Absorption efficiency, ingestion rate, gut passage time and scope for growth in suspension- and deposit-feeding *Yoldia hyperborea*

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ABSTRACT: Laboratory feeding experiments were conducted to study the importance of suspension-feeding in the protobranch bivalve *Yoldia hyperborea* at different suspended particle concentrations in order to evaluate the importance of this feeding strategy when compared with its known strategy of deposit feeding. Standard feeding variables (absorption efficiency, AE; gut passage time, GPT; ingestion rate, IR) were estimated by quantifying ^{68}Ge/^{14}C in dual-labelled *Thalassiosira nordenski-oldii* fed to *Y. hyperborea*. For the first time, results were also used to estimate scope for growth (SFG) in a protobranch bivalve. Absorption efficiency was higher when *Y. hyperborea* was deposit feeding (87.7 to 94.8%) than it was during suspension feeding (50.1 to 71.7%), whereas GPT was similar in most cases and ranged between 8.15 and 20.11 h. However, IRs for suspended particulate matter (SPM, dry weight) were mostly negligible (<0.01 to 5.77 µg PM h^{-1}) when compared with deposit feeding (2067.4 to 6872.3 µg PM h^{-1}), although in one case suspension-feeding individuals ingested 93.7 µg PM h^{-1}. Scope for growth was always positive in deposit feeders (113.8 to 372.4 J d^{-1}), whereas under suspension-feeding conditions it was mostly negative and could not meet metabolic requirements. In addition, mortality of *Y. hyperborea* increased at suspended particle concentrations above 0.085 mg ml^{-1}. Although deposit feeding is the principal feeding strategy followed by *Yoldia hyperborea*, suspension feeding is invoked at low suspended particle loads and may serve as a strategy for capturing highly nutritional particles suspended at the sediment–water interface.

KEY WORDS: *Yoldia* · Protobranchia · Deposit-feeding · Suspension-feeding · Absorption efficiency · Ingestion rate · Gut passage time · Scope for growth

INTRODUCTION

Deposit-feeders ingest a complex assortment of mineral grains and organically dilute detritus, some of which is refractory material of low nutritional value (Lopez & Levinton 1987, Jumars 1993). However, they show a considerable diversity of feeding mechanisms and specialisation, enabling them to survive in an apparently nutritionally deficient environment. The supply of food to a deposit-feeding community occurs mainly through lateral and vertical advection (Snelgrove & Butman 1994) or microbial regeneration within the sediment (Newell 1979). Benthic communities dominated by deposit-feeders, such as the deep sea, are considered to be food-limited and depend on the amount of food that reaches the sediment surface, primarily through processes occurring in the photic zone of the water column (Gooday & Turley 1990). In temperate and high latitude areas, where input of particulate food matter is highly seasonal (Clarke 1988, Wassmann 1991, Boon et al. 1998), benthic invertebrates tend to accumulate energy reserves when food is available for use in maintenance, growth and reproduction during periods of low food availability (Nakaoka 1992, Brockington & Clarke 2001). Thus, benthic invertebrates must utilise food material efficiently when

particulate material (PM) is especially nutritious, e.g. during phytoplankton fallout events. Strategies may include physiological adaptations, such as high absorption efficiency (AE) and long gut passage time (GPT) (or vice versa), particle selection before ingestion and behavioural plasticity (Lopez & Levinton 1987, Levinton 1989, Taghon & Greene 1992).

There are many examples of animals that show behavioural plasticity when acquiring food. Dauer et al. (1981) used the term 'interface-feeders' to refer to species that are not obligatory suspension or deposit-feeders. A combination of suspension and deposit-feeding has been observed in many invertebrate taxa (Lopez & Levinton 1987, Taghon & Greene 1992, Bock & Miller 1996), including several bivalves, all of which belong to the super-family Tellinacea (Pohlo 1969, Ólafsson 1986, Levinton 1991). Ólafsson (1986) found that switching from deposit- to suspension-feeding in *Macoma balthica* occurred with changes in flow velocity. He further suggested that suspension-feeding in this species is a response to higher amounts of suspended particles present in high flows, whereas deposit-feeding is a response to a decrease in the concentration of suspended material, a view later substantiated by Lin & Hines (1994). However, Hummel (1985) indicated that although *M. balthica* behaves as a deposit-feeder most of the time, it depends largely on food present in the water column.

Although protobranch bivalves have usually been considered to be deposit-feeders (Rhoads & Young 1970, Lopez 1988), some authors have suggested that *Yoldia* spp. may be capable of suspension-feeding, based on anatomical features of the gills and palps (Kellogg 1915, Stasek 1965). However, Levinton et al. (1996) suggested that the gills only have a role in the removal of particles from the gill surface and mantle cavity. Furthermore, qualitative observations on *Yoldia eightsii* by Davenport (1988) suggest that this species is capable of passively trapping phytoplankton when ventilating, whereas Nakaoka (1992) indicated that *Y. notabilis* is capable of suspension-feeding, but did not explain how he reached this conclusion.

Although no study has yet provided an accurate account of suspension-feeding behaviour in any protobranch bivalve, personal observations on the nuculanid *Yoldia hyperborea* suggest that it can produce faeces when deprived of sediment but in the presence of suspended particles. Protobranchs are one of the dominant infaunal taxa in muddy sediments, but little is known about their feeding physiology, particularly aspects such as ingestion and assimilation of organic carbon (Lopez & Cheng 1982, 1983, Cheng & Lopez 1991). However, these variables are used for estimating the energy budget of a species in conjunction with other physiological variables such as oxygen uptake and nitrogen excretion (Widdows 1985b). The estimation of a species' energy budget can contribute towards an overall comprehension of its feeding strategies and behaviour, as well as its strategies for energy storage in a nutrient-limited environment.

The purpose of this study is to establish the importance of suspension-feeding in *Yoldia hyperborea* at different particle concentrations, and to compare this strategy with deposit-feeding through the quantification of ingestion rate (IR), AE and GPT. In addition, an energy budget is also derived for inferring the potential impact of feeding strategy and variation of food supply on the feeding activity, energy gain and expenditure of *Yoldia hyperborea.*

MATERIALS AND METHODS

Collection and handling of animals. *Yoldia hyperborea* were obtained by dredge from the deep-depositional zone of Conception Bay, Newfoundland (250 m, 47° 34.0′ N, 53° 08.1′ W) (Stead & Thompson 2003a) and placed in sediment within a refrigerated holding tank (0.0 ± 1.0°C; ambient temperature) at the Ocean Sciences Centre in Logy Bay. Since most physiological rates vary with body size, only large *Y. hyperborea* of similar size were used for feeding experiments (mean shell length = 28.96 mm, SD = 2.14, n = 96).

