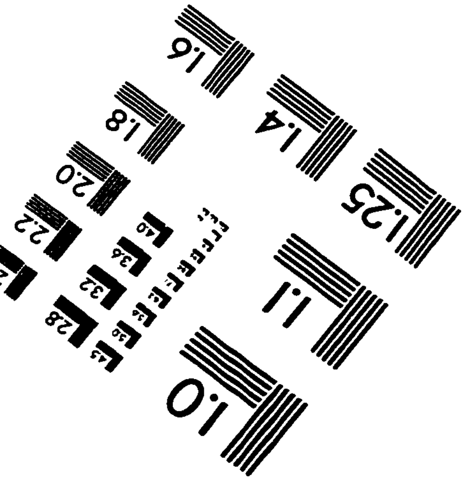

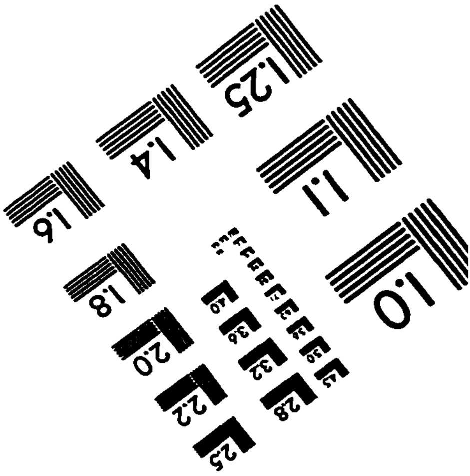

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