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Variation in food quality and particle selectivity in the sea scallop *Placopecten magellanicus* (Mollusca: Bivalvia)

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ABSTRACT: The sea scallop *Placopecten magellanicus* (Gmelin) is a suspension-feeding bivalve, common in subtidal regions in the northwest Atlantic. In this study, we examined the feeding responses of scallops to changes in the quantity and quality of natural seston under field and laboratory conditions. Concentrations of natural suspended particles at our study site were < 5 mg l^{-1}, and chlorophyll *a* concentrations were < 1.4 µg mg^{-1}. Under these seston quantities and qualities, clearance rates were positively correlated with the total amount of chlorophyll-containing particles in the water (µg l^{-1}), while ingestion rates increased with increasing concentration of total suspended particulate matter (mg l^{-1}). Scallops were able to select high-quality chlorophyll-*a*-containing particles and significantly improve the quality of material ingested. Pseudofaeces production increased slightly with increasing particle concentration, and selection was not based on the size of particles. We suggest that during conditions when the ingestive capacity of scallops is not exceeded, qualitative factors of the seston are more important than quantitative ones in mediating feeding processes.

KEY WORDS: Suspension-feeding · Selection · Pseudofaeces · Food quality · Bivalve

INTRODUCTION

Bivalve molluscs are dominant members of many infaunal and epibenthic marine communities. At high densities, suspension-feeding bivalves may alter the quantity and composition of seston in the overlying water column, and they represent an important mechanism for coupling pelagic and benthic processes (Dame et al. 1980, Kemp et al. 1990, Dame 1993). Depletion of suspended food particles can suppress growth rates of other suspension-feeders in the community (Peterson 1982, Frechette & Bourget 1985), and can also significantly influence population dynamics of the plankton (Cloern 1982, Peterson & Black 1987). Establishing the relationship between the concentration and quality of suspended particulate matter and the uptake of this material by bivalves is important to the understanding of energy flow not only through this major group of marine primary consumers (Kiørboe et al. 1980), but also through the benthic community as a whole (e.g. Herman 1993).

In nature, suspension-feeding bivalves are exposed to a food supply that fluctuates unpredictably in both quantity and quality. Many previous studies, however, have examined bivalve feeding responses in the laboratory using only monocultured phytoplankton (for review see Winter 1978, Bayne & Newell 1983). While a reasonable starting point, there have always been technical and conceptual difficulties in predicting an organism's response in the natural environment from data measured in the laboratory (Bayne et al. 1977, Doering & Oviatt 1986, Bayne & Hawkins 1992). One reason for this is that the natural food supply consists of a complex mixture of organic and inorganic particles that is difficult to mimic in the laboratory. Another is that laboratory studies often use formulated seston concentrations that are much higher than natural concentrations available in the field. Despite these differences, few workers have conducted studies on the feeding strategies of bivalves using natural seston, and even fewer have evaluated feeding activity when food varies temporally (Stenton-Dozey & Brown 1992,

Newell & Shumway 1993). Information regarding changes in feeding behaviour under natural conditions is critical to the analysis of bivalve energetics (Bayne et al. 1988).

In general, suspension-feeding bivalves have adopted several strategies for controlling the ingestion of particulate matter including regulation of (1) feeding duration (Foster-Smith 1975), (2) clearance rates (Bayne & Newell 1983), and (3) pseudofaeces production (particles cleared but rejected before ingestion; Kiørboe et al. 1980, Newell & Jordan 1983). Regulation of clearance rates and duration of feeding can only alter the quantity of material ingested by the bivalve. Regulation of pseudofaeces production, however, can prevent particle overload, eliminate material that exceeds the animal's ingestive capacity (Beninger et al. 1992), and facilitate selective rejection of less nutritious particles and enhance the quality of material ingested (e.g. Kiørboe et al. 1980, Newell & Jordan 1983). Thus, production of pseudofaeces can alter both the quantity and quality of material ingested, and it allows certain species to compensate for dilution of food quality due to increases in the proportion of particulate inorganic matter (PIM; Widdows et al. 1979, Kiørboe et al. 1980, Kiørboe & Møhlenberg 1981, Bricelj & Malouf 1984). This strategy is viewed as an adaptive feature that enables the bivalve to maintain a positive flow of energy into growth and reproduction even during periods of poor seston conditions (Bayne & Newell 1983). The importance of such behavioural responses to the overall feeding strategy in many bivalves, however, is not clear. This is especially true for bivalves exposed to natural seston at low particle concentrations (< 5 mg l^{-1}).

The sea scallop *Placopecten magellanicus* (Gmelin) is a benthic suspension-feeder that is exposed to a wide range of pelagic and resuspended benthic material (Shumway et al. 1987). Although scallops consume a variety of organisms and detritus, phytoplankton and benthic microalgae seem to be a major food resource (Shumway et al. 1987, Cranford & Grant 1990). The goal of this research was to determine the pre-ingestive feeding strategies of *P. magellanicus* when exposed to quantitatively and qualitatively different assemblages of natural particles. Both field and laboratory experiments were conducted using natural seston, or natural seston supplemented with microalgae and silt.

MATERIALS AND METHODS

General procedures. Feeding activity in scallops was measured seasonally in the field at Sunnyside, Trinity Bay, Newfoundland, Canada, and at the Marine Sciences Research Laboratory (MSRL), Memorial University of Newfoundland, Logy Bay, in 1990. Scallops were collected at Sunnyside by SCUBA divers from a water depth of 10 to 15 m. Epibiota were cleaned from the shell surface of 9 haphazardly selected individuals ranging in size from 120 to 160 mm in shell height. Collection and cleaning of scallops were always carried out at least 1 d prior to the experiment, and animals were held at the experimental site overnight. This procedure allowed scallops to recover from any stress associated with handling and pre-exposed them to experimental conditions for at least 12 h before measurements were made. Experiments were conducted in the field using natural assemblages of particles on April 18 and 19, at the beginning of the spring phytoplankton bloom, and on August 14 and 15. Experiments were conducted at the MSRL using natural seston supplemented with cultured microalgal cells on May 3, and supplemented with a mixture of microalgae and silt on November 15.

Measurements of clearance rate and retention efficiency. At Sunnyside, seawater from approximately 5 cm above the bottom of a scallop bed was pumped into a 25 l header tank of the experimental apparatus, situated on the deck of a small stationary boat. Analyses of particle size distributions of unfiltered seawater, using an electronic particle counter/sizer (Coulter Multisizer) fitted with a 280 µm aperture, revealed that particles > 60 µm were very rare in the seston. Therefore, the water was passed through a 100 µm screen semi-submerged in the header tank to prevent suspended debris or flocs from clogging the apparatus. Seawater from the header tank was distributed via Tygon tubing to a series of 10 chambers (MacDonald 1984). Flow rates were held fairly constant, between 200 and 300 ml min^{-1}, by maintaining head pressure and using plastic flow-restricting plugs inserted in the Tygon delivery lines. Within 1 h of placing scallops in individual 'experimental' chambers, quantitative water samples were simultaneously collected from the standpipe drain of each chamber. This was done over a recorded time interval to allow calculation of flow rates. Samples were taken hourly over a 4 to 8 h experimental period. The concentration of particles in the outflowing water of an empty 'reference' chamber and 9 experimental chambers was determined using the particle counter equipped with a 100 µm aperture. Differences in the concentration of particles between the reference and experimental chambers were used to calculate clearance rates (see below). The high water flow and exchange rates in the chambers prevented scallops from removing more than ~30 % of the particles. Analysis of water collected inside the containers suggested that dilution of the inflowing water by outflowing water (i.e. partially filtered) was minimal.