Feeding experiments. *Method:* Most feeding studies on deposit-feeders have used various techniques involving radiolabelled food material to determine IR, GPT and AE (Forbes & Lopez 1989, Kofoed et al. 1989, Decho & Luoma 1991, Charles et al. 1995). The advantage of this approach over gravimetric and indicator methods (sensu Lopez et al. 1989) is its increased sensitivity for measuring small changes (Calow & Fletcher 1972). Dual-labelled food is particularly useful as it can be partitioned into an absorbed (organic) and an unabsorbed (conservative) fraction. One such technique is that developed for diatoms by Rivkin (1986) and Bochdansky et al. (1999), using ^{14}C to label the organic fraction and ^{68}Ge the inorganic, since germanium is incorporated into the structure of the frustule, and thus cannot be absorbed by the animal (Bochdansky et al. 1999).

The maximum energies for ^{14}C and ^{68}Ge are 156 and 1900 keV, respectively. The ratio of ^{68}Ge:^{14}C maximum energies (i.e. 12.2) is high enough for complete separation of the 2 isotopes (Bochdansky et al. 1999). Standard quench curves were constructed for each isotope using internal standards and chloroform as quenching agent. The procedure outlined in the Packard Tri-Carb® liquid scintillation counter manual was followed.

Preparation of experimental food source: Laboratory experiments were carried out with the cold-water diatom *Thalassiosira nordenskioldii* as a food source. This species was chosen because of its size (equivalent spherical diameter = 15 µm) and its frequent presence in Newfoundland waters. Cultures were grown under continuous light in f/2+ medium (33‰ salinity) at 5 to 8°C. Cell counts were routinely done on a haemocytometer with a Neubauer grid. Once the culture entered the exponential growth phase it was inoculated with $^{68}Ge(OH)_4$ (Brookhaven National Laboratories) and $NaH^{14}CO_3$ to a final concentration of 80 to 100 µCi l^{-1} for ^{14}C (Nielsen & Olsen 1989) and 40 to 60 µCi l^{-1} for ^{68}Ge (Penry & Frost 1991). No detectable effects of these isotope concentrations on the rate of algal growth have been found in previous studies (Rivkin 1986, Nielsen & Olsen 1989, Penry & Frost 1991, Bochdansky et al. 1999). ^{68}Ge acts as an unabsorbed marker which passes through the gut and is recovered in the faeces. Unbound, dissolved label was removed after 8 to 13 d from inoculation by a series of reversed flow filtrations, using a 5 µm Nitex mesh, until the label was not more than 3% higher than background levels.

Suspension-feeding experiments: Seven days before the start of each experiment, experimental animals were transferred to individual cups overlying a stirbar and lying within a glass jar (200 ml) containing filtered seawater (2 µm) and unlabelled *Thalassiosira nordenskioldii* cells. Containers were kept in an incubator (0 ± 1°C) in the dark and placed on a magnetic stirring plate that maintained the algae in suspension. This set-up allowed the *Yoldia hyperborea* to maintain

the orientation they most frequently adopt when in sediment, but prevented them from reaching any deposited algae with their palp proboscides. Filtered seawater with algae was renewed daily.

The experiment began after filtered seawater (Whatman GF/F) had been renewed and dual-labelled and unlabelled algae introduced into the jars. A total of 11 experiments was carried out on 5 different occasions (Table 1). Experiments on each date included a treatment with a fixed, low algal density (7.54 to 9.94 cells μl^{-1}), whereas an additional 6 treatments with 19.51 to 170.87 cells μl^{-1} were included to test the effect of varying algal concentration on the feeding physiology of the protobranch (Table 1). A range of 4 to 17 replicates of each algal concentration was used on each occasion. Replicate water samples (n = 3) were taken at the beginning of the experiment for cell counts, whereas suspended particulate matter (SPM) was estimated by filtering 50 to 100 ml of unlabelled algae on a GF/F filter, followed by drying (60°C, 72 h) and combustion at 450°C (6 h) for the determination of dry weight (DW) and ash-free dry weight (AFDW).

Faeces were collected every hour for the first 5 h and then every 3 h until the end of the experiment (66.5 to 82.5 h). All faecal pellets produced were removed from the jar with Pasteur pipettes and washed 3 times with 20 ml GF/F-filtered seawater to remove attached algae before transferring onto a 25 mm GF/F filter. A 2 ml water sample was also removed from the jar and passed through a glass fibre filter (GF/F) at the beginning of the experiment and also when faeces were present, in order to monitor any change in the $^{68}Ge:^{14}C$ ratio of sus-

Table 1. *Yoldia hyperborea.* Main characteristics of food provided in suspension- and deposit-feeding experiments. POM = particulate organic matter (% dry weight)

Expt	*T. nordenskioldii* density (cells μl^{-1})		*T. nordenskioldii* $^{68}Ge:^{14}C$ ratio		Particle concentration		Food value
	$\bar{x}$	(SD, n)	$\bar{x}$	(SD, n)	(mg ml^{-1})	(%POM, n)	(J mg^{-1})
Suspension-feeding							
1	8.69	(1.29, 20)	0.123	(0.005, 6)	0.016	(36.54, 3)	7.593
2	9.94	(2.48, 20)	0.312	(0.035, 41)	0.020	(37.48, 3)	7.788
3	7.54	(2.43, 24)	0.317	(0.034, 23)	0.022	(35.32, 3)	7.339
4	89.21	(11.33, 24)	0.317	(0.034, 23)	0.257	(35.32, 3)	7.339
5	170.87	(22.66, 24)	0.317	(0.034, 23)	0.493	(35.32, 3)	7.339
6	9.52	(2.61, 20)	0.666	(0.114, 34)	0.020	(40.59, 3)	8.435
7	19.51	(2.82, 20)	0.666	(0.114, 34)	0.042	(40.59, 3)	8.435
8	39.51	(3.23, 20)	0.666	(0.114, 34)	0.085	(40.59, 3)	8.435
9	9.80	(1.10, 20)	0.526	(0.045, 19)	0.021	(36.54, 3)	7.593
10	29.55	(3.94, 20)	0.526	(0.045, 19)	0.063	(36.54, 3)	7.593
11	49.89	(6.87, 20)	0.526	(0.045, 19)	0.107	(36.54, 3)	7.593
Deposit-feeding							
12			5.544	(3.905, 9)	491.000	(11.88, 8)	2.468
13			7.191	(1.071, 28)	491.000	(11.88, 8)	2.468
14			9.140	(0.661, 46)	491.000	(11.88, 8)	2.468

pended algae. Residual $NaH^{14}CO_3$ was removed by adding 0.25 ml of 0.2 N perchloric acid to the sample. Vials were left loosely capped for 12 h and 5 ml of scintillation cocktail (Ecolume) was then added. Samples were stored for 48 h to ensure that ^{68}Ge attained a transient equilibrium with ^{68}Ga (Rivkin 1986), and radiolabel counted with a Packard Tri-Carb® liquid scintillation spectrometer (model TR 2500); all sample counts were corrected for both quench (external standard method) and background activity.

