

The effect of the sinking spring diatom bloom on digestive processes of the cold-water protobranch *Yoldia hyperborea*

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Abstract

Periodic sampling from April 1997 to December 1998 of a population of the deposit-feeding protobranch *Yoldia hyperborea* from the deep depositional zone (250 m) of Conception Bay, Newfoundland, indicated that this species was exposed to subzero temperatures (-0.63°C) throughout the year. However, the standing stock of phytoplankton in the photic zone showed strong seasonal fluctuations with primary peaks always occurring in April (4.26 and $5.09 \mu\text{g L}^{-1}$ chlorophyll *a* in 1997 and 1998, respectively). In addition, sediment chlorophyll *a* started to increase (from a low of $\sim 6 \text{ ng mg}^{-1}$ dry weight of sediment) as the sinking of a smaller, secondary bloom, reached the bottom in the first 2 months of 1997 and 1998, although higher concentrations were reached by mid-April and May 1997 (21.32 ng mg^{-1} sediment) and remained relatively high until February 1998. An increase of digestive cell height and protein content occurred as soon as sinking organic material from the spring bloom reached the benthic zone, suggesting storage of metabolic energy during spring and summer. Sharp increases in digestive enzyme activity occurred primarily in early spring of each year, coinciding with the timing of the primary spring bloom fallout, suggesting activation of the formerly depressed digestive system after a prolonged period of low food availability (i.e., late summer to autumn). Results suggest that *Y. hyperborea* strongly depends on the input of fresh algal material despite the high availability of organic matter in the sediment.

Carbon supply to the aphotic benthic zone of the sea is largely based on the timing of climatic events (e.g., snow and ice melt, rainfall), tidal exchange, and, most importantly, the sinking of phytoplankton blooms (Wassman 1991; Graf 1992). The organic fraction of the particle input to the sediment is a potential energy source for benthic organisms. It is well established that in shallow water the input of fresh organic matter of high nutritional value from primary production creates a burst of activity in the benthic population (Clarke 1988; Boon et al. 1998). Graf et al. (1982) showed that the response to organic matter input is more rapid in those species that utilize the organic matter directly rather than those species that feed on meiofauna and sediment. However, the availability of food particles decreases with increasing depth and becomes more episodic at higher latitudes, imposing specific constraints on the organisms, which must be able to withstand periods of reduced food availability. Thus energy-demanding metabolic processes such as growth and reproduction are often restricted to periods of high food abundance. For example, antarctic suspension feeders show a marked seasonal variation in feeding rates, with the highest activity occurring in the short but very productive summer, whereas most animals cease feeding during

the winter months in order to reduce metabolic costs when food is scarce (Barnes and Clarke 1995). In some crustaceans that maintain high metabolic activity during winter, energy is provided from large lipid stores, whereas metabolic costs in other species, such as bivalves, can be met from normal lipid, glycogen, and protein pools (Vassallo 1973; Clarke 1983; Henry et al. 1991). Thus the seasonal pattern of growth in many species, together with the frequent limitation of reproduction to the summer months, suggests that many processes are strictly regulated by the availability of food. However, the degree of seasonality in the biology of polar marine organisms varies with their position in the food web (Clarke 1988).

Deposit feeders can use either organic matter as it arrives at the sediment surface or the fraction that has been buried through bioturbation (Middelburg et al. 2000). Although the quality of organic matter in the underlying sediment layers can differ from that of recently deposited material (Graf 1992; Mayer 1994), deposit feeders can maintain a relatively constant feeding activity throughout the year, resulting in a continuous storage and utilization of energy reserves and a reproductive pattern marked by nonseasonal or continuous spawning in the population (Taghon et al. 1994). As a result, metabolic processes should reflect a weak seasonal pattern. However, the quality and the relative importance of the various components (algal, bacterial, and detrital) of the POM available for benthic invertebrate growth and reproduction remains unclear (Boon et al. 1998). Furthermore, the time scales for the accumulation and use of energy stores in deposit feeders and the effects of environmental factors, especially food supply, are poorly known (Taghon et al. 1994).

Monitoring reproduction or feeding activity has become a useful tool for evaluating the response of a population to quantitative and qualitative variability in food resources (e.g., Karrh and Miller 1994; Boon et al. 1998). For example, bivalves respond to variations in food availability by exhib-

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iting changes at cellular and organ level (Owen 1974; Thompson et al. 1974; Langton 1975) but can also exhibit cellular changes resulting from stressors such as oil pollution (Widdows et al. 1982), spawning (Bayne et al. 1978), or temperature (Thompson et al. 1978). These changes can be used as indicators of whole-organism responses to environmental changes, particularly in seasonal food supply.

The digestive gland of bivalves, in addition to its digestive role, acts as a site for the storage of metabolic reserves that are later used for gametogenesis or growth or during periods of physiological stress (Thompson et al. 1974). The height of the digestive cells also varies according to the phase of intracellular digestion (Langton 1975; Lowe and Moore 1985). On the other hand, enzymes produced by the digestive gland undergo fluctuations in activity that have been related not only to changes in food supply (Ibarrola et al. 1998, 2000b), but also to temperature (Seiderer et al. 1982), anoxia (Greenway and Storey 1999), nutritional regime (Reid and Rauchert 1976), pollutants (Widdows et al. 1982), and requirements for specific biochemical components (Cancio et al. 1999). However, all these studies were conducted on suspension-feeding lamellibranch species, and there are no data for deposit-feeding bivalves such as protobranchs.

The benthic community of the deep depositional zone of Conception Bay (Newfoundland, Canada) is dominated by deposit feeders (50–60%), whereas suspension feeders make up only 8–25% of the species in the area (Scheibe 1991). Because phytoplankton biomass at this latitude is highly seasonal (Navarro and Thompson 1995), benthic animals should experience a strong seasonal input of organic matter that accumulates because bacterial turnover is strongly reduced at low temperatures (Pomeroy and Deibel 1986). Hence, deposit feeders should be able to utilize the potential food source over an extended period before depleting it.

In this study, the feeding response of the protobranch *Yoldia hyperborea* from Conception Bay was studied indirectly by quantifying enzymatic and cellular changes in the digestive gland in relation to seasonal changes in the transfer of organic matter from the water column to the benthos.