The size-frequency distribution of the particulate matter in the reference chamber was determined periodically using the particle counter/sizer. Water samples from representative scallop chambers were also analyzed for particle size distributions, and compared to that of the seston. These comparisons were used to calculate retention efficiencies (*RE*) of scallops for particles in the size classes 2.0–3.0, 3.1–4.0, 4.1–5.0, 5.1–6.0, 6.1–10.0, and 10.1–64.0 µm (see below). Using Coulter Accucomp software, the size-frequency distribution of particles from each scallop chamber was then subtracted from that of the reference chamber. These calculations yielded the size-frequency distribution of particles retained by each scallop.

In the laboratory, unfiltered water was supplied to the same header tank and feeding apparatus used in the field through a direct seawater intake line submerged 5 m below the water surface in Logy Bay. On May 3, feeding behaviour under good dietary conditions was evaluated by continuously adding cells of the diatom *Chaetoceros muelleri* Lemmermann to the header tank using a peristaltic pump. These cells are approximately 5 µm in diameter and are efficiently retained by sea scallops (Cranford & Grant 1990). This addition increased the background particle concentration approximately 370% to ~14.0×10^3 particles ml^{-1}. On November 15, scallops were again exposed to natural seston supplemented with microalgae. This addition increased the background particle concentration by only 55% to ~7.0×10^3 particles ml^{-1}. After approximately 4 h, the quality of food was then decreased by continuously pumping a silt slurry (or potters clay), ranging in size from 2 to 20 µm with a peak between 5 and 10 µm, to the header tank. This addition further increased the particle concentration by approximately 86% to ~13.0×10^3 particles ml^{-1}. Silt particles were kept in suspension by placing a submersible stirrer in the header tank and by agitating the tank with a plunger every 15 min. The slurry was pumped to the header tank at a velocity sufficient to prevent settling in the delivery line. Measurements of clearance rates were resumed within 1.5 h of exposure to the diatom/silt combination, and the experiment continued for an additional 5 h. Clearance rates and retention efficiencies were determined in the same manner as in field experiments described above. After the completion of each set of experiments, the somatic tissue of each scallop was dried to a constant weight at 80°C and the value recorded.

Collection and analysis of seston. Seston samples were collected from the overflow hose of the header tank every hour during feeding experiments to determine concentrations of total particulates, chloropigments, and particulate organic matter. Replicate samples of known volume were filtered onto pre-ashed 47 mm GF/C grade filters under vacuum. Filters were washed with approximately 5 ml of isotonic ammonium formate, added to the last few millilitres of sample, to remove residual salts. Filters were then frozen on dry ice and stored in the dark until they were transported back to the laboratory for processing. Filters from each sampling period were separated and used in one of several analyses (2 to 3 filters per analysis).

The concentrations of total particulate matter (TPM) in the seston were determined after drying filters at 55°C for 48 h and weighing. These filters were then ashed in a muffle furnace at 450°C, and particulate organic matter (POM) content determined by weight loss after ignition. Particulate chlorophyll *a* concentrations (PCC) were determined by extracting filters in 6 ml of 90% HPLC grade acetone at –20°C for 14 to 16 h. The filters were then pelleted out at approximately 7000 × *g* for 5 min at 4°C. Chlorophyll *a* concentration was measured using a Turner Designs Model 10 fluorometer calibrated against a chlorophyll *a* standard (Yentsch & Menzel 1963).

Chlorophyll *a* was used as the indicator of food quality because it can be accurately measured in small quantities of sample, and we have observed a significant, positive correlation between chlorophyll *a* concentration and percent organics in the local seston ($r = 0.72$, $n = 31$, $p < 0.001$). Consequently, seston quality was expressed as PCC in µg chl *a* l^{-1}, or as the ratio of PCC to TPM in µg chl *a* mg^{-1} (SES_Q). For selection and preferential ingestion data, SES_Q was used to express quality. Based on this estimator, all experiments were grouped into 1 of 5 different experimental conditions (see Tables 1 & 2): *natural* seston at (1) high quality (>1.0 µg chl *a* mg^{-1}), (2) medium quality (0.1 to 1.0 µg chl *a* mg^{-1}), or (3) low quality (<0.1 µg chl *a* mg^{-1}); or *supplemented* seston at (4) high quality, or (5) medium quality.

Collection and analysis of pseudofaeces. Pseudofaeces were quantitatively collected from each chamber during the experimental period and placed in separate vials. At the termination of an experiment, each scallop was removed from its chamber, turned on its anterior edge to drain the pallial water and quickly placed back into the chamber. This procedure induced rapid valve adductions which expelled any remaining pseudofaeces from the pallial cavity. The ejected material was collected and added to the appropriate vial. Pseudofaeces were treated with several drops of Coulter Electronics type IC dispersant (Newell & Jordan 1983) and shaken vigorously for 5 to 10 min. Preliminary trials indicated that this procedure did not disrupt phytoplankton cells, but it did disperse pseudofaecal particles so they could be counted using the Multisizer (Ward et al. 1992). The volume of each sample was determined just prior to counting so we could calculate

the total number of particles expelled as pseudofaeces. The relative size-frequency distribution of particles in each sample was also recorded and compared to the relative distribution of material retained by the scallop. After counting, pseudofaeces from 4 to 7 of the most active scallops were collected onto individual 25 mm GF/C filters under vacuum. These filters were then processed in the same manner as the seston samples above and analyzed for chloropigments as described previously. The quality of pseudofaeces (PS_Q) was expressed as the concentration of chlorophyll *a* per weight of pseudofaeces produced (µg mg^{-1}).

Calculations. Clearance rate (*CR1*) is defined as the volume of water cleared of suspended particles >2 µm in diameter per unit time (l h^{-1}; Bayne et al. 1977), and it was calculated as follows:

$$CR1 = F \times (C_1 - C_2)/C_1, \quad (1)$$

where *F* is the flow rate of water through the containers (l h^{-1}), C_1 is the particle concentration (counts ml^{-1}) in the inflowing seawater, and C_2 is the particle concentration (counts ml^{-1}) in the outflowing water after it has been processed by the scallop. The *CR1* values obtained for each scallop during the experimental period were averaged and the mean used for further calculations. In order to compare *CR1* of different sized scallops, it was necessary to correct for differences in tissue weight. This was done by standardizing all rates to a 15 g, dry soma weight animal using the following equation:

$$CR1_S = (W_S/W_O)^b \times CR1_O, \quad (2)$$

where $CR1_S$ (l h^{-1}) is the clearance rate for a standard scallop of dry tissue weight W_S (15 g), $CR1_O$ (l h^{-1}) is the observed clearance rate for a scallop of dry tissue weight W_O (g), and *b* is the weight exponent. An exponent of 0.68, previously described by MacDonald & Thompson (1986) for this species feeding on natural seston, was used for standardization.

Scallop retention efficiencies (*RE*) for each of the 6 size classes were calculated as follows:

$$RE = 1 - (C_2/C_1). \quad (3)$$

Values of *RE* were then standardized (RE_S) by setting the highest *RE* of each scallop to 1 and increasing the *RE* values for the other size classes proportionately (Cranford & Grant 1990, Cranford & Gordon 1992). This procedure reduces variation due to differences in the size-frequency distribution of seston and differences in flow rate through the holding chambers.

Ingestion rate (*IR*) for each scallop was defined as the dry weight of seston ingested per unit time (mg h^{-1}), and it was calculated as follows:

$$IR = CR2 - PSR, \quad (4)$$

where *CR2* is the weight of seston cleared per unit time (mg h^{-1}), calculated as the product of *CR1* (l h^{-1}) and the concentration of total particulate matter (TPM) in the seston (mg l^{-1}), and *PSR* is the rate of pseudofaeces production (mg h^{-1}). *IR* was also corrected for differences in tissue weight using the equation and exponent given above for $CR1_S$. This standardized ingestion rate was designated IR_S.