Deposit-feeding experiments: Ambient sediment, which had been previously frozen (–20°C) to eliminate all fauna, was used to fill the bottom of the experimental jars (~8 cm layer). All jars were kept in an incubator at 0°C (±1) in total darkness. After sediment had settled in the jars, the overlying water (~130 ml) was removed and replaced with filtered seawater (2 µm). An equal amount of dual-labelled *Thalassiosira nordenskioldii* was mixed with the sediment from each jar. After confirming that the seawater contained no traces of radiolabel, animals were carefully placed on the sediment surface and allowed to bury. Five replicate jars, each containing 1 animal, were used on each occasion. Jars were checked for the presence of faeces every hour for the first 5 h and every 3 h thereafter until the end of the experiment (46 to 99.5 h). To detect any changes in the $^{68}Ge:^{14}C$ ratio and concentration of algae, sediment samples were taken with a glass microcore (3 mm diameter) from the top 7 mm layer at the beginning of the experiment and each time faeces were observed on the sediment surface. Sediment samples and faeces were processed as in the suspension-feeding experiments.

Handling of animals after the experiment: At the end of each experiment (i.e. after 68.5 to 82 h), *Yoldia hyperborea* were removed from the experimental jars, placed in filtered seawater (2 µm) and examined to verify that they were in good condition. To confirm ingestion of algae by *Yoldia hyperborea*, a small portion of the digestive gland was removed from each individual after this period and separately processed for counting as described above for labelled algae, faeces and sediment. The transfer of ^{14}C and absence of ^{68}Ge in tissues not involved in the processing of food was confirmed in gonad and gill sections.

Physiological measurements. *AE:* AE of labelled microalgae was calculated from an equation devised by Conover (1966) and modified by Calow & Fletcher (1972):

$$AE = 1 - \frac{^{68}Ge_a:^{14}C_a}{^{68}Ge_f:^{14}C_f} \times 100 \qquad (1)$$

where AE is absorption efficiency of organic carbon (%), $^{68}Ge_a:^{14}C_a$ is the ratio of ^{68}Ge to ^{14}C in dual-

labelled algae, $^{68}Ge_f:^{14}C_f$ is the ratio of ^{68}Ge to ^{14}C in faeces. Mean AE was calculated from values obtained each time faeces were collected.

GPT: Minimum GPT was defined by the time elapsed between ingestion of radiolabelled algae and the first appearance of ^{68}Ge in the faeces.

IR: IR was calculated from the total amount of ^{68}Ge (dpm) defecated during the experiment, after correcting for PM (dry weight) concentration (see Eq. 2). GPT provided a correction for material still in the digestive tract as indicated in the equation:

$$IR = \frac{(\sigma^{68}Ge) \times (1 + U_a)}{(\delta t - GPT)} \times \frac{1}{LPM} \qquad (2)$$

where IR is ingestion rate (mg PM h^{-1}), $\sigma^{68}Ge$ is the sum of ^{68}Ge activity in all collected faeces (dpm), U_a is the number of unlabelled cells per labelled *Thalassiosira nordenskioldii* cell, δt is the duration of each experiment (h), GPT is gut passage time (h), LPM is concentration of labelled PM (dpm mg^{-1}). No unlabelled *T. nordenskioldii* cells were added to the sediment in deposit-feeding experiments.

Scope for growth: The physiological index of energy balance given by scope for growth (SFG) represents the energy available for growth and reproduction of an individual after all the physiological demands of respiration and excretion have been met (Widdows 1985a). Rates of standard oxygen consumption (VO_2) and excretion (VNH_4-N) were derived for each individual from our previously published data (Stead 2001, Stead & Thompson 2003b) and converted to energy equivalents (J h^{-1}) using the conversion factors suggested by Widdows (1985b):

$$SFG = C - F = A - (R + U) \qquad (3)$$

where C is the product of ingestion rate (mg PM d^{-1}) and the energy content of food (J mg^{-1}), F is the energy lost as faeces (J d^{-1}), A is energy absorbed (C × AE) (J d^{-1}), R is the oxygen uptake (ml O_2 d^{-1}, × 20.33 J), U is ammonia nitrogen excretion rate (µg NH_4-N d^{-1}, × 24.87 × 10^{-4} J) and SFG is scope for growth (J d^{-1}). Particulate organic matter (POM) was converted to energy equivalents by considering 1 mg of POM as 20.78 J (Crisp 1984).

Statistical analysis. The effect of food conditions (i.e. food source and particle concentration) on AE (%), GPT (h) and IR (mg PM h^{-1}) was examined with a general linear model (GLM) after normalisation with arcsine square-root or log_{10} transformations when appropriate (Sokal & Rohlf 1995). In cases where ANOVA revealed significant differences, *a posteriori* pair-wise comparisons of each independent variable (AE, GPT, IR) were performed between experiments (= food conditions), with the Tukey-Kramer HSD test (Sokal

& Rohlf 1995). As food conditions and all other experimental conditions were similar in all 3 deposit-feeding experiments, the experiments were considered as replicates. All data transformations and analyses were conducted using the SPSS® ver. 10 statistical analysis package (SPSS).

RESULTS

Absorption efficiency (AE)

Faecal pellets collected from both suspension- and deposit-feeding individuals varied in length from 0.5 to 15 mm, although most were around 2 mm. Pellets of similar size were also observed in *Yoldia hyperborea* deposit-feeding in unlabelled mud (Stead 2001). Faecal pellets were easily obtained from the sediment surface in deposit-feeding experiments as the sediment surface was not greatly disturbed. In addition, faeces were not buried by particles from the pseudofaecal plume, as previous observations on *Y. hyperborea* feeding on unenriched sediment had shown, indicating that no significant amounts of pseudofaeces were produced during the experiments.

The AE (%) for *Thalassiosira nordenskioldii* carbon was 50.06 to 71.70 % ($\bar{x}$ = 62.74, SD = 7.12) in suspension-feeding and 87.68 to 94.76 % ($\bar{x}$ = 93.65, SD = 4.49)

in deposit-feeding experiments (Table 2). Since *Yoldia hyperborea* fed the 2 highest seston concentrations in suspension-feeding experiments (Expts 4 and 5) did not ingest algae, for statistical purposes only an AE of 0 % was assumed in their case (Table 2). Significantly different AEs were observed between Expts 1 and 3, although both had similar feeding conditions, and the difference in AE may have resulted from the high variability in individual response to SPM. AEs for *T. nordenskioldii* carbon were significantly higher in deposit- than suspension-feeding animals, except for Expts 3 and 10 (0.022 and 0.063 mg PM ml^{-1}) (cf. Tables 2 & 3).