Material and methods

Study site—All sampling was carried out in the depositional zone of Conception Bay, Newfoundland, Canada (250–270 m) (Fig. 1). This bay is 60 km long and 23 km wide and is exposed to the Atlantic Ocean (orientation NE–SW). Its mouth has a sill at 150 m depth that closes off isobaths in the bay and restricts entry of water from the inshore Labrador current (−1.7 to +2.0°C, 32.6 psu) (de Young and Sanderson 1995). Pack ice often covers the bay from mid-March to late April, but little of it is formed locally. Local freshwater is relatively unimportant compared to the influence of ice melt upstream of the bay, which accounts for most of the variability in salinity (de Young and Sanderson 1995).

The depositional zone of Conception Bay is characterized by muddy sediment (92% of particles <63 μm) with 60–70% water content and 20% organic matter in the upper 10 cm (Scheibe 1991). The protobranch bivalve *Y. hyperborea*

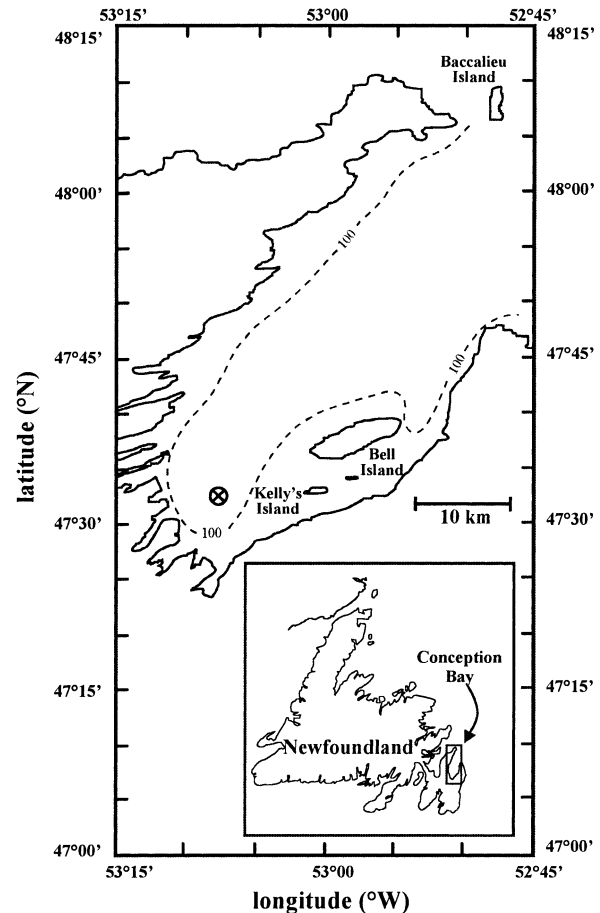


Fig. 1. Map of Conception Bay on the east coast of Newfoundland, Canada, showing the location of the sampling site (X).

at this station attained a dominance of 6.1%, a mean abundance of 12 individuals m^{-2} and a mean biomass of 1.38 g ash-free dry weight (AFDW) m^{-2} (Scheibe 1991).

Water column—The water column was sampled with a Seabird SBE25 CTD equipped with a SeaTech fluorometer. Temperature (°C), salinity (psu), in situ fluorescence (RFU), and light transmission (%) were measured. Relative fluorescence units (RFU) were converted to chlorophyll *a* (Chl *a*) concentration (μg Chl *a* L^{-1}) through the equation $Chl\ a = 0.3973 \cdot RFU + 0.3015$ ($r^2 = 0.65$, $n = 253$) (Ru Cheng Tian pers. comm.). Measurements were made 49 times between March 1996 and December 1998, with more casts during the spring and summer months than in autumn and winter.

Sediment—Sediment samples were obtained with corers (5 cm internal diameter, $n = 3$) 23 times from March 1996 to December 1998 from the deep depositional zone of the study area. Sediment cores were fractionated (0–1, 1–2, 2–3, 3–5, 5–7, and 7–9 cm from the sediment surface), each slice was lyophilized separately, and Chl *a* and pheopigments were determined on a weighed subsample (dry weight [DW]) with the fluorometric method of Holm-Hansen and Riemann (1978) after extraction in 90% acetone.

Sampling of *Y. hyperborea*—A 1.2-m-wide dredge fitted with a 2.54-cm mesh was towed from the R/V *Karl & Jackie* for 20 min from 47°34.0'N, 53°08.1'W to 47°32.5'N, 53°07.8'W. Adult *Y. hyperborea* (>23-mm shell length) were removed from the sediment and transferred to a refrigerated holding tank ($0.0 \pm 1.0^\circ\text{C}$) at the Ocean Sciences Centre in Logy Bay (Newfoundland, Canada).

Protein content and enzyme assays—Protein content and the activity of acid protease and α -amylase were determined in the digestive gland tissue (DG) after each sampling trip. The complete digestive gland (without stomach) was excised from four to eight large animals (shell length mean \pm SD, 32.71 ± 3.54 mm), weighed (± 0.001 g wet weight [WW]), and homogenized.

Each tissue homogenate was used to determine its protein content with the Lowry method as modified by Hartree (1972) using bovine serum albumin (BSA) as a standard (Sigma B-6917). Acid protease activity was determined by a method based on Anson (1939) using 2% azocasein (Sigma A2765) as a substrate. The method for determining α -amylase was based on Rinderknecht et al. (1967), with amylopectin azure (2%) (Sigma A6808) as a substrate. The concentration in solution of the products of digestion (amino acids and glucose, respectively) were determined by reading absorbance at 366 nm and 595 nm for the acid protease and α -amylase assays, respectively. All assays were carried out in duplicate at 25°C . Reactions were stopped after 0.5 and 2.5 h in the case of acid protease and 5 and 20 h in the case of α -amylase assays after initial trials indicated that reaction velocity did not change within the respective time frame. Specific activity ($U \text{ mg}^{-1}$) was related to protein content of the tissue homogenate supernatant and was calculated using Eq. 1.

$$U \text{ mg}^{-1} = \frac{\Delta A(t_2) - \Delta A(t_1)}{\alpha \cdot p \cdot \Delta t} \quad (1)$$

U is the product equivalent (amino acids, glucose) obtained ($\mu\text{mol min}^{-1}$), $\Delta A(t_i)$ is the difference between absorbance values of the sample mean and the blank mean after the reaction was stopped at times t_1 and t_2 , α is the slope of the reaction between times t_1 and t_2 , p is the protein content in the extract (mg), and Δt is the incubation time (min).

