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Seasonal variation in food utilization by the suspension-feeding bivalve molluscs *Mytilus edulis* and *Placopecten magellanicus*

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ABSTRACT: Seston utilization by adult *Mytilus edulis* and *Placopecten magellanicus* cohorts was measured using an *in situ* method over a total period of 139 d 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 during the study varied between 30 (summer) and 90% (spring) organic content. 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 changes in seston utilization and related growth were 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 absorption 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 observed clearance behaviour. Clearance rate predictions based on algal cell rations greatly overestimated *in situ* clearance at all times of the year and appear to be of limited application for predicting feeding activity in nature. Current theories on the ecological role of bivalve communities in coastal regions are questionable as they commonly depend on the assumption that clearance capacity is fully exploited.

KEY WORDS: Physiological ecology · Suspension-feeding · Absorption · Bivalve molluscs · Natural seston

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, Prins et al. 1998). Numerous speculations on the capacity of dense bivalve communities to control phytoplankton and seston at the coastal ecosystem scale (e.g. Cloern 1982, Officer et al. 1982, Nichols 1985, Hily 1991,

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Dame & Prins, 1998, reviews by Dame 1993, 1996) are based largely on a much simpler modelling approach which conforms to the theory advanced by Jørgensen (1990, 1996) that water processing by bivalve filter-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 & Newell 1983, Griffiths & Griffiths 1987, Hawkins & Bayne 1992, Bayne 1998) and observations that natural seston is generally cleared at much lower rates than pure algal cell suspensions (Doering & Oviatt 1986, Riemann et al. 1988, Cranford & Gordon 1992, Iglesias et al. 1992, Navarro et al. 1992, Cranford & Hargrave 1994, Prins et al. 1994, Hawkins et al. 1996). Jørgensen, however, maintains in a recent review (1996) that clearance values below capacity 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 & Larsen 1995, Clausen & Riisgård 1996).

Confidence in feeding behaviour and growth models, whether developed for eutrophication and 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 4 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 & Vonck (1997) did not detect a relationship between clearance rate and reproductive condition in *M. edulis*.

Few studies have been conducted on 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 & Widdows 1978, Widdows et al. 1979, MacDonald & Thompson 1986, Kreeger 1993, Prins et al. 1994, 1995, Kreeger et al. 1995, Smaal & Vonck 1997, Smaal et al. 1997). The present study utilizes the *in situ* biodeposition approach of Cranford & 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 (hours to days). Daily measurements of food utilization by *Mytilus edulis* and sea scallop *Placopecten magellanicus* cohorts were obtained during the present study. In addition to permitting automated 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 short-term variations in feeding/digestion responses that may be attributed to endogenous rhythms, exogenous influences, and inter-individual variability (Hawkins & Bayne 1992, Cranford & Hargrave 1994, Cranford et al. 1998). The observed high precision of the *in situ* method (SE < 4% of mean responses; Cranford 1998) is attributed to each measurement representing the integrated average response of a cohort of bivalves over each sampling interval.

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 abundance and composition (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. Furthermore, *in situ* clearance rate estimates for each species were compared with potential clearance rates calculated using *in vivo* clearance rate models to explore the hypothesis of Jørgensen (1990, 1996) and others that bivalve filter feeders exploit the full capacity of the 'filter-pump' in nature.

MATERIALS AND METHODS

Experimental conditions. Time-series of scallop and mussel feeding and digestion responses were obtained over a total period of 139 d during the spring, summer and fall of 1995. Daily estimates of clearance, ingestion and absorption rates and absorption efficiency were determined according to the sequentially sampling biodeposition method described in Cranford & Har-

grave (1994) and Cranford et al. (1998). A new type of sediment trap was designed and constructed specifically for bivalve studies (Fig. 1). Improvements over the trap described in Cranford & Hargrave (1994) include an increase in the number of sample cups from 14 to 39, weight and height reductions, 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. 1) to remove the need to tie the animals in place (see Fig. 1 of Cranford & Hargrave 1994). Three identical traps were constructed so that 2 of them could be used to monitor bivalve biodeposition (1 for each species) while a third trap could serve as a control measuring natural particle sedimentation (no animals).

The 3 traps were deployed for 40 d periods on 4 separate occasions (Table 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 1 d delayed start to allow the animals an opportunity to recover from any handling stress.

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 Scotia, and held in pearl nets at the study site for approximately 1 mo prior to being transferred to the sediment trap cages. The Graves Shoal, Mahone Bay site is adjacent to a bivalve 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 (±0.01 g). 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

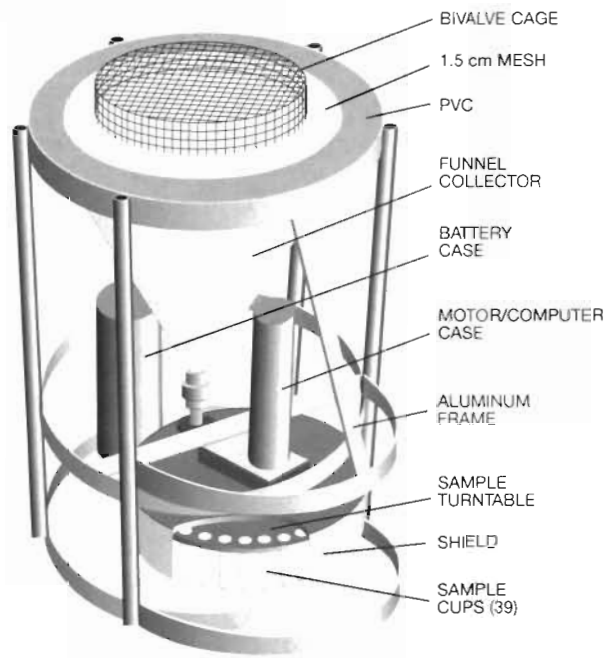

Fig. 1. The sediment trap used to collect sequential samples of faeces produced by a cohort of bivalves. The trap is 1.0 m high with an aperture area of 0.29 m^2 and a capacity to collect 39 faeces samples in 50 ml cups containing a dense preservative (0.1% wt/vol HgCl in 35‰ NaCl). The animals under 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

Table 1. Timing of environmental sensor and sediment trap deployments at the 2 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 parentheses are ±1 SD. BB: Bedford Basin; MB: Mahone Bay

	BB	MB1	MB2	MB3
Duration:	Apr 21–May 30	Jun 14–Jul 21	Sep 15–Oct 24	Oct 27–Dec 4
Start/end time (h):	12:00	12:00	12:00	12:00
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)

experiment is given in Table 1. The same cohort of animals was used during the final 2 Mahone Bay sampling periods (August to December).