A sorting efficiency (*SE*; Iglesias et al. 1992) was calculated to express the difference in quality between the seston and pseudofaeces as a ratio of the seston. The equation was of the form:

$$SE = 1 - (PS_Q/SES_Q), \quad (5)$$

where PS_Q is the quality of the pseudofaeces, and SES_Q is the quality of the seston. Values of *SE* range from 1 for the case when there is total selection and no chlorophyll *a* remains in the pseudofaeces, to 0 for the case when the chlorophyll content of pseudofaeces and seston are equal.

Selection may be defined as the retention, discrimination, and ingestion of one particle type in preference to another, but it only considers the quality of the pseudofaeces. Therefore, to obtain a realistic estimate of the biological significance of selection to the net energy balance of the scallop, we considered the rate of ingestion plus the quality and quantity of pseudofaeces produced. This was expressed as the change in the quantity of chlorophyll *a* content ingested (I_Q) in µg mg^{-1}. I_Q was calculated for each scallop as follows:

$$I_Q = [(SES_Q \times CR2) - (PS_Q \times PSR)]/IR. \quad (6)$$

Finally, we calculated a compensation index (*CI*) that describes the physiologically useful change in chlorophyll *a* content of the ingested ration relative to levels observed in the seston. The estimate of *CI* not only takes into consideration the quality of seston and pseudofaeces, but also the quantities of material cleared and rejected. It can be expressed as follows:

$$CI = (I_Q/SES_Q) - 1. \quad (7)$$

Our *CI* is the same as that calculated by Navarro et al. (1992) and is similar to the benefit ratio (*BR*) given by Iglesias et al. (1992). Values of *CI*, however, express the increase in quality of food ingested relative to that in the seston, whereas *BR* calculated by Iglesias et al. (1992) expresses the increase in quality of food ingested relative to the total quality of material ingested.

Statistical analyses. The effects of changes in seston characteristics on scallop feeding behaviour were determined by plotting and then examining the relationships that existed between these variables. Because some scallops were used in more than one experiment, the data were not entirely independent. Therefore, only

correlation analyses were performed in which we treated both X and Y variables as random factors (Pearson correlation coefficient; Zar 1984). The null hypothesis for these analyses was that the correlation coefficient (r) was equal to zero. Data used to compare clearance rates ($CR1_S$) with the change in the proportion of chlorophyll *a* ingested (CI) were subjected to a reciprocal transformation ($1/X$) prior to analysis (Zar 1984).

Selection of material by each scallop was determined by comparing the quality of the seston (SES_Q) with the quality of material in the pseudofaeces (PS_Q). If there was a significant difference in chlorophyll *a* concentration between seston and pseudofaeces, then selection and preferential ingestion of particles containing chlorophyll had occurred. The null hypothesis for the selection analyses was that PS_Q was equal to SES_Q. To test this hypothesis, values of PS_Q produced by scallops from each experiment were compared to SES_Q values measured during the day using a 2-tailed Student's *t*-test. During the supplemented high-quality conditions, very little pseudofaeces were produced. In order to obtain an accurate measure of PS_Q, pseudofaeces from all scallops were pooled within each experiment and tested against the mean of their respective SES_Q using the procedures outlined by Sokal & Rohlf (1981, p. 231). Two assumptions of selection experiments such as these are: (1) the mucus secreted in the pseudofaeces has negligible dry weight; and (2) all particles of any given size have an equal chance of being retained by the gill (Kiørboe & Møhlenberg 1981, Newell & Jordan 1983).

It was not possible to test for differences between quality of material ingested (I_Q) and that in the seston (SES_Q), nor pseudofaeces (PS_Q), because ingestion is a derived variable and is not independent from the other two. Instead, we examined the change in the proportion of chlorophyll *a* ingested by scallops (CI). The null hypotheses for the compensation analyses were that CI values of scallops were equal to zero, and CI values of scallops under natural, high- and medium-quality conditions were equal to their respective supplemented conditions. The CI values of scallops under similar experimental conditions (e.g. natural seston, medium quality) were combined and tested against zero using a 2-tailed, 1 sample *t*-test. CI values produced under natural, high and medium conditions were compared to their respective supplemented conditions using a 2-tailed Student's *t*-test. Ratios were arcsine transformed prior to analysis (Zar 1984).

Where appropriate, data were tested for normality and homoscedasticity prior to statistical comparisons (Shapiro-Wilk test, *F*-max test; Zar 1984). In all statistical tests, a significance level of $\alpha = 0.05$ was used.

RESULTS

Experimental conditions

A summary of the experimental conditions, including ambient temperature, concentration of total particulate matter of the seston (TPM), particulate chlorophyll *a* concentration per volume of water (PCC) and per mg of seston (SES_Q), and percent organics is reported in Table 1. Seston TPM concentrations were consistently in the 2 to 5 mg l^{-1} range with the exception of the November 15 sample (silt added) when levels reached 15 mg l^{-1}. This high load is comparable to a maximum of 14.5 mg l^{-1} recorded at Sunnyside in a study of natural seston in 1982 (MacDonald 1984). Levels of PCC in the natural seston during our study ranged from 0.39 in August to 4.77 µg l^{-1} in April during the spring phytoplankton bloom. Levels of PCC reached a high of 6.86 µg l^{-1} during the diatom supplemented experimental conditions in May (Table 1). These concentrations are comparable to seasonal values of chlorophyll *a*, ranging from 0.30 to 5.5 µg l^{-1}, previously recorded for natural seston at the Sunnyside site (MacDonald & Thompson 1985).

With the exception of the 2 August samples, which consistently appeared to have the poorest quality conditions, assessing the quality of the seston depended on the indicator used. PCC can be a convenient indica-

Table 1. Experimental parameters and measures of seston quantity and quality. Supplemented experimental conditions were those in which cultured microalgae and/or silt particles were added to the natural seston. TPM: total particulate matter; PCC: particulate chlorophyll *a* concentration; SES_Q: seston quality based on chlorophyll *a* content; POM: particulate organic matter

Date 1990	Experimental conditions	Temp. (°C)	TPM (mg l^{-1})	PCC (µg l^{-1})	SES_Q (µg mg^{-1})	POM (%)
Apr 18	Natural	2.0	2	1.83	0.71	36.6
Apr 19	Natural	2.0	3	4.77	1.38	42.6
May 3	Supplemented (with algae)	2.0	5	6.86	1.26	31.0
Aug 14	Natural	9.0	2	0.39	0.18	34.2
Aug 15	Natural	14.5	4	0.47	0.08	30.0
Nov 15, a.m.	Supplemented (with algae)	4.5	3	4.12	1.17	58.0
Nov 15, p.m.	Supplemented (with algae + silt)	5.0	15	4.11	0.27	78.3

tor but it ignores the quantity of non-chlorophyll-containing particles available to suspension-feeders. For example, the 2 November experiments had the same PCC ($\mu g\ l^{-1}$) levels, but there was approximately 5 times more particulate matter in the afternoon sample (p.m.) due to the addition of silt which greatly diluted the high-quality particles (Table 1). Taking this into consideration, by expressing chlorophyll *a* per unit weight of seston (SES_Q), reveals that the best quality conditions occurred on April 19 and when we supplemented the seston with microalgae (May 3, November 15 a.m.; Table 1). As will be demonstrated below, both measures of quality are useful in analyzing feeding responses of scallops.