Histology—Histological examination of the digestive gland of *Y. hyperborea* was carried out on 13 occasions from April 1997 to the end of October 1998 on animals ($n = 30$) selected from within the 24–42-mm shell length range. The digestive gland was weighed, fixed in Baker's formol calcium with 2.5% sodium chloride, and refrigerated at 4°C (Lowe and Moore 1985) prior to dehydration, clearing, and embedding in paraffin wax. Hematoxylin and eosin-stained sections (7 μm) from 6–10 randomly selected individuals from each sample were examined at $\times 250$ magnification. Five to seven different portions of the tissue were analyzed to complete a minimum of 50 tubule measurements (Lowe and Moore 1985).

Results

Water column—Temperature: Water temperature in Conception Bay showed a seasonal pattern with surface values that fluctuated from 15.9°C in summer (19 August 1997, 0–8 m) to -1.5°C in late winter (21 March 1997, 22–40 m) (Fig. 2A). Although this pattern was similar for most years, a maximum surface temperature of only 11.6°C was observed in the summer of 1998.

The thermocline started to develop within the top 25–40 m of the water column in mid-May in 1996 and 1997 and at the beginning of May in 1998. The thermocline persisted throughout the late summer, autumn, and early winter to mid-January (1997, 1998) as autumn and winter mixing occurred to depths of 90–125 m (see 0°C isotherm, Fig. 2A). Bottom temperature remained fairly stable throughout the year, averaging -0.63°C (± 0.15 , $n = 732$, minimum = -1.12°C , maximum = -0.36°C) below 200 m depth. A cold water mass with temperatures below -1°C developed during winter at the surface and sank below the thermocline by March but was never found close to the bottom.

Salinity: Salinity fluctuated between 24.97 and 33.27 psu between March 1996 and December 1998. However, much of this fluctuation corresponded to one observed event (24 February 1998) in which salinity ranged from 24.97 psu at the surface to 32.09 psu at 58 m. Throughout the rest of the study period, the salinity of the top 15 m remained between 30.91 and 32.15 psu. Surface salinity values >31 psu were observed only during late winter and early spring. Highest salinity values (31.78–33.23 psu) were always observed below 150 m. Lowest values at this depth were recorded on one sampling occasion (June 1998, 31.78 psu) and otherwise ranged from 32.89 to 33.23 psu.

Light transmission: Light transmission is related to the presence of particulate matter in the water column, decreasing values representing an increase in suspended particulate material (Siegel et al. 1989). From March 1996 to December 1998, light transmission within the water column ranged from 0.08 to 91.18% but averaged 75.92% (± 16.57). Most of the water column always showed light transmission values between 70 and 90% and only occasionally were lower values recorded (Fig. 2B). Values below 20%, when observed, were usually found near the surface, as in March 1997; February, June–August, and November 1997; and July and August 1998. In February 1998, the 20% isopleth could be seen extending from the surface to around 120 m, whereas in August 1997 it extended from 150 m to the bottom of the bay. In contrast, isopleths between 20 and 60% were observed at the surface at the same times as the isopleths below 20%, but they also developed from the bottom of the bay to around 100 m from July to mid-October 1996, March 1997 to March 1998, and again from July to the end of 1998.

Chlorophyll *a*: Chl *a* concentration ranged from 0.138 to $5.090 \mu\text{g L}^{-1}$ in 1996–1998 ($0.414 \pm 0.399 \mu\text{g L}^{-1}$; Fig. 2C). Maximum values were always observed between 24 and 50 m during the third week of April of each year and reached 3.370, 4.260, and $5.090 \mu\text{g L}^{-1}$ in 1996–1998, re-