Gut passage time (GPT)

GPT ranged from 8.15 to 57.31 h in suspension-feeding experiments and 9.81 to 17.31 h in deposit-feeding experiments, although mean values were similar (excluding values for Expt 11, $\bar{x}$ = 14.61 h, SD = 3.51 and $\bar{x}$ = 13.80 h, SD = 3.31, for suspension- and deposit-feeding groups, respectively) (Table 2). The highest GPT ($\bar{x}$ = 57.31 h, SD = 31.93) was observed in *Yoldia hyperborea* from Expt 11 fed with 0.107 mg ml^{-1} of suspended particles. The high variability in GPT observed in animals from this experiment may have resulted from the fact that they were exposed to a high

Table 2. *Yoldia hyperborea.* Suspension- and deposit-feeding experiments using suspended or sediment-mixed ^{68}Ge:^{14}C dual-labelled *Thalassiosira nordenskioldii* as food. Experiments were conducted in the dark at 0°C. ^{68}Ge:^{14}C is the ratio of the isotopes in the faeces. AE = absorption efficiency of carbon contained in *Thalassiosira nordenskioldii.* PM = dry particulate matter, ni = ingestion not observed. Total time = experimental period. t_2 = time after removal from experimental set-up. Sig. = experiment significantly different to experiment number in superscript. + = Expts 4 and 5, All+ = all experiments except for Expts 4 and 5, All = all experiments, 12 = Expts 12 to 14

Expt	Total time (h)	*Y. hyperborea* shell length (mm) $\bar{x}$	(SD, n)	Ingestion rate (µg PM h^{-1}) $\bar{x}$	(SD, n)	Sig.	AE (%) $\bar{x}$	(SD, n)	Sig.	Gut passage time (h) $\bar{x}$	(SD, n)	Sig.	Mortality rate at t_2 (%)	t_2 (h)
Suspension-feeding														
1	82.5	32.98	(1.68, 11)	1.91	(0.90, 8)	[12]	50.06	(7.68, 11)	[+, 3, 12]	20.11	(11.73, 11)	[+]	0.00	152.0
2	74.0	30.35	(1.30, 17)	3.25	(2.47, 11)	[12]	59.55	(12.33, 17)	[+, 12]	18.50	(12.18, 11)	[+, 11]	0.00	147.5
3	66.5	27.93	(0.56, 6)	<0.01	(0.00, 4)	[12]	67.77	(15.56, 6)	[+]	15.20	(14.78, 5)	[+, 11]	0.00	148.5
4	66.5	28.12	(0.55, 6)	0.00	(0.00, 6)	[12]	ni	(0.00, 4)	[All+]	ni	(0.00, 4)	[All+]	66.66	148.5
5	66.5	27.77	(0.49, 6)	0.00	(0.00, 6)	[12]	ni	(0.00, 6)	[All+]	ni	(0.00, 6)	[All+]	50.00	148.5
6	77.3	25.78	(0.53, 5)	0.18	(0.09, 5)	[12]	55.30	(14.14, 5)	[+, 12]	14.63	(13.51, 4)	[+, 11]	0.00	151.3
7	77.3	27.44	(0.59, 6)	5.77	(4.99, 5)	[12]	70.20	(6.41, 6)	[+, 12]	12.75	(11.30, 5)	[+, 11]	0.00	151.3
8	77.3	28.76	(1.42, 5)	93.66	(95.42, 5)	[12]	71.70	(14.42, 5)	[+, 12]	8.15	(7.90, 5)	[+, 11]	16.66	151.3
9	75.8	28.20	(0.87, 5)	0.19	(0.18, 5)	[12]	58.40	(20.28, 4)	[+, 12]	12.01	(6.81, 3)	[+, 11]	0.00	149.5
10	75.8	28.70	(1.43, 4)	<0.01	(0.00, 3)	[12]	61.96	(13.27, 4)	[+]	15.50	(20.93, 4)	[+]	0.00	149.5
11	75.8	27.74	(0.93, 5)	<0.01	(0.00, 5)	[12]	69.76	(8.96, 5)	[+, 12]	57.31	(31.93, 4)	[+, 2, 3, 6, 7, 8, 9, 12]	0.00	149.5
Deposit-feeding														
12	99.0	26.58	(0.93, 3)	4135.0	(1734.8, 3)	[All]	87.68	(5.96, 3)	[+, 1, 2, 6, 8, 9, 11]	13.67	(2.49, 3)	[+, 11]	0.00	99.0
13	46.8	29.80	(1.99, 4)	2067.4	(2670.3, 3)		98.52	(0.04, 3)		17.92	(3.77, 3)		0.00	46.8
14	99.5	30.98	(1.28, 4)	6872.3	(6050.8, 4)		94.76	(3.39, 4)		9.81	(4.59, 4)		0.00	168.0

Table 3. *Yoldia hyperborea.* Scope for growth (SFG) calculated for individuals in suspension- and deposit-feeding experiments. Mean shell length of all experimental animals was 28.50 mm (SD = 1.93). Values for VO_2 and VNH_4-N were obtained elsewhere (Stead 2001, Stead & Thompson 2003b)

Expt ($J\ d^{-1}$)	VO_2 ($J\ d^{-1}$)		VNH_4-N ($J\ d^{-1}$)		Ingestion rate (IR) ($J\ d^{-1}$)		Absorption rate ($J\ d^{-1}$)		SFG ($J\ d^{-1}$)	
	$\overline{x}$	(SD, n)	$\overline{x}$	(SD, n)	$\overline{x}$	(SD, n)	$\overline{x}$	(SD, n)	$\overline{x}$	(SD, n)
Suspension-feeding										
1	7.86	(0.58, 8)	0.035	(0.005, 8)	0.35	(0.17, 8)	0.18	(0.11, 8)	−7.71	(0.66, 8)
2	7.08	(0.61, 11)	0.029	(0.004, 11)	0.61	(0.46, 11)	0.41	(0.38, 11)	−6.69	(0.49, 11)
3	6.05	(0.26, 4)	0.022	(0.002, 4)	0.54	(0.52, 4)	0.46	(0.46, 4)	−5.62	(0.31, 4)
4	6.18	(0.07, 6)	0.023	(0.000, 6)	0.00	(0.00, 6)	0.00	(0.00, 6)	−6.20	(0.07, 6)
5	6.03	(0.22, 6)	0.022	(0.001, 6)	0.00	(0.00, 6)	0.00	(0.00, 6)	−6.06	(0.22, 6)
6	5.25	(0.19, 5)	0.018	(0.001, 5)	0.04	(0.02, 5)	0.02	(0.01, 5)	−5.25	(0.19, 5)
7	5.87	(0.23, 5)	0.021	(0.001, 5)	1.17	(1.01, 5)	0.80	(0.69, 5)	−5.09	(0.77, 5)
8	6.51	(0.28, 5)	0.025	(0.002, 5)	18.97	(19.32, 5)	16.10	(16.40, 5)	9.57	(16.14, 5)
9	6.22	(0.59, 5)	0.024	(0.004, 5)	0.04	(0.03, 5)	0.02	(0.02, 5)	−6.23	(0.60, 5)
10	6.49	(0.36, 3)	0.025	(0.012, 3)	0.13	(0.09, 3)	0.09	(0.05, 3)	−6.43	(0.33, 3)
11	6.03	(0.59, 5)	0.022	(0.004, 5)	0.15	(0.11, 5)	0.12	(0.10, 5)	−5.94	(0.51, 5)
Deposit-feeding										
12	5.61	(1.08, 3)	0.020	(0.006, 3)	244.97	(102.78, 3)	216.67	(94.60, 3)	211.04	(95.51, 3)
13	6.91	(0.87, 3)	0.028	(0.006, 3)	122.48	(155.95, 3)	120.73	(155.95, 3)	113.79	(156.05, 3)
14	8.06	(1.25, 4)	0.037	(0.010, 4)	407.14	(358.47, 4)	380.48	(337.38, 4)	372.38	(337.98, 4)

particle concentration (0.107 mg ml^{-1}). GPT from Expt 11 was significantly different to all others, except Expts 1, 3 and 10, possibly as a result of their high variability and low sample size (Table 2).

