

Growth and production of *Hiatella arctica* (Bivalvia) in a high-Arctic fjord (Young Sound, Northeast Greenland)

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ABSTRACT: Abundance and biomass of the bivalve *Hiatella arctica* (L.) was investigated at depths from 10 to 80 m along 6 transects in the high-Arctic fjord Young Sound, NE Greenland (74° 18.58' N, 20° 15.04' W). The highest abundance was found at a depth of 20 m, and the mean intertransect density at this depth was found to be 57 ind. m⁻² with a biomass of 6.2 g shell-free dry weight (SFDW) m⁻². Age was estimated by counting annual growth rings in acetate peels made by cutting through the umbo region. The age of the oldest individual was estimated to be 126 yr. The Von Bertalanffy growth function fitted to length-at-age data showed that a maximum shell length (L_{∞}) of 37 mm was attained in approximately 35 yr. The mean annual growth rate was 0.14 yr⁻¹ corresponding to a mean annual production of 0.30 g SFDW m⁻² (depth 10 to 60 m). The annual somatic production-to-biomass ratio was 0.095. The size distribution of clams was bimodal with a group of very small (shell length 6 to 8 mm) individuals and another group of individuals around the maximum shell length. Large individuals are relatively abundant as a result of their long life span and the absence of significant mortality agents in this area. Based on production estimates, the carbon demand of the *H. arctica* population accounts for 3.6% of pelagic production in outer Young Sound.

KEY WORDS: *Hiatella arctica* · Arctic · Growth · Production · Age · Bivalve · Carbon

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INTRODUCTION

The Arctic region is characterised by low temperatures and large seasonal variation in primary production. Despite the seemingly harsh environment, several studies have documented high standing stocks of benthic fauna in this region (Thomson et al. 1986, Grebmeier et al. 1988, Ambrose & Renaud 1995, Piepenburg & Schmid 1996). Close benthic-pelagic coupling ensures that organic matter produced in the

water column is transferred efficiently to the sea floor. Together with the low benthic fauna metabolism this is one reason why high benthic biomasses can be maintained in low productive areas (Grebmeier & Barry 1991, Brey & Clarke 1993, Ambrose & Renaud 1995).

Despite permanently low temperatures, nearshore Arctic benthic communities mineralise organic matter as efficiently and as rapidly as communities in lower latitudes (Grebmeier et al. 1989, Rysgaard et al. 1998, Glud et al. 2000). Macrobenthic organisms contribute significantly to total benthic mineralisation (Piepenburg et al. 1995, Piepenburg & Schmid 1996, Bluhm et al. 1998, Ambrose et al. 2001). Although research on

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distributional patterns and mineralisation potential of Arctic benthos has improved during the last decade, few studies have dealt with growth and production of individual species. Studies such as these are necessary to further elucidate the ecological role of macrobenthos in the Arctic food chain.

The bivalve *Hiatella arctica* (L.) is an important component of the benthic fauna in many coastal areas of the Arctic (Ockelmann 1958, Thomson et al. 1986, Schiøtte 1989, Welch et al. 1992); it is circumpolar in distribution and extends from the shore down to a maximum depth of approximately 175 m (Ockelmann 1958). Despite its wide distribution and frequent occurrence, little is known about the ecological importance of this species. In Young Sound, NE Greenland, *H. arctica* is an abundant member of the benthic fauna (Sejr et al. 2000). As part of a multidisciplinary ecosystem study of Young Sound, *H. arctica* has been focused on as one of the most abundant infauna species. In this paper, we present data on its abundance, life span, growth and production and discuss its role in this high-Arctic system.

MATERIALS AND METHODS

The study was carried out in the outer part of Young Sound, Northeast Greenland ($74^{\circ} 18.58' \text{N}$, $20^{\circ} 15.04' \text{W}$) (Fig. 1) in August 1999 and August 2000. Specimens of *Hiatella arctica* were collected at depths of 10, 20, 40, 60 and 80 m along 6 transects. Ten replicate samples were collected at each depth using a 0.04 m^2 Van Veen grab. Samples were sieved through a 0.5 mm screen and preserved in borax-buffered formaldehyde. In the laboratory, all specimens were removed from the substrate and the maximum length across the shell was measured.