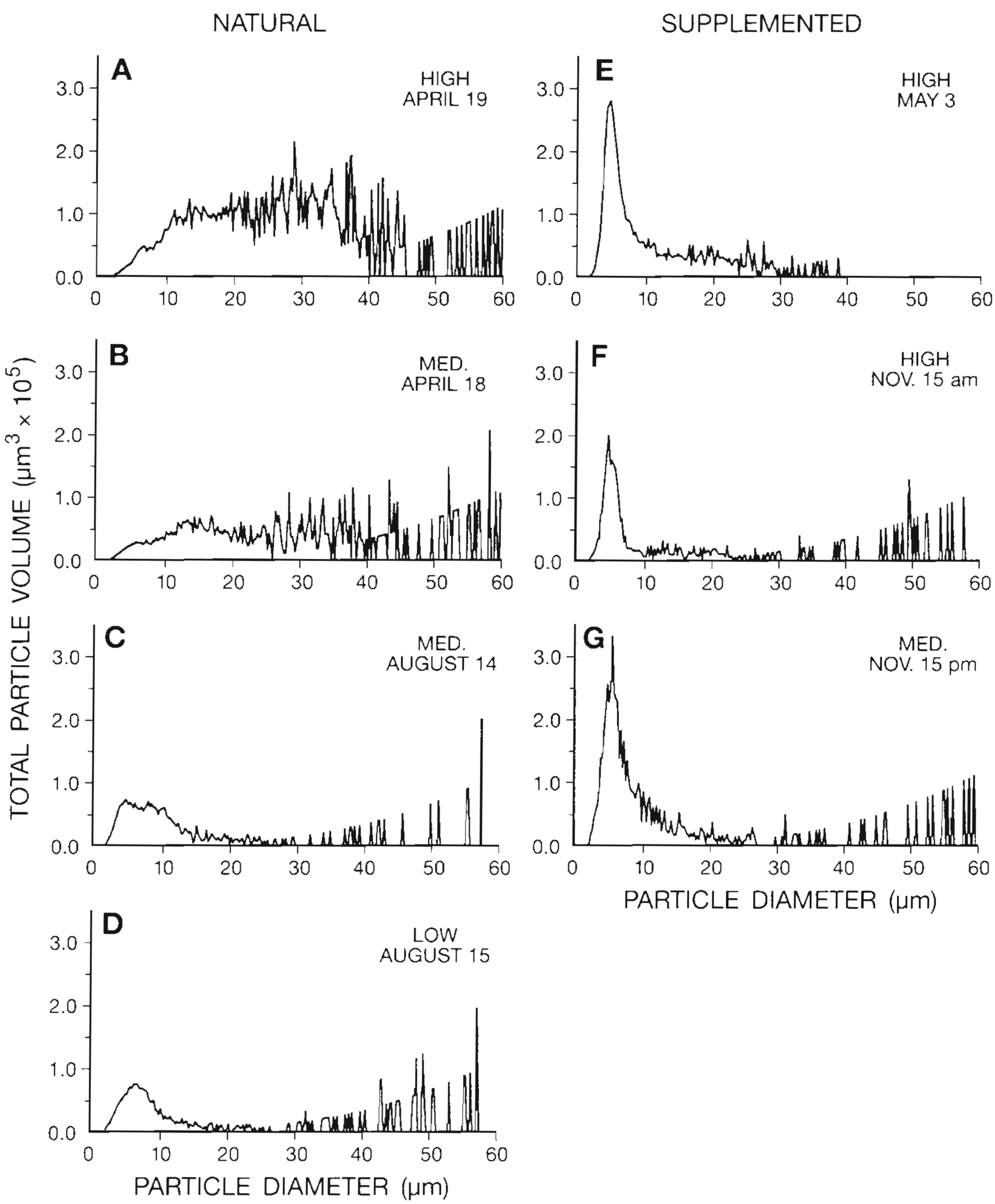

Fig. 1. Representative size-frequency distribution of particles (presented as volume) in the seston during each of the 7 experimental periods. Spectrum obtained using a Coulter Multisizer fitted with a 100 µm aperture. (A) April 19; natural, high-quality seston ($= 3.0 \times 10^3$ particles ml^{-1}). (B) April 18; natural, medium-quality seston ($= 2.1 \times 10^3$ particles ml^{-1}). (C) August 14; natural, medium-quality seston ($= 6.6 \times 10^3$ particles ml^{-1}). (D) August 15; natural, low-quality seston ($= 5.0 \times 10^3$ particles ml^{-1}). (E) May 3; microalgae supplemented, high-quality seston ($= 14.0 \times 10^3$ particles ml^{-1}). (F) November 15 a.m.; microalgae supplemented, high-quality seston ($= 7.0 \times 10^3$ particles ml^{-1}). (G) November 15 p.m.; microalgae and silt supplemented, medium-quality seston ($= 13.0 \times 10^3$ particles ml^{-1})

Representative size-frequency distributions of particles in the seston, presented as particle volume, are shown in Fig. 1. The greatest volume of particles fell in the < 20 µm size range during all conditions except the spring phytoplankton bloom in April (Fig. 1). On these 2 d, a large portion of the seston volume consisted of particles up to 40 µm in size (Fig. 1A, B). The addition of *Chaetoceros muelleri* in the May and November experiments (Fig. 1E, F, G) produced obvious peaks in the smaller size ranges of 4 to 6 µm in diameter. Particle size distributions similar to those in Fig. 1E, F, G have been observed for natural seston at the Sunnyside site during different times of the year (MacDonald & Thompson 1985).

Retention efficiency

Standardized retention efficiencies (RE_S) of scallops generally increased with increasing particle diameter (Fig. 2). For the largest size class (10.1–64.0 µm), however, RE_S values decreased slightly. An apparent decrease in retention efficiency was also observed by Cranford & Grant (1990) for *Placopecten magellanicus* feeding on resuspended sediment and kelp powder. This finding may be an artifact caused by the lower numbers of particles in larger size classes. Scallops feeding on natural seston produced mean RE_S values that were lower than those of scallops feeding on supplemented seston, especially in the 2 to 6 µm size range. These data suggest that (1) scallops were able to retain all particles in the size range analyzed, and (2) scallops were slightly more efficient at retaining particulate matter when the seston was supplemented with diatoms or silt and the majority of particles were less than 10 µm in diameter (Fig. 1).

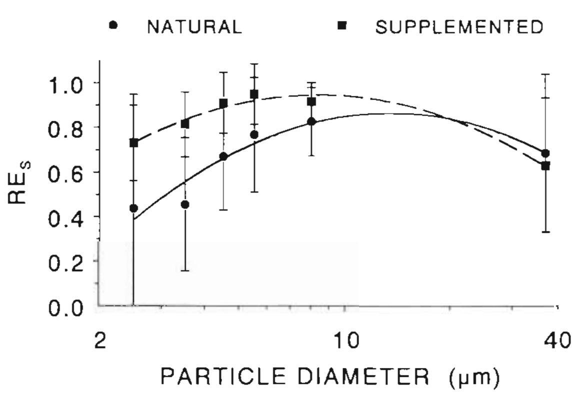

Fig. 2. *Placopecten magellanicus*. Standardized, particle retention efficiencies (RE_S) as a function of selected size ranges of the seston. RE_S data are presented as $\bar{x}$ ± SD, and are plotted in the middle of each size class. Lines of fit through each data set are drawn by eye