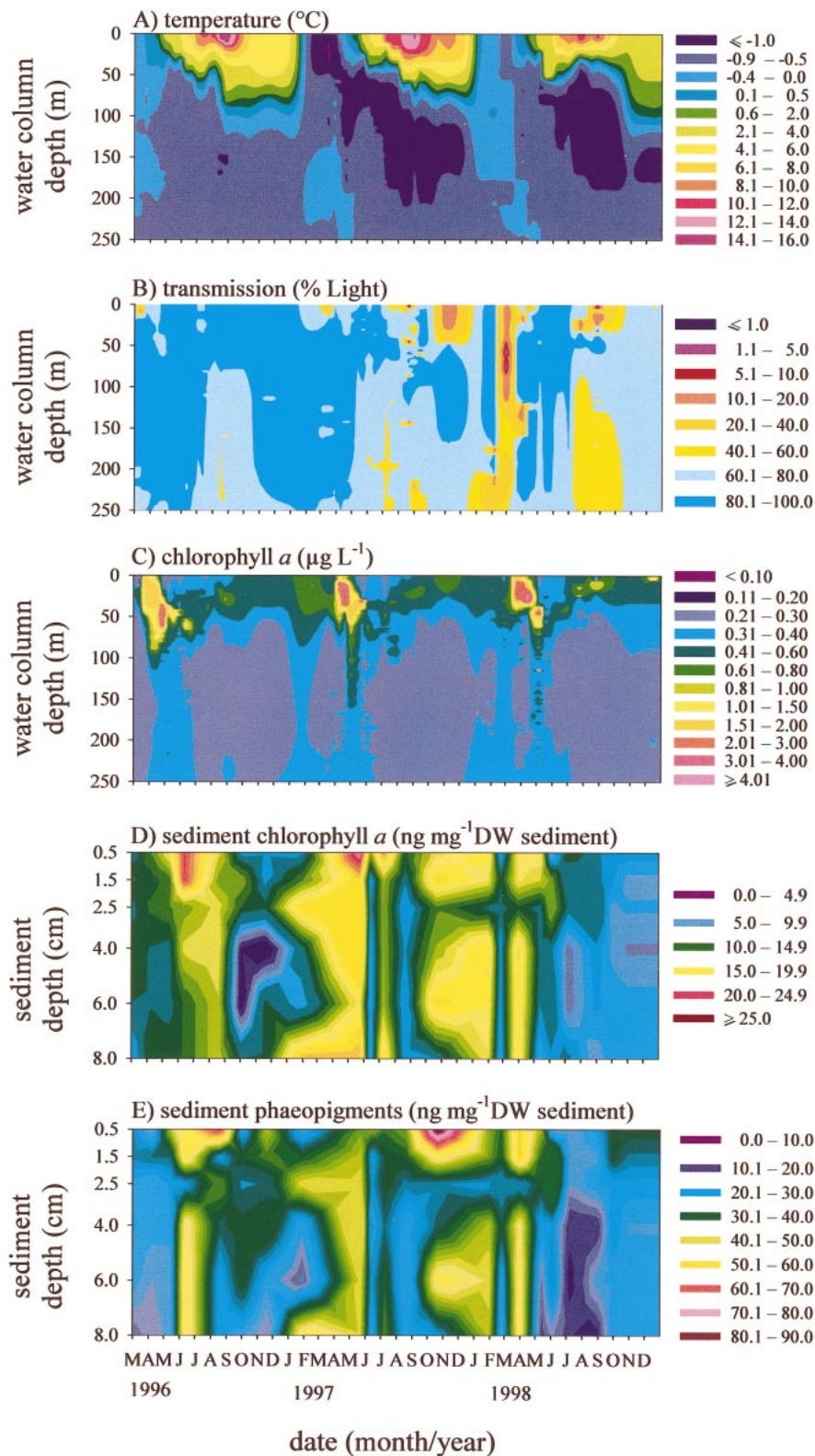


Fig. 2. Temporal variation of (A) temperature ($^{\circ}\text{C}$), (B) light transmission (%), and (C) Chl a concentration ($\mu\text{g L}^{-1}$) in the water column and of (D) Chl a ($\text{ng mg}^{-1}\text{DW sediment}$) and (E) pheopigments ($\text{ng mg}^{-1}\text{DW sediment}$) from sediment cores taken from the sampling area in Conception Bay, Newfoundland. Note that isopleth intervals for water column Chl a are not equal.

spectively. Lowest values were invariably observed near the surface during the summer months and below 60 m from June–July to late December.

The development of the spring bloom was usually rapid, starting in mid-March or early April and extending to mid-April or May of each year. An exception to this pattern was observed in 1997, when the spring bloom showed a gradual development starting as early as mid-January, with Chl *a* values $>0.6 \mu\text{g L}^{-1}$ from the surface to around 40 m depth.

A smaller, secondary bloom can be observed by following the $0.6\text{-}\mu\text{g L}^{-1}$ isopleth, although this bloom is more patchy and variable from year to year. In 1996, the secondary bloom was observed from mid-August to mid-September. This pattern was repeated in 1997 and included a third bloom event from mid-October to November. However, in 1998 the secondary bloom started in early July and extended to late September, peaking in late August with Chl *a* concentrations near $1 \mu\text{g L}^{-1}$. In December of the same year a less prolonged increase was observed, but Chl *a* again reached concentrations up to $1 \mu\text{g L}^{-1}$.

Phytoplankton bloom fallout events can be clearly observed by following the $0.3\text{-}\mu\text{g L}^{-1}$ isopleth, which appears from ~ 50 m to the bottom shortly after the full development of the primary bloom in early April to around June of each year. Furthermore, an earlier, secondary sinking event in 1997 and 1998 probably occurred from January to early March of both years, as evidenced by an increase of Chl *a* concentrations above $0.3 \mu\text{g L}^{-1}$ observed below 200 m from around early January to early June of each year.

Sediment—Pigments: As soon as Chl *a* reached the sediment surface it was quickly mixed throughout the measured sediment profile (Fig. 2D,E). A gradual increase of Chl *a* concentration in surface sediment was observed from March 1996, coinciding with the bloom formation in surface water. However, the maximum concentration of Chl *a* occurred in mid-June 1996 ($19.26 \text{ ng mg}^{-1} \text{ DW sediment [sed]}$), 2.5 months after the peak observed in the water column. On the other hand, the highest surface pheopigment concentration was observed in August of the same year. Lowest surface Chl *a* values were observed between mid-September 1996 and the end of January 1997 ($\sim 6 \text{ ng mg}^{-1} \text{ DW sed}$). An increase in Chl *a* values was observed from early February 1997, whereas the highest values occurred from the beginning of April until late May 1997 ($21.32 \text{ ng mg}^{-1} \text{ DW sed}$) and again throughout July. The increase in sediment Chl *a* concentration during this year closely coincided with the bloom formation and peak observed in the water column.

From mid-September to the end of February 1998, sediment Chl *a* remained high relative to the same period in 1996. Lowest Chl *a* values in early 1998 were observed for a short period in late February, and a marked increase occurred in early March. However, the Chl *a* maximum in the spring of 1998 ($13.89 \text{ ng mg}^{-1} \text{ DW sed}$, May 1998) was lower than in 1996 and 1997 and persisted only until May. Low pigment values were evident from mid-May until the end of the study period ($<8 \text{ ng mg}^{-1} \text{ DW sed}$), except for a short and slight increase in June 1998.