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* (chl *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), chl *a*, organic carbon (POC) and nitrogen (PN) concentrations were determined for seston filtered onto 1.2 µm filters (Whatman GF/C) according to Cranford & 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 & 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 2 min prior to size analysis using an ultrasonic sapphire-tipped probe (Misonix®).

Physiological rates and efficiencies. Daily weight-specific egestion rate (mg dry weight g^{-1} dry tissue 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^{-1} dry tissue d^{-1}) was calculated according to Cranford & Hargrave (1994) as:

$$I_T = E_{ash}/F_{ash} \quad (1)$$

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. Gut passage times reported for *Mytilus edulis* and *Placopecten magellanicus* are shorter than the daily sampling periods (Hawkins et al. 1990, Cranford et al. 1998), so no correction was made to I_T calculations for the time lag between food ingestion and egestion (see Cranford et al. 1998). As the deposition of pseudofaeces into sample cups would have caused I_T estimates to be underestimated (Cranford et al. 1998), the contents of each sample cup were examined to confirm the absence of pseudofaeces, which is readily distinguishable from faeces.

Ingestion 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 *Placopecten magellanicus* (Cranford & Grant 1990) and 3 µm for *Mytilus edulis* (Riisgård 1988). Ingestion rates obtained for sea scallops using Eq. (1) may be susceptible to significant error if a high proportion of total inorganic seston grains are between 1 and 5 µm diameter. The magnitude of error therefore depends on the size distributions of seston and inorganic particles.

A quantitative analysis of potential error in ingestion rates was performed by calculating the retainable fractions of inorganic and total particles assuming conventional size distributions for PIM and TPM and using a simple diameter-dependent expression for retention efficiency. The degree of error in ingestion rate estimates was assessed by calculating the ratio of calculated (I_c) and actual (I_a) particle ingestion rates as

$$\frac{I_c}{I_c} = \frac{\ln d_2/d_r \ln d_3/d_1}{\ln d_2/d_1 \ln d_3/d_r} \quad (2)$$

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 derivation of this equation is given in the Appendix. The quantitative effect of a variable size distribution of particles on sea scallop (potential for error is greater than for mussels) ingestion rate calculations was examined using a wide range of values for d_2 and d_3. Considering that a simplistic expression for retention efficiency was used to derive Eq. (2) (retention efficiency is 0 for particles smaller than d_r), a value of 3 µm was used for d_r to account for ~50% retention by sea scallops of particles between 1 and 5 µm.

Clearance rate (C: l g^{-1} dry weight 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 to Cranford & Hargrave (1994). Absorption rates (mg POM g^{-1} d^{-1}) were estimated as the product of daily POM ingestion rate and AE_{POM}.

Potential clearance rates. *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 *C* (filtration) models. Potential *C* estimates were divided into 2 categories (Table 2). The first category included models derived from observations in which bivalves were fed optimal concentrations of cultured microalgae in the laboratory. These measurements represent the full capacity of the filter pump, and are referred to here as 'clearance capacity' models. These models have frequently been applied in the calculation of population and community clearance rates (e.g. Cloern 1982, Officer et al. 1982, Cohen et al. 1984, Nichols 1985, Fréchette et al. 1989, Hily 1991, Dame & Prins 1998, Meeuwig et al. 1998). For *Mytilus edulis*, allometric equation parameters reported in Table 2 are based on Riisgård & Møhlenberg (1979), and were confirmed by Riisgård (1991). As no direct observations are available for *Placopecten magellanicus* fed optimal diets, potential *C* was calculated using a generic equation (Table 2) that represents the average response of 5 species of bivalve filter feeders (Møhlenberg & Riisgård 1979). These authors observed scallop (*Pecten furtivus* and *P. opercularis*) *C* to be about twice the rate predicted using this model so potential *C* for *P. magellanicus* was increased by a factor of 2 (H. U. Riisgård pers. comm.). Jørgenson et al. (1990) and Riisgård (1991) reported that bivalves fed optimal algal cell diets in the laboratory respond to temperature changes, and a Q_{10} of 2 was employed (Jørgenson et al. 1990) to correct potential *C* measured at 10 to 15°C to temperatures observed in the present study.

The second category of potential *C* estimates, referred to here as 'natural diet' predictions, are based on the average allometric equations of MacDonald & Thomp-

Table 2. Average weight-specific clearance rate (*C*, l g^{-1} dry weight 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* (B). Daily model predictions for both species were averaged over the total 139 d sampling period. *W*: dry tissue weight (g), *L*: shell length (mm), and *T*: temperature (°C)