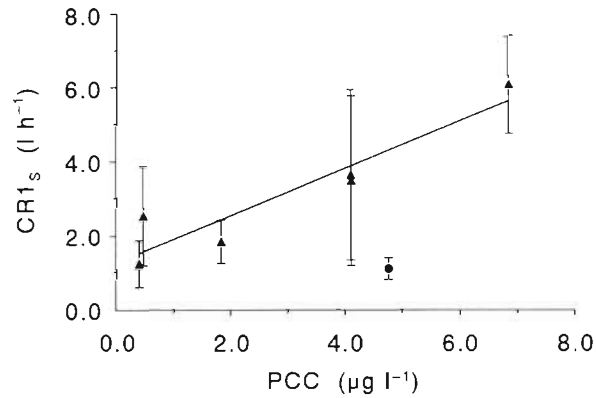

Fig. 3. *Placopecten magellanicus*. Relationship between standardized clearance rate ($CR1_S$) and particulate chlorophyll *a* concentration (PCC) of the seston. $CR1_S$ data are presented as $\bar{x}$ ± SD. A significant, positive relationship exists between the 2 variables. Values for r are 0.52 with the April 19 data (●) included, and 0.70 without (see text for explanation)

Clearance and ingestion rates

Clearance rates of scallops ($CR1_S$) were positively correlated with levels of PCC (µg l^{-1}) encountered in the study (Fig. 3). This relationship was significant when all data sets were used ($r = 0.52$, $n = 59$, $p < 0.001$), and improved considerably when the April 19 data were removed ($r = 0.70$, $n = 50$, $p < 0.001$). During the April 19 experiment scallops produced the highest mean *CI* value (0.396; Table 2), increasing the proportion of chlorophyll *a* ingested the most by means of particle selection. As will be explained below, high *CI* values are associated with lower clearance rates. $CR1_S$ values were not significantly correlated with levels of TPM ($r = 0.25$, $n = 59$, $p > 0.05$), SES_Q ($r = 0.22$, $n = 59$, $p > 0.05$), nor with temperature ($r = -0.17$, $n = 59$, $p > 0.05$) over the range observed in our study.

Pseudofaeces production rates of scallops (*PSR*) were positively correlated with the concentration of TPM (mg l^{-1}) observed in the study ($r = 0.73$, $n = 27$, $p < 0.001$). The amount of pseudofaeces produced as a percentage of the amount of seston retained ranged from < 1 to 85% during the 7 experimental periods. At the highest TPM concentration (15 mg l^{-1}; Table 1), mean pseudofaeces production was only 7.5% (± 3.6%, SD) of that cleared.

Despite the significant increase in *PSR*, ingestion rates of scallops (IR_S) also increased with an increasing concentration of TPM (mg l^{-1}; $r = 0.77$, $n = 32$, no test possible due to lack of independence; Fig. 4). This was simply a consequence of increasing seston concentration because $CR1_S$ were independent of TPM levels (see above) and *PSR* were not high enough to moder-

Table 2. *Placopecten magellanicus*. Summary of selection responses grouped into 1 of 5 different experimental conditions. Statistical test 1 (Sig. 1) compares seston quality (SES_Q) with quality of the pseudofaeces (PS_Q). Statistical test 2 (Sig. 2) compares the compensation indices (CI) with zero. Relative seston quality levels are: high, >1.0 µg chl *a* mg^{-1}; medium, 0.1 to 1.0 µg chl *a* mg^{-1}; low, <0.1 µg chl *a* mg^{-1}. Data are presented as $\bar{x} \pm$ SD

Date 1990	Relative quality	Mean SES_Q (µg mg^{-1})	Mean PS_Q (µg mg^{-1})	Sig. 1	Mean CI	Sig. 2	n
Natural							
Apr 19	High	1.38 ± 0.42	0.42 ± 0.11	**	0.396 ± 0.325	*	5
Apr 18	Medium	0.71 ± 0.23	0.36 ± 0.16	*	0.237 ± 0.170[b]	*	8
Aug 14	Medium	0.18 ± 0.07	0.05 ± 0.01	**			
Aug 15	Low	0.08 ± 0.04	0.11 ± 0.11	ns	0.047 ± 0.141	ns	4
Supplemented							
May 3	High	1.26 ± 0.37	0.10[a]	*	0.011 ± 0.010[b]	**	7
Nov 15, a.m.	High	1.17 ± 0.40	0.02[a]	*			
Nov 15, p.m.	Medium	0.27 ± 0.10	0.05 ± 0.06	**	0.069 ± 0.041	**	7

[a]Pseudofaeces pooled within experiment. [b]Data pooled for Sig. 2. *$p < 0.05$; **$p < 0.01$; ns: not significant

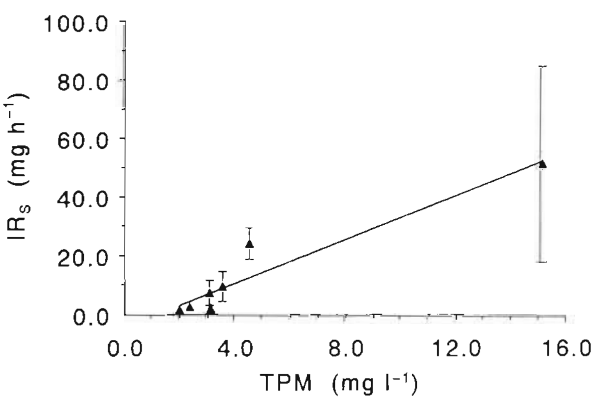

Fig. 4. *Placopecten magellanicus*. Relationship between standardized ingestion rate (IR_S) and total particulate matter (TPM) concentration of the seston. IR_S data are presented as $\bar{x} \pm$ SD. A positive relationship exists between the 2 variables ($r = 0.77$)

ate the increased load being captured and transported to the mouth (see Eq. 4). IR_S values, however, showed no significant relationship with levels of PCC ($r = 0.32$, $n = 32$, $p > 0.05$), SES_Q ($r = 0.24$, $n = 32$, $p > 0.05$), nor with temperature ($r = 0.07$, $n = 32$, $p > 0.05$) over the range measured in our study.

Particle selection

The quality of pseudofaeces (PS_Q) was significantly lower than that of the seston (SES_Q) under both natural and supplemented, high- and medium-quality experimental conditions (Table 2, Fig. 5A, B). These results indicate that scallops have the capability of altering the quality of material ingested by rejecting proportionally more of the non-chlorophyll particles in pseudofaeces. There was no evidence of selection when pseudofaeces were produced during August 15, when SES_Q was at its lowest (Table 2, Fig. 5A). The quality of material ingested (I_Q) can be visually compared to SES_Q in Fig. 5, the difference of which represents the enhanced proportion of chlorophyll *a* ingested.

Mean sorting efficiencies (SE) of scallops ranged from a low of 0.06 (±0.73, SD), when exposed to low-quality conditions, to a high of 0.95 (±0.04), when exposed to diatom supplemented, high-quality conditions (Fig. 6). Values of SE increased with increasing SES_Q and then plateaued (Fig. 6). SE values, however, were not significantly correlated with the percentage of material rejected in pseudofaeces ($r = 0.01$, $n = 32$, $p > 0.05$). Therefore, scallops that rejected up to 85% of the retained seston were no more efficient at selecting chlorophyll *a* particles than those that rejected <10% of the retained material. These data suggest that at low seston qualities scallops are less efficient at sorting, but become more efficient at selecting chlorophyll *a* containing particles when seston quality is above a threshold level.