Ingestion rate (IR)

IR varied considerably between individuals in all suspension-feeding experiments (Table 2). *Yoldia hyperborea* fed low seston concentrations (0.016 to 0.022 mg PM ml^{-1}) ingested <0.01 to 3.25 µg PM h^{-1}, whereas at intermediate seston concentrations of 0.042 and 0.085 mg ml^{-1}, IRs increased to 5.77 and 93.66 µgPM h^{-1}, respectively. However, this increase was not apparent at 0.063 mg PM ml^{-1} (IRs of 7 × 10^{-4} mg PM h^{-1}). A low value of IR (8 × 10^{-4} mg PM h^{-1}, Expt 11; Table 2) was observed at a seston concentration of 0.107 mg PM ml^{-1} (Table 1), and animals ceased to ingest suspended particles at higher concentrations.

In contrast, *Yoldia hyperborea* from all deposit-feeding experiments showed high mean IRs, although the food value was only 31.86% (SD = 1.69) (see Table 1) of that offered to suspension-feeders. However, mean IR values also varied considerably between individuals (Table 2) and ranged from 2.07 to 6.87 mg PM h^{-1}.

IRs were not significantly different between suspension-feeding experiments, as a result of the high variability of the individual response to SPM. Significant differences were, however, observed between suspension- and deposit-feeding experiments (Table 2).

Scope for growth (SFG)

SFG for *Yoldia hyperborea* under different feeding conditions is presented in Table 3. The metabolic cost of excretion and oxygen uptake corresponds to standard metabolic rates and therefore does not include the cost of handling and digestion of PM (Stead & Thompson 2003b). POM in the sediment was 32% of that contained in suspended particles (Table 1). Mean oxygen uptake varied between 5.25 and 8.06 J d^{-1}, and ammonia excretion rates were between 0.018 and 0.037 J d^{-1} (Table 3). IR of organic matter varied between 0.04 and 0.61 J d^{-1} at low suspended particle concentrations (0.016 to 0.022 mg PM ml^{-1}). Suspension-feeding animals showed the highest IRs (18.97 and 1.17 J d^{-1}) when exposed to seston concentrations of 0.085 and 0.042 mg PM ml^{-1}, respectively. However, at all other intermediate seston concentrations IR was always below 0.15 J d^{-1}. No ingestion was observed at seston values above 0.257 mg PM ml^{-1}. In contrast, deposit-feeding *Y. hyperborea* ingested 122.48 to 407.14 J d^{-1}. A similar trend was observed for absorption rate of organic carbon in all experiments.

Deposit-feeding *Yoldia hyperborea* had a much higher SFG than suspension-feeding individuals. SFG for deposit-feeders ranged between 113.79 and 372.38 J d^{-1}, although supplementary food remained constant in all 3 experiments (2.468 J d^{-1}). SFG in suspension-feeding animals was slightly negative except at a particle concentration of 0.85 mg ml^{-1} ($\overline{x}$ = 9.57 J d^{-1}, SD = 16.14).

DISCUSSION

Absorption efficiency (AE)

Mean AE of organic carbon was 62.74% (SD = 7.12) for suspension-feeding *Yoldia hyperborea* and 93.65% (SD = 4.49) when the animal was deposit-feeding on sediment enriched with *Thalassiosira nordenskioldii*. In contrast, only 50% of sedimentary organic matter and 51% of sedimentary protein is absorbed by the protobranch *Portlandia arctica* (Bubnova 1972). Furthermore, Lopez & Cheng (1983) found a mean AE of 72.1% (range: 66.0 to 78.2%) for the nuculid *Nucula annulata* feeding on sediment-associated bacteria, whereas *Nucula proxima* (Cheng & Lopez 1991) absorbed bacteria with 65.25% (SD = 15.93) efficiency. These values from the literature are the only ones available for protobranchs, and are comparable to those obtained from *Y. hyperborea* suspension-feeding on the diatom *T. nordenskioldii* in this study (see Table 4). However, under natural conditions *Y. hyperborea* ingests sediment containing a variety of organic compounds of potentially different, mostly lower, digestibility and thus, should exhibit lower AE values when feeding on bulk sediment. Cheng & Lopez (1991) recorded a mean AE of only 18.85% (SD = 15.24) in natural sediment detritus containing 10.5% POM; however, their values showed high seasonal variation, ranging between 1.42 and 42%. Seasonal variation should also be observed in the AE of *Y. hyperborea*, as sediments from Conception Bay contain a high proportion of algae from the spring-bloom fallout during a short period in May and June of each year. During this time, high AE values are expected, but should decline thereafter as food quality decreases (Stead & Thompson 2003a).

To meet metabolic demands, *Yoldia hyperborea* must attain a minimum AE for carbon, which may range between 4 and 13% of ingested food (Cammen 1989). Cammen (1989) indicated that because non-living detritus is less well absorbed than microbes (primarily bacteria and microalgae), it may be assumed that microbes form the major food source for deposit-feeders. Although bacteria may contribute some essential nutrients, such as B-complex vitamins, they lack the polyunsaturated fatty acids (PUFAs)

Table 4. Comparison of ingestion rates (IR) in different bivalves species when suspension- (susp.) or deposit-feeding (dep.). Values of IR refer to 1 mg tissue DW) are shown as indicated by each source or estimated (e) with the equation $IR_e = IR_o (DW_e/DW_o)^{0.579}$, where IR_e and IR_o are the estimated and observed IRs, respectively, and DW_e and DW_o are the estimated and observed tissue dry weights, respectively. The exponent 0.579 was obtained from Bayne & Newell (1983). MD = macrophytic detritus (source algae indicated); PM = dry particulate matter in suspension; POM = organic content of particulate matter (%); SPM = suspended particulate matter; nd = no available data. Parenthesis following species name indicates superfamily: T = Tellinacea, M = Mytilacea, C = Cardiacea, P = Pectinacea, Nc = Nuculacea, Ncn = Nuculanacea. *Values calculated by Lopez & Levinton (1987) from indicated source