Specimens for growth analyses were collected at Transect 2 in the 15 to 25 m depth interval in August 1999. This depth interval is the key distribution area of the species and was expected to give typical values of growth within its distributional zone. Length was measured using a digital caliper and individual shell-free dry weight (SFDW) was determined by drying specimens at 80°C for 24 h.

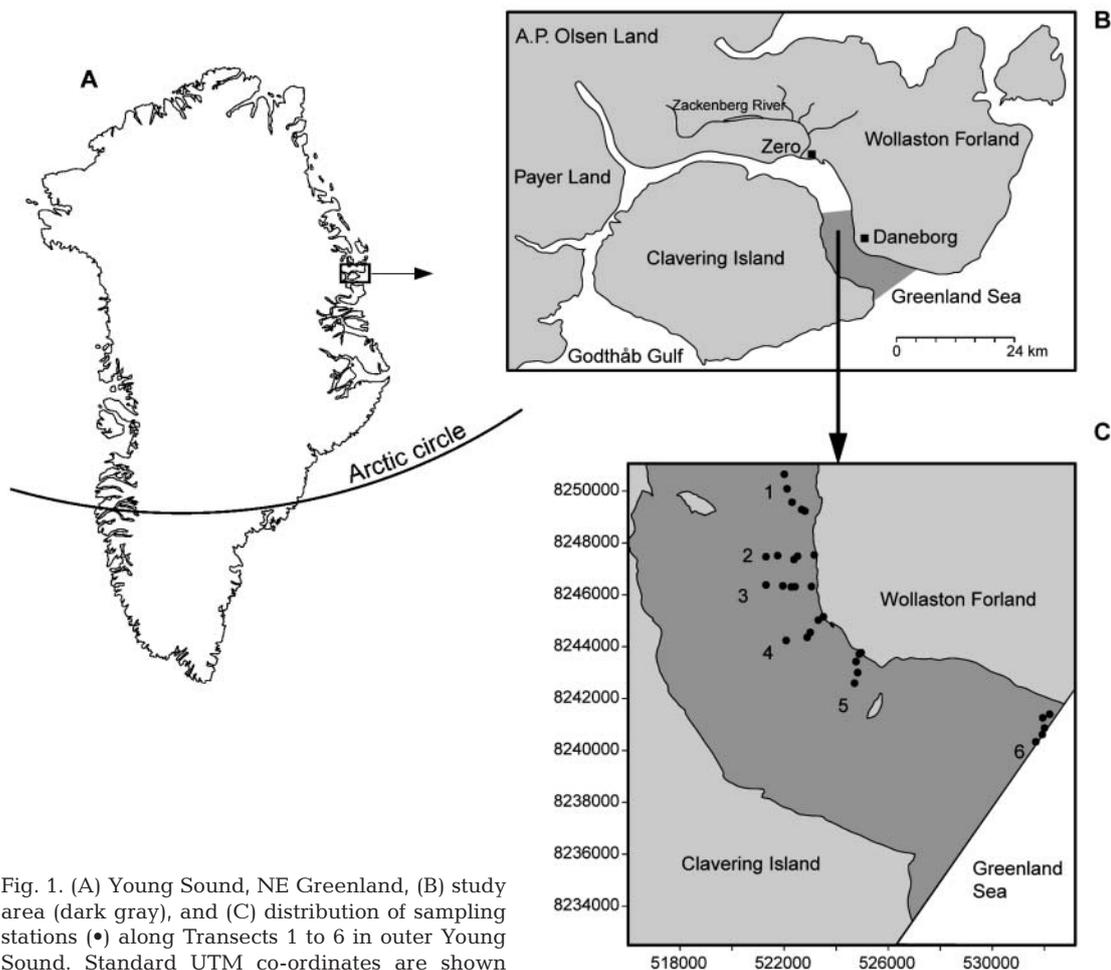


Fig. 1. (A) Young Sound, NE Greenland, (B) study area (dark gray), and (C) distribution of sampling stations (•) along Transects 1 to 6 in outer Young Sound. Standard UTM co-ordinates are shown