The pattern of pheopigment concentration was similar to that of Chl *a*, but highest values were observed in summer

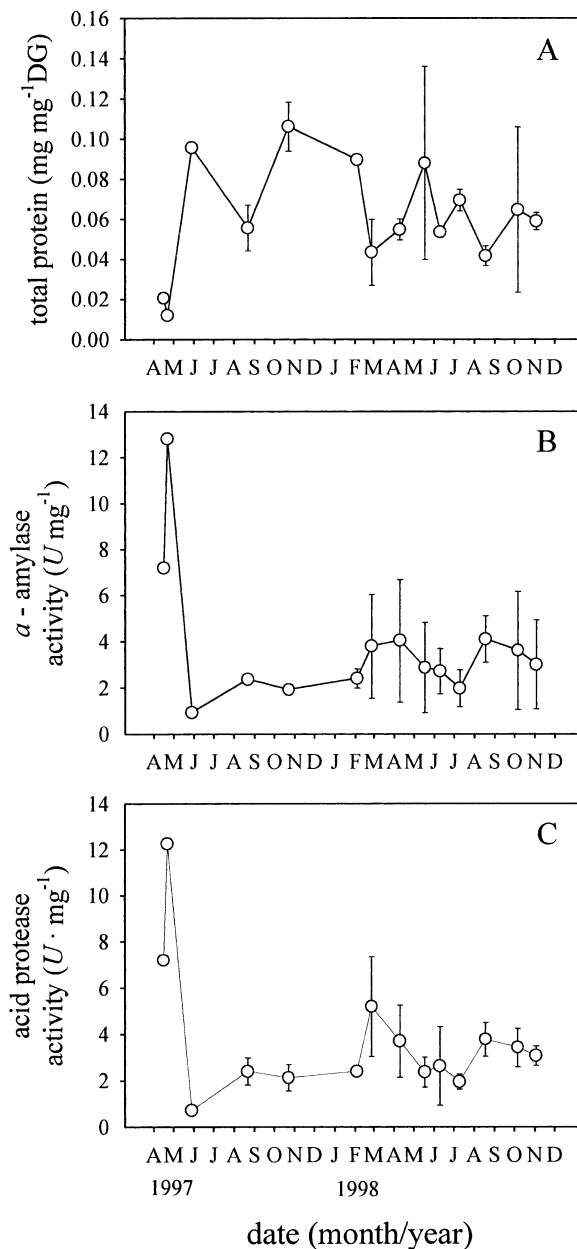


Fig. 3. *Yoldia hyperborea*. Temporal variation of digestive gland (A) protein content ($\text{mg mg}^{-1} \text{ DG}$), (B) relative activity of α -amylase ($\text{U mg}^{-1} \text{ protein in extract}$), and (C) relative activity of acid protease ($\text{U mg}^{-1} \text{ protein in extract}$). All values are means \pm SD.

1996 ($72.38 \text{ ng mg}^{-1} \text{ DW sed}$, August 1996) and autumn 1997 ($89.29 \text{ ng mg}^{-1} \text{ DW sed}$; i.e., 1.5 and 5 months, respectively, after the observed Chl *a* peaks).

Protein content and enzyme activities—The mean protein concentration in the digestive gland of *Y. hyperborea* was $0.0610 \pm 0.0264 \text{ mg mg}^{-1} \text{ DG}$ (Fig. 3A). Lowest monthly means were observed in April 1997 ($0.0118 \text{ mg mg}^{-1} \text{ DG}$), whereas maximum means occurred in May and October of that year (0.0957 and $0.1061 \pm 0.0121 \text{ mg mg}^{-1} \text{ DG}$).

Acid protease and α -amylase activity followed a similar

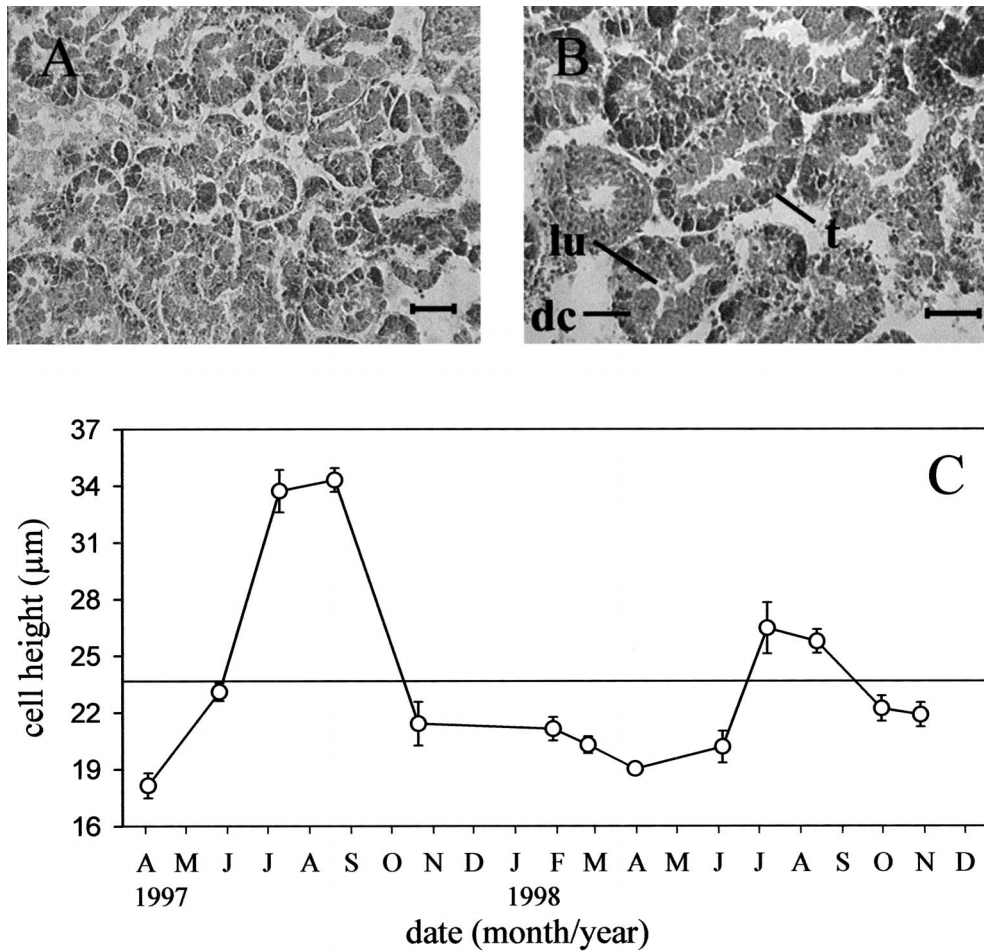


Fig. 4. *Yoldia hyperborea*. (A) Holding phase: digestive gland tubules from animals obtained on 3 March 1997, (B) early absorptive phase: digestive gland cells, 26 May 1997, and (C) temporal variability of digestive gland cell height (mean \pm SD, μm) in individuals obtained from Conception Bay. The horizontal line represents the grand mean for all data. dc, digestive cell; tu, tubule; lu, lumen. Scale bar = 50 μm .