Category and source	Species	Sampling site and period BB Apr–May	MB1 Jun–Jul	MB2 Aug–Oct	MB3 Oct–Dec	Mean (n = 139)
(A) *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
(B) 'Clearance Capacity' Models						
Möhlenberg & Riisgård (1979); 6.96 $W^{0.67}$, $Q_{10} = 2$						
	P. m[a]	4.822	4.584	8.836	6.374	6.154
	M. e	3.152	3.463	6.474	4.662	4.276
Riisgård & Möhlenberg (1979)[b]; $0.85(W \times 10^3)^{0.72} \times 0.06$, $Q_{10} = 2$						
	M. e	3.521	3.856	7.124	5.167	4.741
Powell et al. (1992); $-1.199 + 0.121(L) + 8.165 \times 10^{-5}(L^2)$						
	P. m	1.616	1.184	1.599	1.391	1.439
	M. e	2.980	3.179	4.105	3.757	3.451
(C) 'Natural Diet' Models						
MacDonald & Thompson (1986); 0.94 $W^{0.67}$						
	P. m	0.507	0.446	0.498	0.476	0.481
Smaal et al. (1997); 1.52 $W^{0.51}$						
	M. e	0.903	0.931	1.043	0.974	0.956
Doering & Oviatt (1986)[a]; $(\{[(L/10)^{0.96}](T^{0.95})\}/2.95) \times 0.06$						
	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); $-0.074 + 0.013(L) + 1.796 \times 10^{-4}(L^2)$						
	P. m	0.403	0.303	0.405	0.351	0.363
	M. e	0.696	0.742	0.957	0.899	0.813

[a]Model prediction increased by factor of 2 (see text)
[b]The 0.06 factor converts model output in units of ml $ind.^{-1}$ min^{-1} to l $ind.^{-1}$ h^{-1}

son (1986) for *Placopenten magellanicus* and Smaal et al. (1997) for *Mytilus edulis* (Table 2). Model parameters reported by Smaal et al. (1997) are similar to the average values suggested for suspension-feeding bivalves by Bayne & 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 fed natural diets (Widdows & Bayne 1971, Bayne & Newell 1983, Smaal et al. 1997, B. MacDonald pers. comm.). The *C* equation of Doering & Oviatt (1986) was employed as a generic bivalve model for predicting *C* responses to natural diets. This equation accounts for the effects of both body size and temperature on *C*. While this model was developed specifically for the hard clam *Mercenaria mercenaria*, it has also 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 2 curves to data from a wide range of bivalve filter feeders. These generic equations are given in Table 2, with the 'high gear' and 'low gear' models presented in the 'clearance capacity' and 'natural diet' categories, respectively (Table 2B,C).

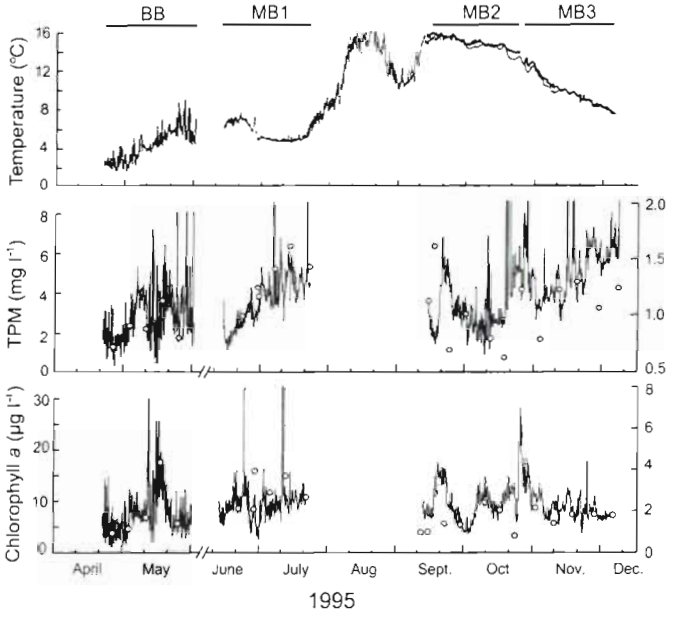

Fig. 2. Time-series of environmental data from *in situ* instruments in Bedford Basin (BB; 5 m depth) and Graves Shoal, Mahone Bay (MB; 12.7 m depth). Horizontal lines at the top of the figure identify the sites and timing of the 4 instrument deployment periods listed in Table 1. Seawater temperatures 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 chl *a* concentrations were measured at 1 h intervals with moored instruments. Results from the analysis of water samples (o) 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)

Statistical analysis. All statistical tests were performed at $\alpha = 0.05$ with SYSTAT Version 6.1 (SPSS, Inc., Chicago, IL). Prior to performing any analysis, each variable was screened for normality and homoscedasticity 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).

It was necessary to normalise ingestion rates of both species with a log transformation. Environmental variables significantly related to scallop and mussel ingestion rates were identified from a Pearson correlation matrix using Bonferroni-adjusted probabilities. 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.

RESULTS

Environmental conditions

The experimental animals held in Bedford Basin and Mahone Bay were exposed to seawater 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 2 Mahone Bay sites during the MB2 and MB3 sampling periods showed similar temperature time-series (Fig. 2). Salinity at 5 m depth in Bedford Basin was between 28.0 and 30.5 psu and current speeds averaged 3.8 cm s^{-1} (SD = 4.1 cm s^{-1}). Salinity at the Graves Shoal, Mahone Bay site was