A separate study on this species has been conducted in Young Sound (Sejr et al. 2001). Marked individuals were collected after 2 yr of *in situ* growth. The shell section produced during this period was clearly visible. Due to methodological problems relating to the small increment produced, images of the banding pattern could be produced in only 2 individuals. However, the banding pattern in these 2 individuals clearly showed growth lines to be formed annually. We assume that this banding pattern is representative of the entire population and have adopted it as a tool for estimating clam age. Growth lines were examined using the acetate peel method described by Ropes (1985). The right shell was cut through the umbo to the ventral margin and embedded in epoxy (Epofix, Struers). The embedded shell was then polished using carborundum paper (600 and 800 grit). The polished cut edge of the shell was etched by submerging the blocks in a mixture of 4 ml 30% hydrochloric acid and 5 ml 85% formic acid in 1000 ml demineralised water for 5 min. The blocks were allowed to dry before being flooded with acetone, after which a sheet of acetate (Schwan Stabilo triacetate film 0.08 mm) was applied. After drying, the acetate peel was placed in slide mounts for examination under a stereomicroscope.

The Von Bertalanffy growth function is defined as follows:

$$L_t = L_\infty \times [1 - e^{-K(t-t_0)}] \quad (1)$$

where L_t is the shell length at time t , L_∞ is the asymptotic shell length, and K the annual growth coefficient. This was fitted to the length-at-age data by the iterative non-linear Newton algorithm (Strum & Kirk 1988). The Von Bertalanffy growth function was chosen because it gives a marginally better fit compared to the Gompertz ($R^2 = 0.54$) and logistic ($R^2 = 0.52$) functions. In addition, its widespread use allows comparisons to be made easily. Somatic production was calculated by the weight-specific growth rate method (Crisp 1984, Brey & Hain 1992) using: (1) the pooled length frequency samples; (2) the Von Bertalanffy growth function; and (3) the length-mass relation:

$$P = \sum N_i \times M_i \times G_i \quad (2)$$

where P is the production per total sample, N_i and M_i are the number of bivalves and mean individual mass, respectively, in size class i , and G_i is the weight-specific growth rate yr^{-1} calculated by:

$$G_i = b \times K \times (L_\infty - L_i)/L_i \quad (3)$$

where b is the exponent of the length-mass relation, K and L_∞ are parameters from the Von Bertalanffy function and L_i is the mean length of size class i . Production

estimates are calculated on the basis of the pooled abundance in all 10 grab samples collected at each station, giving production per 0.4 m^2 . Production in g SFDW was converted into g C using conversion values for this species. Organic C and N contents were determined on 5 replicate individuals. Prior to analysis, soft parts were removed, freeze-dried, homogenised and weighed into sample boats. Analyses were performed on a C/N elemental analyser (RoboPrep-C/N, Europa Scientific).

RESULTS

Abundance and biomass of *Hiatella arctica* were extremely variable (Fig. 2). This variability was in part due to the grab size being insufficient, as a result of which many samples contained no specimens. In general, abundance and biomass peaked at a depth of 20 m. Intertransect means of biomass and abundance at each depth are given in Table 1.

The pooled size distribution exhibited a marked bimodal pattern (Fig. 3). Large proportions of the population consist of small specimens with a shell length of around 6 mm and of large individuals close to maximum shell length. The decrease in abundance of small individuals, from 28 individuals with a shell length of 6 mm to 4 individuals with a shell length of 18 mm, is most probably due to mortality. In contrast, the decrease in number of individuals >30 mm in shell length is most likely due to variation in the maximum shell length attained by this species.

Growth lines are clearly distinguishable, with the first 6 to 10 increments being somewhat more diffuse compared to lines deposited later (Fig. 4). Thus, the growth lines provide a relatively precise estimate of maximum age at 126 yr. The length-mass relationship found in specimens used in the growth analysis was $M = 2.80 \cdot 10^{-5} \times L^{2.635}$ (g SFDW) for 108 specimens ($R^2 = 0.63$, weight range 0.046 to 0.985 g dry weight).