pattern throughout the study period (Fig. 3B,C). Mean activity of α -amylase was $3.90 \pm 2.86 U \text{ mg}^{-1}$, and a maximum activity was observed at the end of April 1997 ($12.81 U \text{ mg}^{-1}$). The lowest α -amylase activity was observed in May 1997 ($0.93 U \text{ mg}^{-1}$). In 1998, activity of this enzyme showed very little fluctuation, ranging between $1.97 U \text{ mg}^{-1}$ in June and $4.10 U \text{ mg}^{-1}$ in July. Acid protease activity ranged between $0.71 U \text{ mg}^{-1}$ (May 1997) and $12.25 U \text{ mg}^{-1}$ (April 1997) but averaged $3.80 \pm 2.79 U \text{ mg}^{-1}$ throughout the period. As with α -amylase, acid protease activity did not fluctuate as strongly in 1998, showing values in the range of $1.96 U \text{ mg}^{-1}$ (July) to $5.19 U \text{ mg}^{-1}$ (February). High activities of acid protease and α -amylase were recorded from April to May 1997, sharply decreasing in late May 1997 (Fig. 3B,C). From late August 1997 to early February 1998 activity levels remained around $2 U \text{ mg}^{-1}$ and more than doubled in late February, only to decline steadily until early July. An increase was observed in late August 1998 and values progressively declined thereafter.

Histology—Digestive tubules from *Y. hyperborea* were well organized, with the prominent digestive cells being eas-

ily distinguishable from the basophil cells. A conspicuous feature was the large number of darkly staining inclusions in the basal region of the digestive cells. The principal feeding and digestive phases in the digestive cells appeared to be synchronized and did not vary significantly between individuals sampled at the same time.

Although the digestive phases described by Owen (1974) and Langton (1975) in shallow-water bivalves correspond to short-term changes occurring within hours of food intake, in *Y. hyperborea* each phase progressed in an annual cycle as food energy was ingested, stored, and later used as food quality decreased. Similar results have been obtained for subtidal *Pecten maximus*, where seasonal variations in both cell structure and biochemical composition are independent of the tidal cycle but, instead, correspond to phytoplankton abundance (Le Pennec et al. 2001).

In tissue sections, the phases of the digestive tubules (holding, absorption, disintegrating, and reconstituting, sensu Langton 1975) were strongly correlated to the digestive cell height (Stead 2001) (Fig. 4A,B). In April 1997, the digestive cells were in a holding phase (Fig. 4A) but rapidly increased

in size as they stored food, giving way to the absorptive phase, which continued until late August when the cells were so large that the lumina of the diverticuli were barely visible (Fig. 4B). However, this late absorptive phase also contained some tubules undergoing disintegration. The disintegrating phase became more apparent shortly afterward as cell height decreased and the tubule lumen became visible again. As stored nutrients in the cell became depleted, the tubules entered the reconstituting phase, reaching the holding state in late March, after which a new cycle began. However in 1998 the increase in digestive cell height was not as marked, leading to a more ambiguous interpretation of the different descriptive phases.

Digestive gland cell height showed a strongly seasonal pattern with smaller cells observed in winter and early spring and larger cells occurring in summer (Fig. 4C). Mean cell height throughout the period was $23.67 \pm 4.96 \mu\text{m}$ with highest values in July and August 1997 (33.72 and 34.31 μm , respectively) and again in July and August 1998 (26.47 and 25.77 μm , respectively). Cell height was at its minimum in early April 1997 (18.15 μm) and in late March 1998 (19.03 μm). Because qualitative observations also indicated that tubule diameter was directly proportional to cell height (Stead 2001), this measurement could be useful as an alternative or as a supplement to cell height.

Discussion

The spring diatom bloom in Conception Bay began to develop between mid-March and early April when the water temperature was $<0^\circ\text{C}$. The bloom continued until it was disrupted by an increase in water temperature followed by water column stratification in mid-April or May of each year. This pattern is typical of this area, since de Young and Sanderson (1995) showed that the head of the bay is normally sheltered from the winds in spring, leading to reduced mixing and increased thermal stratification.

The timing of the spring bloom coincided with observations by Deibel et al. (1992), who sampled the same area from March to June 1986, 1988, and 1990. Thus, conditions for the development of the primary bloom in Conception Bay include the absence of thermal stratification in early winter, a water temperature near 0°C , and an increase of photosynthetically active radiation to around $100 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Deibel et al. 1992; this study). Photosynthetically active radiation above $100 \mu\text{mol m}^{-2} \text{s}^{-1}$ was observed in February of each year, and Deibel et al. (1992) indicated that light intensity and inorganic nutrients are sufficient in January and February to initiate the bloom, but this does not happen until the wind velocity decreases in late March to mid-April.

In this study, spring Chl *a* maxima always occurred in the third week of April when water temperature was $<0.5^\circ\text{C}$. However, Chl *a* concentrations were considerably lower than in 1986, 1988, and 1990 when values of 24, 8, and 12 $\mu\text{g L}^{-1}$, respectively, were recorded by Deibel et al. (1992). Thus, Conception Bay is a cold-water system, and although the bay has a midlatitude light regime, the spring bloom occurs at polar temperatures, a characteristic only shared in the northern hemisphere with parts of the Sea of Okhotsk

(Shiomoto 1997). The development of a secondary bloom in late summer or autumn was usually associated with water temperatures between 4 and 6°C in 1996 and 1997. However in 1998 a bloom that peaked in August occurred when water temperature was between 6 and 10°C , whereas the December bloom occurred at $\sim 2^\circ\text{C}$.