Species	Feeding mode	Temperature (°C)	Animal DW (mg)	Food source	PM (mg l⁻¹)	POM (%)	IR (mg PM ind.⁻¹ h⁻¹)	IR (mg PM mg⁻¹ DW d⁻¹)	Source
Abra ovata (T)	dep.	nd	1	MD: *Ulva rigida*	nd	68.5	0.0085	0.204	Charles et al. (1996)
Abra ovata (T)	dep.	nd	1	MD: *Cystoseira mediterranea* and *Dilophys spiralis*	nd	70.3	0.0002	0.004	Charles et al. (1996)
Macoma balthica (T)	dep.	6	1	nd	nd	nd	0.375	9.000	L. Kofoed unpubl. cited in Lopez & Levinton (1987)
Macoma balthica (T)	dep.	6	5.1	Ambient sediment	nd	20	0.187	1.748 e	Bubnova (1972)
Macoma nasuta (T)	dep.	nd	1	Ambient sediment	nd	nd	0.042–0.083	1–2	Hylleberg & Galluci (1975) (*)
Scrobicularia plana (T)	dep.	15	380	Ambient sediment	nd	3.4	1.792	1.380 e	Hughes (1969)
Cerastoderma edule (C)	susp.	17	200	Suspended silt + microalgae	2.191	56.14	4.465	4.986 e	Navarro et al. (1994)
Modiolus modiolus (M)	susp.	0–15	2000	Ambient SPM	1.203	64.5*	0.821	0.242 e	Navarro & Thompson (1996)
Mytilus galloprovincialis (M)	susp.	14.5	1000	Sediment + microalgae	1.035	56.21	2.265	0.054	Labarta et al. (1997)
Placopecten magellanicus (P)	susp.	9.7	42000	Ambient SPM	1.5	58	47.900	0.026	Cranford & Hargrave (1994)
Nucula proxima (Nc)	dep.	12–25	1	Ambient sediment + bacteria	nd	9–13	0.32–0.45	7.68–10.8	Cheng & Lopez (1991)
Nucula annulata (Nc)	dep.	15	1	Ambient sediment + bacteria	nd	19.3	0.3	7.201	Lopez & Cheng (1983)
Portlandia arctica (Ncm)	dep.	6	19.9	Ambient sediment	nd	8.8	0.148	0.627 e	Bubnova (1972)
Yoldia limatula (Ncm)	dep.	8–24	1	Ambient sediment	nd	nd	0.417–0.833	10–20	Bender & Davis (1984) (*)
Yoldia hyperborea (Ncn)	susp.	0	161.8	Suspended diatoms	85	40.59	0.094	0.118 e	This study
Yoldia hyperborea (Ncn)	dep.	0	162.1	Ambient sediment + diatoms	nd	11.88	4.358	5.497 e	This study

which are essential to most metazoans, but which are abundant in diatoms (Phillips 1984). The sediment used in our experiments was highly refractory (Stead 2001) and thus, it may be assumed that most of the digestible components obtained by *Y. hyperborea* were provided by *Thalassiosira nordenskioldii* in the sediment. In another experiment, where *Y. hyperborea* was placed in sediment with and without addition of *T. nordenskioldii*, a large accumulation of glycogen and triacylglycerides (TAGs) was observed in the digestive glands of individuals exposed to the algae, but not in the digestive glands of the control group (Stead 2001).

Food quality also affects AE in deposit-feeding lamellibranchs. Charles et al. (1996) investigated this by feeding *Abra ovata* with detritus from 11 macrophytes labelled with ^{14}C-formaldehyde. Whereas detrital food from 5 of the macroalgae resulted in an AE below 3.9%, 4 other diets showed AEs between 7.0 and 12.1%, and the remaining 2 diets were hardly ingested (Charles 1993). On the other hand, when *A. ovata* was fed with detritus derived from the microalga *Pavlova lutherii* the authors observed AEs that ranged between 13 and 24% (Charles et al. 1995). However, these results may have been confounded by methodological problems (Charles et al. 1996) as well as by an indirect method for calculating AE (see Kofoed et al. 1989 for method).

AE values between 30 and 60% are typically found in bivalves feeding on natural seston, but values are usually higher (~80%) for suspension-feeders feeding on fresh algal diets, except at high concentrations (Bayne & Newell 1983). Thus *M. edulis* showed AEs between ca. 81 and 87% and ca. 65 and 74% when fed with 1500 and 5500 cells ml^{-1}, respectively, of the alga *Tetraselmis suecica* (Widdows & Bayne 1971). However, high AE can also be found under natural conditions, as demonstrated by Navarro & Thompson (1996) for *Modiolus modiolus* from Newfoundland, which exhibited a seasonal variation in AE between 50.3 and 93.3%. The authors suggested that these high values may have been the result of low particle loads.

Although AE normally declines with higher particle concentrations in lamellibranch bivalves (Widdows & Bayne 1971, Bayne & Newell 1983), this was not observed for the protobranch *Yoldia hyperborea* in the present study. Similar results were obtained by Cheng & Lopez (1991), who found that AE was not related to bacterial abundance in the protobranch *Nucula proxima*.

The partitioning of food into a rapidly processed fraction in the intestine and a slowly digested fraction in the digestive gland was not immediately observable in these experiments, as faeces egested at the beginning of the experiment did not show lower AE values than faeces obtained subsequently. Intestinal and

glandular digestion (sensu Widdows et al. 1979) has been demonstrated for a number of suspension- and deposit-feeding lamellibranch bivalves (e.g. Decho & Luoma 1991, see also Bayne & Newell 1983), suggesting that particles can be selectively channelled into the digestive gland, allowing the animal to increase its digestive capacity without compromising effective absorption of nutrients.

However, the relative ^{68}Ge:^{14}C ratios in digestive gland and faeces indicated that glandular digestion was occurring in *Yoldia hyperborea*. If the algae frustules had not passed through the digestive gland, no ^{68}Ge should have been observed in this tissue. Thus it is likely that under deposit- and suspension-feeding conditions most of the ingested algae was digested in the digestive gland, resulting in high AE values.

Gut passage time (GPT)

GPT was approximately the same in deposit- and suspension-feeding *Yoldia hyperborea* individuals. Mean GPT from all experiments (except Expt 11) was 14.39 h (SD = 3.47). These data are the first for a protobranch bivalve, and compare with 9.6 h (SD = 1.8) for the facultative deposit-feeding *Macoma balthica* and contrast with 0.86 h (SD = 0.8) for the suspension-feeding *Potamocarbula amurensis* (Decho & Luoma 1991). However, Hummel (1985) recorded a GPT of only 1.6 h for *M. balthica*, although this occurred under suspension-feeding conditions. Navarro et al. (1992) reported a GPT for the suspension-feeder *Cerastoderma edule* between 2.28 and 4.85 h, with higher values observed at lower concentrations of suspended particles. Levinton et al. (1996) calculated gut residence times for *M. nasuta* of 8.92 h, whereas Hughes (1969) recorded times of 8 to 48 h in the deposit-feeding *Scrobicularia plana*. On the other hand, Charles (1993) indicated that the GPT in the deposit-feeding *Abra ovata* is inversely correlated with ingestion rate, and is normally between 2 and 14 h.

Bayne et al. (1989) suggested that bivalves balance variations in GPT and filtration (= clearance) rate to achieve relatively constant AEs under different feeding conditions, although Decho & Luoma (1991) consider that such a balance can also be achieved by partitioning food into digestive compartments with different absorption capabilities.