Comparison of the size-frequency distributions of particles retained by scallops with those of particles rejected in pseudofaeces indicates that the selection of chlorophyll *a* containing particles was not based entirely on size (Fig. 7A, B, C). Particles of all sizes were rejected in pseudofaeces, and in many instances the relative number rejected at any size was similar to that retained (e.g. Fig. 7A). The differences that were found were common to all experimental conditions and included a shift in the pseudofaeces distribution to either a smaller (e.g. Fig. 7B) or larger (e.g. Fig 7C) size range of particles. It should be emphasized that

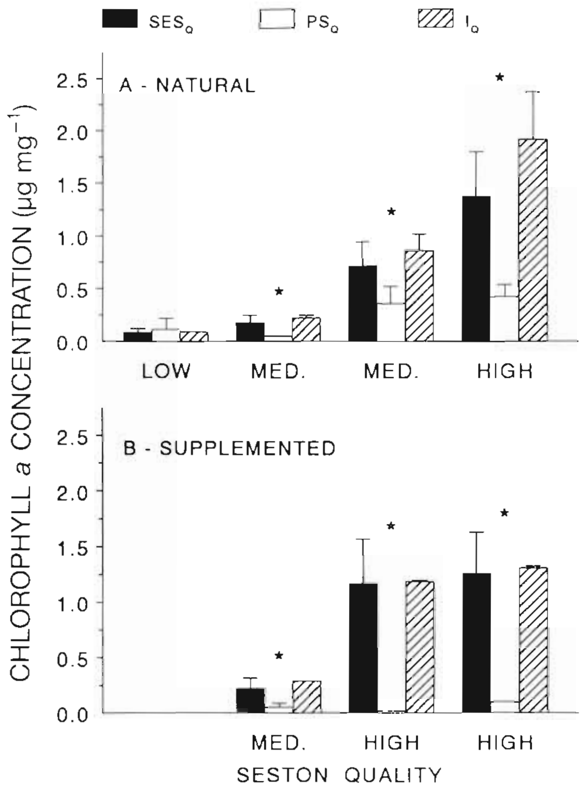

Fig. 5. *Placopecten magellanicus*. Comparisons of the quality of material in the seston (SES_Q), with that in the pseudofaeces (PS_Q) and that ingested (I_Q) during each of the 7 experimental periods. Data are presented as $\bar{x}$ ± SD, and are grouped according to the 5 different experimental conditions based on relative seston quality. *Significant difference between SES_Q and PS_Q (see Table 2 for details)

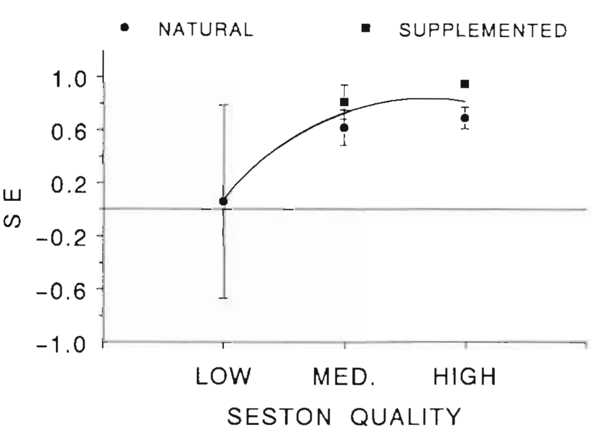

Fig. 6. *Placopecten magellanicus*. Relationship between sorting efficiency (*SE*) and relative seston quality. *SE* data are presented as $\bar{x}$ ± SD. Line of fit through data set is drawn by eye

the particle distribution in pseudofaeces represent the accumulation of particles over the entire experimental period, while the distribution of particles retained is a more instantaneous measure for a given hour.

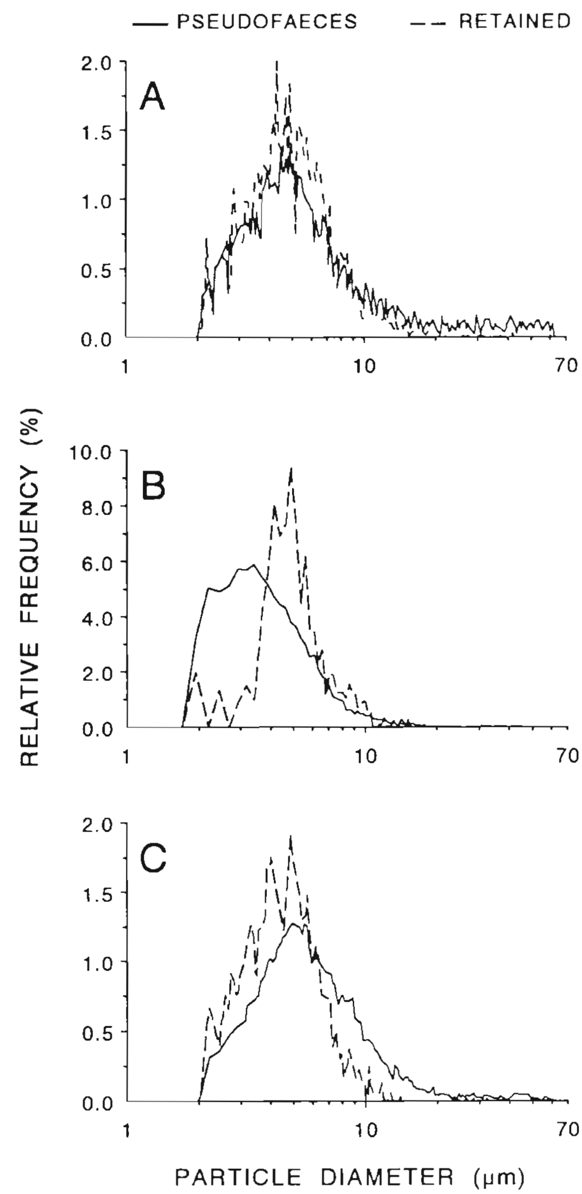

Fig. 7 *Placopecten magellanicus*. Comparisons of the size-frequency distributions of particles retained and those rejected in the pseudofaeces of 3 specimens. Spectrum obtained using a Coulter multisizer fitted with a 100 µm aperture. Comparisons are representative of data obtained during all 7 experimental periods. (A) Relative particle distribution of pseudofaeces equals that retained. (B) Relative particle distribution of pseudofaeces is shifted towards the smaller size particles. (C) Relative particle distribution of pseudofaeces is shifted towards the larger size particles

Ingestion compensation

Scallops significantly enhanced the proportion of chlorophyll *a* ingested under both natural and supplemented, high- and medium-quality experimental conditions (Table 2, Fig. 8). Compensation indices

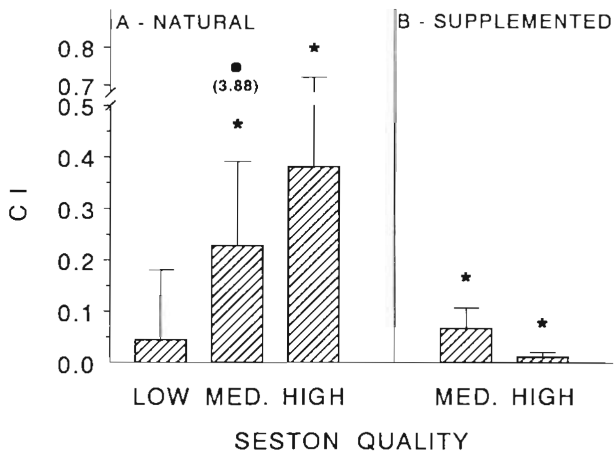

Fig. 8. *Placopecten magellanicus.* Compensation indices (*CI*) produced under the 5 different experimental conditions. *CI* data are presented as $\bar{x} \pm$ SD. **CI* values are significantly different from zero (see Table 2 for details)

(*CI*) were highest when scallops were exposed to natural seston of high quality. Under this condition, scallops increased the chlorophyll *a* content ingested between 9.5 and 86.4% ($\bar{x}$ = 39.6%). Scallops exposed to natural seston of medium quality also had high *CI* values, ranging from 4.0 to 46.7% ($\bar{x}$ = 23.7%). In addition, under this condition 1 individual produced a *CI* of 388%. This datum point, however, was not used for statistical analysis, but it does indicate the broad individual variation possible under similar conditions. Scallops demonstrated no significant compensation under the low-quality experimental conditions (Table 2, Fig. 8). In fact, in some cases *CI* values were negative indicating that scallops rejected more chlorophyll *a* containing particles in the pseudofaeces and decreased the quality of material ingested.