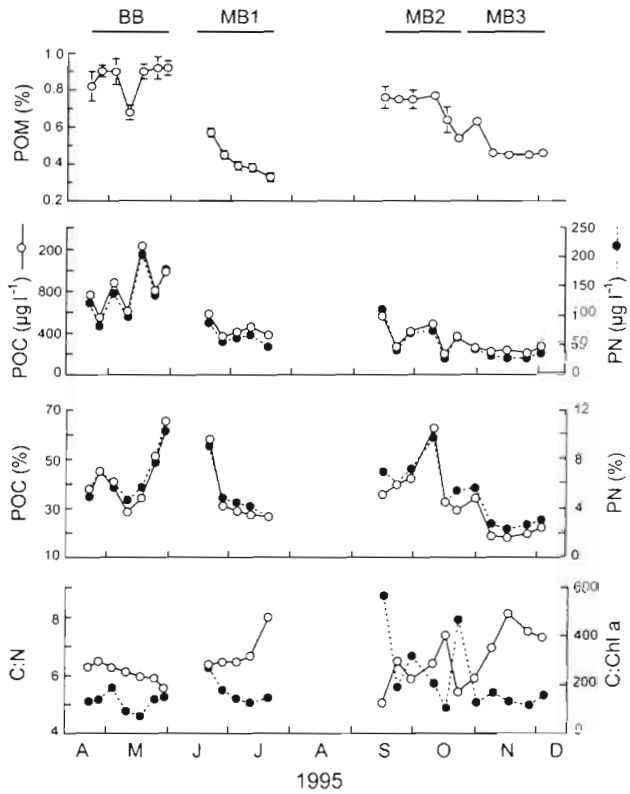

Fig. 3. Composition of seston collected at approximately weekly intervals from 5 m depth in Bedford Basin (BB) and 12.7 m depth in Mahone Bay (MB). Horizontal lines at the top of the figure designate the periods sampled during each instrument deployment. POM: particulate organic matter (mean ± SD); POC: particulate organic carbon; PN: particulate nitrogen; C:chl *a*: ratio of carbon to chl *a*; and C:N: ratio of POC to chl *a*. Percent of total seston was calculated from total particulate matter (TPM) data shown in Fig. 2

higher (30.5 ± 0.13 psu) than at the Bedford Basin site and current speeds were lower (2.4 ± 0.9 cm s^{-1}).

Hourly *in situ* fluorometer and transmissometer data from both sites were converted to chl *a* and TPM concentrations, respectively, using regression equations describing the relationship between instrument voltage output and data on chl *a* ($r^2 = 0.770$, $p < 0.001$) and TPM ($r^2 = 0.745$, $p < 0.001$) concentrations in water samples were collected weekly with Niskin bottles. A phytoplankton bloom was observed in Bedford Basin between May 10 and 20 when chl *a* levels reached 30 µg l^{-1} (Fig. 2). Chlorophyll concentrations at the Mahone Bay site were lower than in Bedford Basin (note the different vertical scales used in Fig. 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 µg l^{-1} in late October (Fig. 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 chl *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. 3).

Several estimates of seston quality were calculated to assess the nutritive value of the seston for experimental animals. Large variations in the POM, POC, and PN content of seston were observed both within and between the 2 sites (Fig. 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:chl *a* 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 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 a values averaged 226 (SD = 142).

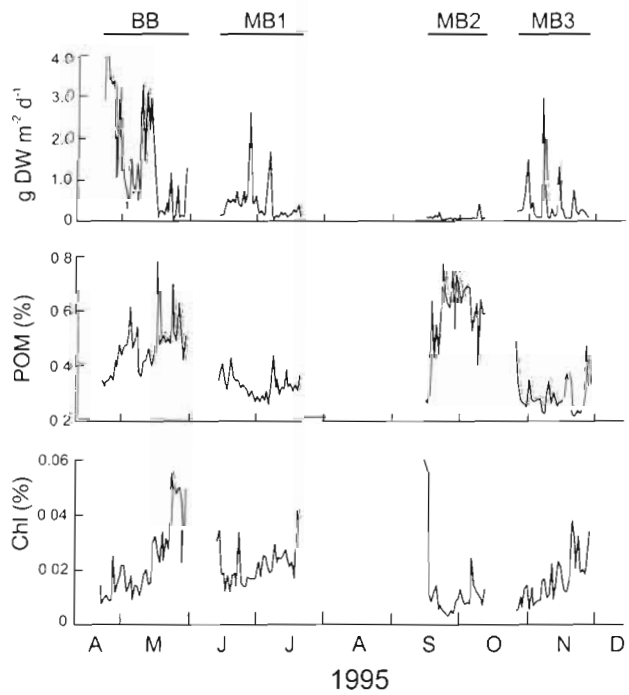

Fig. 4. Daily sedimentation rates of particulate matter (DW: dry weight) and the organic (POM) and chl *a* content of settled material collected at 5 m depth in Bedford Basin (BB) and at 12.7 m depth in Mahone Bay (MB) by the sediment traps described in the text. Data are plotted at the midpoint of each daily sampling interval

Daily vertical particle flux and settled particle composition data, shown in Fig. 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 d, 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. 2 & 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. The chl *a* content of settled particles increased during the spring bloom and continued to increase after the bloom subsided (Fig. 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 Fig. 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 in both Bedford Basin and Mahone Bay. The May phytoplankton bloom in Bedford Basin coincided with a high proportion of particle concentrations in the 9 to 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 to 12 µm range between September and December (Fig. 5).

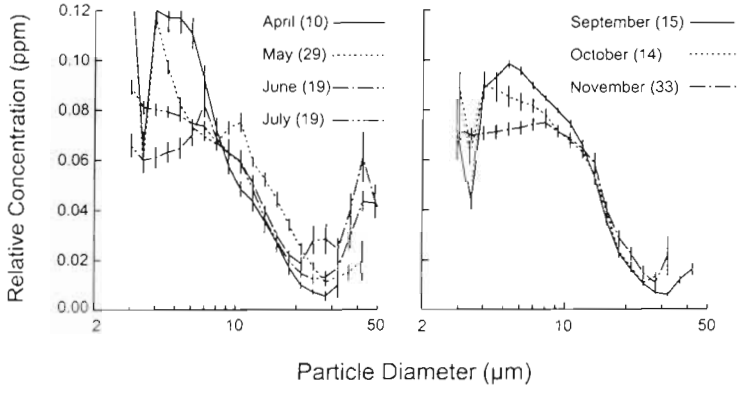

Fig. 5. Grain size distributions obtained by Coulter Multisizer analysis of disaggregated sediment collected by the control (no animals) sediment trap. Particle concentrations, relative to total concentration, are an average (±1 SE) of all daily samples (sample size given) collected within the indicated monthly period. April and May data are from Bedford Basin and all other data are from Mahone Bay

Bivalve growth and physiological responses

Sea scallop biomass increased during all sampling periods (Table 1), with gonad development accounting for the majority of total tissue growth (73%) during the spring 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 1).