Table 1. *Hiatella arctica*. Mean abundance and biomass and production for 10 grab samples collected at different depths along 6 transects in outer Young Sound. Total production was $14.9 \text{ t SFDW yr}^{-1}$, or 4.3 t C yr^{-1} ; production/biomass ratio (P/B) = 0.095 yr^{-1}

Depth (m)	Biomass (g SFDW m^{-2})	Abundance (ind. m^{-2})	Production (g SFDW $\text{m}^{-2} \text{ yr}^{-1}$)
10	0.4	2.5	0.02
20	6.2	57	0.30
40	6.0	32	0.61
60	3.1	15	0.28
80	0	0	0

There is a considerable variation around the Von Bertalanffy growth function fitted to the length-at-age data (Fig. 5), due mainly to variation in the maximum length attained by the collected individuals. The scatter around L_{∞} is caused to a large extent by the variability in shell shape, which makes change in shell length a poor predictor of growth. Shell height, width and weight were recorded as well, but did not improve the estimate considerably when plotted against age. Shell weight would most likely have provided the best estimate of growth, but due to sediment trapped between shell layers, the shell weight was highly variable. The parameters applied in the Von Bertalanffy growth function are $L_{\infty} = 37.2$ mm, $K =$

0.14 yr^{-1} and $t_0 = -1.4$. The maximum shell length (L_{∞}) from the fitted growth function is smaller than the observed maximum length of about 45 mm. This discrepancy poses a problem with regard to calculations of production. Production was calculated by transforming the Von Bertalanffy growth function into an individual weight-specific growth rate (Fig. 6), where the individual annual growth (in SFDW) is depicted as a function of shell length. Growth becomes negative in individuals with shell lengths above 37.2 mm. In calculations of mean production, negative values of individual weight-specific production were treated as 0. This causes production (Table 1) to be underestimated, as 10% of the sampled individuals were longer than 37.2 mm. Total production was calculated by multiplying mean production in a given depth interval with the corresponding sea-floor area at that depth, as given by Glud et al. (2000). Production at 10 m is assumed to represent production at depths from 0 to 10 m, production at 20 m to represent production between 10 and 20 m etc.

DISCUSSION

The abundance and biomass of *Hiatella arctica* in Young Sound resemble those previously reported from the Scoresby Sound and Franz Joseph Fjord systems in East Greenland (Thorson 1933, 1934), Disko Bay (Godhavn), West Greenland (Petersen 1978) and Lancaster Sound and Baffin Island, Canada (Thomson et al. 1986).

The occurrence of *Hiatella arctica* is concentrated in the 20 to 60 m depth interval, with no specimens being found at 80 m. This is similar to the distribution of *H. arctica* found in Lancaster Sound, Canada (Welch et al. 1992). Absence of suitable substratum may be the factor limiting the depth distribution of *H. arctica*, as the species shows a preference for coarse-grained or stony substrata (Thompson et al. 1986). According to Glud et al. (2000), the stone fraction decreases with depth in the Young Sound area.

The size distribution of *Hiatella arctica* is probably a result of high and low mortality rates in small (<20 mm) and large clams (>20 mm), respectively. The high proportion of large individuals and their long life span suggests that mortality is low once individuals reach a certain size. Apart from ice-induced disturbance, predation on small individuals is probably an important mortality factor. A variety of benthic animals may consume young bivalves. In Young Sound, the brittle stars *Ophiacten sericeum* and *Ophiura robusta* occur at densities around 30 and 40 ind. m^{-2} at a depth of 20 and 30 m, respectively, and up to 250 ind. m^{-2} at 60 m (Sejr et al. 2000). Specimens of *H. arctica* have been