Although scallops had significant *CI* values under high- and medium-quality conditions, obvious differences existed in the ability to enhance the material ingested when exposed to natural and supplemented seston. Under natural conditions, *CI* increased with increasing seston quality (Fig. 8). The opposite trend was observed under the supplemented conditions. In addition, *CI* values of scallops under natural, high- and medium-quality conditions were significantly higher than *CI* values under the respective supplemented conditions ($p < 0.002$ and $p < 0.05$ respectively).

Finally, a significant negative relationship was found between *CI* and $CR1_S$ ($r = -0.46$, $n = 32$, $p < 0.01$; Fig. 9). Small changes in the proportion of chlorophyll *a* ingested (<10%) could be achieved by scallops over a wide range of clearance rates, between 1 and 8 l h^{-1}. Large changes in the proportion of chlorophyll *a* ingested (>20%), however, could only be achieved if the bivalve was clearing particles at relatively low rates of <2 l h^{-1}.

DISCUSSION

The quality of suspended particles, as well as the quantity of seston, are important factors mediating the feeding behaviour and physiology of suspension-feeding animals (Bayne & Hawkins 1992). This is particularly true for bivalves, which can regulate both the rate of food uptake and the quality of material ingested. Behavioural responses such as changes in clearance and ingestion rates, and active particle selection are thought to be particularly advantageous to bivalve species that occur in turbid environments, such as oysters, mussels and clams. As indicated by our study, however, even species that live in low turbidity environments, such as *Placopecten magellanicus*, respond to subtle changes of the seston and can substantially increase the quality of food ingested by adjusting feeding behaviour. Because phytoplankton and benthic microalgae are important components of the food resource for both inshore and offshore populations of scallops (Shumway et al. 1987, Cranford & Grant 1990), chlorophyll *a* appears to be a useful indicator of the factors that mediate some feeding responses.

Clearance rates of scallops increased with increasing concentration of particulate chlorophyll *a* (PCC; µg l^{-1}; Fig. 3), but showed no trend when analyzed based on seston quality (SES_Q; µg ml^{-1}). Therefore, in *Placopecten magellanicus* the rate at which seston is cleared from suspension is related more to the total

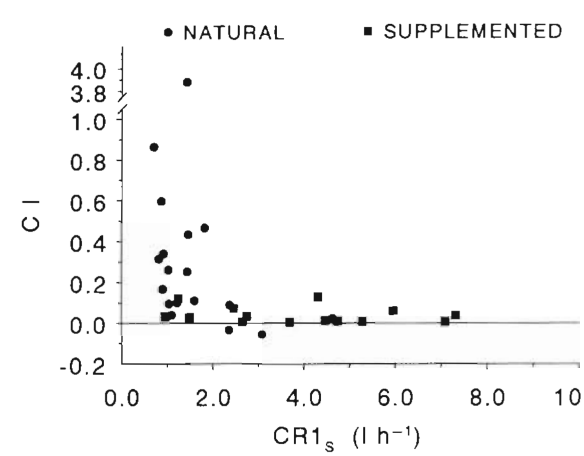

Fig. 9. *Placopecten magellanicus.* Relationship between compensation index (*CI*) and standardized clearance rate ($CR1_S$). Data are presented for individual scallops. A significant, negative relationship exists between the 2 variables when linearized using $1/X$ transformation (r = 0.46)

amount of chlorophyll *a* in the water than to how diluted this food resource is with non-chlorophyll-containing particles. Our findings are consistent with recent studies by Ward et al. (1992) who found that clearance and ingestion rates of *P. magellanicus* are stimulated by dissolved metabolites from the diatom *Chaetoceros muelleri*. Taken together, these results suggest that the initial stage of suspension-feeding in scallops (i.e. clearance rate) is mediated in part by the concentration of phytoplankton in the water, which is probably assessed by means of distance chemoreception. Results of the present study also support aspects of the functional model of bivalve feeding recently developed by Willows (1992), in which clearance rates are predicted to increase initially with increasing food concentration (J l^{-1}).

When exposed to increasing seston concentrations, many bivalve species control ingestion by either increasing pseudofaeces production, reducing clearance rates, or both (e.g. Foster-Smith 1975, Winter 1978, Kiørboe et al. 1980, Møhlenberg & Kiørboe 1981, Bricelj & Malouf 1984). Under our experimental conditions (2 to 15 mg l^{-1}), however, clearance rates of *Placopecten magellanicus* were independent of seston concentration, and ingestion rates simply increased with increasing levels of total particulate matter (TPM; Fig. 4). Even with the addition of ~12 mg l^{-1} silt, clearance rates remained constant (Fig. 3; cf. rates at PCC 4.1 µg l^{-1}), a response not found when scallops were exposed to bentonite clay at concentrations >2 mg l^{-1} (Cranford & Gordon 1992). Nevertheless, our findings are consistent with previous results obtained for *P. magellanicus* feeding on cultured phytoplankton, pulverized kelp, and resuspended sediment (Cranford & Grant 1990). Furthermore, in our study pseudofaeces were produced by scallops even at low concentrations of natural seston (~2 mg l^{-1}), and the rate of pseudofaeces production increased only slightly with increasing levels of TPM. These results suggest that the ingestive capacity of *P. magellanicus* was not exceeded over the time period measured. The production of pseudofaeces served to alter the quality of material ingested by means of selective rejection, rather than to simply eliminate material in excess of the ingestive capacity by means of bulk rejection. Therefore, we suggest that at TPM concentrations of 2 to 15 mg l^{-1}, qualitative factors of the seston are more important in regulating clearance and pseudofaeces production rates of scallops than quantitative factors.

Although mediated to some degree by qualitative components of the seston, it is apparent that clearance rates are also affected by the secondary stages of feeding (i.e. particle selection, preferential ingestion). For example, scallops exposed to natural, high-quality seston had high compensation indices (*CI*; Table 2), but had clearance rates ($CR1_S$) that were lower than expected based on PCC (Fig. 3). In addition, there was a negative relationship between *CI* and $CR1_S$ (Fig. 9). These results suggest that particle sorting on the labial palps is one of the limiting steps in the feeding process. In order to increase the quality of material ingested above 20% by means of particle selection, scallops must reduce the volume of material entering the palps by reducing the clearance rate. At this stage, both contact chemoreception and post-ingestive feedback mechanisms may be operating. Similar feeding 'trade-offs' have been reported for certain species of zooplankton. Richman & Dodson (1983) showed that the filtering and ingestion rates of *Daphnia pulex* decrease as rejection activities increase. While the energetic costs of selection in bivalves are unknown, models of suspension-feeding zooplankton suggest that selective feeders have lower feeding rates than nonselective feeders under all but the poorest food quality conditions (Sierszen & Frost 1992).

The efficiency of particle selection in marine bivalves has been shown to be quite variable both within and between species, and it may be related to labial palp size or seston conditions (Kiørboe & Møhlenberg 1981, Iglesias et al. 1992). For example, Newell et al. (1989) reported that *Mytilus edulis* did not always display selective capabilities, especially when food quality was low (POM < 20%). Iglesias et al. (1992) observed that selection efficiencies (*SE*) of *Cerastoderma edule* increased with increasing organic content of the food to a maximum at intermediate diet qualities, and then declined at the highest organic concentrations. For scallops, we obtained a similar trend for *SE* as a function of SES_Q (Fig. 6), although we did not find a decrease in *SE* at the high-quality conditions. These results indicate that food quality plays an important role in the efficiency of particle selection.