The phytoplankton bloom fallout to the benthos in early April of each year began $<2\text{--}3$ weeks after its initial development. Chlorophyll *a* concentrations in the bottom 50 m at this time were 5.89–14.73% (1998 and 1999, respectively) of surface concentration maxima. However, an earlier phytoplankton bloom fallout starting in January 1997 and February 1998 was observed in which $\sim 50\%$ of surface Chl *a* concentration was found at the hyperbenthos, resulting in a similar degree of Chl *a* input. This also coincided with the increase in Chl *a* observed in surface sediments at the same time of the year (Fig. 2E). The difference in the magnitude of these fallout events is partly attributable to the higher zooplankton abundance at the time of the primary spring bloom (Davis 1982). Thus grazing pressure in the water column in January and February is relatively low, so that a large proportion of the algae reaches the bottom. According to Pomeroy and Deibel (1986), the bacterial population of Conception Bay utilizes particulate material at very low rates when temperature is as low as -0.2°C , which suggests that most of the primary production is available to zooplanktonic and benthic animals.

The decrease in light transmission from spring to early summer can be explained by the increased phytoplankton concentration followed by a rapid proliferation of microzooplankton and microaggregates (McKenzie et al. 1997), as well as the resulting increase in zooplankton fecal pellet production. Deibel et al. (1992) suggested that copepods are not significant grazers in the water column of Conception Bay until June and July because of their temperature-dependent hatching rates. This pattern would lead to increased fecal pellet production after the bloom has subsided, consistent with the reduced light transmission values observed in Conception Bay (see Fig. 2B).

The reduced light transmission and increased Chl *a* values observed near the bottom during the summers of 1996 and 1997 and throughout most of 1998 (Fig. 2B,C) suggest that resuspension of bottom sediments was taking place. A slight but constant bedload transport or resuspension of particulate material and microalgae could be promoted by weak tidal currents observed in this area ($1\text{--}2 \text{ cm s}^{-1}$, de Young and Sanderson 1995). Resuspension of sediment organic matter also provides higher concentrations of POM for hyperbenthic suspension-feeding invertebrates, thus helping to sustain the high biomass typically found in the benthic boundary layer in Conception Bay (Choe and Deibel 2000).

An unusual event was observed on 24 February 1998. At this time, temperature was completely uniform throughout the water column to 180 m and was also homogenous below that depth between March and early May of that year (see 0°C -isopleth, Fig. 2A). A high particle load (sensu Siegel et al. 1989) was also observed throughout the water column until early March, whereas dredge samples and sediment cores from May showed that the top 25 cm of sediment had been completely mixed, as evidenced by its high water con-

tent and low compactness, whereas in the following months (June and July) mixing was only observed in the top 7 and 3 cm, respectively. Furthermore, *Y. hyperborea* collected in May 1998 were sluggish and showed a strong tendency to gape, which resulted in 100% mortality within a week of collection. Sediment disturbance of this magnitude was not observed throughout the rest of the study period and has not been reported in previous years. The anomaly observed in the water column from February 1998 could have triggered bottom turbidity currents, leading to strong sediment disturbance and particle resuspension. Data collected from sediment traps deployed in the same area at 50 and 220 m depth shortly after the bloom peak of April 1996 and April 1998 indicated three times more material in April 1998 than in April 1996 (C. C. Parrish unpubl. data). Lipid analysis of settling particles captured in April 1996 showed a high content of total polyunsaturated fatty acids (PUFAs) (>32.8%) and a high concentration of fresh and relatively undegraded material throughout the water column. In contrast, trap material obtained in April 1998 contained a higher proportion of refractory material with a lower concentration of total PUFAs (23.18% at 50 m and 16.14% at 100 m), which might have resulted from a massive resuspension of bottom sediments.

The digestive gland of *Y. hyperborea* from Conception Bay shows marked seasonal variation, particularly in digestive cell height, which is interpreted as a cycle of uptake, storage, and use of energy reserves. Changes in the biochemical composition of the digestive gland in *Mytilus edulis* led Thompson et al. (1974) to suggest that it stores metabolic energy reserves that are subsequently transferred to the gonad during gametogenesis. Carbohydrates accumulated in the digestive gland are transferred to the gonad during vitellogenesis or in response to stress. Furthermore, when carbohydrate reserves are low, lipids are synthesized and stored for subsequent distribution to other tissues (Vassallo 1973; Thompson et al. 1974). Similarities between the fatty acid composition of the triacylglyceride fraction (TAG) of the gonad and the digestive gland in the scallop *Argopecten purpuratus* demonstrate the transfer of lipids from the lipid-rich digestive gland to the gonad for gametogenesis (Caers et al. 1999). However, the digestive gland also plays a major role in the storage of lipids originating from phytoplankton (Soudant et al. 1999).

An increase in digestive cell volume was observed after April 1997 and 1998 as soon as the phytoplankton cells from the spring bloom fallout reached the benthos, and values increased dramatically thereafter, suggesting a storage of metabolic reserves until July (1998) or late August (1997). Ibarrola et al. (2000b) demonstrated that the presence of food affected the characteristics of the lysosomal system of *Cardium edule* in less than 3 d and that the lysosomal volume density was significantly lower in starved than in fed cockles, although it increased with improved food conditions.

Aljetlawi et al. (2000) stressed the importance of defining whether phytoplankton is available as food as soon as it reaches the sediment or whether some degradation is necessary before it can be utilized. Results obtained here strongly suggest that *Y. hyperborea* uses phytodetritus as soon as it is available, although the bivalve also depends on the an-

nual cycle of phytoplankton production for storage of metabolic reserves, growth, and reproduction despite the high organic content of sediment (see Scheibe 1991). The less productive months of the year (i.e., autumn and winter) were marked by utilization of what was left of the metabolic energy reserves in the digestive gland and a decrease in size of the digestive tissue. Thompson et al. (1974) also noted a decrease in size and number of the digestive cells of laboratory-fed *M. edulis* and also found that the structural integrity of digestive tubules was lost in individuals starved for 5 months.

Although the pattern of phytoplankton production in both years was somewhat similar, the difference in maximum digestive cell height between years suggests that accumulation of metabolic reserves was greater in 1997 than 1998. Smaller cell height in 1998 is probably attributable to less phytoplankton reaching the benthos. However, an alternative but nonexclusive explanation can be found in stress induced by the strong sediment disturbance that occurred in early May 1998. Animals that survived such a disturbance might have been unable to feed until most of the particle load had settled. Observations during subsequent feeding experiments with *Y. hyperborea* (Stead 2001) indicated no fecal production and increasing high mortalities when suspended particle load was higher than 84.5 mg L⁻¹ for prolonged periods (>96 h).