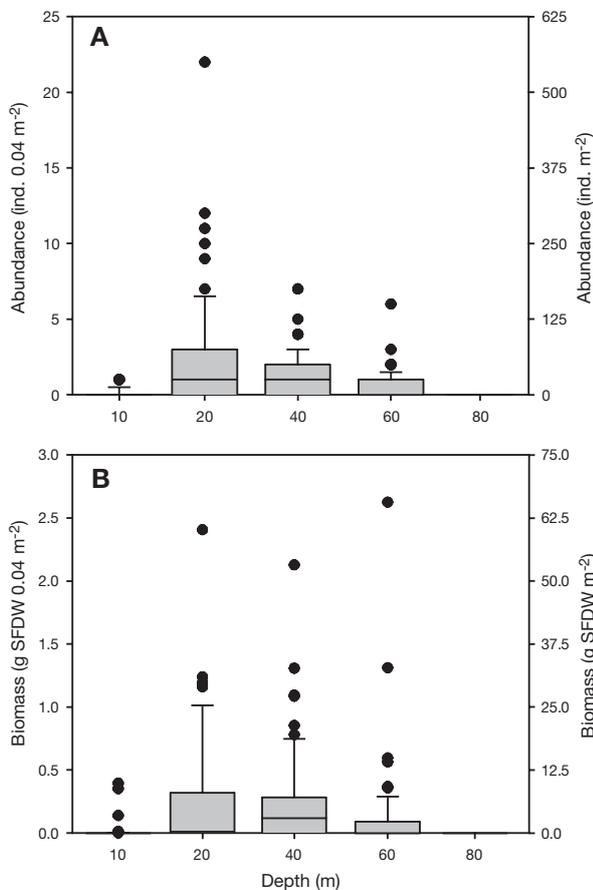


Fig. 2. *Hiatella arctica*. (A) Abundance (ind. 0.04 m^{-2}) and (B) biomass (g shell-free dry weight [SFDW] 0.04 m^{-2}) in 60 grab samples of 0.04 m^2 collected at different depths along 6 transects in outer Young Sound. The box represents the inter-quartile range, which contains 50% of the values. The whiskers are lines extending from the box to the highest and lowest values with the exclusion of outliers. A line across the box indicates the median. Outliers (●) are cases in which values lie between 1.5 and 3 box lengths from the upper or lower edge of the box. Abundance and biomass per m^2 are included for comparison

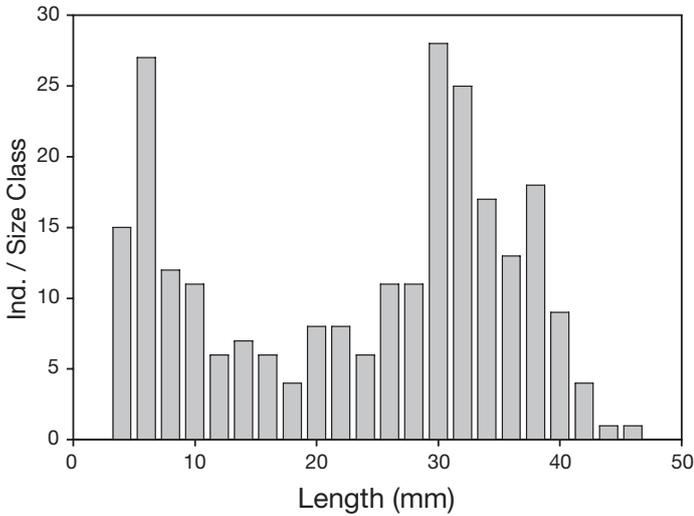


Fig. 3. *Hiatella arctica*. Pooled size frequency distribution in Young Sound (2 mm size classes)

found in the stomach content of *O. sericeum* (Forbes & Hanley 1853, in Ockelmann 1958) from East Greenland. Furthermore, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analyses of a wide range of species in Young Sound placed *O. sericeum* at the same trophic level as known bivalve predators such as walrus and eider duck (S. Rysgaard & M. K. Sejr unpubl.). Since predatory brittle stars engulf their prey whole (Feder 1981), there is an upper size limit to their prey. Predation by the brittle star *O. sericeum* is proposed to be the main cause of mortality among small (<20 mm) *H. arctica* specimens. The high abundance of brittle stars at 60 m may also limit