Averaged over each instrument deployment period (Table 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 d during MB2 and after 34 d 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. Observations of sedimented material collected in sample cups under animals showed that pseudofaeces were not present in detectable amounts.

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. 6 & 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 throughout the year and ranged between 20 and 70% of total dry weight (Figs. 6 & 7). Mussels and scallops generally produced faeces of similar organic content, except during MB2 when the organic content of mussel faeces was relatively high.

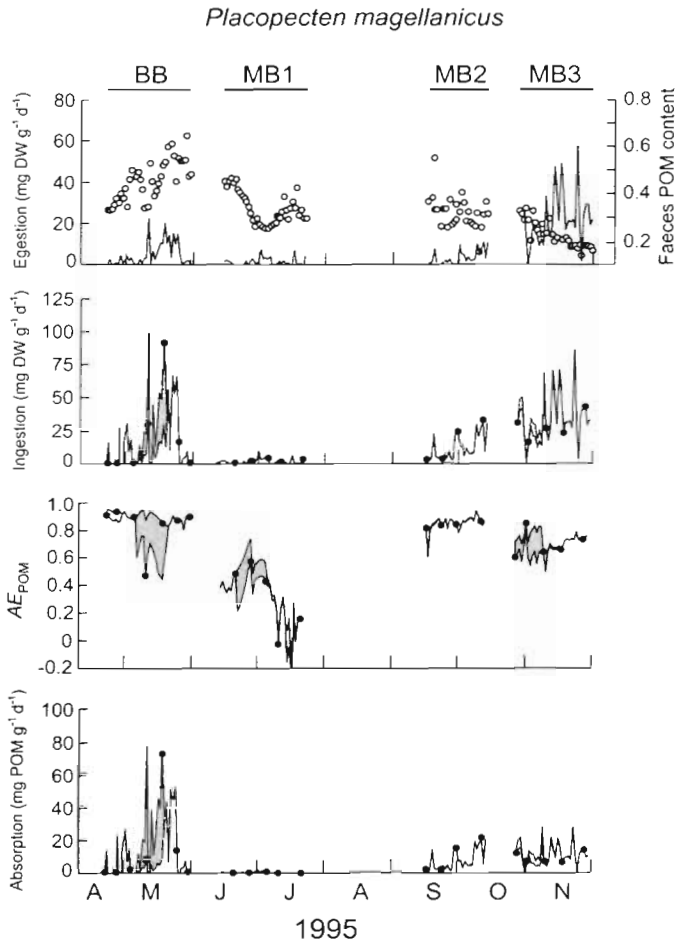

Fig. 6. Daily weight-standardized egestion (DW: dry weight), ingestion and absorption (POM: particulate organic matter) rates and absorption efficiency (*AE*) of sea scallops *Placopecten magellanicus* held at 5 m depth in Bedford Basin (BB) and at 12.7 m depth in Mahone Bay (MB). The proportion of organic matter in daily faeces samples is shown in the top panel (o). 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 (●). All data are plotted at the midpoint of daily sampling intervals

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 were 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 2 wk running average of maximum and minimum observations of seston PIM content. The difference in daily maximum and minimum I_T estimates was generally low (Figs. 6 & 7) owing to the low short-term variability in seston organic content at both sites (Fig. 3). Mussel and scallop I_T estimates generally followed similar temporal patterns as with egestion rate (Figs. 6 & 7), except that the low seston ash content in Bedford Basin during spring resulted in high I_T estimates.

Results of the analysis of potential errors in *in situ* sea scallop ingestion rates, based on solving Eq. (2) for a wide range of particle diameters, are summarized in Fig. 8. The largest error in calculated ingestion rate occurs when seston particles are relatively large and inorganic particles are relatively small (Fig. 9). The largest inorganic particles observed at similar low-energy coastal sites on the eastern coast of Nova Scotia are <20 µm diameter (Cranford et al. 1998) and seston particles at the site were smaller than 50 µm (Fig. 5), resulting in calculated sea scallop ingestion rates generally being underestimated by 1 to 15% (Fig. 9). Errors in *in situ* mussel ingestion rates are subject to even less error as they retain fine particles more effectively than scallops.

The net absorption efficiency of POM (AE_{POM}) was highest during the spring and lowest during the sum-