Jumars (1993) suggested that deposit-feeders in general have short gut residence times in order to process large numbers of particles. However, this is not true for *Yoldia hyperborea* and other deposit-feeding bivalves, as they exhibit longer GPTs than suspension-feeding bivalves and bulk deposit-feeders (see Bayne & Newell 1983). Allen (1992) argued that the maximisation of

extracellular digestion of refractive food material or of that attached to silt particles requires increased residence time within the gut, which in protobranchs is facilitated by an elongated hindgut for more complete digestion and absorption. Lopez & Levinton (1987) stated that gut morphology reflects the adaptation of an animal to the availability of labile organic matter. Thus animals exposed to high amounts of digestible food possess short and wide digestive tracts and are adapted to high feeding rates and low GPTs, whereas the contrary is observed in species with narrow and long intestines, such as *Y. hyperborea*.

Although GPT was highly variable between individuals, no difference was observed between suspension- and deposit-feeding groups or among animals exposed to different particle concentrations. Kofoed et al. (1989) argued that rapid saturation of the absorption mechanism is likely to occur with easily absorbed food types such as diatoms and bacteria, and thus AE should not change considerably over a wide range of GPTs.

Ingestion rate (IR)

The data suggest that ingestion of SPM by *Yoldia hyperborea* is possible, but the rates observed were very low, although in one case where *Y. hyperborea* was offered a seston concentration of 0.085 mg ml^{-1} mean ingestion rate was 93.66 µg h^{-1}. IRs per unit tissue dry weight (0.118 mg PM mg^{-1} DW d^{-1}) during suspension feeding are much lower than values obtained for the suspension feeding cockle *Cerastoderma edule* (4.986 mg PM mg^{-1} DW d^{-1}) (Navarro et al. 1994) and the horse mussel *Modiolus modiolus* (0.242 mg PM mg^{-1} DW d^{-1}) (Navarro & Thompson 1996), but higher than in *Mytilus galloprovincialis* (Labarta et al. 1997) and *Placopecten magellanicus* (Cranford & Hargrave 1994) (0.054 and 0.026 mg PM mg^{-1} DW d^{-1}, respectively) (Table 4). However, our observed rates occurred at SPM concentrations ~50 times higher than those normally encountered by suspension-feeders, which indicates a low efficiency of suspended particle capture. Although these results reinforce the idea that suspended particles are only passively taken into the mantle cavity during ventilation as suggested by Levinton et al. (1996), *Y. hyperborea* was observed extending its siphons into the water column as if actively capturing these particles. This active behaviour could have been the result of stimuli other than particle concentration associated with the type of food offered to *Y. hyperborea*. Jumars (1993) indicated that at least 4 sets of stimuli may affect ingestion rate: smell, taste, distention of the gut and internal detection of the levels of absorbed products in body fluids. A good example is given by Charles et al. (1996), who offered

sediment mixed with detritus derived from different macrophytes to the deposit-feeding *Abra ovata*: whereas maximum IR values were observed when individuals were feeding on detritus derived from *Ulva rigida* (0.204 mg PM mg^{-1} DW d^{-1}), very low IRs were observed when sediment was mixed with either *Cystoseira mediterranea* or *Dylophis spiralis* (0.004 mg PM mg^{-1} DW d^{-1}) (Table 4).

Cammen (1980, 1989) pointed out that the importance of a particular diet to an individual is reflected in the resulting IR and AE. However, IR and AE are in turn affected by digestive system morphology, gut residence time and digestive processing, which are unique and complicated in bivalves (Owen 1974, Bayne & Newell 1983, Decho & Luoma 1996). Most bivalves are selective feeders, as food is pre-sorted on the basis of size and organic content at 1 or both of the following stages: (1) before ingestion (on the gills and labial palps, and additionally on the palp proboscides in the case of protobranchs); and (2) after ingestion (in the stomach and digestive gland for glandular and intestinal digestion). However, because of this feeding strategy, bivalves also exhibit the lowest ingestion rates observed within the deposit-feeding guild (for review see Cammen 1980, Bayne & Newell 1983). In contrast, bulk deposit-feeders such as some polychaetes usually have high IRs to compensate for high inorganic content of their food (Linton & Taghon 2000a). However, feeding rates in polychaetes can also increase progressively with rising protein concentration until a plateau is reached (Grémare et al. 1991, Linton & Taghon 2000b).

Mean IR per body mass of *Yoldia hyperborea* during deposit-feeding was 5.497 mg PM mg^{-1} DW d^{-1}, which is similar to values recorded for other deposit-feeding protobranchs such as *Nucula proxima* (7.68 to 10.8 mg PM mg^{-1} DW d^{-1}) and *N. annulata* (7.201 mg PM mg^{-1} DW d^{-1}), but higher than in other deposit-feeding bivalves (0.004 to 1.748 mg PM mg^{-1} DW d^{-1}; Table 4). Higher IRs were reported by Lopez & Levinton (1987) and Cammen (1980) for *Y. limatula* and *Macoma balthica* (10–20, 9 mg PM mg^{-1} DW d^{-1}, respectively). However, these values were not provided by the original authors (Hylleberg & Galluci 1975, Bender & Davis 1984) but calculated from information contained in their published work after making some necessary assumptions; hence, they should be accepted with some caution. On the other hand, descriptions of deposit-feeding in *Y. limatula* indicate that it is a more active species than *Y. hyperborea* (Drew 1899, Rhoads 1963, Bender & Davis 1984) and is therefore likely to exhibit higher IRs.

During deposit-feeding experiments, *Yoldia hyperborea* consumed 20 to 70 times more particles per unit time than it did at the highest IR observed during sus-

pension-feeding. However, deposit-feeding is carried out primarily by the palp proboscides on a physically stable food source, as opposed to the involvement of the gill during suspension-feeding (see Levinton et al. 1996). In addition, intake of food by the palp proboscides is coupled to the particle load on the labial palps, so that particle capture does not occur at a constant rate, being limited by the handling capabilities of the labial palps as well as by GPT.

Mortality

During the course of the experiments some individuals modified their usual behaviour and subsequently died when exposed to certain experimental conditions. These individuals were separated and not considered in AE, GPT, IR and SFG calculations.

No mortality was observed in *Yoldia hyperborea* from deposit-feeding and suspension-feeding experiments with low seston concentrations (Table 2). One individual (16.66%) died at 0.85 mg PM ml^{-1} but no mortality was observed at the slightly higher concentration of 0.107 mg PM ml^{-1}. However, 50 to 67% of experimental animals exposed to the highest seston concentrations (0.493 and 0.257 mg PM ml^{-1}, respectively) died during the experiment or within 150 h of its beginning. Death of an individual at high suspended particle concentration was usually preceded by behavioural changes such as increased valve gaping and a strong loss of orientation. In the latter case, individuals were usually found inverted within the holding cup, with the anterior end towards the bottom of the jar and the foot slightly outside the valves, pointing upwards. Individual orientation was corrected each time an animal was found in this position, but without effect, as the animal always returned to the inverted position. Although deposit-feeders are adapted to handling high particle loads, the high mortalities recorded at SPM levels above 0.085 mg PM ml^{-1} indicate a negative impact of these conditions on *Y. hyperborea* which may result from structural limitations. These results suggest that a heavy particle load is not normally encountered, thus giving some insight into the dynamics of their habitat (e.g. Conception Bay, Newfoundland). However, field data indicate that on one occasion during 1998, significant *Y. hyperborea* mortality occurred after an unusually high particle load was detected in the water column and near the sediment surface of Conception Bay (Stead & Thompson 2003a), which may be explained through the results obtained here.