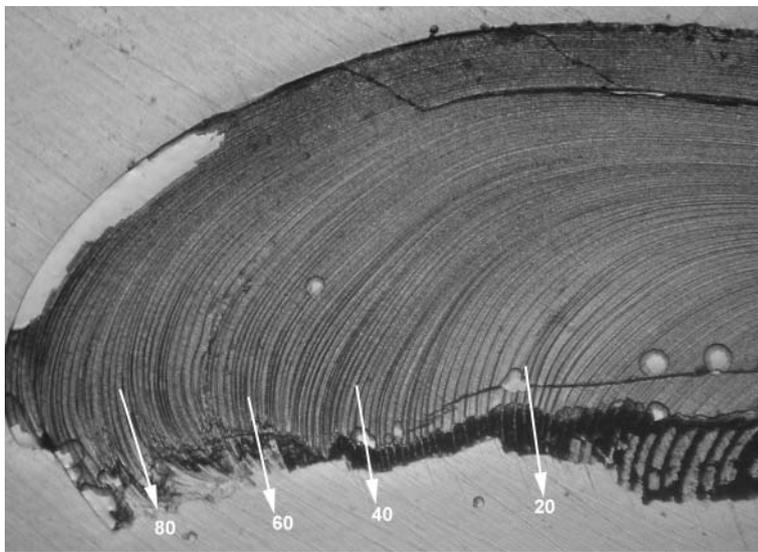


Fig. 4. *Hiatella arctica*. Photomicrograph of acetate peel showing internal annual growth bands; 50 \times magnification. Age was estimated at 104 yr

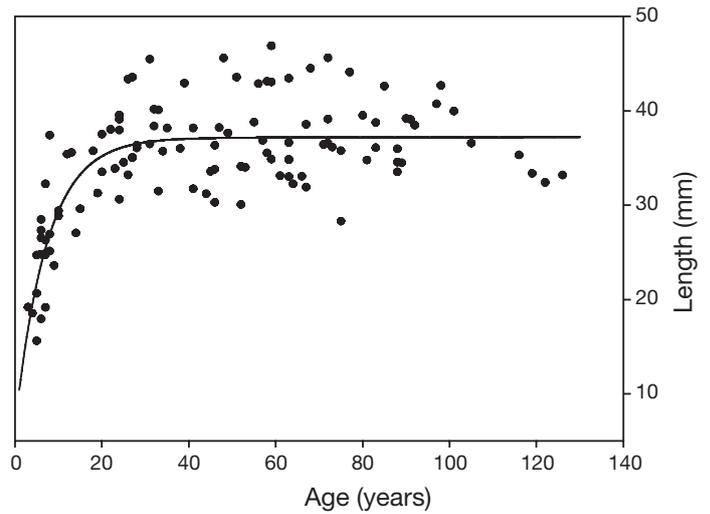


Fig. 5. *Hiatella arctica*. Von Bertalanffy growth curve fitted to length at age. Age estimated from internal growth bands in the shell. $L_{\infty} = 37.2$ mm, $K = 0.14$ yr $^{-1}$, $t_0 = -1.4$ yr; $R^2 = 0.56$

the lower distribution of *H. arctica*. Possible predators on adult bivalves include walrus and eider duck (Fisher & Stewart 1997, Larsen & Guillemette 2000, Born et al. unpubl.), but they are not considered important in structuring the pooled size composition of *H. arctica* because of their low abundance and seasonally varying consumption. Strong year-round predation seems to be exerted only on small individuals and this allows a high standing stock of old and large individuals to build up.

The maximum age estimate of 126 yr is high, but not extreme for bivalves (e.g. Ropes 1985, Peck & Bullough 1993). The estimated growth coefficient ($K = 0.14$ yr $^{-1}$) is within the range of values reported for 6 Antarctic bivalves (0.085 to 0.345 yr $^{-1}$; Brey & Clarke 1993) and comparable to growth of the Iceland scallop *Chlamys islandica* from West Greenland (0.12 yr $^{-1}$; Petersen 1994). However, it is lower than growth rates from temperate areas. Typical growth rates estimated from the Von Bertalanffy growth equation range from 0.20 to 1.5, e.g. *Mytilus edulis* (Dolmer 1998), *Pinna nobilis* (Richardson et al. 1999), *Venus verrucosa* (Arneri et al. 1998), *Ruditapes decussatus* (Garcia & Plante 1993), *Spisula solidissima* (Weinberg 1998) and *Donax trunculus* (Gaspar et al. 1999). The mean P/B ratio of 0.095 is lower than estimates for *Hiatella bysifera* (P/B = 0.15), *Mya truncata* (0.15 to 0.17) and *Macoma calcarea* (0.16 to 0.33) from Disko Bay, West Greenland