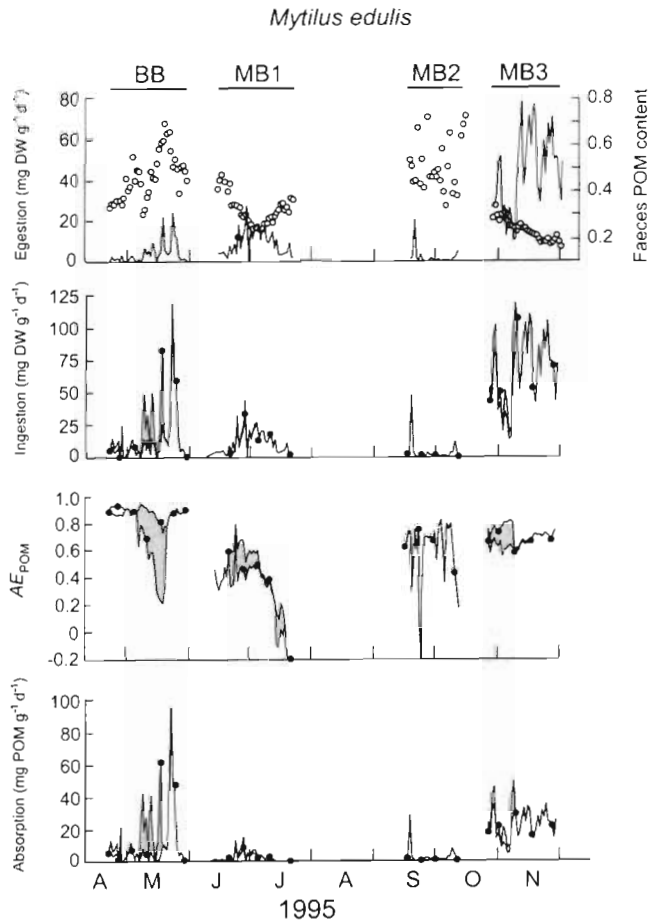

Fig. 7. As in Fig. 6, except that data are for blue mussels *Mytilus edulis*

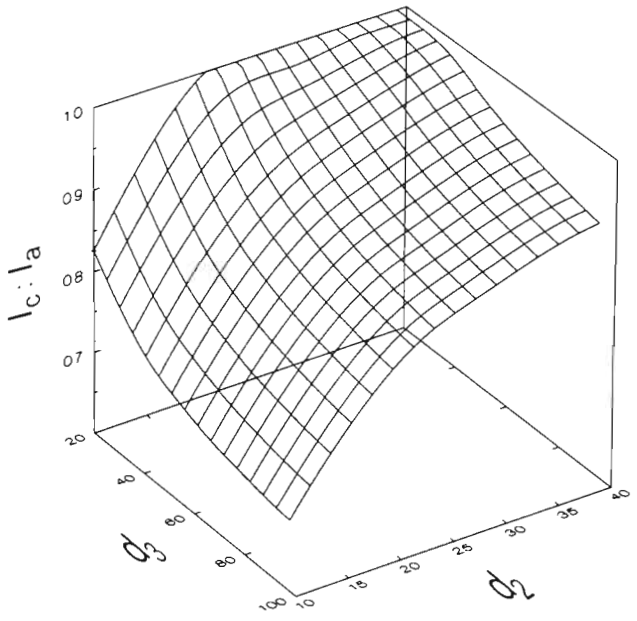

Fig. 8. Quantitative effect of different values for the largest particle (d_3) and inorganic particle (d_2) in the seston on the ratio of calculated (I_c) and actual (I_a) ingestion rates. The ratio was calculated using Eq. (2) assuming values for the smallest particle on the filter (d_1) was 1 µm (pore 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)

mer (Figs. 6 & 7), generally reflecting differences in seston POM content (Fig. 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. 9). The relatively low AE of the mussels during MB2, compared to scallops, also resulted from differences in faeces POM content (Figs. 6 & 7). Functional relationships between each species net AE and seston quality were described by the exponential equations:

$$\text{Scallop } AE_{POM} = 0.886\ (\pm 0.163) \times (1 - e^{-6.052\ (\pm 5.213)\ [POM - 0.307\ (\pm 0.069)]}) \quad (3)$$

$$\text{Mussel } AE_{POM} = 0.759\ (\pm 0.077) \times (1 - e^{-15.911\ (\pm 8.205)\ [POM - 0.342\ (\pm 0.016)]}) \quad (4)$$

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 Fig. 9, 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 that of 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. 3); however, the high ingestion rates resulted in elevated absorption rates during this period. Approximately 36% of the POM absorbed by both species during the 139 d 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 ~40 and 53% of total scallop and mussel absorption, respectively.

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 chl *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 & 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 ($r = -0.306$, $p = 0.017$).

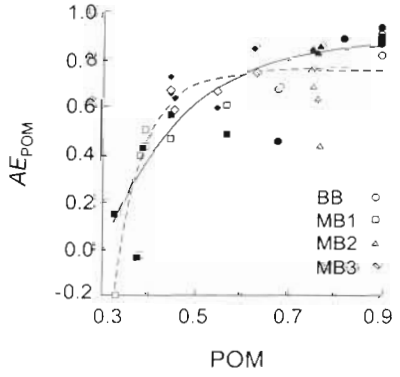

Fig. 9. Net absorption efficiency of particulate organic matter (AE_{POM}) by *Mytilus edulis* (open symbols, broken line) and *Placopecten magellanicus* (closed symbols, solid line) as a function of the POM content of seston during the 4 sampling periods defined in Table 1. The lines were fitted by least squares, and the equations (Eqs. 1 & 2) and fit statistics are given in the text

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).

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:

$$\text{Scallop, } \ln I_T = 0.042\,(\text{SIZE}) + 0.065\,(\text{TEMP}) - 1.882 \quad (5)$$

$$\text{Mussel, } \ln I_T = -3.028\,(\text{SEDPOM}) + 2.186 \quad (6)$$

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. 1 & 2) also showed seston quantity variables (TPM and chl *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.

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 2. Although ingestion rates of both species were relatively high during the spring in Bedford Basin (Figs. 6 & 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 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 'clearance capacity' models overestimated *in situ* C by a factor of between 3.2 and 6.6 (Table 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 Møhlenberg & Riisgård (1979) and Riisgård & Møhlenberg (1979).

The 'natural diet' models were generally more accurate at predicting the average *in situ* C of both species (Table 2), with the exception of the Doering & 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 & Thompson (1986) and Smaal et al. (1997). It is important to note, however, that all these comparisons were based on average C responses. Daily and seasonal *in situ* C estimates often deviated markedly from all predicted values (Table 2).

DISCUSSION

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 temperature and food supply variations (Hawkins & Bayne 1992). Empirical models of food ingestion by *Placopecten magellanicus* and *Mytilus 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.

Ambient water temperature was significantly correlated with sea scallop ingestion (Pearson's $r = 0.399$, $p < 0.001$). However, the apparent relationship was driven by the high leverage exerted by a few observations and high and low ingestion rates were observed at both temperature extremes (Figs. 2 & 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

(Widdows & Bayne 1971, Bayne & Newell, 1983, Smaal et. al. 1997, B. MacDonald pers. comm., but see Jørgensen et al. 1990 and Riisgård 1991). Viscosity changes have been cited to account for a large proportion of the effects of temperature on feeding performance and are believed to limit the effectiveness of physiological compensation responses (Jørgensen et al. 1990, Podolsky 1994). This is reasonable if the animals are feeding at full capacity; however, given observations that bivalves seldom utilize their full clearance potential in nature (see below), there appears to be considerable scope for compensatory physiological responses (e.g. regulation of enzyme reaction rates) to achieve thermal independence in feeding performance.