The protobranch families Nuculidae and Nuculanidae have a ctenidial-palp association similar to that found in lamellibranch bivalves (Stasek 1965,

Levinton et al. 1996). Furthermore, endoscopic observations of *Yoldia limatula* indicated that during deposit-feeding the mantle cavity is relatively free of suspended material (Levinton et al. 1996). However, suspended particle concentration increases after digging action by the foot or during particle ejection via the siphon. These suspended particles are rapidly captured and sorted by size on the ctenidia and later transported to a point near the 15th ctenidial plate, where they form a mucous-bound ball before being transferred to the labial palps for ingestion (Stasek 1965, Levinton et al. 1996). Thus an increase in particle concentration within the mantle cavity is a common occurrence, albeit of short duration. However, in those of our experiments where *Y. hyperborea* were exposed to particle concentrations exceeding 0.107 mg PM ml^{-1}, it is possible that the ctenidial-palp association system could have become overloaded, causing it to shut down altogether. It is likely that due to the lack of sediment, animals were not capable of isolating themselves from their external environment by sealing off the mantle cavity and maintaining ventilation at a minimum rate. At high particle concentrations, *Y. hyperborea* increased the valve gape, suggesting a lack of oxygen, probably as a result of increased numbers of particles on the gill surface, which may have reduced gas exchange significantly.

Differences in individual survival may be explained by variations in ciliation of the ctenidia. After observing several individuals of *Yoldia scissurata*, Stasek (1965) indicated that the ctenidia of 1 individual contained complete ciliation, whereas cilia in another were restricted to some platelets near the 15th plate. If these differences also occur in *Y. hyperborea*, it could be argued that some individuals are more capable of coping with higher suspended particles than others. A closer examination of ctenidial morphology should clarify this point.

Scope for growth (SFG)

This is the first report of SFG for a protobranch bivalve. However, these results must be interpreted with some caution as the measurements from which SFG was derived were carried out independently on different sets of *Yoldia hyperborea* (VO$_2$ and VNH$_4$-N vs AE and IR), under unfed but otherwise similar conditions (Stead 2001, Stead & Thompson 2003b).

Ammonia excretion has a low impact on the energy budget, accounting for less than 0.5% of metabolic losses in non-feeding animals. Because of its low impact, the energy lost in excretion has not been considered in SFG calculations by many authors (Bayne & Newell 1983), but was included in this study.

Mucus production may be a significant source of energy loss and is usually ignored in energy balance studies (Bayne & Newell 1983). Although much of the mucus produced by bivalves during feeding may be reingested, a considerable amount is lost during the production of pseudofaeces. However, energy loss due to mucus production is likely to be negligible in *Yoldia hyperborea*, because sediment particles in pseudofaeces are not bound together when expelled as a jet from the exhalent siphon.

The fraction of energy expenditure resulting from oxygen consumption depends on the amount of POM ingested, and in suspension-feeding *Yoldia hyperborea* it amounted to 68% of the total energy budget at 0.085 mg ml^{-1} and over 99% in all other experiments. During deposit-feeding, *Y. hyperborea* ingested more POM, and oxygen consumption accounted for less than 5% of the total energy budget. However, these values do not include the cost of feeding and processing of food. Bayne et al. (1976) found that standard respiration values increased 2 to 4 times in *Mytilus californianus* after initiation of feeding, whereas Navarro et al. (1992) showed that particle concentration affects oxygen uptake in *Cardium* (= *Cerastoderma*) *edule*. In contrast, other studies have found that oxygen consumption of some bivalve species, such as *Aulacomya ater* (Stuart et al. 1982), *Mytilus edulis* (Widdows et al. 1979) and *Spisula subtruncata* (Møhlenberg & Kiørboe 1981), is independent of the concentrations of suspended microalgae and sediment. The scallop *Placopecten magellanicus* also shows oxygen uptake rates that are independent of seston concentration and quality, in contrast to values obtained at the same time in the clam *Mya arenaria*, which doubled VO$_2$ when the scallops were exposed to increased seston concentrations and food of higher quality (MacDonald et al. 1998).

Hummel (1985) studied a population of *Macoma balthica* that alternated between suspension and deposit-feeding, and concluded that oxygen uptake in this species increased 3 to 5 times from the standard (i.e. no feeding) value during suspension-feeding and 4 to 9 times during deposit-feeding. If the cost of metabolism in *Yoldia hyperborea* were arbitrarily increased to 9 times the standard value obtained here, it would only account for 19.5 to 43.8% of the energy budget during deposit-feeding. However, SFG also depends on the organic content of food, and the estimations obtained here are for sediments containing around 12% POM. Seasonal values for organic matter from Conception Bay sediments range between 8 and 13% DW (Stead & Thompson 2003a), with the highest POM values typically found after the fallout of the spring-bloom, and the lowest values between the end of summer and late winter. Thus the SFG of *Y. hyper-*

borea from Conception Bay probably varies with the organic content of the sediment.

Yoldia hyperborea needs to ingest a minimal amount of POM in order to meet its metabolic requirements. Even if absorption rates were to decrease 20-fold to account for a decrease in sediment quality, individuals would still maintain a positive SFG. The experimental conditions included enriched sediment or suspended particles that simulated conditions that would be observed only during the phytoplankton bloom fallout, so that a reduction in energy acquisition would be expected at most times of the year.

SFG calculations assume that all the POM is metabolisable. However, POM in sediment includes refractory organic matter, which was not quantified separately but which could account for a significant proportion of the organic matter ingested by *Y. hyperborea* in its natural habitat. Rice & Rhoads (1989) assumed that 33% of deposited POC is metabolisable, whereas Mayer (1989) suggested that the fraction of sediment POM utilisable by deposit-feeders is only 5 to 30%. Thus if standard respiration rates were to increase 5-fold and only 20% of ingested POM were metabolised (see Table 2), *Y. hyperborea* would still be able to meet its minimum metabolic demands.

Since 60 to 80% of suspended POM is usually metabolisable (e.g. Navarro & Thompson 1996), suspension-feeding could become a beneficial strategy during the first bloom fallout, when sediment quality is at its lowest, but not once the sediment has been enriched. Although deposit-feeding is the main strategy followed by *Yoldia hyperborea* and related species (Bender & Davis 1984, Davenport 1988, Stead 2001), our data suggest that suspension-feeding can be advantageous under certain conditions, possibly as a response to water-borne chemical cues released by settling microalgae after a prolonged period of low food availability (Ward & Targett 1989). However, these conditions are likely to be sporadic and of short duration (Stead & Thompson 2003a). In addition, because capture of suspended particles by *Yoldia hyperborea* is not an efficient mechanism, only very low ingestion rates are observed, the view that protobranch bivalves are primarily deposit-feeders is thus reinforced. However, suspension-feeding may be beneficial in order to capture high quality food particles before they are ingested by competitors (e.g. benthic and hyperbenthic species).

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