The low protein content of the digestive gland in April 1997 and the qualitative and quantitative histological examination, demonstrating a low value for digestive cell height, suggest that animals had experienced a period of low food availability. This interpretation is supported by the prolonged period of low sediment Chl *a* concentrations observed throughout autumn and early winter (September 1996–January 1997). The sharp increase in protein content (about ninefold) in late May of that year shows that growth of the digestive gland coincides with the arrival of the spring bloom fallout. Ibarrola et al. (1998) showed that digestive gland protein levels in the cockle *Cerastoderma edule* rise with enhanced food quality. The protein content of the digestive gland from *Y. hyperborea* decreased shortly after the initiation of gametogenesis in late August of each year (Jaramillo 2001), a pattern observed in other bivalve species and that may be linked to the high protein demands of gametogenesis (reviewed by Newell and Bayne 1980). During this time, the digestive cells were still large but some tubules had started to disintegrate (Stead 2001).

The next important drop in digestive gland protein content was observed toward the end of February 1998 as digestive cells were reaching their minimum size and the early bloom fallout was beginning to reach the benthos. During the early and spring bloom fallout of 1998, protein content doubled but varied considerably between individuals, probably as a result of a differential effect on individuals of the sediment disturbances observed in May.

Attempts to establish a correlation between feeding mode and digestive capacity in benthic invertebrates have been contradictory. Whereas Teo and Sabapathy (1990) reported high carbohydrase and low protease activity in mussels (*Perna viridis*), Ibarrola et al. (2000a) found high protease activities in the suspension-feeding bivalve *Cardium edule*. On

the other hand, Brock and Kennedy (1992) found no differences in enzyme activity between suspension- and deposit-feeding bivalves. Owen (1974) noted that digestive gland extracts of a number of bivalve species show relatively weak proteolytic activities.

It appears that in the majority of molluscs the secretion of enzymes is frequently a rhythmic process accelerated by feeding (Bayne et al. 1989; Brock 1989). Furthermore, enzyme composition and activity levels tend to reflect the biochemical nature of the digestible food substrate, regardless of the feeding mode of the animal (Mayer et al. 1997). For example, Stuart et al. (1985) demonstrated that in the amphipod *Corophium volutator* enzyme production is regulated by external factors such as food availability and composition.

The ability to regulate the rate of digestive enzyme production has frequently been proposed as a possible mechanism to maximize absorption (Bayne et al. 1989; Navarro et al. 1994). Moreover, advantages derived from increasing digestive activity in response to enhanced food quality have been analyzed in terms of an optimal feeding behavior (Willows 1992). Changes in the rate of digestive enzyme production might operate only as a long-term response in bivalves (Newell et al. 1980). However, a few studies have attempted to establish a relationship between digestive enzyme activity and nutritional status in bivalves. Brock (1989) observed that digestive glands of *Crassostrea gigas* individuals acclimated for 3 weeks to a diet of *Tetraselmis suecica* showed a significantly higher capacity to hydrolyze phytoplankton cells than did glands of starved oysters. Furthermore, Ibarrola et al. (1996) described variations in total cellulase activity in the digestive gland of the cockle *Cerastoderma edule* (L.) during a short-term response to simultaneous changes in food organic content and particle concentration, and showed that the acute response to increasing food quality included an increase in digestive gland weight as well as an adjustment in digestive enzyme activities.

Digestive enzyme activities in *Y. hyperborea* were highest in April 1997, probably because the animals had undergone a prolonged period of low-quality food from September 1996 to January 1997, whereas the main part of the bloom did not settle until May. At this time, the digestive cells attained the minimum size and tubules were in the holding phase. Experiments in which the bivalve *Cerastoderma edule* was starved for 20 d and then fed showed that a long starvation period induced a rapid increase in protease activity and a gradual but significant increase in amylase activity as soon as feeding was resumed (Ibarrola et al. 1999). However, after continued feeding, protease activity quickly returned to the prestarvation levels. A similar pattern was also observed here: in May 1997 activities of acid protease and α -amylase reached the lowest values recorded, although sediment Chl *a* concentration and digestive cell size had started to increase. Ibarrola et al. (1999) suggested that because most protein digestion in bivalves occurs through the action of lysosomal proteases (Reid and Rauchert 1976), the recorded fast reaction of proteases might reflect activation of the formerly depressed lysosomal system.

Acid protease and α -amylase activity remained relatively

constant from August 1997 to the beginning of February 1998, then doubled in the third week of February. This pattern is explained by an increase of food quality in late February 1998. Although stronger activities were always observed at the end of winter of each year, minor increases were observed between June and late August 1997 and between July and late August 1998, coinciding with the times that the secondary summer bloom fallout reached the benthos. Ibarrola et al. (1999) also found that enzyme activity in the digestive gland of *C. edule* was greater in winter (i.e., after a prolonged period of starvation), especially in the case of protease.

Thus, activities of acid protease and α -amylase are potential indicators of the physiological state of *Y. hyperborea*, high activities following periods of starvation or decreased food quality. The magnitude of the difference between low and subsequent high activities might be a good indicator of the degree of reduced food quality in the preceding months. Enzyme activity in late February 1998 did not increase as sharply as in April 1997 because *Y. hyperborea* would have accumulated a lot of energy reserves, such as lipids and glycogen (R. Stead unpubl. data), during the spring and early summer of 1997. In addition, the higher Chl *a* concentration in sediments during autumn and winter 1997 might have moderated the effect of starvation on the physiological state of the animals.

The patterns of enzymatic response and the cycle of uptake, storage, and use of energy reserves in the digestive gland (i.e., digestive cell height) in *Y. hyperborea* are closely linked to the seasonality and magnitude of the phytoplankton bloom reaching the benthos. Although the food preferences of benthic deposit feeders are still a matter of debate, this study suggests that the strong seasonal burst of activity reflects a strong dependence of this species on fresh algal material.

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