Scallops were highly efficient at selecting chlorophyll-*a*-containing particles under both natural and supplemented, high- and medium-quality conditions (Fig. 6). This selection led to the preferential rejection of a significantly higher proportion of non-chlorophyll-containing particles in the pseudofaeces (PS_Q; Fig. 5). Under laboratory conditions, *Placopecten magellanicus* has been shown to selectively ingest certain dinoflagellate species in preference to others (Shumway et al. 1985), and *Tetraselmis suecica* cells over similar size bentonite clay particles (Cranford & Gordon 1992). In the present study, *P. magellanicus* has been shown to have the capability of particle selection over a wide range of natural conditions.

In addition to qualitative selection, under most conditions scallops produced sufficient amounts of pseudofaeces to significantly increase the quality of mater-

ial ingested on a quantitative basis (Fig. 8). Under some conditions, there was on average a 7%, 24%, and 40% increase in the quality of material ingested over that which would have been ingested if selection had not taken place (*CI*; Table 2). Therefore, the selection process of scallops was successful in altering the ingested ration over time. This point has not been thoroughly addressed by many previous workers, and is particularly important. To the bivalve, there is no energetic benefit to altering the quality of material in the pseudofaeces if it is not produced in high enough quantities to significantly enhance the quality of material ingested. Newell & Jordan (1983) showed that the oyster *Crassostrea virginica* has the ability to sort different types of particles, but they emphasized that this selective mechanism is only meaningful if the oyster produces significant amounts of pseudofaeces at low ambient particle concentrations. Our work supports their contention. For example, scallops under the supplemented, high-quality conditions exhibited the highest *SE* values (Fig. 6), and demonstrated statistically significant selection (Fig. 5) and ingestion compensation (Fig 8). Despite this, the amount of material rejected as pseudofaeces was low compared to that cleared (<1%), and consequently the increased proportion of chlorophyll *a* ingested was also very low (*CI* ~1.0%; Table 2). Therefore, the biological significance of the selection process of these scallops is questionable. On the other hand, the high *CI* values produced by scallops under natural conditions emphasizes the importance of considering particle selection when calculating absorption efficiencies. Traditional methods such as the Conover ratio (Conover 1966), assume non-selective feeding and may seriously underestimate the efficiency of digestive processes.

It was previously thought that *Placopecten magellanicus* rarely produce pseudofaeces when feeding on natural particulates in Newfoundland waters (MacDonald & Thompson 1986). This assumption was based on previous reports which indicate that for many bivalve species pseudofaeces are not produced below a certain threshold concentration of seston (e.g. 1 to 6 mg l^{-1}; Griffiths & Griffiths 1987). Such reports, however, can be misleading. As shown in the present study, production of pseudofaeces at low TPM concentrations can be important. In fact, one of the highest mean *CI* values (~24%) was produced by scallops feeding on seston at the lowest TPM concentration (natural seston, medium quality; Tables 1 & 2). Much lower amounts of pseudofaeces and lower *CI* values were produced by scallops feeding at higher TPM concentrations (e.g. natural seston, low quality; supplemented seston, high quality).

The type of suspended particles encountered by scallops also seems to affect the selection process (Fig. 8). *CI* values of scallops under natural, high- and medium-quality conditions were significantly higher than those of scallops under comparable, but supplemented, conditions. During the supplemented experiments the seston was dominated by small, uniform particles (Fig 1). This narrow particle distribution seemed to increase retention efficiency (RE_S; Fig. 2) and may have influenced the production of pseudofaeces. One possibility is that when exposed to relatively high numbers of small, good quality particles (i.e. cultured microalgae) the selection process is not needed to maintain a high energy intake. Alternatively, selection between small, similar sized particles may be difficult and result in a reduced pseudofaeces production rate. It is clear that more research is needed to understand the principles underlying these observed difference. Our findings, however, indicate the dynamic nature of the selection process and point to the problem of using laboratory mixtures of narrow ranged particles to determine the consequences of selection under natural conditions.

There are 2 ways in which scallops can improve the quality of material ingested: (1) preferential clearance of chlorophyll containing particles on the gill (Shumway et al. 1985, Newell et al. 1989); and (2) selection on the labial palps and preferential rejection of non-chlorophyll-containing particles in the pseudofaeces (Kiørboe & Møhlenberg 1981, Newell & Jordan 1983). While the exact mechanisms involved in the discrimination of particles have yet to be described, recent endoscopic studies have demonstrated that particles on the ridged surfaces of the labial palps of *Crassostrea virginica* and *Placopecten magellanicus* are not tightly bound in mucus. Therefore, discrimination of individual particles is possible (Beninger et al. 1992, Ward et al. 1993, 1994). Comparison of the particle size distributions of seston retained by scallops with those of the pseudofaeces indicates that the selection process was not based entirely on particle size (Fig. 7). Instead, we suggest that qualitative factors of the particles and contact chemoreception were involved in the preferential ingestion of chlorophyll-*a*-containing particles. Such a selection mechanism has been reported for other species of bivalves (e.g. Newell & Jordan 1983, Ward & Targett 1989).

The lack of particle selection and ingestion compensation observed at low SES_Q conditions may be explained by considering that selection through pseudofaeces production is a process of rejection. Under these conditions, poor-quality particles dominate the seston and scallops may attempt to reject a high proportion of these particles in order to increase the quality of material ingested. It may not be possible, however, to retain the relatively few high-quality particles

while rejecting the majority of low-quality ones. This high rate of rejection may overwhelm the capacity of the system and result in non-selection or even a negative selection. In contrast, when the seston contains a higher proportion of high-quality particles it may be easier to improve on the mixture by rejecting just some of the poor-quality particles at a lower and more acceptable rate. Thus, it may be more feasible to retain most of the high-quality particles while rejecting just some of the low-quality particles. Because moderate amounts of pseudofaeces were produced under the low-quality conditions (~10% of the retained seston), we assume that scallops were attempting to reject poor-quality particles. Therefore, under these conditions the lack of selection and ingestion compensation may be due to an inability to reject efficiently the poor-quality particles rather than a behavioural response to retain all particles and maximize energy gain (see Willows 1992). This idea is supported by the fact that under low-quality conditions some scallops produced negative *CI* values and decreased the quality of material ingested. It is important to remember that selection is rarely an all (100%) or nothing (0%) response, but rather a process to improve the ingested ration, the efficiency of which varies with environmental conditions.

Bivalve species that produce pseudofaeces to regulate ingestion may be better adapted to periods of increasing TPM concentrations than species that control ingestion mainly by reducing clearance rate (e.g. Bricelj & Malouf 1984) The strategy a bivalve uses to deal with increasing particle concentrations may be related to the composition of the food supply and the habitat in which the bivalve is found (e.g. high or low turbidity water). The majority of studies on the relationships between bivalve feeding activity and variation in particle concentrations have routinely used species from coastal habitats, estuarine conditions, or those found above fine sedimentary bottoms which regularly experience resuspension events. While sea scallops may be exposed to high seston concentrations in some coastal habitats, many populations are exposed to comparatively low concentrations. With the exception of bloom conditions and periodic storm events, TPM concentrations near the bottom are routinely low (< 5 mg l^{-1}) in coastal regions of Newfoundland (MacDonald & Thompson 1985) and on the Georges Bank (Bothner et al. 1981). To regulate ingestion and maximize energy intake under these conditions, sea scallops adjust their clearance rates to optimize uptake of phytoplankton and produce pseudofaeces to improve the quality of material ingested. Energetic cost-efficient strategies such as these have recently been predicted in functional models of bivalve feeding (Willows 1992).

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