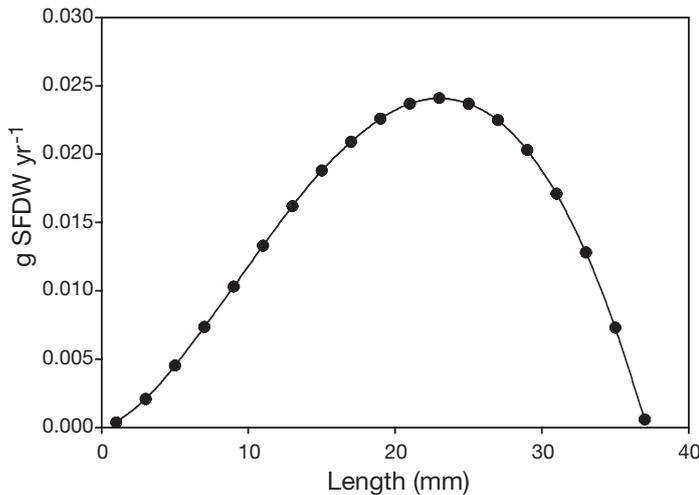


Fig. 6. *Hiattella arctica*. Relationship between shell length (mm) and annual individual production (g shell-free dry weight, SFDW)

(Petersen 1978). It is also low compared to P/B values of Antarctic bivalve species (Brey & Clarke 1993; range 0.117 to 0.664). The relatively low P/B ratio of the Young Sound clams may be a result of the high latitude, dominance of old clams and the underestimate of production. Low temperature combined with a short period of food supply is the most probable explanation of the low annual growth rates of polar organisms (Brey & Clarke 1993, Arntz et al. 1994). In Young Sound, where the temperature at 15 m is -1.2°C throughout the year (Rysgaard et al. 1999), annual pelagic primary production is estimated at 10 g C m^{-2} and takes place in July and August. At present, the relative importance of food and temperature as regulators of growth in *Hiattella arctica* cannot be assessed.

To assess the importance of *Hiattella arctica* in the carbon budget of the Young Sound ecosystem, the annual carbon uptake of the clam population can be estimated. To produce 4.3 t C (somatic production), a carbon uptake of 17.9 t C yr^{-1} is required, assuming an assimilation efficiency of 80% and a net growth efficiency of 30%. To include reproductive production in the total carbon demand for *H. arctica*, a value for gonad production in relation to biomass (P_g/B) of 0.1 was used. P_g/B values from 0.11 to 0.13 have been reported for Antarctic bivalves (Brey & Clarke 1993). When gonad production is included, annual total production (somatic + gonad) is estimated at 8.8 t C in outer Young Sound, corresponding to an estimated carbon input of 37 t C yr^{-1} . This is 3.6% of the annual microalgal (benthic and pelagic) production in outer Young Sound (Glud et al. 2002). While the carbon demand of *H. arctica* matches estimates of Arctic sea urchins and brittle stars (Table 2), it is much lower than the annual bacterial mineralisation in Young Sound, which has been estimated at 312 t C (Glud et al. 2000).

The principal importance of *Hiattella arctica* to this coastal ecosystem consists in its role as a food item for walrus during summer. Of the estimated total production of 8.8 t C , 0.9 t C are consumed in summer by a population of approximately 50 walrus that use this easily accessible food source to replenish their energy stores (Born et al. unpubl.)

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Table 2. Comparison of standing stock and estimated daily carbon requirement of Arctic macrobenthos. Values for *Mya truncata* were converted into carbon units by multiplying shell-free dry weight (SFDW) by a factor of 0.43 (Clausen & Riisgård 1996)

Taxon	Biomass (g C m ⁻²)	C input (mg C m ⁻² d ⁻¹)	Location	Depth (m)	Method	Source
<i>Hiattella arctica</i>	1.7	2.5	Young Sound NE Greenland	0–60	Annual production estimate	This study
<i>Strongylocentrotus pallidus</i>	0.5	2.8	N Barents Sea	80–360	Annual production estimate	Bluhm et al. (1998)
Brittle stars	0.64	5.3	NE Greenland shelf, banks	40–150	Abundance and mean respiration rates	Piepenburg (2000)
Brittle stars	0.46	3.6	Barents Sea	80–100	Abundance and mean respiration rates	Piepenburg (2000)
<i>Mya truncata</i>	49.5	19.10	Lancaster Sound Canada	0–100	Annual production estimate	Welch et al. (1992)
Brittle stars	0.7	1.9	Chuckchi Sea	36–212	Abundance and mean respiration rates	Ambrose et al. (2001)

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