The results of multiple regression analysis indicate that daily sea scallop and mussel food intake was not passively (autonomous view of filter-feeding behaviour) driven by the abundance or composition of the food supply. For example, large differences in clearance and ingestion rates were observed in Mahone Bay during the summer (MB1) and late autumn (MB3) (Figs. 6 & 7, Table 2) when the food supply was similar in abundance and quality (Figs. 2 & 3). A positive relationship between ingestion rate and food quality was predicted by Taghon (1981) and this has been confirmed empirically for sea scallops and mussels (Bayne et al. 1987, Cranford & Grant 1990). However, no clear relationship between ingestion rate and seston POM, POC or PN content was observed in the present study. It may not be valid to compare daily food acquisition responses with average daily food supplies, as it is possible that a short period of rapid food intake, caused by short-term changes in food supplies, could account for much of the total daily food intake (Cranford & Hargrave 1994). However, this would not explain the observed seasonal variations in ingestion rate, as the magnitude of short-term fluctuations in TPM and chl *a* remained relatively low and constant throughout the study period (Fig. 2). Riisgård & Møhlenberg (1979) suggested that variable feeding behaviour in bivalves 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. 2).

The independence of scallop and mussel food intake from observed environmental changes may also be related to an overly simplistic characterization of the nature of the particulate food (Grant & Bacher 1998). Prins et al. (1994) had similar problems finding a relation between mussel feeding behaviour and seston composition and suggested that this resulted from the inhibitory effect of a *Phaeocystis* bloom on feeding behaviour. Poor relationships between food supplies and feeding behaviour may also stem from the influence of feeding history (e.g. time-averaged feeding behaviour), a feedback on feeding behaviour imposed by the regulation of digestive processes, and/or endogenous regulation of food intake based on seasonal changes in energy/nutrient demands (see below).

Post-ingestive processes appear to be more directly related to the ambient food supply than clearance and ingestion rates. Previous observations of scallop and mussel *AE* responses to short-term changes in diet quality generally reveal a high correlation between *AE* and seston organic content (Hawkins et al. 1996, Cranford 1998). The relatively poor relationships observed here between *AE* and POM (Fig. 9) appear to result from a high flexibility of absorptive responses to compensate for seasonally changing rations. A gradual decline in the organic content of scallop and mussel faeces was observed during November when seston POM content remained constant (Figs. 6 & 7), resulting in increased *AE*. Similarly, scallops and mussels increased faeces organic content during April and May when Bedford Basin seston was generally of high quality, resulting in decreased *AE*. Bivalves fed high-quality diets in the laboratory have also been observed to reduce *AE* (Kreeger 1993, Cranford 1995 and references therein). These observations suggest that the animals maximize absorption by regulating metabolic energy losses to faeces. The capacity to acclimate absorption has previously been observed in the laboratory for mussels (Bayne et al. 1987, 1993) and sea scallops (Cranford 1995) and the time-course for absorptive acclimation observed in the laboratory (several days) is consistent with *in situ* observations.

The feeding behaviour of bivalve filter feeders is conceptualized by Bayne (1998) as a linked series of behavioural and physiological functions, from food capture and selection, through ingestion, digestion, absorption and defecation, that are varied to compensate in terms of net energy gain for changes in the food environment. Willows (1992) applied this theory to model the behaviour and physiology of *Mytilus edulis* under a wide range of dietary conditions, providing an opportunity to compare theoretical predictions with our observed responses. Feeding rate at low food availability is predicted to be constrained by the high energetic costs of food processing such that a high flexibility of digestive energetic investments is believed to be an important compensatory mechanism (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 & Newell 1983). The observation that absorption efficiency was reduced during the spring phytoplankton bloom (Figs. 6 & 7) is typical of 'exploiter' species (Bayne & Newell 1983) that conserve energy under favorable dietary conditions by reducing digestive energy investment to maximize energy gain from the food supply. During pro-

longed 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. *In situ AE* observations generally support theoretical predictions.

Observed seasonal changes in bivalve feeding rates cannot be explained solely by the energetic constraints of food processing costs at low food availability. The highest feeding rates were observed in November when food abundance was low and the low 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 & Widdows 1978, Thompson 1984, Grant et al. 1993, Hatcher et al. 1997, Smaal et al. 1997) and sea scallops (MacDonald & Thompson 1986, Shumway et al. 1988). Gametogenesis in *Mytilus 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 & Carver 1993). *Placopecten magellanicus* initiate gametogensis during early winter, growth and ripening of the gonad occurs during the spring and summer, and spawning takes place from August to September (Robinson et al. 1981, MacDonald & Thompson 1986, Barber et al. 1988). The decrease in scallop and mussel tissue weight during the fall and summer, respectively, (Table 1) are consistent with these spawning 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 maximizing energy intake. This is consistent with empirical observations of bivalve feeding responses to maintenance rations or partial starvation (Bayne & 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 (low food quantity and quality) 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. The fact that no clear relationship has been observed between clearance rate and reproductive condition (Smaal & Vonck 1997, Smaal et al. 1997) likely stems from endogenous demands being only one of several factors that may constrain or influence feeding (see above).

Accuracy of *in situ* clearance rate estimates

Substantial errors in ingestion rate estimates can result from differential particle retention by bivalves and the GF/C filters typically used to characterize their food supplies (Fig. 8). However, typical size distributions of seston and inorganic particles at Nova Scotia coastal sites indicate that the largest inorganic particles typically observed at similar coastal environments are <20 µm (Cranford et al. 1998) and seston particles during this study are generally smaller than 30 to 50 µm (Fig. 5), resulting in an underestimation of ingestion rate estimates of 7 to 12% (Eq. 2 assuming $d_l = 1$ and $d_r = 3$).

To further assess the accuracy of absorption rate estimates the actual growth of individual scallops and mussels (Table 1) was compared with growth estimates calculated by summing daily absorption rates ($C \times TPM \times AE$) and subtracting daily respiration rate (R). This is the same approach as that used by Clausen and Riisgård (1996) to compare mussel growth in nature with growth estimates based on the assumption of maximum clearance rate. For consistency, growth estimates for *Mytilus edulis* were calculated using the same allometric relationship for R (ml O_2 h^{-1} = $0.475\ W^{0.663}$) and the same energy equivalents for oxygen and dry tissue mass as used by these authors. *Placopecten magellanicus* tissue was assumed to be 24.5 J mg^{-1} (MacDonald & Thompson 1985) and routine oxygen consumption was estimated using an average allometric relationship with dry weight (W, g), where $R = 0.35\ W^{0.81}$ (Bricelj & 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 1) as these periods do not include spawning. The resulting mussel growth estimate of 23.0 kJ over the 99 d period examined was 20% greater than observed (0.9 g tissue growth × 20.5 J mg^{-1} = 18.5 kJ). Sea scallop growth was estimated at 38.4 kJ over the 39 d 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* clearance, ingestion and absorption rates.

Accuracy of potential clearance rate estimates

Species-specific and generic clearance models were 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 d 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 2). The 'clearance capacity' models overestimated *in situ* clearance by 320 to 1365%. The fact that the generic 'low gear' model of Powell et al. (1992) provided clearance rates that were at least as accurate as those provided by species-specific allometric clearance relationships (MacDonald & 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 conclusion of Clausen & Riisgård (1996) that food uptake by *Mytilus edulis* in nature is characterized by the full exploitation of their filtration capacity depends on their assumption that living phytoplankton were the sole trophic resource of the mussels. A lower clearance rate could explain actual growth if a greater proportion of detrital POM was also utilized as a food source. Much of the material characterized as POM consists of organic mineral aggregates of phytoplankton, protozoans, bacteria, colloids and detrital organic matter, some of which is adsorbed to mineral particles (reviewed by Grant & Bacher, 1998). The C:chl *a* 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 & 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 food sources is demonstrated by the high *AE* observed during September and October (*AE* > 80% in scallops and >60% in mussels, Figs. 6 & 7) when seston phytoplankton content was lowest (C:chl ratio often exceeded 300).

Jørgenson (1990, 1996) and Riisgård & Larsen (1995) have speculated that the low clearance rate measurements prevalent in the literature reflect suboptimal 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 & 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 'clearance capacity' models in predicting mussel and scallop clearance behaviour in nature (Table 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 & 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, and numerous other examples are available (Dame 1996, Prins & Dame 1998). 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 substantially 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 2), the time scale on which bivalve populations feed at a rate sufficient to deplete phytoplankton and allochthonous 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 affect 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 & 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 &

Smaal 1998). To this end, the present study has made progress in resolving 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; and (3) food utilization strategies of different bivalve species. 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.

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Appendix: Derivation of Eq. (2)

Actual and calculated ingestion rates are defined as

$$I_a = \frac{E_{ash}}{(F_{ash})_{retained}} \quad \text{(A1)}$$

$$I_c = \frac{E_{ash}}{(F_{ash})_{filtered}} \quad \text{(A2)}$$

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

$$(F_{ash})_{retained} = \frac{(PIM)_{retained}}{(TPM)_{retained}} \quad \text{(A3)}$$

$$(F_{ash})_{filtered} = \frac{(PIM)_{filtered}}{(TPM)_{filtered}} \quad \text{(A4)}$$

where PIM and TPM are mass concentrations of particulate inorganic matter and total particulate matter, respectively. Eqs. (A1) to (A4) were combined to define the ratio

$$\frac{I_c}{I_a} = \frac{(PIM)_{retained}(TPM)_{filtered}}{(PIM)_{filtered}(TPM)_{retained}} \quad \text{(A5)}$$

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

$$n(d) = Ad^{-4}, \quad \text{(A6)}$$

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 m in diameter d is then

$$m(d) = \frac{(\rho \pi A)}{6} d^{-1} \quad \text{(A7)}$$

where ρ is the density of the material in question. The mass in a size interval in the seston from diameter d_i to d_j is

$$\frac{\rho \pi A}{6} \int_{di}^{dj} d^{-1} dd \quad \text{(A8)}$$

which upon integration yields

$$\frac{\rho \pi A}{6} \ln d_j / d_i \quad \text{(A9)}$$

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

$$\frac{\rho \pi A}{6} \int_{di}^{dj} RE(d) d^{-1} dd \quad \text{(A10)}$$

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

$$RE(d) = 0 \text{ if } d < d_r \text{, and 1 otherwise} \quad \text{(A11)}$$

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

$$\frac{\rho \pi A}{6} \ln d_j / d_r \quad \text{(A12)}$$

By assigning some diameters, Eq. (A5) is rewritten in terms of particle diameters. Let

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

With these definitions, the quantities in Eq. (A5) become

$$(PIM)_{retained} = \frac{\rho_{PIM} \pi A_{PIM}}{6} \ln d_2/d_r \quad \text{(A13)}$$

$$(PIM)_{filtered} = \frac{\rho_{PIM} \pi A_{PIM}}{6} \ln d_2/d_1 \quad \text{(A14)}$$

$$(TPM)_{retained} = \frac{\rho_{TPM} \pi A_{TPM}}{6} \ln d_3/d_r \quad \text{(A15)}$$

$$(TPM)_{filtered} = \frac{\rho_{TPM} \pi A_{TPM}}{6} \ln d_3/d_1 \quad \text{(A16)}$$

and Eq. (A5) becomes

$$\frac{I_c}{I_a} = \frac{\ln d_2/d_r \ln d_3/d_1}{\ln d_2/d_1 \ln d_3/d_r} \quad \text{(Eq. 2 in text)}$$

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